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Review

Assessing Ungulate Populations in Temperate North America

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Abstract

Ungulates are among the most intensively managed wildlife in North America because they are both keystone and umbrella species, and because of their importance as game species for subsistence and sport hunters. To manage ungulate populations effectively, wildlife managers must employ survey methods that can provide population estimations that are accurate and precise enough to achieve management goals, yet efficient and economical enough to remain practical. In this paper, we review major methods for estimating both absolute and relative abundance of ungulate populations across temperate North America, where season and habitat provide a further challenge to selecting and developing an appropriate survey method for a given species. We consider physiological and behavioural differences among species that influence the relative effectiveness of one method over another, and make recommendations accordingly. Identifying the best method for surveying a given ungulate population ensures that long-term management is both effective and sustainable.

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INTRODUCTION

By nature of their size and pivotal trophic position as both keystone herbivores and major prey for apex predators, but also because they are a primary game species for subsistence and sport hunters, many ungulates are among the most highly managed wildlife across North America (Krausman and Bleich, 2013). Whether the overarching objectives are the conservation of rare species, such as woodland caribou (*Rangifer tarandus*), or the regulation of abundant species that are important targets for hunting by humans, such as moose (*Alces americanus*) and deer (*Odocoileus* spp.), ungulate management invariably requires some quantification of local populations (Williams 2011). The most accurate way to determine the population of a given species is to count every individual within a management area (i.e., a census), but this is prohibitively expensive, and rarely conceivable in large areas because of the time and labour required. As such, most ungulate populations must be enumerated using estimates derived from sampling (Cochran 1977). The challenge facing managers is therefore to identify survey and sampling methods that are both effective and efficient. This task is further complicated by the wide variety of potential strategies that can be implemented in a given situation, site-specific factors that should give managers pause before they simply implement the same methods as used in other jurisdictions, and advances in technologies that make the best approach today different from the best approaches of 10 years ago. In this review, we attempt to make sense of the multitude of choices available to managers by outlining each method that can be used to estimate ungulate abundance, why and when it should or should not be implemented, and by illustrating many of the factors that should go into selection of an abundance estimation method. The overall steps one must take, from defining survey objectives, through to the implementation stage, are summarized in Figure 1.

SURVEY OBJECTIVES

Wildlife management is inevitably a trade-off between objectives, where cost-effectiveness can be a deciding factor as to how or even whether a population can be counted or estimated with enough accuracy to accomplish a given management goal (Wu *et al.* 2000). There are 2 broad categories of population surveys that need to be considered from the outset – measures of relative versus absolute abundance. Indicators of relative abundance track population trends through count comparisons, and tend to be cost-effective because issues of sample size and reducing bias are less important than making sure that all compared surveys have the same sample size and bias (O'Brien 2011). Relative abundance measures can allow tracking of spatial or temporal population trends, and then only as far as the methods for multiple relative abundance surveys are standardized. For example, a roadside count can only be compared to another roadside count if the time of day, road section, season, etc. are all the same in each year. The biggest drawback of relative abundance measures is perhaps their lack of a probability-based design, though this allows them to be employed on much smaller scales. Conversely, measures of absolute abundance are invariably more expensive to obtain because their purpose is to estimate the population size or density, where accuracy and precision often depend on sampling effort, and a probability-based survey design is paramount (Williams *et al.* 2002). Standardization of methods is still important, but it is the random sampling design that allows them to be conducted on and applied on much larger scales, and to allow comparisons between different study areas.

As a general, but somewhat arbitrary guideline originally proposed for mark-recapture studies, Robson and Regier (1964) suggested 25% accuracy (an estimate within 25% of true population) is needed for effective ongoing wildlife management programs. In most cases, the true population value is not or cannot be known, but the relative robustness of different estimates can be compared using standardized measures of the precision of the estimate. A population estimate is based on a sample of the total population. These samples vary, so the resulting population estimate is actually a mean value bound by confidence intervals calculated from the sample variance. We can therefore evaluate the relative precision of different sampling methods by comparing each survey's coefficient of variation (CV), which is a unitless ratio between the estimate's standard deviation and mean. It is commonly desired that the CV of a useful population estimate be < 0.20 (Eberhardt 1978; Nakagawa and Cuthill 2007), though different, often lower CV targets may be chosen depending on one's desired use of the CV metric.

Ultimately the choice of a sampling technique depends on a combination of available resources, the ecology of target species, habitat type and variability, and how best to achieve specific management goals (Lancia *et al.* 1994). Certain survey methods can only provide population estimates, while others can provide a wealth of additional demographic information, such as sex ratio, calf:cow ratios (i.e., fecundity), age classification (i.e., recruitment), and measures of male antler class (i.e., optimal population growth via mature bulls), but also spatial metrics such as seasonal range sizes (Boulanger *et al.* 2017). However, in many cases, the collection of additional data requires increases in the time, effort, and expense of the survey.

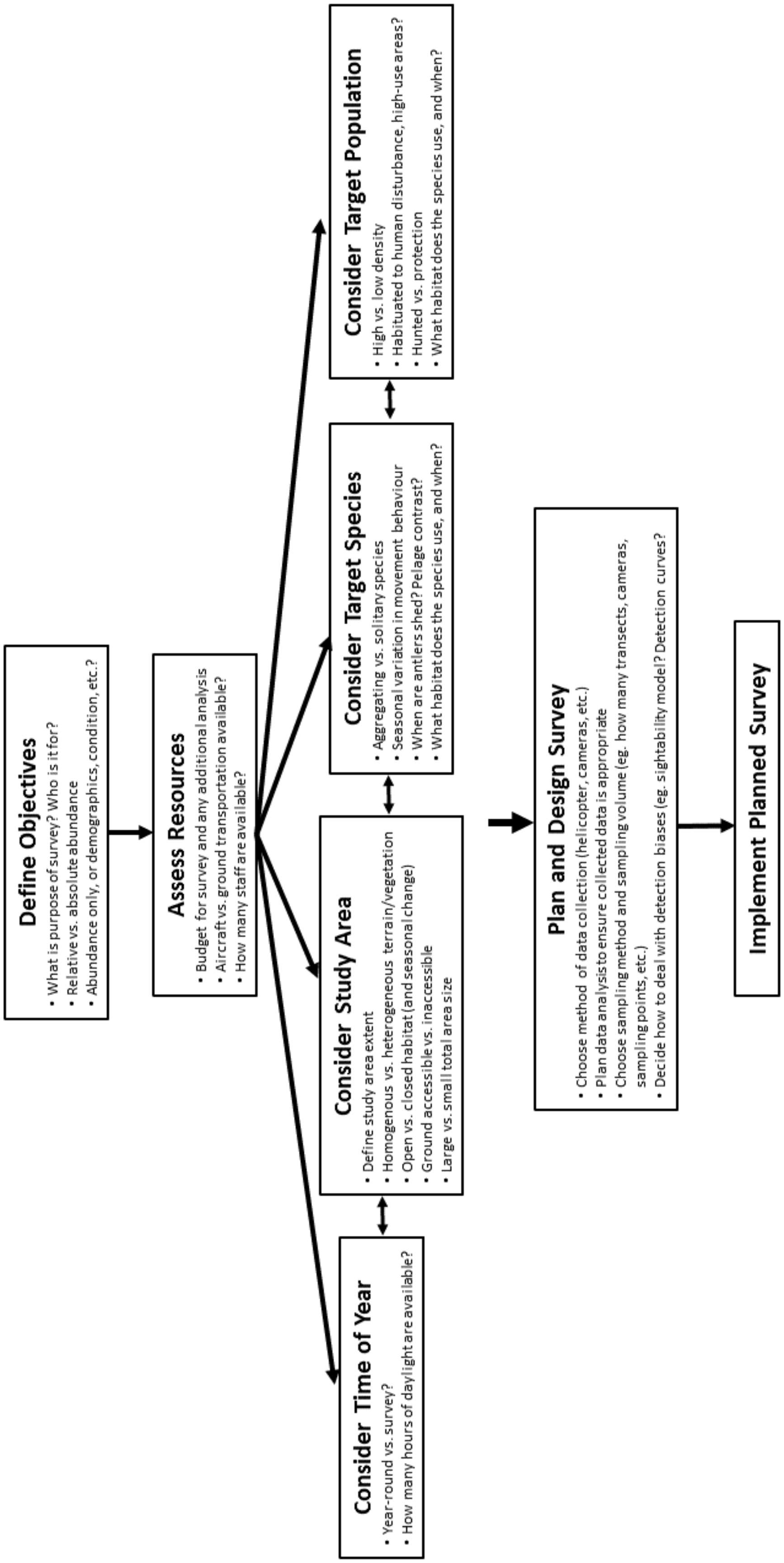

Figure 1. Flow chart for choosing and designing an ungulate survey.

Survey objectives should be defined first because these will guide the timing of the survey. In temperate areas, seasonal differences in weather will influence the choice of field methods. Snow both hides (e.g., covers fecal pellets) and reveals (e.g., footprints) animal sign, and short winter days limit daily operational duration; on the other hand, animals are easier to see from the air if there is snow on the ground, and no leaves on the trees. One of the biggest factors influencing the timing of surveys in relation to the survey objectives is, however, the species one wishes to survey.

ANIMAL BEHAVIOUR AND SPECIES DIFFERENCES

Managers should not assume that if they use the same survey objectives for different species, the timing and field methods will also be the same for those species. Surveying more than 1 species simultaneously is appealing because it can seem more cost-effective, but because of inter-species variation in behaviour, size, and colour, and also variation in the optimal times and places to survey different species, simultaneous surveys tend to be less effective than surveys of multiple species (Matulich and Hanson 1986; BC 2002). Observers tend to develop stronger search images for species that are seen more frequently, so the species that is easier to see in the first place (e.g., pelage that better contrasts the background, use of more open habitat with less cover, larger body size) becomes even easier to see, at the expense of missing observations of the less common or more cryptic species (ASRD 2010). For example, in a comparison of ground-based scat sampling with simultaneous aerial surveys of deer, elk (*Cervus canadensis*), moose, and American bison (*Bison bison*) in Elk Island National Park, it was found that deer populations were significantly underestimated whereas bison (largest, darkest) were most accurately estimated (Found 2017). However, ungulates in temperate North America share some broad seasonal behavioural characteristics; thus, they can be considered collectively when choosing and planning a survey. In North America, ungulates generally mate in late summer to early autumn, antlers are shed in late winter, and calves are born in late spring and early summer. Migratory animals tend to leave for summer ranges shortly before calving and return to winter ranges in late autumn (Houston *et al.* 1986). It is of course important to identify local variations in these patterns, as they may vary even within the same species.

Surveys are rarely conducted more than once per year (and often less) and are often conducted in winter because the season provides the best compromise of population estimation, sex/age classification, and measures of mortality. Ungulates often aggregate in winter, which makes it easier to detect them visually (Bartmann *et al.* 1986). These months also have more reliable snow cover, which provides strong contrast that increases visibility of animals from both the air and ground, and at this time deciduous trees are without foliage (Unsworth *et al.* 1990). The winter period tends to be outside the hunting seasons of most ungulates, yet allows for population estimation in time to allocate hunting quotas for the following hunting season. Mountain goats (*Oreamnos americanus*) and pronghorn antelope (*Antilocapra americana*) are exceptions to this timing recommendation. Because their light pelages do not contrast well against snow, they tend to be best surveyed in summer (BC 2002).

There are further behavioural considerations for timing ungulate surveys. If the snow cover is too deep, both deer (mule, *O. hemionus*; white-tailed, *O. virginianus*) and elk tend to shift from a graze-based to browse-based diet, and so will select for denser forests where sightability is reduced (Debyle and Winokur 1985; Jenkins *et al.* 2007). Mountain sheep (*Ovis* spp.) have more consistent foraging patterns, but their low tolerance for snow motivates them to seek out sunny and snow-free slopes, which can be advantageous during targeted counts, but could result in high inter-annual variation due to weather and snow conditions (BC 2002). Extremely cold temperatures, high winds, and extreme heat (in summer), may drive ungulates to select dense cover (ASRD 2010), which can reduce sightability during those periods; thus, optimal timing of surveys may require rapid schedule adaptations.

Differences in species behaviour also partly dictate how a population is best surveyed. Moose may be found either alone, or in small family groups, and are generally uniformly distributed. This favours random sampling methods (Peters *et al.* 2014). Elk, caribou, bison and sheep all tend to aggregate into groups that can be very large and easy to detect, but such patchy distributions can complicate or even preclude certain population estimation methods (Boulanger *et al.* 2017). For example, if a study area is randomly sub-sampled and by chance the biggest aggregations were not counted, the population would be severely underestimated. Conversely, if the biggest aggregations happened to fall within the randomly sampled areas only, the size of the population would be severely overestimated. For this reason, some jurisdictions simply avoid random sampling methods entirely for aggregating species, and instead use trend counts or total counts of targeted areas (Rabe *et al.* 2002). These methods survey only those areas with the greatest expected aggregations which can be compared to previous surveys of those same high-aggregation areas (i.e., a relative abundance measure), or approximate minimum counts by simply counting animals in those areas where you expect to see most of them. These methods are more effective and useful when populations have high site fidelity, such as with mountain sheep, and caribou in winter (BC 2002). Deer and moose may also aggregate in winter into "wintering yards", though there is high variability in this behaviour (Proulx and Joyal 1981; Messier and Barrette 1985; Nelson and Sargeant 2008; Hurst and Porter 2008). There are also seasonal intra-specific behavioural variations that can further influence these factors. For example, sedentary caribou populations in northern Ontario have more consistent distributions that facilitate random sampling. Conversely migratory caribou in northern Ontario can be entirely absent from sampling areas, or be seasonally aggregated, both of which can lead to biased population estimates (Newton *et al.* 2015).

METHODOLOGICAL SAMPLING AND STATISTICAL APPROACHES

Sampling schemes and statistical methods should be considered after the survey objectives are established, and before choosing the method of data collection (below). Survey objectives will determine whether the survey must produce absolute abundance data, or whether relative abundance data can suffice (Table 1). Consideration of peripheral data needs, such as demographic information, will further indicate which methodological, sampling, and statistical approaches will be preferred.

Relative Abundance

If the desired measure is relative abundance, rather than absolute abundance, then there are many different surveying methods available that can be applied quickly, cheaply, and easily (Krebs 1999). A measure of abundance is considered relative when the value is only relevant in the context of comparison to similarly standardized measure, and is largely uninformative on its own. For example, a person can drive a road through a protected area and count the number of deer, but that value only tells us how many deer are beside that road, at that time of year, at that time of day. However, if one repeats the count driving at the same speed, at the same time of year, at the same time of day, one can now compare the 2 counts. When the methods are standardized enough to allow such comparisons, one can obtain measures of the amount of change by that sampling of the population, and potentially extend those trend inferences to the entire population (i.e., if there are twice as many deer seen during the roadside count there are likely more deer elsewhere). By contrast, an absolute measure of abundance would aim to quantify the actual population value each year and should use a probability-based sampling design to achieve a spatially representative count. Relative abundance estimates can be achieved with non-random sampling, where the goal is to quantify relative change in the population over some time interval. Many survey methods can be used to estimate both absolute and relative abundance, where the main differences are the randomness of design and the sampling sizes required. For example, a single linear transect counting ungulate fecal pellets could, in theory, be used as an annual relative abundance indicator, but more labour intensive, random designs must be employed in order to obtain absolute abundance estimates (see below).

With a relative abundance measure, the desired number of sampling plots or transects is more subjective and can actually be as low as 1, though sample size can still be important. It may also be more difficult to estimate accuracy with respect to the "true" population value, since the nature of relative abundance counts means one cannot usually extrapolate that value to a larger area. For example, if there are 50 deer seen along a roadway passing through a study area, one cannot estimate the population of deer within the entire study area because the road is not representative of the entire area. While a survey with just a single plot would be very cheap and easy to implement, sample size also matters when it comes to relative abundance indicators. A review of American ungulate surveys found that most states used non-random sampling methods, and thus were obtaining only relative abundance measures of their ungulate populations (Rabe *et al.* 2002). Besides cost, another advantage of relative abundance surveys is that one is not restricted to the use of just a single method. For example, Banff National Park quantifies elk populations by using both winter track counts along non-random transects, and spring roadside counting from automobiles (Ham 2011). In longitudinal studies based on relative abundance methods the choice of survey method, sampling design, field methods, etc. are less important than they are with absolute abundance measures. Rather than attempting to measure the bias in the estimate, the objective of relative abundance measures is to minimize the variation in the observation process so that any biases in the survey are consistent.

Census vs. Sampling

Absolute abundance can be determined either by looking everywhere in a study area and simply counting how many animals are there (a census), or by looking in only a portion of the study area and using that sample to estimate the population. Censuses, which are complete counts that can be thought of as sampling of 100% of the study area, are usually only effective when the population is geographically closed, and the study area relatively small. For example, Elk Island National Parks is 194 km^2 and surrounded by fencing largely impermeable to bison, moose, and elk, and managers are thus able to survey the entire park via helicopter in less than 2 d (Parks Canada 2018). Still, less than 100% of the animals in the study area are actually detected, most censuses are

Table 1. Summary of advantages and disadvantages of different ungulate survey methods used across Canada and United States.

Method	Advantages	Disadvantages	Best for	Worst for
		Relative abundance		
Roadside counts [1,2,3]	> fast, cheap, and logistically simple > can be used all year	> biased towards species and individuals using roadside habitat > limited management applications because of narrow roadside scope	> abundant species (e.g., deer) > populations adapted to human-disturbed areas	> remote habitat > species that avoid roads (e.g., caribou, mountain goats)
Track counts (aerial) [4.5,6]	> potentially fast, and relatively cheap method to survey large and remote areas	> difficulty in identifying separate species by tracks alone, from air > aerial tracks surveys better coupled with actual animal observation > dependent on snow cover	> abundant but only moderately-aggregating species (e.g., white-tailed deer) > large areas with challenging access	> species using broken terrain (e.g., mountain goats, bighorn sheep) > aggregating species (e.g., bison, elk)
Track counts (ground) [4,5]	> low cost method to survey reasonably accessible areas > easy to identify and count tracks of multiple species	> labour intensive to conduct winter ground transects > often relies on winter snow cover	> multi-species systems > ground accessible terrain	> species using less accessible terrain (e.g., goats, caribou) > aggregating species (e.g., bison, elk)
Hunter harvest [1,7]	> low cost, low effort, easily coupled with other socio-biological information obtained from hunter surveys > can survey very large areas pre-divided into management units	> reliability of collected data (hunting success and/or effort) is often questionable > information biased towards hunter targets (e.g., antlered males) > sample sizes dependent on hunting tag allocations	> abundant species > very large areas divided into management units > heavily hunted populations	> rare species with minimal or no hunting season (e.g., woodland caribou) > populations in protected areas
Camera Surveys [5,8,9]	> can be used all year > can survey multiple species simultaneously > can obtain detailed demographic and body condition data > low ongoing costs	> requires ongoing labour to maintain cameras and process data > access to camera sites may be limited on private property or remote terrain	> accessible habitat with well-used game trails > multi-species surveys > continuous monitoring	> open habitat where animals do notuse easily identified corridors or locales (e.g., bison and plains/tundra species)

Table 1, cont'd. Summary of advantages and disadvantages of different ungulate survey methods used across Canada and United States.

Method	Advantages	Disadvantages	Best for	Worst for
		Absolute abundance		
Mark-recapture/re-sight (10,11,12,13)	> cost effective on marked population > may require less time than other aerial methods	> expensive to maintain adequat sample size of marked individuals > estimates highly dependent on difficult-to-meet assumptions > not feasible to identify without artificial marking	> closed populations or those occurring in discrete blocks (e.g., mountain goats) > populations with a high proportion of marked individuals	> low density populations > larger survey areas
DNA mark-recapture [14,15]	> non-invasive (assuming hair or fecal pellets used) > can be combined with other bio-sampling (e.g., stable isotope and diet analysis) > no capture/collar costs	> lab analysis is expensive > estimates highly dependent on difficult-to-meet assumptions > demographic information difficult to obtain	> closed populations or those occurring in discrete blocks > populations difficult to capture	> low density populations > large survey areas > elk (DNA issues)
Camera surveys (mark-recapture or occupancy modeling) [8,12]	> non-invasive > can get individual-level information and detailed demographics > can be done at any time of year	> expensive to maintain adequate sample size of marked individuals, yet unreliable/not feasible to identify ungulates without artificial marking assumptions of mark-recapture are difficult to meet > cost of cameras, labour to maintain cameras and process images	> populations occurring in discrete blocks (e.g., mountain goats) > populations difficult to capture > areas with high ungulate diversity	> low density populations > large survey areas
Fecal pellet counts [4,13,16]	> non-invasive > can acquire biological samples at same time > requires no specialized equipment	> very difficult to obtain demographic information > very labour intensive, particularly if "clearance" method is used > rates of fecal deposition difficult to know, introduces high uncertainty	> easily accessible areas > areas with low ungulate diversity > medium density populations	> large survey areas and/or low density populations > densely aggregating species (e.g., elk)

Table 1, cont'd. Summary of advantages and disadvantages of different ungulate survey methods used across Canada and United States.

Method	Advantages	Disadvantages	Best for	Worst for
Track counts (FMP) [5,6]	> accurate with low flying kilometers > cost effective	> unlikely to obtain demographic information > estimates of daily travel distances for ungulates are variable and introduce high levels of uncertainty, and may be locally unknown > vulnerable to snow conditions	> highly mobile species > large and open areas	> low-density populations > aggregating species (e.g., elk, caribou)
Fixed-width transects [1,17,18,19,20,21]	> can census an area > easily adapted for relative abundance approaches > aerial method can be very fast	> more costly than stratified random block and distance sampling > assumes homogeneity in animal density > risk of periodicity where systematic linear features are present	> homogenous habitats > areas small enough to census > species with individuals often found alone (e.g., moose)	> heterogeneously distributed and/or aggregating populations
Distance sampling (aerial) [17,18,20,22,23]	> can require less flying kms than SRB > addresses sightability issues prevalent other aerial methods; as few as 20% of animals need to be sighted.	> 100% sightability along the transect line unlikely, requires sightability adjustment in most cases > assumes homogeneity in habitat (sightability) and population density	> homogenous habitats > hard to see animals > evenly distributed species (e.g., moose)	> aggregating and/or low density >species with few "detection events" (e.g., sheep, goats, possibly elk)
Distance sampling (ground) [12,20,22]	> driving or walking does not require specialist (pilot) > addresses sightability issues; as few as 20% of animals need to be sighted.	> 100% sightability along the transect line unlikely, requires sightability adjustment in most cases > assumes homogeneity in sightability and population density > using roads introduce habitat biases	> homogenous habitats > open habitats	> aggregating and/or low density > species with few "detection events" > mountainous terrain (e.g. goat, sheep)
Thermal imaging (in general) [24,25]	> not dependent on snow or daylight for sightability	> more expensive than naked-eye spotting > image processing and interpretation is time-consuming > does not outperform sightability-corrected naked-eye surveys	> deciduous habitats > areas small enough to census > areas with low ungulate diversity	> coniferous forests > species with body sizes similar to those of sympatric species

Table 1, cont'd. Summary of advantages and disadvantages of different ungulate survey methods used across Canada and United States.

Method	Advantages	Disadvantages	Best for	Worst for
Stratified random block [18,21,22,23,26,27]	> reduced variance leads to very precise estimates > adaptable to heterogenous and changing habitats > cheaper than fixed-width transects	> estimates vulnerable to choice of block size and stratification > can require more flying that distance sampling	> large areas > species with patchy distributions (e.g., sheep, caribou, elk)	> areas lacking any past landscape/population data for stratification

[1]Rabe *et al.* 2002, [2]Drysdale 1986, [3]Grosman *et al.*, 2011, [4]Mooty and Karns 1984, [5]Ham 2011, [6]Stephens *et al.* 2006,[7]Putman *et al.* 2011, [8]Rovero *et al.* 2013, [9]Brinkman *et al.* 2011, [10]Bear *et al.* 1989, [11]Mahoney *et al.* 1998, [12]Zero *et al.* 2013, [13]Urbanek *et al.* 2012, [14]Hamrick *et al.* 2013, [15]Maudet *et al.* 2004, [16]Campbell *et al.* 2004, [17]ASRD 2010,[18]BC 2002,[19]Dalton 1990, [20]Ogutu *et al.* 2007, [21]Unsworth *et al.* 1994, [22]Buckland 2001 ,[23]Peters *et al.* 2014, [24]Franke *et al.* 2012,[25]Millette *et al.* 2011,[26]Gasaway *et al.* 1986,[27]Samuel *et al.* 1987.

essentially *minimum counts*, where the minimum count is simply very close to the true population size (see DeCesare *et al.* 2016).

Sampling is cheaper than a census because managers only have to count ungulates or ungulate signs in a portion of the study area. The trade-off is that sampling provides population estimates only through extrapolation, and with these come estimate errors beyond the sightability errors inherent to both sampling and censuses.

Random vs. Systematic Sampling

Bias is a consequence of any sampling approach, but poor sampling design may lead to errors which get magnified when extrapolated to produce the population estimate. In this way, sampling biases can result in population overestimates or underestimates. Random sampling is generally preferred for population estimation, since it is the least biased. Random sampling is a particularly efficient way to sample representative habitat of more homogenously-distributed ungulates. For patchily-distributed ungulates, random sampling is still preferred for its lack of bias, but can become logistically inefficient because one inevitably samples many areas where no animals are present, and one must increase the number of sampling sites if too many of them contain 0 counts. The alternative, however, would place emphasis on sites more likely to have animals, and such a non-random sampling scheme would produce overestimates of the population.

Systematic sampling using an evenly distributed grid or plot system is a simple way to sample a larger area (e.g., flying linear transects covering a portion of the overall study area), but can be plagued by the introduction of periodicity to the sampling, whereby the systematic arrangement of transects or sampling points aligns with other systematic elements within the survey area (Thompson 2002). Periodicity is more common in human-disturbed areas in both Canada and the USA, where farmland and road networks form nation-wide grid systems. Since these same grid systems are often used for defining at least some of the boundaries of survey areas, a transect survey that starts aligned (or not) with a road allowance will likely have further transects continually aligning (or not) over other road allowances. Surveys that systematically sample or avoid sampling roadside habitat will be as biased as the biases in ungulate use of those habitats, and these can be very significant because of attractants (e.g., salt; Leblond *et al.* 2007), variation in plant distribution (Kadmon *et al.* 2004), or roadside reduction in predation risk (Mulero-Pazmany *et al.* 2005). Similarly, transects grids should be aligned perpendicularly to major landscape features, such as rivers, to minimize natural habitat biases.

Rate-based Sampling

Rate-based sampling is a broad category for methods that use the time and/or location of collected animal occurrence data to estimate how many animals were required to produce said occurrence data. In other words, what population of animals is necessary to create that occurrence data? These data, outlined in detail below, can include scat, DNA, images from automated wildlife camera, and animal tracks, among others.

Fecal Pellet Counts

One of the oldest forms of rate-based sampling to estimate ungulate populations is the use of fecal pellet counting. Fecal depositions can be used to estimate absolute animal abundance if the daily defecation rate and total accumulation time are both known. Most typically, fecal samples are collected by walking transects randomly distributed across a survey area, and a simple formula is used to estimate how many individuals were necessary to produce that number of fecal piles over the specified period (White and Eberhardt 1980). Defecation by most wild ungulates in North America takes the form of fecal pellets, which are found in piles (single dung piles of bison can be counted similarly). To ensure optimal detection of pellet groups, transect widths are typically no more than 2 m wide, so that the entire width of the transect can be observed during a single sweep (Marques *et al.* 2001). Transect length can vary, as been as short as 50 m in high density areas, but when transects become too long (e.g., > 1km) error rates can increase (Marques *et al.* 2001). As transect length increases, the proportion of edge to area of the transect becomes very high, and it becomes more difficult to lay a straight transect for its entire length. It becomes more important yet more difficult to confidently determine whether a pellet group is within the 2 m transect band or not. Though transects are perhaps most common, pellets can also be counted within grids (e.g., Gopalaswamy *et al.* 2012). There is a trade-off between the number and total length of transects – where high transect frequency provides a more robust sampling of a landscape, longer transects more efficiently survey larger areas.

Estimates from both white-tailed and mule deer suggest that 13 pellet groups/day is an average defecation rate (e.g., Mooty andand Karns 1984), though estimates have been as high as 25 pellet groups/day for some cervids (Mayle *et al.* 1999). This variability translates directly into uncertainty surrounding any population estimate relying on daily defecation rates as a calculation variable. There are 2 ways to determine the time over which the counted pellet groups accumulated. The "standing crop" method visits transects just once, but it requires estimating the age of each pellet group. This is done with parallel experimental plots, in similar habitats, from which one can quantify the decay rates for the fecal pellets. This method is highly vulnerable to both the high variability in decay rates between pellet groups even when found in the same area, and the in-field biases of the observer (Mayle *et al.* 1999). The “clearance” method addresses both of these concerns by removing all pellets on the initial visit to the transect, then making a second visit to count new pellet groups that had accumulated. Typically, there is a 2-month accumulation period between visits, which is based on the typical rate of pellet degradation in a temperate climate (for comparison, in equatorial regions deer pellets can degrade in as little as 1-2 weeks during the rainy season; Rivero *et al.* 2004). The clearance method is much less prone to bias, and produces more accurate estimates, but takes more time and is thus more expensive (Campbell *et al.* 2004).

Track Counts

Track counts estimate absolute density based on the ratio of crossings/km of transects, divided by the estimated daily travel distance of the species of interest. Extensive field and simulation modeling by Stephens *et al.* (2006) found that 2 km was a suitable transect length for maximizing efficiency and confidence intervals. Their study found that a < 25% error could be achieved with total transect distances of 250 km, for regions of 2,500 km^2 in total area (Stephens *et al.*, 2006). However, they also concluded that this method would be unsuitable for ungulates at densities lower than 0.5/km^2. For red deer (*Cervus elaphus*), and presumably in North America for elk, confidence intervals were unacceptably wide unless their density was over 1 animal/km^2 (Stephens *et al.* 2006). While track counts are rarely used in North America to estimate absolute ungulate abundance, ungulate populations are often estimated in Russia and former Soviet regions using the Formozov–Malyshev–Pereleshin (FMP) formula (Kuzyakin 1983).

Random Encounter Modeling

There have been many efforts to develop analytical methods to estimate absolute abundance from spatially-explicit presence-absence data (Royle and Nichols 2003; Roberts *et al.* 2006). Random encounter models (REM) attempt to use encounter rates to estimate the density of animals in an area by using the presence or absence of an animal as recorded by wildlife cameras (Rowcliffe *et al.* 2008). This method requires assumptions about the variability in group size and travel speed. Average travel speeds can be estimated from GPS data, though this requires live animal captures. Captured individuals are assumed to be representative, and step lengths must be measured on a short enough scale to match photo frequencies and camera trap densities. A study extracting these data from 7 radio-collared Grevy’s zebra (*Equus grevyi*) found very high variation in both mean group size and travel speed (Zero *et al.* 2013). This high variation resulted in population estimates that were less precise than mark-resight methods using the same data.

Zebras are an interesting example of one of the few ungulates that can be individually identified by appearance alone; automated software exists for this purpose (e.g., Hiby 2010). North American ungulates cannot be identified in this way, though in some cases it is possible to identify adult males by antler pattern (Hamrick *et al.* 2013). This method is complicated by the fact that antlers grow in size and shape from spring through to fall, and are then shed sometime from late winter to spring. The method of estimating absolute abundance from demographic ratios also requires assumptions regarding the homogeneity of camera site distribution relative to "available" locations for an animal to be present, which is almost certainly not true when it comes to baited sites (see Found and St. Clair 2016). These methods may also require a prohibitively large number of cameras to adequately survey most management units. For example, a review of camera-trap protocols suggested 1 camera per 2 km^2 for medium-large animals (Rovero 2013), which for the average wildlife management unit in Alberta (4,400 km^2; Alberta Environment and Parks 2019), would equate to >2,000 cameras.

Mark-recapture

In its most basic form, mark-recapture sampling "marks" a sub-sample of the population in some way, and then during further captures extrapolates the ratio of marked:unmarked animals to the total population (Strandgaard 1967). This method was originally developed for estimating the populations of small mammals that could be caught in traps and marked manually, but more recently has been used to count ungulates where the "recapture" is done by remotely resighting marked individuals during aerial or ground counts (e.g., Bear *et al.* 1989; Rosatte 2007). When trail cameras can be used for the re-sighting, antler patterns have allowed the individual identification of male deer, which can provide a mark-resight estimate of the population of males. With the population of males thus estimated, and the ratio of males:females known, one can estimate the total population (Oetgen *et al.* 2008). However, this method makes significant assumptions about male versus female movement behaviour that are almost certainly violated. Such violations would be even more pronounced when bait is used to attract animals to camera sites, as inter-sex and inter-individual variation in this behaviour should be expected (Found and St. Clair 2016). Image collection for this method is therefore restricted to a known period when male antler patterns remain unchanged, which can be highly variable.

Theoretical models show that both precision and accuracy increase when higher proportions of the population are marked (Hestbeck and Malecki 1989), at least up to some plateau. Mahoney *et al.* (1988) found that marking > 25% of initially-sighted caribou did not affect either the precision or accuracy of their estimates. Nevertheless, marking even 25% of an ungulate population (others recommend as much as 40%; Krebs 1999), can become prohibitively expensive, particularly for large populations. Although mark-recapture methods can and have been demonstrably accurate and precise, the quality and validity of such population estimates depend on several important assumptions that are likely to be violated when applied to surveys of ungulates: 1) populations are assumed to be geographically and demographically closed, but this is rarely the case for large, wide-ranging, and long-lived species, except when the marking and resight can be completed within a short period of time (i.e., days); 2), it is assumed that there are no capture bias during either the marking or the resight, but individual variation in ungulate behaviour precludes this because, as examples, both ground-based darting of ungulates and baited trapping tends to target ungulates with particularly personality types, to the exclusion of other personality types (Found and St. Clair 2016) ; and 3) sampling is assumed to be random, but the tendency towards convenience sampling reduces this randomness. For example, Roberts *et al.* (2006) compared roadside counts to camera trapping of key deer (*O. virginianus clavium*) marked with radio collars, and found that because initial captures targeted easy to find and highly visible animals along roadways, there was a higher proportion of resights of marked deer than there was through the more random re-sighting using cameras.

DNA mark-recapture uses individual DNA signatures to uniquely identify biological samples, and random but systematic collection of DNA as the individual “recaptures”. This method has been used successfully on a variety of species, perhaps most often on carnivores (e.g., Sharma *et al.* 2010; Whittington andand Sawaya 2015), but also on ungulates (Brinkman *et al.* 2011). When coupled with spatial information for the captures/recaptures, spatially-explicit mark-recapture estimators can provide more biologically meaningful estimates of population size in which some of the traditional limitations of mark-recapture (i.e., assumption of closed populations) can be overcome (Jůnek *et al.* 2015).

Sightability Models

One issue with applying probability-based sampling schemes to the counting of animals is that, in practice, most samples are incomplete; while in theory one is supposed to count all animals along a transect or at a point count, some animals that were present invariably go undetected (i.e., false negatives). Sightability models adjust observed counts to account for this detection bias. They can be developed for specific species and areas, where the final population estimate is the product of a sample-based estimate, and a correction factor determined from a separate sightability model (Samuel *et al.* 1987). As an example, a sightability model for elk in Ontario found individuals were more likely to be seen if elk were: in larger groups, upright (as opposed to bedded), in deciduous habitats (compared to coniferous), and in areas where canopy cover was < 50% (Mckintosh *et al.* 2009). Sightability models for moose also included canopy cover (Quayle *et al.* 2001; Peters *et al.* 2014). The importance of group size was emphasized by Peters *et al.* (2014), who reported that lone moose were missed 75% of the time.

Sightability models are most commonly derived from and applied to ungulate data from aerial surveys, but could be derived from and applied to other observation-based data. These models are essentially logistic regression models, where various landscape and behavioural parameters are used to predict binary data signifying detection or not. Constructing the model thus requires counting all observed animals, but also knowing how many animals were available to be observed. With these 2 pieces of information, one can determine what environmental/behavioural factors influence whether an animal is observed or not. The standard approach is to use radio-marked animals to build the sightability model. However, other methods are possible, such double sampling with more intensive searches, ground-based surveys (in small areas), and the use of infrared cameras to detect animals that were not observable to the naked eye (see below). Similarly, and clearly only opportunistically, when a new population is introduced and is entirely marked with radio/GPS collars, their true locations can be known, regardless of whether they are sighted or not during the survey. The second component to making a sightability model is to collect potential predictor variables at each location where any animal or animal clusters were sighted. Lastly, during the survey itself those same predictor variables must be collected at each observation.

Distance Sampling

Distance sampling can correct some sightability issues in an entirely different way than described above, using the assumption that distance between the ungulate and the observer is the major factor determining whether an animal will be observed. Distance sampling is therefore a popular method of estimating animal abundance (Nielson *et al.* 2004). In distance sampling, an observer will travel along a transect, often by motor-vehicle (e.g., Larue *et al.* 2007), or aircraft (e.g. Peters *et al.* 2014), and record the distance between observer and each detection. Usually the detection is the animal itself, but ground-based methods can also use detections of fecal pellet groups (Urbanek *et al.* 2012). A point sampling strategy can be similarly applied by measuring the distance in an outward radius, using either visual or acoustic sampling (Sebastian-Gonzalez *et al.* 2018), though is most often done in avian studies (Applegate *et al.* 2011). Distances do not even need to be measured precisely, as confidence intervals often do not grow appreciably when distances are "binned" (Buckland *et al.* 2004). In either case, the frequency distribution of the observer-animal distances are used to generate a detection function, which can then be applied throughout the sampling area to estimate the density and total population of animals (Buckland *et al.* 2001). A great strength of distance methods is that population estimates can remain robust even if only 20-40% of available individuals are observed during the survey, since detection curves can be derived from a sampling of available animals along each transect (Buckland *et al.* 1993). It then follows that if such a small portion of the animals need to be seen, in most cases a smaller portion of the study area needs to be sampled, which tends to reduce the cost of the survey compared to many other observation-based methods (Dalton 1990; Peters *et al.* 2014).

An important assumption behind distance sampling is that detection is 100% along the transect line, but this assumption is often violated because environmental factors reducing sightability elsewhere on the transect are also present on the transect centre line, but also because it can be difficult to observe wildlife directly below a helicopter or airplane (Burt *et al.* 2014). Distance sampling of moose in west-central Alberta found that detection along the transect line was 67% in one year, and just 46% in the next (Peters *et al.* 2014). More recently, Burt *et al.* (2014) used a hybrid of mark-recapture methods and distance sampling to model sighted vs. not-sighted moose along the transect line to correct for detection at distance "0" (Burt *et al.* 2014). It is generally recommended that a distance-sampling scheme have a total sample size of at least 60 observations to achieve acceptable precision (Buckland *et al.* 2001). This may be more difficult when surveying highly aggregated species, like sheep and elk, and the increased sampling intensity might erase any flying-time advantage. A comparison by Peters *et al.* (2014) found that distance sampling required 20% less total flying than a stratified random block survey (described below) of the same area. However, that survey was of moose, which are more evenly dispersed than other ungulate species, so the challenge of using distance sampling on gregarious species remains. In distance sampling, the precision of the population estimate is dependent on animal encounter rates, rather than the actual proportion of the population that is surveyed. We should therefore expect distance sampling to outperform stratified random block (SRB, below) surveys for medium to high population densities (Buckland *et al.* 2001), but fail where encounter rates are expected to be quite low.

Stratified Sampling

Stratified sampling addresses a major problem inherent in random sampling, which is that variation in habitat and population density limits realistic extrapolation of sampled densities to other areas within a survey region (Caughley 1977). The goal of stratification is to identify areas expected to have similar population densities, which leads to a smaller sampling variance, and therefore more precise population estimates. Stratification improves precision by calculating variances for each stratum independently, thereby reducing overall (Gasaway *et al.* 1986). Variance between strata does not influence the overall population estimate (Gasaway *et al.* 1986). Stratification can be done using resource selection functions (Allen 2005), past survey results, prior knowledge (BC 2002), or stratification flights (ASRD 2010). The number of strata that should be defined partly depends on the type and quality of data available for stratification, but while 2 strata (low-high) is obviously the minimum, 3-stratum configurations (low-medium-high) are more typical (Thompson 2002; Sinclair *et al.* 2006). Sampling allocation across strata is ideally adaptive, whereby it continues until a target variance is reached within each stratum, or for the population estimate (Gasaway *et al.* 1986). The result is that a given level of precision can be achieved with less sampling, and so with lower cost. For example, Gasaway *et al.* (1986) compared a SRB and simple random sampling design for an aerial survey of moose and found the SRB design needed 20 sampling blocks (stratified) to produce a population estimate with ±10% relative error compared to 32 unstratified sample blocks which produced an estimate with ± 20% relative error.

Stratification can also incorporate unique areas that one wishes to sample completely, alleviating the need for randomness in block selection (i.e., 100% of the blocks in the area are sampled). For example, moose surveys in Minnesota designated a stratum consisting only of 9 blocks that had undergone the same unique type of disturbance, and survey all 9 blocks every year (DelGiudice 2014). These blocks need not be the same size, but large variation in block size can increase inter-block population variation in counts. Our review of the literature and operational documents suggests that quadrats in stratified random block surveys typically range in size from 16 to 30 km^2.

DATA COLLECTION

Aerial vs. Ground Methods

Ungulate surveys often must occur over such large or inaccessible areas that an effective population estimate can only be obtained by using aerial census methods. Sampling a given area by car can require as much as 35 times more human-hours than sampling the same area by fixed-wing aircraft, and by foot may require 69 times more human-hours (Gaidet-Drapier *et al.* 2006). Helicopters have the further advantage of being able to hover and make tight turns, which are often necessary when collecting certain demographic information or for improving detection rates (Franke *et al.* 2012). This all comes at a cost that can be as high as 1300 CAN$/h for rotary wing, or $670CAN$/h for fixed wing. Aerial methods may also sacrifice sightability because the observer is typically at least 60 m above the ground (BC 2002; ASRD 2010; MNRF 2012), looking for animals that can be 200-300 m away laterally (see above for transect widths). Aircraft must also travel relatively fast to stall speeds. Beringer *et al.* (1998) observed that aerial methods tend to underestimate deer abundance by more than 20%, and inexperienced observers can miss or misidentify considerably more animals (Gasaway *et al.* 1986). Even an experienced observer's ability to sight wildlife typically deteriorates after 3 h of flying (Samuel *et al.* 1987) and is further affected by the intensity and speed of the search (Unsworth *et al.* 1994).

The effectiveness of aerial surveys is also largely influenced by transect width. Unless in very open habitat, individual ungulates that are available to be detected (i.e., not completely hidden) can only reliably spotted if they are within 200 m of either side of the observer (i.e., a transect strip width of 400 m; *sensu* Wright *et al.* 2011; Peters *et al.* 2014; Haroldson 2013). Likewise, Peters *et al.* (2014) showed that detection of moose was essentially 100% within a transect strip width of 400 m, but incomplete beyond that. In other words, if an entire area is surveyed completely using linear transects spaced 400 m apart, that count would represent a census of the population, and not just a sample (though if animals moved to the next transect after counting, and were thus double-counted, the census could still be inaccurate). If those transects were spaced 800 m apart, however, the raw count would be a sample of just 50% of the total area, and extrapolation to the unsampled 50% of the study area would result in a population estimate.

Ungulate Tracks

Track surveys are most feasible during winter periods when there is adequate snow cover for preserving tracks made during the known intervals between snowfalls (Ham 2011). However, Nelson and Mech (1984) used gravel roads, which they raked clean at known intervals, to count white-tailed deer tracks made in spring and summer. Ungulate tracks can be excellent indicators of presence/absence (e.g., Olsson *et al.* 2008), and effective measures of relative abundance (e.g., Reyna-Hurtado *et al.* 2007). Annually, Parks Canada conducts 10 counts throughout the winter along 15-20 transects, using observers that walk each transect at least 24 h after each snowfall, as a way to monitor predator and prey trends (Ham 2011). Data from these annual surveys have been quantitatively informative for most species using the areas, with the notable exception of elk, which frequently occur in such large herds that individual tracks become impossible to distinguish, and one can only confirm the presence of an unknown group size (Simon Ham, Banff National Park, personal communication, 2012). In snow, differentiating between the tracks of mule and white-tailed deer is also highly unreliable. The use of rocky and often steep terrain by mountain sheep (*Ovis canadensis*) and goats makes this method even less effective for those species.

Roadside Counts

A very cost-effective method is roadside counts, which is where an observer simply drives along roads and counts animals. Roadside counts can produce relative abundance results comparable to aerial surveys, despite costing as little as 1/30th the expense (Caro 2016), assuming a sufficiently large road segment is chosen. Furthermore, Caro (2016) found that, in most cases, a single roadside transect was sufficient to estimate the direction of trends (decrease vs. increase). For many jurisdictions with adequate road coverage, this can be an effective method of counting ungulates, particularly when species are expected to be at high density (Eberhardt *et al.* 1998). This method has been employed by Parks Canada for white-tailed deer (e.g. Drysdale 1986), and is still used for elk in both Banff and Jasper National Parks (John Wilmshurst, Jasper National Park, personal communication, 2014). While roadside surveys can be a quick and cost-effective method, the resulting counts can be biased if roads do not constitute a representative sample of habitats or animals (e.g., animals be attracted to or avoid roads; Garton *et al.* 2004). Demographic information such as calf:cow ratios may also be non-representative if, for example, calf survival is higher near roadsides (Grosman *et al.* 2011). This "convenience sampling" of ungulates using roadside habitat can bias estimates (Roberts *et al.* 2006).

Hunter Harvest

Hunter harvest estimates use annual hunter-reported harvest mortalities to estimate relative changes in populations. This method was implemented in Kentucky following the introduction of elk to that state in the 1990s (Larkin 2001). In the first 3 years, they censused the population and recorded detailed demographic information, which they were able to calibrate to the number of elk reported killed by hunters during the same period. In the years afterwards, they were then able to estimate the population using only mortalities resulting from hunting by humans, after adjusting for annual variation in hunting effort. This technique admittedly suffered from the unreliability of applying demographic information from a founder population (more homogenous demographics and very narrow distribution around introduction sites) to more established populations (more widely distributed and demographically natural). There was also a decline in the accuracy of extrapolations because while they knew the exact population at the time of introduction, they did not know the population size 3 years after introduction (Larkin 2001). As part of this review, we examined hunter-harvest data collected for a similarly introduced elk population in Ontario. Using an aerial mark-resight method the estimated population size was 372 (MNRF 2012. In comparison, we estimated the population size was 332 based on hunter harvest mark-resight methods based on the number of unmarked elk killed versus the number marked elk killed. Considering that the aerial method was believed to be an overestimate because of violations in assumptions regarding the population being closed, and non-random searching for elk resights using radio telemetry (Mcintosh *et al.* 2009), the hunter harvest method may have actually been more accurate, at essentially no cost.

Low cost is the greatest advantage of using hunter harvest data to monitor ungulate populations, and likely why it remains a popular method of estimating relative abundance in established and heavily hunted populations across the USA (Rabe *et al.* 2002). Unfortunately, reported hunter harvest data tends to be both unreliable and biased, and lacks consistency because of variable hunter effort and reporting standards. More detailed information on hunter kills can yield more representative population and demographic information through techniques such as cohort analysis (Fryxell *et al.* 1988), which can calculate spatio-temporal densities of populations (Ueno *et al.* 2014). Population reconstruction is an even more advanced method of estimating longitudinal populations and demographics using a combination of sex, age, and specific cohort harvest rates to model recruitment and birth and mortality rates (Downing 1980; Davis *et al.* 2007; Skalski *et al.* 2012). However, these advanced techniques all require more data, and are therefore even more limited because mandatory reporting of hunter harvest is uncommon across North America, and the precise determination of age from ungulate carcasses requires labour-intensive (and thus costly) techniques (Ueno *et al.* 2014).

Fecal Pellet Counts

Comparisons of population estimates of a known population of introduced red deer in sub-tropical Australia, using CV as a measure of relative survey quality, found that pellet counting (CV=12.3) was provided more precise estimates than roadside counting (CV=18.1), distance sampling during walked transects (CV=23.7), and aerial transects (CV=36.6; Amos *et al.* 2014). Counting fecal pellets is relatively straightforward, but significant uncertainty arises over animal defecation rates, and scat degradation times. Teichman (2013) used a fall clearance of scat followed by spring counting of the accumulations to estimate over-winter populations of bison, elk, moose, and deer in Elk Island National Park, but required assuming pellets did not degrade between September and May. The author's own winter experimental ungulate scat plots in the same park showed this assumption was almost certainly false. Variation in animal defecation rates is further magnified when variations between seasons need be considered.

Using fecal counts to estimate population size may not provide many collateral benefits either. It can be difficult to differentiate ungulate sex using pellets. In a study of captive female reindeer, pellet size alone differentiated between calves, yearlings, and adults (Morden *et al.* 2011), but in practice the presence of males would introduce uncertainty in classification of both age and sex. The difficulty would be magnified where different sized ungulates are sympatric, since large elk pellets may be difficult to differentiate from small moose pellets, large deer pellets look similar to elk calf pellets, and so on. Color differences are unreliable indicators of species, since pellet color changes with ages. Lastly, it is economically unfeasible to use DNA to differentiate sex and species in pellets with a sampling volume sufficient for a robust population estimate.

DNA collection

In ungulates, DNA information is most easily obtained from either hair or fecal pellet samples. Both blood and saliva can also provide useful DNA samples, but these require invasive collection that could only realistically take place during a capture event. Collecting ungulate hair is easiest during winter, when hair is longest; bed sites containing shed guard hairs can be readily identified, and snow itself acts as an abrasive to remove hair, but sample collection is limited to the interval between snow falls. Genetic analysis also requires the root bulb of the hair, which may not be present in shed hair. In addition to DNA analysis, hairs can also provide long-term information from stable isotopes (i.e., diet analysis) and hormones (e.g., cortisol and testosterone). Fecal pellets can also be collected in winter, and are generally easier to find than hair because of their size and the frequency at which they are deposited. Unlike hair samples, fecal pellets can be easily collected in summer, where they can remain visible for months. However, fecal samples are not as durable as hair. One study found that after Sitka deer (*O. hemionus sitkensis*) pellets were exposed to a summer environment for 7 d, only 22% were still useful for microsatellite analysis (Brinkman *et al.* 2009). Samples taken during spring and early-summer greenup are also more likely to fail, as this high-value vegetation is easier and quicker for ungulates to digest, and this leaves less time for genetic material to accumulate on the pellets (Maudet *et al.* 2004).

The majority of ungulates have a polygynous mating system (moose being an exception across most of their distribution), and most individuals found in the same local region have high degrees of interrelatedness (Clutton-Brock 1989). This necessitates using more microsatellite markers (~12) for individual identification than are required for other species such as bears (*Ursus* spp.) and canids (~7), which can increase the analysis cost to approximately $65CAD/sample compared to $47CAD (David Paetkau, Wildlife Genetics International, March 13, 2020). The mark-recapture recommendation of marking 40% of the population would make this a prohibitively expensive method for most ungulate populations.

Trail Cameras

Remote wildlife cameras, triggered by motion and/or heat, have been used to survey a wide diversity of wildlife (Royle *et al.* 2011), including ungulates (e.g., Muhly *et al.* 2011). These cameras can be mounted on fences, trees, or even self-supported stands, and programmed to detect heat and/or motion with variable sensitivity, and take photos according to a pre-chosen image quality, delay interval, and multi-image sequence. In addition to providing data on relative abundance (number of observations by species per unit time), the close range of these cameras can provide clear photos enabling precise evaluation of body condition (e.g., antler-size), and even differentiation between adult and yearling cows. These cameras can also capture images of multiple species during a single camera deployment, and collect data throughout the year and even at night, and independent of weather conditions. Certain research projects may benefit through the use of habitat stratification to guide deployment. For example, if the objective is to detect a decline in occupancy, the optimal strategy is to sample high-quality habitats whereas if the objective is to detect an increase in occupancy, one should sample intermediate-quality habitats (Rhodes *et al.* 2006). One may also want to consider sampling core versus peripheral habitat, depending on species, habitat, and objectives.

Image resolution and camera reliability has steadily improved, while prices have dropped to where an effective camera can be purchased for as little as $100CAD, in addition to costs for batteries and locks. Additional costs include the in-field labour to mount and maintain camera trap locations, and though extracting useful data from raw images can also be labour intensive, automated software may increase efficiency. For example, Willi et al (2018) used machine learning methods to achieve 98% success identify frames with no animals, and up to 93% success in identify wildlife to species.

Thermal Imaging

Thermal imagers, such as FLIR (Forward Looking Infrared Radar) and AIMS (Airborne Image Multispectral Sensor) produce digital images that depict subtle (< 1ºC) changes in temperature. Cameras are typically mounted on fixed or rotary-wing aircraft and capture thermal images along designated survey routes; because mammal body temperatures contrast sharply with those of their surroundings, individual animals can be differentiated from their environment. Species can then be identified by body size comparisons, where the difference is large enough, such as between moose and deer (Potvin and Breton 2005). Overlap in body sizes, such as between small moose and large elk, or even adult deer and elk calves, might require precise temperature measurements in order to differentiate individuals to species (Graves *et al.* 1972), but this is not always necessary. Mule deer and pronghorn have similar body sizes, yet were differentiated using FLIR at an altitude of 600 m in California, where they were also conspecific with bighorn sheep (Bernatas and Nelson 2004). If paired with a visible spectrum camera, the thermal signatures can then be compared to the visible spectrum images to identify animals more definitively (see Franke *et al.* 2012), though the resolution necessary to achieve this can quickly become cost prohibitive. For example, at 5 cm resolution, bison could still not be classed reliably to age class or sex (Jonathan DeMoor, Elk Island National Park, personal communication, 2018).

Pairing with a visible spectrum camera may also be necessary in order to collect demographic data, since heat signatures of antlers are unlikely outside of the velvet period (Wiggers and Beckerman 1993), and because sympatric adult females and yearling males have similar body sizes. Pairing with visible spectrum cameras and adding the extra processing time drive the costs of IR methods even higher. Including the costs of equipment AIMS-T costs about $270CAD/km^2$, and FLIR $123CAD/km^2$, compared to $60CAD/km^2$ for comparable naked-eye observation (Millette *et al.* 2011). It can take 4 h of video/photo processing for every 1 h of actual survey time, and this can amount to an additional $400CAD/hour (Dahl 2008). A FLIR survey of caribou in the Slate Islands of Ontario cost $6,000CAD to survey just 284 km^2, and while this survey successfully achieved a CV less than 0.20, it failed to collect demographic information (Carr *et al.* 2012).

As with most survey methods, detection rates for thermal methods can vary as a function of season, weather, and habitat cover attributes. Detectability using FLIR can be as low as 54% where there is canopy cover (Potvin and Breton 2005), and less than 50% in coniferous forests (Bernatas

2009). The use of FLIR to survey elk in Kentucky achieved 76% detection (Dahl 2008), and here the unit of detection was the entire group. Dahl (2008) also found that 6% of all "elk sightings" were actually white-tailed deer that had been misidentified. This seemingly small error was calculated to have inflated population estimates by 14-64%. Reflected heat on sunny days can also lead to misidentification of inanimate objects as animals (Franke *et al.* 2012). Thermal surveys of both fallow deer (*Dama dama*) and red deer achieved impressive CV values near 0.10 on completely overcast days, but CV values increased to 0.52 when the sky was only partly cloudy (Franke *et al.* 2012). Winter experiments on white-tailed deer in Wisconsin (Storm *et al.* 2011) found that after autumn leaf fall, FLIR could detect no more animals than traditional visual methods, and FLIR surveys only outperformed traditional surveys when there was no snow on the ground. Daily weather conditions can also have a significant effect on FLIR capabilities, since reflected sunshine may also give false heat signatures off of high albedo elements such as white rocks.

CONCLUSION

Knowledge of populations and trends is necessary for the effective and adaptive management of ungulates. Because total counts are prohibitively expensive for all but the smallest management areas, monitoring metrics (e.g., population size or trends) usually must be estimated from samples. Wildlife professionals continue to rely on both absolute and relative abundance survey methods because while the latter is cheaper, the former is more informative. Faced with this choice, managers may find that a combination of the two is more cost effective for achieving management goals (Bowden *et al.* 2000). However, it is important to recognize that there can be such high variability in habitat, species assemblages, and logistical capacity that methods that are useful in one jurisdiction, may fail in another (Rabe *et al.* 2002). Ultimately the choice of survey method and sampling must be guided by management objectives, which provide the lens through which the costs and benefits of different survey methods and sampling designs are evaluated.

LITERATURE CITED

Alberta Sustainable Resource Development (ASRD). 2010. Aerial ungulate survey protocol manual. ASRD, Fish and Wildlife Division, Edmonton, Alberta, Canada.

Alberta Environment and Parks. 2019. Wildlife management unit map. http: https://open.alberta.ca/publications/2015-wildlife-management-unit-map Accessed March 10, 2010.

Allen, J. R. 2005. Use of sightability models and resource selection functions to enhance aerial population surveys of elk (*Cervus elaphus*) in Alberta. MS thesis, University of Alberta, Edmonton, Canada.

Amos, M., G. Baxter, N. Finch, A. Lisle, and and P. Murray. 2014. I just want to count them! Considerations when choosing a deer population monitoring method. Wildlife Biology 20: 362–370.

Applegate, R. D., R. E. Kissell Jr., E. D. Moss, E. L. Warr, and M. L. Kennedy. 2011. Problems with avian point counts for estimating density of northern bobwhite: a case study. Journal of Fish and Wildlife Management 2: 117–121.

Bartmann, R. M., L. H. Carpenter, R. A. Garrott, and D. C. Bowden. 1986. Accuracy of helicopter counts of mule deer in pinyon-juniper woodland. Wildlife Society Bulletin 14: 356–363.

Bear, G. D., G. C. White, L. H. Carpenter, R. B. Gill, and D. J. Essex. 1989. Evaluation of aerial mark-resighting estimates of elk populations. Journal of Wildlife Management 53: 908–915.

Beringer, J., L. P. Hansen, and O. Sexton. 1998. Detection rates of white-tailed deer with helicopter over snow. Wildlife Society Bulletin 26: 24–28.

Bernatas, S. 2009. White-tailed deer population survey. Delaware Division of Fish and Wildlife. Vision Air Research. Boise, Idaho, USA.

Bernatas, S., and L. Nelson. 2004. Sightability model for California bighorn sheep in canyonlands using forward-looking infrared (FLIR). Wildlife Society Bulletin 32:638–647.

Boulanger, J., K. Poole, and C. DeMars. 2017. Review of bison monitoring program for the Northwest Territories. Integrated Ecological Research. Manuscript Report No. 269.

Bowden, D. C., G. C. White, and R. M. Bartmann. 2000. Optimal allocation of sampling effort for monitoring a harvested mule deer population. The Journal of Wildlife Management 64: 1013–1024.

Brinkman, T. J., D. K. Person, F. S. Chapin III, W. Smith, and K. J. Hundertmark. 2011. Estimating abundance of Sitka black-tailed deer using DNA from fecal pellets. Journal of Wildlife Management 75: 232–242.

British Columbia Ministry of Sustainable Resource Management. 2002. Aerial-based inventory methods for selected ungulates: bison, mountain goat, mountain sheep, elk, deer and caribou. Standards for Components of British Columbia's Biodiversity No. 32., Victoria, British Columbia, Canada.

Buckland, S. T., D. R. Anderson, K. P. Burnham and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, New York, New York.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling. Oxford University Press, London, UK.

Burt, M. L., D. L. Borchers, K. J. Jenkins, and T. A. Marques. 2014. Using mark-recapture distance sampling methods on line transect surveys. Methods in Ecology and Evolution 5: 1180–1191.

Campbell, D., G. M. Swanson, and J. Sales. 2004. Comparing the precision and cost-effectiveness of faecal pellet group count methods. Journal of Applied Ecology 41: 1185–1196.

Caro, T. 2016. Guidelines for wildlife monitoring: savannah herbivores. Tropical Conservation Science 9: 1–15.

Carr, N. L., A. R. Rodgers, S. R. Kingston, P. N. Hettinga, L .M. Thompson, J. L. Renton and P. J. Wilson. 2012. Comparative woodland caribou population surveys in Slate Islands Provincial Park, Ontario. Rangifer 32: 205–217.

Caughley, G. 1977. Sampling in aerial survey. Journal of Wildlife Management 41: 605–615.

Clutton-Brock, T. H. 1989. Mammalian mating strategies. Proceedings of the Royal Society B 236: 339–-372.

Cochran, W. G. 1977. Sampling techniques. Wiley, New York, USA.

Creel, S., J. A. Winnie Jr., and D. Christianson. 2010. Glucocorticoid stress hormones and the effect of predation risk on elk production. Proceedings of National Academy of Sciences: www.pnas.org_cgi_doi_10.1073_pnas.0902235106

Dahl, L. M. 2008. Using forward-looking infrared radiography to estimate elk density and distribution in eastern Kentucky. MSc. thesis. University of Kentucky. USA.

Dalton, W. J. 1990. Moose density estimation with line transect survey. Alces 26:129–141.

Davis, M. L., J. Berkson, D. Steffen, and M. K. Tilton. 2007. Evaluation of accuracy and precision of Downing population reconstruction. Journal of Wildlife Management 71: 2297–2303. doi:10.2193/2006-427

Debyle, N. V. and R. P. Winokur . 1985. Aspen: ecology and Management in the Western United States. United States Department of Agriculture, Forest Service:143–144 .

DeCesare, N. J, J. R. Newby, V. J. Boccardori, T. Chilton-Radant, T. Thier, D. Waltee,K. Pdruzny, and J. A. Gude. 2016. Calibrating minimum counts and catch-per-unit-effort as indices of moose population trend. Wildlife Society Bulletin 40: 537–547.

DelGiudice, G. D. 2014. 2014 Aerial moose survey. Minnesota Department of Natural Resources, Section of Wildlife, St. Paul, Minnesota. USA.

Downing, R.L. 1980. Vital statistics of animal populations. Pages 247– 267 *in* S.D. Schemnitz, editor. Wildlife management techniques manual. The Wildlife Society, Washington, D.C.

Drysdale, C. D. 1986. The roadside deer of Kejimkujik National Park. MS thesis, Acadia University, Wolfville, Nova Scotia, Canada.

Eberhardt, L. L. 1978. Appraising variability in population studies. Journal of Wildlife Management 42: 207–238.

Eberhardt, L. L., R. A. Garrott, P. J. White, and P. J. Gogan. 1998. Alternative approaches to aerial censusing of elk. Journal of Wildlife Management 62: 1046–1055.

Found, R. 2017. Ungulate population estimation using fecal pellet counts. Operational Report. Elk Island National Park, Fort Saskatchewan, Alberta, Canada.

Found R. F. and St. Clair C. C. 2016. Behavioural syndromes predict loss of migration in wild elk. Animal Behaviour. 115: 35–46

Franke, U., B. Goll, U. Hohmann, and M. Heurich. 2012. Aerial ungulate surveys with a combination of infrared and high-resolution natural colour images. Animal Biodiversity and Conservation 35: 285–293.

Fryxell, J., W. Mercer, and R. Gellately. 1988. Population dynamics of Newfoundland moose using cohort analysis. Journal of Wildlife Management 52: 14–21.

Gaidet-Drapier, N., H. Fritz, M. Bourgarel, P-C. Renaud, P. Poilecot, D. Poulet, and S. Le Bell. 2006. Cost and efficiency of large mammal census techniques : comparison of methods for a participatory approach in a communal area, Zimbabwe. Biodiversity and Conservation 15:735–754

Garton, E. O., J. T. Ratti, and J. H. Giudice. 2004. Research and experimental design. Chapter 3 *in* C. Braun editor. Techniques for wildlife investigations and management. The Wildlife Society, Bethesda, Maryland, USA.

Gasaway, W.C., D. DuBois, D. J. Reed, and S. J. Harbo. 1986. Estimating moose population parameters from aerial surveys. Biological Papers of the University of Alaska No. 22. Fairbanks or Anchorage, Alaska, USA.

Gopalaswamy, A. M., K.U. Karanth, N. S. Kumar, and D. W. Macdonald. 2012. Estimating tropical forest ungulate densities from sign surveys using abundance models of occupancy. Animal Conservation 15: 669–679.

Graves, H. B., E. D. Bellis, and W. M. Knuth. 1972. Censusing white-tailed deer by airborne thermal infrared imagery. Journal of Wildlife Management, 875–884.

Grosman, P. D., J. A. G. Jaeger, P. M. Biron, C. Dussault, and J. P. Ouellet. 2011. Trade-off between road avoidance and attraction by roadside salt pools in moose: an agent-based model to assess measures for reducing moose-vehicle collisions. Ecological Modelling 222: 1423–1435.

Haroldson, B. S., and J. H. Giudice. 2013. 2013 White-tailed deer surveys. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA.

Ham, S. 2011. Wildlife corridors around developed areas in Banff National Park. Progress report for Parks Canada Warden Service. Winter 2010/2011, Banff, Alberta, Canada.

Hamrick, B., B. Strickland, S. Demarais, W. McKinley, and B. Griffin. 2013. Conducting camera surveys to estimate population characteristics of white-tailed deer. Mississippi State University Extension Service Publication 2788.

Hestbeck, J. B., and R. A. Malecki. 1989. Mark–resight estimate of Canada goose midwinter number. Journal of Wildlife Management 53: 749–752.

Hiby, L. 2010. Downloadable software for automated photo-id of Grevy's zebra. Http://www.Conservationresearch.co.uk/zebra/zebra.htm

Houston, D. B., B. B. Moorhead, and R. W. Olson. 1986. An aerial census of mountain goats in the Olympic Mountain Range, Washington. Northwest Scientist 60: 131–136.

Hurst, J. E., and W. F. Porter. 2008. Evaluation of shifts in white-tailed deer winter yards in the Adirondack region of New York. Journal of Wildlife Management 72: 367–375.

Jenkins, D. A, J. A. Schaefer, R. Rosatte, T. Bellhouse, J. Hamr, and F. F. Mallory. 2007. Winter resource selection of reintroduced elk and sympatric white-tailed deer at multiple spatial scales. Journal of Mammalogy 88: 614–624.

Jůnek T., P. Jůnková Vymyslická, K. Hozdecká, and P. Hejcmanová. 2015. Application of spatial and closed capture-recapture models on known population of the Western Derby Eland (*Taurotragus derbianus derbianus*) in Senegal. PLoS ONE 10(9): e0136525.

Kadmon, R., O. Farber, and A. Danin. 2004. Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. Ecological Applications 14: 401–413.

Krausman, P. R. ,and V. C. Bleich. 2013. Conservation and management of ungulates in North America. International Journal of Environmental Studies 70: 372–382.

Krebs, C. J. 1999. Ecological methodology. 2nd edition. Benjamin/Cummings, Menlo Park, California, USA.

Kuzyakin, V. A. 1983. Results of modelling winter transect counts. Pages 193-229 *in* V.A. Zabrodin, editor. Scientific proceedings: winter transect counts of game animals. Moscow: Central Research Laboratory of Glavokhota, Town, Russia

Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. Pages 215–253 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats, 5th edition The Wildlife Society, Bethesda, Maryland, USA.

Larkin, J. L. 2001. Demographic and spatial characteristics of a reintroduced elk population. PhD dissertation, University of Kentucky, Lexington, Kentucky, USA.

Larue, M. A., C. K. Nielsen and M. D. Grund. 2007. Using distance sampling to estimate densities of white-tailed deer in south-central Minnesota. The Prairie Naturalist 39: 57–68.

Leblond, M., C. Dussault, J-P Ouellet, M. Poulin, R. Courtois, and J. Fortin. 2007. Management of roadside salt pools to reduce moose-vehicle collisions. Journal of Wildlife Management 71: 2304–2310.

Mahoney, S. P., J. A. Virgl, D. W. Fong, A. M. MacCharles, and M. McGrath. 1998. Evaluation of a mark-resighting technique for woodland caribou in Newfoundland. Journal of Wildlife Management 62: 1227–1235.

Marques, F. F. C, S. T. Buckland, D. Goffin, C. E. Dixon, D. L. Borchers, B. A. Mayle, and A. J. Peace. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. Journal of Applied Ecology 38: 349–363.

Matulich, S. C., and J. E. Hanson. 1986. Modelling supply response in bioeconomic research: an example from wildlife enhancement. Land Economics 62: 292–305.

Maudet, C, G. Luikart, and D. Dubray. 2004. Low genotyping error rates in wild ungulate feces sampled in winter. Molecular Ecology Notes 4: 772–775.

Mayle, B. A., A. J. Peace, and R. M. A. Gill. 1999. How many deer? A field guide to estimating deer population size. Field Book 18. Forestry Commission, Edinburgh, UK.

McIntosh, T. E., R. C. Rosatte, J. Hamr, and D. L. Murray. 2009. Development of a sightability model for low-density elk populations in Ontario, Canada. Journal of Wildlife Management 73: 580–585.

Messier, F., and C. Barrette. 1985. The efficiency of yarding behavior by white-tailed deer as an antipredator strategy. Canadian Journal of Zoology 63: 785–789.

Millette, T. L., D. Slaymaker, E. Marcano, C. Alexander, and L. Richardson. 2011. AIMS-Thermal-A thermal and high resolution color camera system integrated with GIS for aerial moose and deer census in northeastern Vermont. Alces 47: 27‒37.

Ministry of Natural Resources and Forestry (MNRF). 2012. Elk aerial index based on moose survey methodology. Unpublished report, Bancroft, Ontario, Canada.

Mooty, J. J., and P. D. Karns. 1984. The relationship between white-tailed deer track counts and pellet-group surveys. Journal of Wildlife Management 48: 275‒278.

Morden, C. J., R. B. Weladji, E. Ropstad, E. Dahl, and H. Oystein. 2011. Use of faecal pellet size to differentiate age classes in female Svalbard reindeer *Rangifer tarandus platyrhynchus*. Wildlife Biology 17: 441‒448.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. PLoS ONE, 6: e17050

Mulero-Pazmany, M, M. D'Amico, and M. Gonzalez-Suarez, M. 2016. Journal of Zoology 298: 233‒240.

Nakagawa, S., and I. C. Cuthill. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biological Reviews 82: 591‒605.

Nelson, M.E., and L.D. Mech. 1984. Deer social organization and wolf predation in Minnesota. Wildlife Monographs 77: 1–53.

Nelson, M. E., and G. A. Sargeant. 2008. Spatial interactions of yarded white-tailed deer, Odocoileus virginianus. Canadian Field-Naturalist 122: 221‒225.

Newton, E., K. Abraham, J. Schaefer, B. Pond, G. Brown, and J. Thompson. 2015. Causes and consequences of broad-scale changes in the distribution of migratory Caribou (*Rangifer tarandus*) of Southern Hudson Bay. Arctic 68: 472‒485.

Nielson, R. M., R. T. Sugihara, T. J. Boardman, and R. M. Engeman. 2004. Optimization or ordered distance sampling. Environmetrics 15: 119‒128.

O'Brien, T. G. 2011. Abundance, density and relative abundance: A conceptual framework. Pages 71‒96 *in* A. F. O'Connell, J. D. Nichols and K. U. Karanth, editors. Camera traps in animal ecology: methods and analyses. Springer-Verlag, Tokyo, Japan.

Oetgen, J. G., B. C. Lambert Jr., and J. D. Whiteside. 2008. Surveying white-tailed deer populations using infrared-triggered cameras. Texas Parks and Wildlife. Austin, USA.

Ogutu, J. O., N. Bhola, H-P Piepho, and R. Reid. 2007. Efficiency of strip and line transect surveys of African savanna mammals. Journal of Zoology 269: 149‒160.

Olsson, M. P. O., P. Widen, and J. L. Larkin. 2008. Effectiveness of a highway overpass to promote landscape connectivity and movement of moose and roe deer in Sweden. Landscape and Urban Planning 85: 133‒139.

Parks Canada. 2018. Elk Island National Park ungulate population monitoring: aerial survey protocol. Elk Island National Park, Fort Saskatchewan, Alberta, Canada.

Peters, W., M. Hebblewhite, K. G. Smith, S. M. Webb, N. Webb, M. Russell, C. Stambaugh, and R. B. Anderson. 2014. Contrasting aerial moose population estimation methods and evaluating sightability in West-Central Alberta, Canada. Wildlife Society Bulletin 38: 639‒649.

Potvin, F., and L. Breton. 2005. Testing 2 aerial survey techniques on deer in fenced enclosures-visual double-counts and thermal infrared sensing. Wildlife Society Bulletin 33: 317‒325.

Proulx, G., and R. Joyal. 1981. Forestry maps as an information source for description of moose winter yards. Canadian Journal of Zoology 59: 75–80.

Putman, R., P. Watson, and J. Langbein. 2011. Assessing deer densities and impacts at the appropriate level for management: a review of methodologies for use beyond the site scale. Mammal Review 41: 197‒219.

Quayle, J. F., A. G. MacHutchon, and D. N. Jury. 2001. Modeling moose sightability in south-central British Columbia. Alces 37: 43‒54.

Rabe, M. J., S. S. Rosenstock and J. C. deVos Jr. 2002. Review of big-game survey methods used by wildlife agencies of the western United States. Wildlife Society Bulletin 30: 46‒52.

Reyna-Hurtado, R., and G. W. Tanner. 2007. Ungulate relative abundance in hunted and non-hunted sites in Calakmul Forest (Southern Mexico). Biodiversity and Conservation 16: 743‒756.

Rhodes, J. R., A. J. Tyre, N. Jonzen, C. A. McAlpine, and H. P. Possingham. 2006. Optimizing presence-absence surveys for detecting population trends. Journal of Wildlife Management 70: 8‒18.

Rivero, K., D. I. Rumiz, and A. B. Taber. 2004. Estimating brocket deer (*Mazama gouazoubira* and *M. americana*) abundance by dung pellet counts and other indices in seasonal Chiquitano forest habitats of Santa Cruz, Bolivia. European Journal of Wildlife Research 50: 161‒167.

Roberts, C. W., B. L. Pierce, A. W. Braden, R. R. Lopez, N. J. Silvy, P. A. Frank, and D. Ransom Jr. 2006. Comparison of camera and road survey estimates for white-tailed deer. Journal of Wildlife Management 70: 263‒267.

Robson, D. S., and H. A. Regier. 1964. Sample size in Petersen mark-recapture experiments. Transactions of the American Fisheries Society 93: 215‒226.

Rosatte, R., J. Young, J. Hamr, and I. Filion. 2007. The restoration of elk (*Cervus elaphus*) in Ontario, Canada: 1998-2005. Restoration Ecology 15: 34‒43.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek. 2013. "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. Hystrix 24: 148‒156.

Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. Journal of Applied Ecology 45: 1228‒1236.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84: 777‒790.

Royle, J. A., A. J. Magoun, B. Gardner, P. Valkenburg, and R. E. Lowell. 2011. Density estimation in a wolverine population using spatial capture-recapture models. Journal of Wildlife Management 75: 604–611.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in Northcentral Idaho. Journal of Wildlife Management 51: 622‒630.

Sebastian-Gonzalez, E., R. J. Camp, A. M. Tanimoto, P. M. de Oliveira, B. B. Lima, T. A. Marques, and P. J. Hart. 2018. Density estimate of sound-producing terrestrial animals using single automatic acoustic recorded and distance sampling. Avian Conservation and Ecology 13: 7. doi.org/10.5751/ACE-01224-130207

Sharma R., Y. Jhala, Q. Qureshi, J. Vattakaven, R. Gopal, and K. Nayak. 2010. Evaluating capture–recapture population and density estimation of tigers in a population with known parameters. Animal Conservation 13: 94–103.

Sinclair, A. R. E., J. M. Fryxell, and G. Caughley. 2006. Wildlife ecology, conservation, and management. 2nd edition. Blackwell Publishing. Malden, USA.

Skalski, J. R., J. J. Millspaugh, and M. V. Clawson. 2012. Comparison of statistical population reconstruction using full and pooled adult age-class data. PLoS One 7, e33910. doi:10.1371/journal.pone.0033910.

Stephens, P. A., O. Y. Zaumyslova, D. G. Miquelle, A. I. Myslenkov, and G. D. Hayward. 2006. Estimating population density from indirect sign: track counts and the Formozov-Malyshev-Pereleshin formula. Animal Conservation 9: 339‒348.

Storm, D. J., M. D. Samuel, T. R. Van Deelen, K. D. Malcolm, R. E. Rolley, N. A. Frost, D. P. Bates, and B. J. Richards. 2011. Comparison of visual-based helicopter and fixed-wing forward looking infrared surveys for counting white-tailed deer *Odocoileus virginianus* Wildlife Biology 17: 431‒440.

Strandgaard, H. 1967. Reliability of the Petersen method tested on a roe-deer population. Journal of Wildlife Management.31: 643‒651.

Teichman, K. J. 2013. Trophic cascades: Linking ungulates to shrub-dependent birds and butterflies. MS thesis. University of Alberta. Edmonton, Canada.

Thompson, S. K. 2002. Sampling. 2nd edition. John Wiley and Sons. New York, USA.

Ueno, M., E. J. Solberg, H. Iijima, C. M. Rolandsen, and L. E. Gangsei. 2014. Performance of hunting statistics as spatiotemporal density indices of moose (*Alces alces*) in Norway. Ecosphere 5, e-Article 13. doi:10.1890/ES13-00083.1.

Unsworth, J. W., F. A. Leban, D. A. Leptich, E. O. Garton, and P. Zager. 1994. Aerial survey: user's manual, 2nd edition. Idaho Department of Fish and Game, Boise, Idaho.

Urbanek, R. E., C. K. Nielsen, T. S. Preuss, and G. A. Glowacki. 2012. Comparison of aerial surveys and pellet-based distance sampling methods for estimating deer density. Wildlife Society Bulletin 36: 100‒106.

White, G. C. and L. E. Eberhardt. 1980. Statistical analysis of deer and elk pellet-group data. Journal of Wildlife Management 44: 121‒131.

Whittington, J. and M. A. Sawaya. 2015. A comparison of grizzly bear demographic parameters estimated from non-spatial and spatial open population capture-recapture models. PLoS ONE 10(7): Doi: 10.1371/ journal.pone.0134446.

Wiggers, E. P., and S. F. Beckerman. 1993. Use of thermal infrared sensing to survey white-tailed deer populations. Wildlife Society Bulletin: 263‒268.

Willi, M., R. T. Pitman, A. W. Cardoso, C. Locke, A. Swanson, A. Boyer, M. Veldhuis, and L. Fortson. 2018. Identifying animal species in camera trap images using deep learning and citizen science. Methods in Ecology and Evolution 10: 80‒91.

Williams, B. K., J. D. Nichols and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Williams, B. K. 2011. Passive and active adaptive management: approaches and an example. Journal of Environmental Management 92: 1371‒1378.

Wright, R. G., B. S. Haroldson and C. Pouliot. 2011. DNR Survey–moving map software for aerial surveys. Pages 271‒275 *in* G. DelGiudice, M. Grund, L. Lawrence, and M. Lenarz, editors. Summaries of wildlife research findings, 2010. Division of Fish and Wildlife, Minnesota Department of Natural Resources, St. Paul, Minnesota, USA.

Wu, J., R. M. Adams, and W. G. Boggess. 2000. Cumulative effects and optimal target of conservation efforts: steelhead trout habitat enhancement in Oregon. American Journal of Agricultural Economics 82: 400–413.

Zero, V. H., S. R. Sundaresan, T. G. O'Brien and M. F. Kinnaird. 2013. Monitoring an endangered savannah ungulate, Grevy's zebra (*Equus grevyi*): choosing a method for estimating population densities. Oryx 47: 410–419.

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