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Review of Bison Monitoring Program for the Northwest Territories

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ABSTRACT

Population monitoring of wood bison is challenging because of their clumped distribution within a landscape composed of a matrix of open and forested habitats. Here, we review recent advances in methods for monitoring ungulate populations which are often clumped in distribution due to their gregarious nature or due to smaller-scale habitat selection. We began with an overview of common sampling designs and methods for collecting relevant data. We then examine statistical methods for estimating the population characteristics of spatial distribution, size and trend. Included in this review is discussion of main demographic indicators and methods to assess distribution. One of our main conclusions is that management should be based on use of all population indictors. If there are estimates of population size, survival estimates, and recruitment rates then it is possible to fit multiple-data source models to further model demography and population trends. A variety of methods are available to estimate abundance and density of bison. Of these, distance sampling is most advantageous because it does not involve marking individual bison but still allows an estimate of detection probability needed to ensure robust estimates. It also allows further modeling of density within the survey area using density surface modeling. The main challenge for distance sampling is collection of field data that meets distance sampling assumptions as well as confronting variation in density due to aggregation of bison into larger groups. Power analyses suggest that annual abundance surveys are unlikely to detect year-to-year changes in population size. Anthrax outbreaks (detected by summer surveillance flights) will trigger the need for more intensive monitoring, but otherwise herd abundance should not change dramatically year to year. We proposed various improvements for field-based methodologies as well as estimation methods to optimize survey design for monitoring bison populations.

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Introduction

Effective wildlife management requires monitoring changes in the spatial distribution of species, their population size and their population trend (Williams et al. 2002, Sinclair et al. 2006). Reliable estimates of these population characteristics are necessary for determining current population status and providing a basis for evaluating management decisions in an adaptive management framework (Holling 1978) obtaining reliable estimates of population distribution, size or trend; however, it is not a trivial task. Surveys designed to collect the relevant data are often costly and challenged by environmental factors (e.g. weather, land cover) and animal behaviours that can cause imperfect detection of all individuals, leading to estimates that are biased and/or imprecise (Williams et al. 2002).

Three subpopulations of wood bison (*Bison bison athabascae*) occur within the Northwest Territories (NWT) (COSEWIC 2013). The first goal of the *NWT Wood Bison Management Strategy* is to recover free-ranging, genetically diverse, healthy wood bison throughout their historic range in the NWT, which can sustain on-going harvests for the benefit of all NWT residents (Species at Risk 2010). Population estimates and composition surveys are integral parts of the strategy. Population monitoring of wood bison is challenging because of their clumped distribution within a landscape composed of a matrix of open and forested habitats. Here, we review recent advances in methods for monitoring ungulate populations which are often clumped in distribution due to their gregarious nature or due to smaller-scale habitat selection. We begin with an overview of common sampling designs and methods for collecting relevant data. We then examine statistical methods for estimating the population characteristics of spatial distribution, size and trend.

Traditional knowledge systems employ a variety of approaches for monitoring wildlife populations (Berkes et al. 2000, Berkes 2008). Traditional monitoring methods are primarily aimed at understanding population changes in harvestable species (Moller et al. 2004). Bison have always played a central role in Dene culture, and as such Aboriginal peoples have had a long interest in the species (e.g. Athabasca Chipewyan First Nation 2012, ENR 2013). Traditional ecological knowledge has become an important part of wood bison monitoring, research and management (Moesker 2004, Parks Canada 2010). We reviewed the literature (see Appendix A for search sources) for information directly applicable to monitoring bison distribution, population size and trend; where applicable, these data are incorporated into the appropriate sections of this report.

Challenges of Data Collection for Clustered Species

Effective monitoring of wildlife populations requires estimates of key population metrics that are reliable and cost-efficient. Achieving such estimates depends critically on survey designs that aim to minimize bias and maximize precision by taking into account the metric of interest and the biology of the target species. For ungulates, the most prevalent survey designs have been aerial-based and generally involve delineating a predefined study area into either transects (e.g. Caughley 1977) or blocks (e.g. Gasaway et al. 1986). For species with a relatively uniform distribution within the study area, a simple transect or random block design may be sufficient to achieve estimates with acceptable precision (e.g. coefficients of variation [CV] ≤20%; Pollock et al. 1990). Species that are spatially clustered, however, present a number of challenges to such designs. First, spatial clustering may result in the target species being absent in a large percentage of transects or blocks. Because of this low rate of encounter, estimates of the targeted population metric will likely be imprecise because the survey data will contain a high number of zeroes, a scenario that confounds many statistical estimation procedures (Thompson 2004). This problem may be exacerbated by species that occur in groups. For these species, the group rather than the individual becomes the encounter unit and increasing aggregation into groups will result in a further lowering of encounter rates (Ioannou et al. 2011). Group-living can also generate biased estimates of population metrics if large groups are more easily detected than small groups (Royle 2008) or if groups are too large to practically enumerate all individuals (Cogan and Diefenbach 1998). Biases related to imperfect detection and enumeration can be accounted for with specific sampling and statistical techniques developed for the metric of interest (see Distribution, Range Size and Habitat Selection). Here, we focus on general survey designs that aim to increase estimated precision by increasing encounter rates with spatially clustered species.

Sampling Designs for Spatially Clustered Species

For most wide-ranging animals, surveys focused on a total count or censuses of all individuals are infeasible logistically. Moreover, the resulting estimates of such surveys lack measures of precision and therefore are scientifically questionable (Williams et al. 2002). Consequently, most surveys employ a sampling design to collect the relevant data and to make inferences across the study area. For spatially clustered species, sampling designs primarily focus on directing survey effort to where species are, or are predicted to be, to increase encounter rates. In general, these designs fall into two categories: those that stratify the study area either pre- or post-survey, and those that use adaptive sampling.

Stratified sampling designs involve partitioning the study area into regions (or strata) based on expected similarities among within-strata sample units (e.g. transects or blocks; Lohr 1999). By doing so, a proportion of the total variance is assigned to differences among strata. Because this proportion does not contribute to the variance of the targeted estimate, estimate precision is increased. Pre-stratification is inherent to the stratified random block design of Gasaway et al. (1986), one of the most widely used methods for surveying ungulates. In this design, stratification is conducted during a pre-survey flight of the study area and sample units are assigned to different strata based on perceived species-habitat relationships. Pre-stratification can also be done if species-habitat spatial models are available for the targeted species within the study area (e.g. Allen et al. 2008). In both cases, the success of pre-stratification designs depends on the strength of the species-habitat relationship; however, even in situations where this relationship is well understood, stratification may not result in precise estimates if animals are spatially clustered within strata and/or well below the carrying capacity of their habitat (Rachlow and Svancara 2006). Stratification can also be done post-survey where sample units are grouped based on similar rates of animal encounter or on environmental attributes collected during the survey (Anganuzzi and Buckland 1993, Allen et al. 2008). Post-stratification should be approached cautiously, though, as post-hoc “data snooping” may lead to an overestimation of parameter precision (Lohr 1999).

Stratification designs have been used to estimate population sizes of bison. Rowe (2006) employed a stratified random block design to estimate the population size of plains bison in northeast British Columbia (BC). The study area consisted of 54 blocks which were divided into two strata (high [n=28] and low [n=26] suitability). Because variability among blocks was expected to be high due to the grouping nature of bison, all high stratum blocks were surveyed, which resulted in an estimate that had an extremely low CV (±2.6%). Kindopp and Vassal (2010) used stratification to estimate the population size of wood bison in Wood Buffalo National Park (WBNP). In this study, stratification was based on the method used to survey four areas within the park. These methods included strip transects, 100% coverage, a combination of strip transect and 100% coverage, and reconnaissance flights. The reconnaissance flights and the 100% coverage areas were considered minimum counts with no accompanying estimates of precision. Nevertheless, this design resulted in an estimate with a CV of ±9.3%. Stratification designs have also been used to estimate population sizes of other ungulates that occur in groups including elk (*Cervus canadensis*; CV=26-28%; Allen et al. 2008); mule deer (*Odocoileus hemionus*; CV=27%; Habib et al. 2013) and elephants (*Loxodonta africana*; CV=24%; Watson et al. 1969).

Adaptive sampling designs are another approach for estimating population metrics of spatially clustered species (Thompson 2012, Brown et al. 2013). A key advantage to these designs is their flexibility, allowing survey effort to be shifted to areas where the target species has been found to occur. In adaptive cluster sampling, an initial set of sample units is selected by a probability-based process (e.g. simple random sampling) and for those units meeting an *a priori* threshold (e.g. species presence), additional units in close proximity receive further survey effort. If any of these additional units meet the threshold, their neighbouring units are surveyed. This process is repeated, allowing for sampled clusters to vary in shape and size (Brown et al. 2013). This variability, however, can be a drawback from a planning perspective because the final sample size, and therefore survey cost, is difficult to estimate. Cost-efficiency of adaptive sampling is further impacted by the necessity of surveying "edge" units (i.e., units that are unoccupied surrounding a cluster) yet information from these units does not contribute to the targeted estimate (Brown et al. 2008).

For estimating metrics of population demography, adaptive cluster sampling has had few empirical tests. Khaemba et al. (2001) used empirical distributions of elephants and zebras (*Equus burchelli*) to assess multiple aerial survey designs for estimating animal abundance. For both species, estimate precision was improved with adaptive cluster sampling. Khaemba and Stein (2002) further assessed the efficacy of adaptive cluster sampling for estimating population sizes of kongoni (*Alcelaphus buselaphus*) and wildebeest (*Connochaetes taurinus*), reporting improved precision in estimates for both species but simulations showed an underestimation of true population size for wildebeest, which occur in large herds. Beyond large herbivores, Sullivan et al. (2008) found increased precision with adaptive cluster sampling when estimating the density of sea lampreys (*Petromyzon marinus*). Smith et al. (2003) and Noon et al. (2006), however, found no increase in precision when estimating densities of freshwater mussels and herpetofauna, respectively. The efficacy of adaptive cluster sampling likely depends on whether the within-cluster variance is similar to the population variance (Smith et al. 1995). For herding species like bison, the efficacy of adaptive sampling also likely depends on the relative degree of aggregation into groups. If spatial clustering predominantly results in most animals occurring in a few large groups and these groups are separated by significant distances, then adaptive cluster sampling will be ineffective; conversely, if bison occur in many smaller groups that are close in space, then survey efficiency may be improved with adaptive cluster sampling.

Adaptive sampling can be extended to other survey designs. In adaptive two-stage sequential sampling, the study area is partitioned into primary sample units which have smaller secondary units nested within them (Brown et al. 2008). In the first stage, an initial subset of secondary units is drawn equally among primary units using a probabilistic sampling process and this subset is then surveyed to determine the number of secondary units meeting an *a priori* criterion (e.g. species presence). In the second stage, additional survey effort is proportionally allocated to primary units based on the number of secondary units meeting the criterion. Thus, the design focuses effort to areas having a higher rate of occurrence of the targeted species. Conroy et al. (2008) used a similar two-stage approach to direct sampling effort to where species occur to efficiently estimate abundance in spatially clustered populations. In their design, an initial set of sample units is surveyed to determine species occupancy. In the second phase, a subset of units predicted to be occupied is surveyed to determine within-unit animal abundance. Population size is then estimated by modeling the occupancy-abundance relationship. The Conroy et al. (2008) design has been successfully used to estimate abundances of endangered golden-cheeked warblers (*Setophaga chrysoparia*; Mathewson et al. 2012) and extended to estimate occupancy patterns (Pacifici et al. 2012). The design, however, produced mixed results when applied to boreal caribou (*Rangifer tarandus caribou*), primarily due to its dependence on sample units being “closed” (i.e., no immigration/emigration) during the first phase of sampling (DeMars and Boutin 2013). We also note that the design requires further testing on herding species because precise estimates may be difficult to obtain if there is large variation in group size, which would result in large variation of within-unit abundances and potentially confound extrapolation of the occupancy-abundance relationship to the larger study area.

Adaptive sampling designs are not limited to estimating metrics of population demography and may be particularly useful for monitoring disease incidence, which tends to have a clustered distribution (Thompson 1990, Turechek and Madden 1999, Gattone et al. 2013). To explicitly model the spatial distribution of disease, adaptive web sampling can be used. This design is similar to adaptive cluster sampling but its advantage is that it is not confined to encountered aggregations (i.e., stopping at edge units) and allows spatial "jumps" to unsampled areas of the study region to more thoroughly map the network of disease incidence (Thompson 2013). For bison, such a design may be useful for monitoring disease outbreaks such as anthrax.

Finally, we note that the general survey designs listed above are not mutually exclusive and designs may be combined to best survey the target species. For example, stratification may be combined with adaptive sampling (Thompson 2012). Prior to applying any survey design, particularly those that are novel, we recommend pilot studies be conducted to determine whether the design is logistically feasible and cost-efficient, and is capable of producing estimates with acceptable precision.

Data Collection Considerations

Survey designs for monitoring wildlife populations must take into consideration potential methods for collecting data on the target species. Historically, monitoring ungulate populations has primarily relied on data collected by direct observation (e.g. aerial surveys), radio collaring programs or, to a lesser extent, counts of fecal deposits (Bailey and Putman 1981, Campbell et al. 2004). Recently, the range of potential methods has expanded due to advances in non-invasive methods, particularly camera trapping (Karanth and Nichols 1998) and genetic approaches using fecal DNA (Kohn et al. 1999). Specific to ungulates, camera traps have been used to estimate distributional patterns (white-tailed deer [*Odocoileus virginianus*], Fisher et al. 2013, Duquette et al. 2014; brocket deer [*Mazama spp*.], Tobler et al. 2009), abundance or density (Harvey's duiker [*Cephalophus harveyi*], Rovero and Marshall 2009; wild boar [*Sus scrofa*], Plhal et al. 2011), population trend (white-tailed deer; Duquette et al. 2014), herd composition (white-tailed deer; Jacobson et al. 1997, Duquette et al. 2014), and productivity (white-tailed deer; Jacobson et al. 1997, Fisher et al. 2013). Most applications of camera traps, however, have been on species that are either solitary or live in small groups and it is therefore unclear as to whether these demographic parameters could be reliably estimated for species that occur in large groups such as bison. In particular, the use of remote cameras may preclude estimating population size as quantifying group size of large herds would be likely infeasible.

Demographic parameters of ungulate populations have also been estimated from data derived from fecal DNA. This approach may be particularly advantageous for species that have low rates of visual detection due to the habitats in which they live (e.g. interior forest species) or cryptic behaviour (e.g. nocturnally active species). Fecal DNA approaches have been used to estimate population size and structure of elephants (Eggert et al. 2003, Hedges et al. 2013), black rhinoceros (*Diceros bicornis*, Cunningham et al. 2001), mountain goats (*Oreamnos americanus,* Poole et al. 2011), argali (*Ovis ammon*, Harris et al. 2010), boreal caribou (*Rangifer tarandus caribou*, Hettinga et al. 2012) and Sitka black-tailed deer (*Odocoileus hemionus sitkensis*, Brinkman et al. 2011). In recent years, the application of fecal DNA methods has steadily increased. These methods, however, are not infallible as genotyping errors can lead to biased estimates if these errors are not explicitly taken into account (Lukacs and Burnham 2005, Lampa et al. 2013).

Demography

Wildlife management depends on reliable demographic data to inform decision-making. Such data can include estimates of population size and trend. Understanding underlying mechanisms driving population trends may further require data on specific vital rates (e.g. age-specific survival and fecundity, Caughley 1974, Gunn and Russell 2008). Local Aboriginal government organizations consider population surveys and monitoring as a priority for bison management in the Slave River Lowlands (ENR 2013). In this section, we review methods for obtaining reliable demographic data, particularly those methods likely to be most appropriate for spatially clustered ungulate populations.

Population Size

Effective management of wildlife populations often requires reliable estimates of population size. Such estimates provide a current assessment of population status – with management actions varying relative to estimated size – and represent a key metric for evaluating a population's ability to withstand natural and human-mediated disturbance (Wittmer et al. 2010). Moreover, repeated estimates of population size provide direct measures of population trend (see Utilization Distributions) and are an effective tool for evaluating management actions. As a consequence, considerable research effort has been directed toward developing effective methods for estimating population size. Inherent to most methods is the accounting of detection bias; that is, the likelihood that not all individuals encountered in a survey are detected perfectly.

Estimating population sizes of spatially clustered species presents additional challenges. As noted above, increasing aggregation of individuals into groups will lower encounter rates (Ioannou et al. 2011), which may result in small samples sizes that confound statistical procedures for estimating population size or decrease estimate precision. For species that occur in large groups, biased estimates may result from imperfect enumeration of group size (Walsh et al. 2009, Griffin et al. 2013). Also, estimate precision may be overestimated because detection of individuals within a group is not independent (Boulanger et al. 2004).

In this section, we review potential methods for estimating population size in ungulates (see Table 1) with a particular emphasis on species that are group-living and spatially clustered. We begin with two of the most commonly used methods, sightability models and mark-resight, then move on to review distance sampling, thermal imaging and non-invasive approaches such as remote camera trapping and mark-recapture methods using fecal DNA. We note that selecting a method to account for imperfect detection is only one aspect of designing surveys to estimate population size or density. Because most of these methods become problematic when detection rates are low, we emphasize the importance of sampling design for increasing detection rates to efficiently estimate population size of spatially clustered species (Couturier et al. 2013). We further note that data for estimating population size does not need to be restricted to one method and estimate precision is often improved if multiple sources of data are used (Gopalaswamy et al. 2012b). The Athabasca Chipewyan First Nation (2012) has proposed collaborative integration of community and science-based monitoring into survey and composition counts.

Sightability Models

During aerial surveys of ungulates, individual detectability will vary depending on environmental and behavioural factors (Samuel et al. 1987, Steinhorst and Samuel 1989). To account for this potential bias, sightability models can be used to adjust the raw counts of animals observed on survey. These models are usually developed using a sample of marked individuals (e.g. radio collars or tags) in a mark-resight framework to estimate a sightability correction factor (Samuel et al. 1987, Steinhorst and Samuel 1989). In most applications, correction factors are based on logistic regression models linking detection probability to a suite of environmental (e.g. forest cover) and behavioural (e.g. walking versus bedding) factors. For herding species, group size can be included as a covariate in the model and Walsh et al. (2009) developed a further extension to account for the uncertainty associated with estimating group size. These models have been applied to a variety of ungulate species including elk (Gilbert and Moeller 2008, McIntosh et al. 2009), bighorn sheep (*Ovis canadensis*; Conroy et al. 2014), mountain goats (Rice et al. 2009), and pronghorn (Jacques et al. 2014). To our knowledge, no sightability models have been developed specifically for bison.

While sightability models are conceptually easy to apply, they do have some potential drawbacks. First, for species residing in environments where sightability is low (e.g. old growth conifer forest), low rates of detection will result in an imprecise estimate of population size (Vander Wal et al. 2011, McCorquodale et al. 2013). Second, the explanatory data (e.g. percent canopy cover in a given radius around an observed animal) has associated measurement error and logistic regression models assume that explanatory variables are fixed and measured without error. Any measurement error of the explanatory variables can therefore produce biased estimates of population size (Johnson 2008, Walsh et al. 2011). Third, sightability models may not translate well through space and time (Vander Wal et al. 2011, McCorquodale et al. 2013) and in the case of stratified sampling designs, the application of single sightability model across all strata may result in estimates of precision that are overly optimistic (Fieberg and Giudice 2008). Thus, sightability models likely preform best in the region in which they were developed and as a consequence, the additional costs of model development should be considered when determining whether to employ a sightability model approach.

Mark-resight

One of the more common approaches for estimating population sizes in ungulates is mark-resight (Bear et al. 1989, Neal et al. 1993, Wittmer et al. 2005). This method involves marking a sample of the target population prior to survey, typically with either radio collars (Bear et al. 1989) or by paintball (Mahoney et al. 1998, Skalski et al. 2005a). After allowing sufficient time for animals to remix in the population, aerial surveys are conducted and the observed numbers of marked and unmarked animals are used to estimate population size. Because animals are usually marked only in an initial session, mark-resight methods differ from traditional mark-recapture methods (see below).

Primary assumptions of mark-resight are that marked and unmarked animals are correctly classified, marks are not lost, and marks do not affect the resighting process. However, if animals are individually identifiable, resighting probabilities can be allowed to vary among individuals (Minta and Mangel 1989, Bowden and Kufeld 1995). Mark-resight methods have also been generalized to include estimators that allow movement to and from the survey area between sampling sessions (Neal et al. 1993). All of these estimators are contained in program NOREMARK (White 1996). Recently, estimators that allow flexible modeling of sightability based on individual covariates (when it is possible to identify individual marked animals during the survey) and temporal covariates (McClintock and White 2009) have been developed and incorporated into program MARK (White and Burnham 1999). The main requirements for mark-resight methods are having enough marked animals, and high enough resighting probabilities, to obtain adequate precision of estimates, which generally requires multiple surveys to achieve a sufficient sample size of resightings.

Mark-resight methods have been used to estimate population sizes of bison in the Yukon on two occasions. Hegel et al. (2012) marked 59 bison using paintballs in July 2009, which combined with previously radio collared animals equated to a marked sample size of 83 animals. They conducted two resighting surveys approximately one and three days after marking by paintball. The derived population estimate had good precision ($\widehat{N}$=1151; 90% CI:998-1,355) and resighting rates for the two sessions were 0.39 and 0.37. Jung and Egli (2012) used a similar approach within the same study area, marking 101 bison with paintballs in July 2011 and conducting a resighting surveys three, four and six days after marking (three total resighting occasions). Resighting rates were more variable (0.26, 0.52, and 0.33, respectively) but the derived estimate of population size ($\widehat{N}$=1,230; 90% CI:1,106-1,385) had greater precision than the estimate of Hegel et al. (2012), perhaps due to the increased sample of marked animals and extra resighting survey.

We note that for herding species like bison, mark-resight estimates have the potential to be biased because animals within a group do not have equal and independent probabilities of being marked and resighted (Skalski et al. 2005a). This bias can be particularly problematic if animals do not remix among groups after marking or if fidelity to a particular group size is high. To reduce such potential bias, animals should be marked when group sizes are smallest and animals within groups should be marked in proportion to group size (Skalski et al. 2005a).

Capture-Mark-Recapture

For estimating population size in difficult-to-observe wildlife species, capture-mark-recapture (CMR) is the most commonly used method in ecological studies. As with mark-resight, CMR involves capturing and marking an initial sample of individuals from the target population; however, in most CMR applications new individuals captured during subsequent resampling occasions are also marked. The recapture data also known as encounter histories, are used to estimate detection rates and derive estimates of population size. Model formulations have progressed beyond simple closed population models (i.e., no births, deaths, immigration or emigration) to include 'robust' designs that incorporate demographic data such as survival (Pollock 1982). Most current modeling approaches are contained in the omnibus software program MARK (White and Burnham 1999). Design is critical to the success of CMR experiments as precision is influenced by the proportion of the true population that is marked, the number of animals recaptured and the number of sampling sessions (Pollock et al. 1990, Rees et al. 2011).

Until recently, classic CMR methods have rarely been used to estimate population sizes of ungulates due to the difficulty and expense of capturing large animals. In the last few years, however, the use of CMR approaches to estimate population size in ungulates has increased due to the development of fecal-based DNA methods that can identify – and hence 'mark' – individuals based on genotype. CMR approaches have been used to estimate population size in mountain goats (Poole et al. 2011), elephants (Hedges et al. 2013), boreal caribou (Carr et al. 2012, Hettinga et al. 2012), and argali (*Ovis ammon*; Harris et al. 2010). Compared to other approaches where the animals are directly observed, fecal-based DNA methods are relatively non-invasive and obtaining sufficient sample sizes may require less effort because fecal deposits are generally easier to find and collect versus sighting the actual animals, particularly for cryptic and elusive species. The main drawbacks to this approach are *i*) the costs associated with genetic analyses (Harris et al. 2010, Carr et al. 2012); and *ii*) the necessity of multiple sampling occasions combined with the time required for genetic analyses equates to a comparatively long time interval between survey initiation and the derivation of the population size estimate. Within NWT bison range it may be costly to obtain the required intensity and optimum spatial distribution of samples because of difficult access.

CMR methods have recently been extended to allow estimation of animal densities by incorporating spatial information. This framework, known as spatially explicit capture-recapture (SECR), uses the spatial coordinates of capture locations to model the spatial distribution of individual home ranges and fits a detection function to the mark-recapture that estimates the decline in detection probability with increasing distance from an individual's home range center (Efford 2004, Efford and Fewster 2013). Using this information, population density on the study area is estimated without the issues of "closure violation" that challenge estimation with traditional closed CMR models (Otis et al. 1978). Early empirical testing suggests that SECR models have similar or better statistical performance than CMR models (e.g. higher precision; Blanc et al. 2013, Efford and Fewster 2013). The main potential issue with SECR is highly non-circular home ranges, which can create bias (Ivan et al. 2013a, b); however, this bias can be offset if covariates are used to account for variation in movement rates and/or densities due to habitat or geographic features. The SECR approach has been adapted to line transect sampling (Efford 2011) but as yet the approach has not been tested for estimating ungulate densities.

CMR estimators for animal density have also been developed that utilize information from radio collared animals. Ivan et al. (2013a) developed an estimator that uses estimates of the mean location of animal detection on the sampling grid (using mark-recapture methods) to estimate residency (using information from radio collared animals). This approach provides an estimate of density that can be compared with SECR methods.

Simulation studies suggest that it provides robust inference; however, it does require that a substantial number of animals are collared in the study area.

Aerial Survey Strip Transect Sampling

Strip transect methods have been used in previous bison aerial surveys in the NWT and continue to be used in barren-ground caribou surveys (Gunn and Russell 2008). Strip transect surveys assume that all animals are sighted within a limited strip of the survey plane (usually 400 m on each side of the plane) with all other observations beyond the strip not being used for estimates. The estimator for abundance then becomes similar to a quadrat or block survey estimator (Krebs 1998) which is simply the number of animals counted divided by the proportion of the survey area covered by the strip transects. The strip transect method is appealing in terms of simplicity and ease of instruction for field observers. One particular advantage is that it allows efficient counting of animals which can be advantageous for species at higher densities such as caribou calving ground surveys. However, it is not statistically efficient in that all observations beyond the survey strip are not considered (Burnham and Anderson 1984). In addition, the assumption of perfect sightability within the survey strip may be violated especially in areas of vegetation cover which will lead to negatively biased estimates. Double-observer methods (Buckland et al. 2010) which estimate sightability using data from two observers on each side of the plane can be used to estimate sightability on the survey strip to reduce bias when sightability is less than one on the survey strip.

Aerial Survey Distance Sampling

Distance sampling has been recently applied to bison and other ungulate populations to provide enhanced abundance estimates from aerial transect surveys. In most applications, a line transect design is used where the distance from the line to a detected individual or group is measured and a detection function is estimated to determine the size of the area sampled (Buckland et al. 1993, Thomas et al. 2010). Compared to mark-resight and mark-recapture approaches, a primary advantage to distance sampling is its efficiency because data can be collected and estimates calculated from a single survey. In addition, distance sampling does not require that individual animals are marked, which therefore reduces overall cost of surveys.

Distance sampling requires that several key assumptions be met. The first is that all individuals centered on the transect (or specified distance from the survey plane to account for the blind spot under the plane) are detected perfectly (i.e., detection probability = 1.0 at a distance of zero), although recent extensions relax this assumption by incorporating either sightability models (Peters et al. 2014), double-observer methods (Conn et al. 2012), or mark-recapture approaches (Borchers et al. 1998, Laake et al. 2008). If habitat is open and sightability is high then this assumption is probably met if observers are focusing their primary attention on areas closest to the plane. If terrain or vegetation is variable, if observers' skill in detecting bison is limited, or if observers do not concentrate their attention on the "zero distance" closest to the plane (even if there are nice, open areas in the middle distance where they are more likely to see bison), then this assumption may be violated. The approach used to estimate detection probability near the plane depends on factors influencing sightability. If it can be assumed that all bison near the plane have a reasonable sighting probability then double-observer methods can be used to estimate sighting probability by comparing observations of the two observers on each side of the plane. This approach works best if the two observers cannot communicate their observations, but can also be applied if communication occurs (Buckland et al. 2010). If vegetation or other factors makes some bison difficult to observe then mark-resight or sightability models with collared or marked bison can be used to estimate sighting probability near the plane and this estimate can be used to scale the distance sampling detection function (Peters et al. 2014).

Accurate measurement of the detection distance is also critical to distance sampling as measurement error can produce biased estimates of population size or density (Marques et al. 2006, Alldredge et al. 2007). Wing strut markers measure distance bins from the survey plane provides one approach to efficiently estimate distances from the survey plane (Buckland et al. 1993.). However, this approach restricts the fitting of detection functions and modeling of covariates in the analysis stage since the number of distance bins is usually restricted to four or five bins. An alternative approach is to measure the angle of groups and altitude above ground level (AGL) for the survey plane and from this estimate distance (Laake et al. 2008). This approach allows continuous estimates of the distance of groups from the plane but also requires a radar altimeter that is cross referenced with field data. Previous surveys of bison in the NWT have flown the survey plane over each bison group and used geographic information system (GIS) waypoints of groups from the survey line to estimate distance. This approach is more time consuming than the bin approach but does allow exact counts of groups and continuous distance measurements.

Distance sampling directly models the effect of different group sizes on sightability through the use of a group size covariate or use of regression-based methods (Buckland et al. 1993, Thomas et al. 2010). This approach allows detectability to vary with group size given that often larger groups are easier to detect than individuals. Both distance sampling and strip-transect sampling are potentially vulnerable to sampling situations where a large number of individuals appear in groups which results in variation between individual transects and higher survey variance. Stratification can be used to confront large-scale differences in density, however, this approach will be limited if aggregation of individuals causes small-scale density variation. Density surface modeling (Miller et al. 2013) is a newer method that allows the use of covariates to describe variation in density within study areas, which can improve estimate precision as well as provide inference about factors affecting abundance (as discussed later in the report).

Similar to other modeling approaches, distance sampling is sensitive to small sample sizes, generally requiring >60 individuals or groups to be encountered to effectively estimate the detection function (Buckland et al. 2001) and achieve acceptable estimate precision (Seddon et al. 2003, Wegge and Storaas 2009, Williams and Thomas 2009). Combining multiple years of data can potentially offset low sample sizes from single surveys as long as methods are standardized and appropriate covariates are collected (Buckland et al. 2004).

Distance sampling has been used to estimate population sizes and densities of a variety of ungulate species including moose (*Alces americanus*; Peters et al. 2014), Dall's sheep (*Ovis dalli*; Schmidt and Rattenbury 2013), mule deer (Koenen et al. 2002), and blue duiker (*Philantomba monticola*; Waltert et al. 2006). Specific to herding species that are spatially clustered, distance sampling has been used to estimate densities of elephants (Kumara et al. 2012), chiru (*Pantholops hodgsonii*; Bårdsen and Fox 2006) and onager (*Equus hemionus onager*; Hemami and Momeni 2013), all with acceptable rates of precision (CV <20%). For bison, Boulanger (2014a) used distance sampling in a post-hoc stratified sampling design to obtain density estimates for the Mackenzie wood bison range. Preliminary results suggest that acceptable rates of precision can be achieved for both population size and density estimates. We discuss distance sampling including recommendations to improve precision in Power Analyses of Abundance Surveys section of this report.

Aerial Surveys Using Thermal Imaging

Thus far, all methods for estimating population size attempt to account for imperfect detection of all individuals, yet these methods produce imprecise estimates when overall detectability is low. For species residing in areas where sightability is low, thermal imaging technology has been used to increase detection rates (Bernatas and Nelson 2004, Kissell and Nimmo 2011, Carr et al. 2012, Franke et al. 2012). In most ungulate applications, surveys are conducted by aircraft using a line-transect sampling design where a thermal imaging camera is mounted on the underside of the aircraft to detect heat emitted from animals situated along each transect. Camera resolution is generally sufficient to discriminate among species that differ substantially in size but additional visual imagery may be required to discriminate among similarly sized species (Franke et al. 2012).

In trials using radio-marked animals, estimates of detection rates using thermal imagery have generally been high (e.g. 89% for bighorn sheep, Bernatas and Nelson 2004; 95% for white-tailed deer, Kissell and Nimmo 2011). Thermal imaging technology has also been used in conjunction with distance sampling to produce estimates with acceptable precision (Bernatas and Nelson 2004, Carr et al. 2012). These applications, however, have been conducted primarily at small spatial scales (Bernatas and Nelson 2004, Carr et al. 2012) and the utility of thermal imaging surveys for estimating population size over large geographic areas has not been widely tested. One potential drawback to extending thermal imaging surveys to larger spatial extents is the narrow field of vision of the camera, which typically yields a transect width of ~100 m (Kissell and Nimmo 2011, Franke et al. 2012). For wide-ranging, spatially clustered species, this narrow transect width may necessitate extensive flying time – and hence survey cost – to achieve estimates with acceptable precision (Ogutu et al. 2006). Thermal imaging has also not been tested on species that occur in large groups (i.e., >20). With a narrow strip width, effectively enumerating all individuals in large groups using thermal imagery may be problematic.

Counts of Fecal Deposits

Using counts of fecal deposits as an index of abundance has a long history in the management of ungulates (Neff 1968). A central assumption in this method is that the count of fecal deposits in a given time period is positively correlated to animal density (Forsyth et al. 2007). Converting fecal counts to an estimate of abundance requires *a priori* knowledge of a species' daily defecation rate and, when the time period is unknown or undefined, an understanding of fecal decay rates (Neff 1968, Campbell et al. 2004). Without this information, fecal counts should be viewed as an index of relative abundance rather than an estimate of true abundance *per se*. Abundance estimates derived from fecal counts are also likely influenced by animal movement rates and estimates may be biased if individuals move into or out of the study area during the sampling interval (i.e., the population is not 'closed'; Gopalaswamy et al. 2012a). Fecal counts have generally been used for environments that have low sightability (e.g. tropical forests; Merz 1986). The method, however, is still susceptible to detection bias because not all fecal deposits will be detected; therefore, sampling designs that incorporate double-observer approaches may be necessary (Nichols et al. 2000).

A primary drawback to using fecal counts is that data collection is labour intensive, particularly over large spatial extents. Moreover, in study areas that are largely inaccessible by ground-based means (e.g. roads or by foot), extensive helicopter use may still be required and as a consequence may be more expensive than standard aerial survey approaches (Forsyth et al. 2014).

Remote Camera Trapping

The use of remote camera traps for estimating population size or density has been primarily restricted to carnivore species, particularly those with individually identifiable markings that allow camera trap data to be used in a mark-recapture framework (Karanth and Nichols 1998, Silver et al. 2004, Long et al. 2008). For many ungulate species, individual recognition from photographs is not possible, which has limited the use of camera trap designs for estimating ungulate population size or density. However, using horn measurement ratios (relative to the distance between the eyes) and a likelihood-based algorithm to calculate a matching score between pairs of photographs, researchers in Prince Albert National Park were able to estimate population size through photographic mark-recapture (Merkle and Fortin 2014). Rowcliffe et al. (2008) also developed a modeling framework – the random encounter model (REM) – that eliminates the requirement of individual recognition to estimate animal density. Their approach models the underlying detection process using expected movement rates and group size of the target species. While the method has not been widely tested, Zero et al. (2013) compared the REM approach to distance sampling for estimating densities of Grévy's zebra (*Equus grevyi*). The two methods produced similar density estimates with the REM estimate having higher precision (CV:27% for REM; 61% for distance sampling).

Compared to other methods, camera trap surveys may have higher initial costs because of the expenses associated with purchasing and deploying cameras (Zero et al. 2013). For short-term surveys, these costs may restrict the application of camera trap designs to elusive species residing in environments with low sightability. For longer term monitoring, however, camera trap designs may be an efficient, cost-effective method for estimating population size, even for species that may be easily observable. We note that the REM method has not been tested on species such as bison that live in large groups and there may be potential for estimate bias and precision to be affected by high variation in group size.

Table 1: Comparison of methods for estimating population size and/or density of wildlife populations with an emphasis on applications to ungulate species.

Method	Framework	Advantages	Disadvantages
Sightability Model	Sightability is modeled as a function of environmental and behavioural covariates.	Sightability correction factors can be applied to raw counts to derive population estimates after a single survey; therefore may be relatively cost efficient (*c.f.* CMR and mark-resight)	Imprecise when sightability is low. Measurement error of explanatory variables can induce bias. Requires marked animals to estimate a sightability model if none exists. Sightability models may not translate well through space and time.
Mark-Resight	Animals are marked during an initial session followed by resighting sessions to estimate detection probabilities.	Extensive use in ungulates and a variety of models are available. Estimates can be derived after each resighting session. Can be used to account for low sightability in closed habitats	Requires a segment of the population be individually marked. May require a high number of animals to be marked. For herding species, non-independence of resighting probabilities may bias estimates. Sensitive to low resighting probabilities. Necessity of multiple resighting surveys may equate to relatively high survey cost (*c.f.* distance sampling).
CMR	Animals are captured, marked and recaptured	Extensive literature support and a wide	Requires marking of individual animals

Method	Framework	Advantages	Disadvantages
	over multiple sessions to estimate detection probabilities.	variety of models are available. SECR can estimate density.	Necessity of multiple recapture sessions may lead to high relative cost. For fecal DNA-based methods, there may be a long time interval between data collection and estimate derivation.
Strip Transect Surveys	For ungulates, generally uses a line-transect design where animals are only counted within a specified strip from the survey plane.	Provides an estimate of density as the count of animals divided by the area sampled by strip transects. Estimates can be calculated after a single survey (*c.f.* CMR above), therefore may be relatively cost-efficient.	Assumes all animals are sighted within the strip which is unlikely in many habitats. Does not use data from animals sighted outside the strip and therefore is not as efficient as distance sampling.
Distance Sampling	For ungulates, generally uses a line-transect design where detectability is estimated as a function of distance off the transect.	Provides an estimate of density as effective transect width is empirically estimated. Estimates can be calculated after a single survey (*c.f.* CMR above) therefore may be relatively cost-efficient.	Sensitive to small sample sizes. Requires accurate measurement of detection distances.
Thermal Imaging	Thermal imaging camera is mounted to aircraft while conducting aerial surveys.	Increases detection rates in environments with low sightability.	Has not been tested at enough large spatial extents. Narrow transect width may equate to high survey costs for spatially clustered species.
Fecal Deposit Counts	Fecal deposits are counted along transects	Suitable for species with low sightability.	Requires knowledge of fecal deposition and decay rates. Labour intensive. May be biased by movements on to/off of the sampling area.
Remote Camera Trapping	An array or grid of cameras are deployed and picture data is generally used in a mark-recapture framework.	Less invasive than other approaches. May increase detection rates for cryptic species. May be cost-efficient for long-term monitoring.	Often requires recognition of individual animals. High initial costs. Limited testing on herding ungulates.

Population Trend

A primary objective of wildlife management is determining population trend, defined as the direction and magnitude of changes in population size through time. Population trend can be estimated by both direct and indirect methods. In direct approaches, trend is estimated by changes in population size estimates obtained from sequential surveys. Indirect methods rely on information such as age ratios and vital rates such as survival to infer trend. Of the two approaches, direct approaches are conceptually easier to understand because interpreting indirect estimates of trend is difficult if there is not a baseline estimation of population size for reference. Consequently, initial efforts should be made to estimate population size – and periodically thereafter – to corroborate indirect trend measurements.

Body condition measures such as body fat, animal size and observations of movement ability (e.g. walking with a limp) have been used by indigenous cultures to infer information about habitat conditions, which are then linked to population dynamics (Kofinas et al. 2003, Parlee et al. 2014). For example, Dene hunters assess the condition of internal organs to assess for diseases that if widespread, give an indication that the ecosystem is "out of balance" (Parlee et al. 2014). Information gained from body condition, however, may be biased because hunters target individuals deemed to be in good condition (Kofinas et al. 2003, Wray and Parlee 2013). Moreover, body condition may not directly relate to whether a population is increasing or decreasing (Moller et al. 2004), because of time lags or lack of synchrony between changes in body condition (from density dependence) and population responses. Disease outbreaks may further confound inferences between body condition and population trend.

Repeated Abundance Surveys

Monitoring trend by direct measures requires repeated estimates of population size such that:

$$\lambda = \frac{\widehat{N}_{t+1}}{\widehat{N}_t}$$

where λ is the estimated population trend, $\widehat{N}_t$ is the initial estimated population size and $\widehat{N}_{t+1}$ is the estimated population size at the next time step. Values of λ >1.0 indicate increasing populations while those <1.0 indicates a decline. For time steps spanning multiple years, an estimate of the average λ can calculated by:

$$\widehat{N}_t * \lambda^x = \widehat{N}_{t+x}$$

where x is the time span in years. Direct estimation of trend can further be estimated by using regression analysis (e.g. Ottichilo et al. 2001) where the slope of the relationship between population size and time is the intrinsic rate of population increase (r), which can be transformed to an estimate of λ by calculating e^r. The method to estimate trends will depend on management objectives and the number of survey points available to estimate trend. If only two surveys have been conducted then a *t*-test can be used to determine if abundance has changed significantly between surveys (Caughley 1977, Thompson et al. 1998). Regression methods can be used to estimate actual trend in the population. The usual approach for this is log-linear modeling with an underlying model of exponential population growth (Buckland et al. 2004) where δ_t is sampling variation and ϵ_t is biological variation or process variance:

$$log_e(\widehat{N}_t) = \beta_0 + \beta_1 t + \delta_t + \epsilon_t$$

The estimate of trend ($\lambda = N_{t+1}/N_t$) is equal to the exponent of β_1. For this procedure abundance estimates will usually be weighted by the inverse of their variance to account for differences in survey variance (Brown and Rothery 1993). Alternatively, generalized linear models (McCullough and Nelder 1989) with a log-link can be used to add flexibility about error distributions. Covariates can be added to further explain temporal variation in trends. If time series are long enough it is also possible to estimate process variance (ϵ_t) separate from sampling variance (δ_t) (Thompson et al. 1998).

Another approach is using Bayesian state-space models (Humbert et al. 2009) that can better account for process and observation error, uneven time series as well as auto-correlated trend estimates. This approach involves the use of Markov-Chain Monte Carlo methods which are more complex than likelihood methods. However, simulation results suggest it may be more robust to various sampling and biological issues with trend data.

Using Composition Counts and/or Telemetry Data

Population trend in ungulates can also be estimated by indirect methods if composition and telemetry data are available. Two common approaches are age ratios and the "R/M" equation developed by Hatter and Bergerud (1991). Age ratios typically consist of juvenile:adult female (J:AF) ratios collected during late-winter. As an index of population trend, J:AF ratios have been criticized because they can mask the underlying mechanisms driving population change and opposite trends can produce the same ratios (Caughley 1974). In particular, McCullough (1994) suggested that ratios can mask changes in adult female survival, which has a strong influence on ungulate population trend (Gaillard et al. 2000). Further, temporal changes in the female-offspring bond and seasonal changes in offspring sightability can bias age ratio estimates (Bonenfant et al. 2005). Nevertheless, recent analyses suggest that age ratios can reliably track population trend in elk (Harris et al. 2008, Christianson and Creel 2014). This correlation, however, may not hold for other species that differ in age structure or have delayed reproductive maturity (Bender 2006, Cameron et al. 2013). Because of these uncertainties, age ratios should periodically be augmented by other data sources to effectively monitor trend (McCullough 1994, Bender 2006).

The R/M equation also uses J:AF ratios but these data are incorporated with adult female survival data to estimate population trend. In its basic formulation, the R/M equation calculates λ by:

$$\lambda = \frac{(1 - \mathrm{M})}{(1 - R)}$$

where M is the finite annual mortality rate and R is the finite annual recruitment rate or proportion recruits in the population (Hatter and Bergerud 1991). The numerator is usually derived from Kaplan-Meier estimates of survival (1–M) from radio collared females. The R/M equation has been used extensively to monitor trend in caribou populations (Hervieux et al. 2013, Larter and Allaire 2013a) and has been applied to moose, elk and deer (Hatter and Janz 1994, Kunkel and Pletscher 1999). While this approach is appealing in the terms of simplicity, it does make a set of assumptions regarding the symmetry of survival rate and recruitment estimates. For example, it assumes that annual J:AF ratios are an unbiased estimate of annual recruitment so that recruitment from this measure is directly comparable to annual rates of female survival (Wasser et al. 2012). The original formulation of the equation also assumes that juveniles are recruited to the population at one year of age. DeCesare et al. (2012a), however, showed that violations of this assumption (e.g. for species with delayed reproductive maturity) are not problematic if the recruitment is expressed as a ratio of the number of female juveniles to the total number of females in the population, i.e.:

$$R = \frac{female\ calves}{(female\ calves + adult\ females)}$$

This reformulation was shown to produce λ values equivalent to those estimated from matrix population projection models (Morris and Doak 2002).

Other indirect methods for estimating population trend require more intensive data inputs. For example, trend can be estimated using demographic models such as those used in population viability analyses (Boyce 1992, Morris and Doak 2002) or life table analyses (Krebs 2008, McMahon et al. 2011). Dawson and Hone (2012) used a modified Lotka equation, as developed by Eberhardt et al. (1994) to estimate trend in feral horses. This equation requires inputs on age at first reproduction, annual adult survival, survival to age at first reproduction and fecundity. If data have been collected via fecal-based DNA methods, CMR models such as the ‘robust’ design (Pollock 1982) and Pradel approach (Pradel 1996) provide a powerful framework by simultaneously estimating yearly population size, trend, apparent survival, and emigration/immigration (e.g. Hettinga et al. 2012).

Inferences from Multiple Data Sources

We note that if there are baseline estimates of population size, survival estimates, and recruitment rate estimates then it is possible to fit multiple-data source models to further model demography and population trends (Buckland et al. 2004, Boulanger et al. 2011). These approaches do not require annual surveys or annual measurements from any of the demographic indicators. They can accommodate sample biases with indicators, such as the effects of differential survival of juveniles and adults on J:AF ratios, and can also incorporate harvest data (Boulanger et al. 2011). This approach utilizes all the data sources in a unified analysis therefore maximizing inference when compared to stand-alone interpretation of single data sources.

Inference from Changes in Distribution

We do note that management objectives often include monitoring trends in species distribution. Changes in distribution can be monitored through repeated occupancy surveys and recent advancements in occupancy methods include dynamic multi-state models that incorporate estimates of site colonization and extinction (MacKenzie et al. 2006, Bailey et al. 2014). Changes in distribution often reflect changes in population size (He and Gaston 2000). This relationship however, is not straight-forward and is particularly problematic across large landscapes and for species that are spatially clustered (He and Gaston 2007, Hui et al. 2009). For example, for group-living species the number of animals per group may decline while the number of groups on the landscape may stay relatively constant; thus, a population could decline while its spatial distribution remains unchanged (McLellan et al. 2010). This process would result in a high-risk strategy of monitoring population change because change may not be detected until a rapid contraction in distribution is observed. Occupancy models that consider counts of animals rather than presence not detected (Royle and Nichols 2003) may be more sensitive to changes in group size; however, the use of this approach assumes that individual groups can be counted adequately during surveys. For wide-ranging species with annual home ranges much larger than occupancy plot sizes, short-term changes in occupancy may reflect temporal variation in annual home range use rather than distributional changes related to changes in abundance. Also, with respect to plot size, unbiased occupancy estimation requires a large "plot size" (Efford and Dawson 2012) and thus inference from occupancy will indicate larger temporal changes in distribution. Therefore, tracking changes in occupancy as a surrogate for population size may result in limited power to detect smaller, short-term change.

Population Composition

Wildlife managers commonly collect herd composition, age and sex ratios to assess status and demographic trends of ungulate populations (McCullough 1994, Skalski et al. 2005b, Bender 2006, Harris et al. 2008). Long-term conservation targets for ungulate populations often include ratio data (Lammers et al. 2013). For ungulates, ratios commonly collected include juveniles, yearlings, and bulls:100 females. These data may be used to determine whether population objectives are being attained (e.g. post-harvest escapement of males), to track productivity, and, as noted in the previous section, can be used to help assess population trend (Harris et al. 2008, Christianson and Creel 2014).

Most sustained-yield management strategies attempt to affect population trend, population age structure, and adult sex ratios (Bender 2006). These three demographics commonly are used as management goals and are each a function of population productivity and adult mortality rates. Each of these parameters (productivity, mortality) can be determined annually from ratio data if ratios are correctly interpreted and collected during biologically meaningful periods when biological bias can be minimized and when ratios can be meaningfully applied to the population as representative of true production, recruitment, or mortality. Use of estimators designed to accommodate heterogeneity of sighting frequencies among animals can reduce bias in estimates (e.g. Bowden's estimator; Bowden and Kufeld 1995, Weaver and Weckerly 2011).

Timing of Composition Surveys

Properly timed, ratio data can provide substantial information beyond trends on which to base management decisions. Juvenile:female ratios obtained soon after the bulk of birthing can provide substantial information on potential mechanisms affecting productivity, e.g. a low ratio could indicate low fecundity or high rates of predation on neonates. These data also provide a baseline to determine potential periods where juvenile mortality might be high (i.e., is mortality more of a concern during the neonate period or overwinter?). Juvenile ratios collected during pre-weaning potentially have bias because in many species of ungulates juveniles are not reliably seen with adults during the pre-weaning period ("hiders") (Bender 2006). Bison calves are generally not "hiders" and may be visible soon after birth following the "follower" strategy). After weaning even "hider" juveniles habitually travel with adults and thus unbiased juvenile ratios are more readily available. These changes in relationship between females and their juveniles can result in seasonal bias in juvenile:female ratios (Bonenfant et al. 2005).

Recruitment of one-year-olds into older age classes can typically be collected concurrent with productivity ratios (Bender 2006). It is important to consider that collecting recruitment ratio data in mid- or late winter, typical timing for some ungulate populations, may not capture potentially significant juvenile mortality associated with late winter and the immediate winter–spring interface. Female bison generally don't reach reproductive age until three to four years of age, and this delay could affect the utility of juvenile:cow ratios for monitoring trend. Specific to bison, Bradley and Wilmshurst (2005) observed that the ratio of yearlings/100 cows to calves/100 cows appeared to be a strong inductor of population trend. However, use of ratios in management has been criticized because the individual components of the ratio can confound its interpretation, particularly when used to assess population trend (see discussion in *Population Trend* section above, Caughley 1974, 1977, McCullough 1994, Bonenfant et al. 2005). As a consequence, ratio data should periodically be augmented with other data sources to effectively monitor trend potentially through the use of an integrated population model (Boulanger et al. 2011).

Sampling Considerations

Social grouping patterns, sexual segregation, and differences in detectability among age-sex groups and among years can often result in biased composition data (McCullough et al. 1996, White et al. 2001, Mitchell 2002, Bender 2006, Gunn and Russell 2008), especially if sampling techniques do not allow easy access to herd range. Unrepresentative distribution of sampling effort can be an issue; for example, bison outside of the main herds at the edges of the range tend to be bulls which frequently travel alone (Mitchell 2002). Differences in calf:female and adult sex ratios among different density strata were evident in West Greenland caribou, with low density stratum having higher calf ratios and lower bull ratios – these were likely sampling issues rather than density dependence issues (Poole et al. 2013). In caribou this sex- and age-biased distribution is compounded if the count is delayed until the onset of spring migration (Valkenburg et al. 2002). One approach to ensure representative sampling of a population is to allocate sampling effort based on relative densities from reconnaissance or population surveys or some other means of assumed population distribution (Gunn and Russell 2008).

Differences in bias and precision can occur between methods used to collect composition data (ground or aerial surveys; Woolley and Lindzey 1997). Composition data collected from the ground may not be as accurate as data collected using helicopters (Bender et al. 2003). Accuracy of age-sex classification should also be tested. Misclassification of mountain goats kids and yearlings and sexes between adults during aerial surveys was evident, resulting in inaccurate conclusions of ratios (Gonzalez-Voyer et al. 2001). Similarly confusion occurs with other ungulate species (Dau 2005). Classification of bison into seven age and sex classes (see below) can ostensibly involve misidentification, especially among bull bison categories (Larter and Allaire 2007).

Accurate estimation of population composition can be affected by sample size. Calculation of variance associated with the estimated ratios is important to demonstrate the range of possible values (Bender 2006), and can be used to assess the survey effort required to obtain statistically defensible composition data for management objectives (e.g. Poole et al. 2013). We provide a case study that estimates variance for composition surveys in Composition Surveys.

Age- and Sex-specific Vital Rates

Vital rates (also called demographic rates) are those components that collectively determine the rates of change – the mechanisms for why populations change in size (Gunn and Russell 2008). The rate of change is the outcome of how many animals are born (birth rate), how many die (death rate) and how many disperse from their birth population (egress or ingress). As such, they can be useful additional data to support whether a population is changing in size as well as indicating the mechanism.

For ungulate populations, vital rates are typically estimated from radio collared individuals or from ratio data, such as juveniles:100 females (Lammers et al. 2013). Ratios can be used to monitor productivity and calf survival (for example comparing neonate ratios to fall and late winter ratios), and to compare male and female survival. As noted in previous sections, inferring demographic trends from ratio data should be done cautiously as ratios can mask important trends in either the numerator or denominator age classes (Caughley 1974, McCullough 1994). For ratios using adult females in the denominator, an estimate of adult female mortality is needed (Caughley 1977, McCullough 1994). As adult female mortality is annually less variable than calf mortality, Harris et al. (2008) demonstrated that juvenile:cow ratios can track calf survival in elk; however, the authors cautioned that age ratios alone should not be used to track trends in population size.

Birth Rates

Birth rate (or natality) is the mean number of live births per female per year, which can be further expressed by age class. For many ungulate species, fecundity tables are usually derived from harvested animals, which in northern bison populations is unlikely to produce sufficient annual sample sizes. Birth rate, birthing location and peak birthing period can also be estimated by movement analyses of radio collared females (Testa et al. 2000, Kelleyhouse 2001, Vore and Schmidt 2001, DeMars et al. 2013) although these analyses may be problematic for herding species where individual movement rates are not independent. Delays in the peak birthing period can indicate density dependent effects affecting female body condition (Skogland 1984).

Pregnancy rate, which differs from the actual birth rate, can be derived from blood serum progesterone levels (Haigh et al. 1982). Progesterone and estrogen conjugates from collected faecal pellet samples during late pregnancy stages can be used as a non-invasive method of detecting pregnancy status (Morden et al. 2011). Pellet collections can be screened using genetic testing to eliminate males from the sample. Pregnancy rates vary among years in caribou populations (Cameron 1994), suggesting that pregnancy rates could be monitored annually to determine whether changes in juvenile:female ratios reflect changes in pregnancy or changes in calf and adult female survival (Gunn and Russell 2008).

Survival

Survival rates are a key demographic factor dictating population trend in most wildlife populations (Morris and Doak 2002). In ungulate populations, small changes in adult female survival can have a large influence on trends in population size (Gaillard et al. 1998, Boulanger et al. 2011). However, because adult female survival has relatively low variability in many populations (Gaillard and Yoccoz 2003), population trend can also be influenced by juvenile survival due to its higher variability (Gaillard et al. 2000, Coulson et al. 2005). Effectively managing ungulate populations therefore requires understanding the relative contribution of age-specific survival rates to population trend and the potential mechanisms influencing these rates.

Adult survival may best be inferred from collar data, but three assumptions should be considered: 1) marking of the individual does not affect its likelihood of dying, either through the capture process or from the effect of the collar (which may not be true in all instances – see Swenson et al. 1999 and Rasiulis et al. 2014); 2) censoring collars is independent of the individual's fate (biases can result if censored records (i.e., the collar signal was lost and therefore the record was censored) are actually deaths and not collar failures (that should be censored), and 3) collared individuals are representative of a population (Gunn and Russell 2008). Sample sizes are usually low relative to population size, either because of budget restrictions or community concerns (as in the case of several northern caribou herds). Although capture costs are generally fixed, long-life, multi-location GPS-satellite uplink collars often cost six to eight times more than VHF collars. Some GPS collars are designed for survival-focused studies (one to two fixes/day) and will last four to five years (e.g. Globalstar collars – Vectronic or Lotek). These collars will email a mortality signal, eliminating aerial telemetry costs, and facilitating prompt mortality investigations.

Juvenile survival in ungulates can also be estimated from radio collared or ear-tagged samples, although these types of studies are relatively uncommon. Juvenile:adult female ratios can give an indication of juvenile survival rates, particularly if estimates of the birth rate are available, although temporal changes in offspring sightability and the female-offspring bond may bias ratio estimates and thus inferences of juvenile survival (Bonenfant et al. 2005). Without birth rate estimates, inferring juvenile survival from changes in juvenile: adult female ratios may be confounded by changes in female survival or fecundity

(Caughley 1974). Harris et al. (2008) suggested that annual estimates of juvenile: adult female ratios may only be useful for detecting severe declines in juvenile survival. Repeated intra-annual estimates of these ratios, however, can yield seasonal estimates of juvenile survival (e.g. subtracting late winter ratios from fall ratios can estimate overwinter survival) although a correction factor to account for adult female mortality during the same time period may be necessary to reduce bias (Bender 2006). Boulanger et al (2011) used an integrated population model to estimate juvenile survival in unison with adult female survival rates therefore reducing potential bias due to female mortality.

The primary methods to estimate survival are Kaplan-Meier estimates (Pollock et al. 1989), or known fate binomial models in program MARK (White and Burnham 1999). The Kaplan-Meir estimator is a simple non-parametric estimator that evaluates proportions of animals with collars that were mortalities in a time step (usually a month) to produce an annual survival rate. The known fate estimator treats mortality events like a binomial trial and estimates survival rate using a method similar to logistic regression. The known fate method allows the use of covariates to assess factors influencing survival. If time series of data are available it is also possible to estimate biological process variance through random effects modeling in program MARK (White et al. 2002). Monte Carlo simulations can be run to test precision for estimating survival and cause-specific mortality.

Monitoring the sex ratio can provide insight into relative mortality of the two sexes and, if the trend of the population is known, the ratios can be corrected to estimate mortality for either sex from ratio data (Bender 2006).

Dispersal

Estimates of survival and population trend can be confounded if there are high rates of movement by individuals into and out of the study area (Morris and Doak 2002). Empirical data of dispersal rates are generally rare for most ungulate populations; however, if multiyear mark-recapture data are available, immigration and emigration rates can be estimated using robust design models (Nichols et al. 1992).

Bison populations within the NWT are relatively geographically separated, and although movement between the greater WBNP and the Mackenzie or Nahanni populations may be attempted, animals observed in the Bison Control Area are generally killed (Bidwell et al. 2009), largely eliminating options for dispersal among herds (see below).

Distribution, Range Size, and Habitat Selection

Effectively managing a species' habitat requires understanding its space use and the potential mechanisms driving its observed distribution. Traditional knowledge can help establish historical range and distribution (summarized in Gardner and DeGange 2003). For current distribution, a variety of approaches have been developed to evaluate and predict patterns of species distribution with most relying either on 'presence/absence' data or 'presence-only' data. These approaches can vary from fairly simplistic (e.g. the minimum convex polygon) to more complex modeling frameworks such as spatially explicit capture-recapture which estimates surface of predicted animal densities over the study area. Here, we review six common approaches and provide a summary of the relative advantages and disadvantages of each (Table 2). In addition, traditional and local knowledge can be a valuable source of information for understanding, monitoring and modeling species movements and distribution. Local knowledge can be used to establish and refine boundaries to movement assumptions for modeling (Gates and Wierzchowski 2003), and to delineate ranges, movement corridors and habitat selection (Schramm 2002). Athabasca Dene have established zones within which heightened environmental management and monitoring occurs, including community and science-based Aboriginal government organizations monitoring and enforcement (Athabasca Chipewyan First Nation 2012). Traditional knowledge of species distribution has also compared favourably to distributional models derived from modern scientific methods. For example, Polfus et al. (2014) demonstrated that a distributional map for the northern ecotype of woodland caribou generated from traditional knowledge produced similar predictions to one generated from a resource selection function (RSF) model.

Minimum Convex Polygon

The oldest method for quantifying an animal's space use is the minimum convex polygon (MCP; Hayne 1949). The MCP is the smallest polygon encompassing all recorded locations (generally from radio collars) of an animal (100% MCP) although the outermost 5% of locations are frequently excluded to reduce the influence of outlying locations (95% MCP). While commonly applied to individuals, the MCP can be pooled across all animals to assess a species distribution, an approach that is still used by the IUCN (2012) for assessing trends in a species' extent of occurrence. MCPs, however, have been criticized for a number of reasons. First, they are sensitive to sampling effort and may be biased when sample sizes are small (Börger et al. 2006, Nilsen et al. 2008, Kolodzinski et al. 2010). Second, bias may also be induced by errors in animal spatial locations (Burgman and Fox 2003). Third, MCPs can encompass large areas that are devoid of animal locations, which may be problematic when evaluating for distributional changes (Worton 1987, Burgman and Fox 2003, Barg et al. 2005). A further drawback is that MCPs have limited value in evaluating wildlife-habitat relationships or predicting species occurrence where data are insufficient or non-existent (Nilsen et al. 2008). While assessing compositional differences in home ranges can be accomplished, generating explicit spatial predictions (i.e., a map) from these types of analyses is problematic.

Utilization Distributions

Because of the limitations of MCPs, utilization distributions (UDs) were developed as an alternative approach to home range estimation. UDs typically use a non-parametric approach that estimates a probability density function (PDF) that describes an animal's relative use of space (Worton 1989). Fixed kernel and adaptive kernel techniques are normally used to estimate the PDF. A critical component to UD estimation is determining the appropriate bandwidth or smoothing factor for the kernel estimator (Worton 1989, Gitzen et al. 2006) as the choice of bandwidth dictates the resolution or grain at which animal use is measured. Similar to MCPs, UDs can be estimated at the population-level and probability contours can be used to define the UD boundary. For ungulate species that are non-territorial, Börger et al. (2006) suggest that 80-90% probability contours provide an accurate estimate of home range size and this estimate is less susceptible to bias from small sample sizes than MCPs.

Utilization distributions can also be used to assess factors influencing an animal's spatial distribution by linking the intensity of use to environmental and behavioural variables (i.e., a resource utilization function [RUF]; Marzluff et al. 2004, Millspaugh et al. 2006). RUFs are generally estimated for each individual animal and population inferences are derived by averaging estimates across animals. A key advantage to the RUF approach is that because it estimates a smooth density surface describing animal use, it is less influenced by animal location error compared to other resource selection approaches that rely on correctly classifying environmental variables at an animal's exact observed location (see below; Millspaugh et al. 2006). The RUF approach, however, does not take into account resource availability, which can influence resource use by an individual (Mysterud and Ims 1998). Further, by not scaling resource use by its availability, the RUF approach is problematic for evaluating whether certain resources are relatively avoided by the focal species.

Occupancy

In the last decade, occupancy modeling has become a common method for monitoring species distribution. In this approach, the study area or region of interest is partitioned into sites (or grid cells), which are considered the sampling unit (MacKenzie et al. 2002, 2006). From this sampling frame, a subset of sites is selected by a probability-based process and this subset is repeatedly surveyed to determine species presence/absence. The repeated visits yield an encounter history that is used in a likelihood-based framework to model detection probability and estimate site occupancy (MacKenzie et al. 2002). During the survey period, sites are assumed to be closed (i.e., no immigration or emigration) although recent extensions relax this assumption (Kendall et al. 2013). Ensuring closure requires careful consideration of the survey period and site size (MacKenzie and Royle 2005, Latham et al. 2014). One approach to assure closure of sites as well as efficiently estimate detection rates is to use double independent observers for site visits. This methodology provides an estimate of sighting probabilities if each observer is modeled as a sample session without the requirement of repeated visits.

Typically, site size is set to approximate the average home range size of the focal species; however, for wide-ranging species such as large herbivores, site size is often smaller than the average home range and in these instances the survey period needs to be very short to ensure closure otherwise inferences are restricted to the proportion of the study area used rather than occupancy *per se* (MacKenzie and Royle 2005, Efford and Dawson 2012). To predict occupancy states across the study area and account for heterogeneity in detection probability, habitat covariates can be easily incorporated into the model (MacKenzie et al. 2002, 2006).

While occupancy modeling has been applied to a wide variety of species, we note that its application to ungulates has been more limited. For herding species, occupancy has been used to model the distribution of boreal caribou (Schaefer 2003, Poley et al. 2014) though these studies have had a long-term focus (e.g. decades). This long time frame was likely necessary because sample sites were smaller than home ranges and short-term changes in occupancy may reflect differential home range use rather than actual range changes in the distribution of the population (e.g. retraction or expansion). We further note that spatial clustering may impact occupancy modeling because similar to other modeling approaches, estimation becomes problematic when encounter rates are low (e.g. probability of occupancy <0.2; MacKenzie et al. 2006). Thus, for spatially clustered species, a two-phase adaptive sampling design may be advantageous for assessing distribution based on occupancy (Pacifici et al. 2012).

Resource Selection Functions and Presence-Only Species Distribution Models

Similar to the RUF approach, this suite of models relies on 'presence only' data to evaluate and predict species distribution based on relationships with environmental variables. These modeling approaches include machine learning models that estimate a probability of occurrence distribution based on the principle of maximum entropy (program Maxent; Phillips et al. 2006), resource selection functions (RSFs; Manly et al. 2002) and environmental niche factor analysis (Hirzel et al. 2002). For the latter two approaches, inferences are derived by comparing the distribution of locations used by the focal species to the distribution of available locations at a spatial extent defined by the researcher. Environmental variables (or resources) associated with each location are included in the model and are evaluated to determine their relative influence in explaining differences in these distributions. Unlike RUFs, resource use is scaled by the availability of the particular resource, which means that the relative strength of an animal's resource selection can be dependent on resource availability (Mysterud and Ims 1998).

A primary focus of presence-only models is to generate spatial predictions of habitat suitability. These types of models, particularly RSFs, have been used to assess habitat associations for wide variety of ungulate species (e.g. elk - Hebblewhite et al. 2008; caribou - DeCesare et al. 2012b). Inferences from RSFs, however, fundamentally differ from occupancy. By comparing used resource units (i.e., animal locations) to available resource units, RSFs estimate the probability that a resource unit is selected given that it is encountered by the animal. Occupancy modeling, on the other hand, estimates the probability that a sample site will be occupied during a given time period by the focal species. This distinction is primarily due to differences in the sampling frameworks and because occupancy explicitly incorporates absence data (Lele et al. 2013). In most presence-only models, the sampling unit is a point or pixel, which is generally a much smaller scale than the sample sites used in occupancy modeling; consequently, locations are not considered closed during sampling and unused locations do not equate to being unoccupied. The sampling of "used" locations (animal presence) is also not driven by a probabilistic sampling process and instead is driven by movement of the focal species

(Koper and Manseau 2009). Extrapolating inferences of species distribution to areas without animal location data is therefore problematic for presence-only models and model predictions are rarely validated by assessing whether predicted areas of high suitability actually contain the target species. These key differences make presence-only models less powerful than occupancy models for monitoring changes in species distribution.

Density Surface Modeling from Aerial Survey or Mark-recapture Data

Aerial Survey Data

A more recent approach termed density surface modeling uses data from distance sampling to model distribution and habitat selection (Miller et al. 2013). This approach explicitly models the detection function of animals from aerial transect surveys and factors influencing detection (i.e., canopy cover). The response variable in this case is density rather than selection which potentially allows estimates of population size for sub-regions of the study area. We suggest this approach is useful for partitioning densities within study areas but also potentially useful for assessing areas of higher habitat quality outside of study areas. We provide further exploration of this approach in Power Analyses of Abundance Surveys.

We note that density surface modeling is similar to RSF modeling discussed in Resource Selection Functions and Presence-Only Species Distribution Models with availability of habitat types defined by habitats sampled within transects where no animals were detected. Boulanger et al. (2011) applied this type of approach to derive RSF's for barren-ground caribou from strip transect surveys. The key difference is that detection of caribou was not incorporated into this analysis and instead assumed to be constant for all habitat types (given that all habitat types were above timberline). Because detection was not estimated the model could only estimate relative use of habitat types rather than probability of occurrence.

Mark Recapture Data

If individuals are marked and sampling occurs over multiple sessions then SECR models can be used to fit density surface modeling. Under the SECR paradigm, inference can be expanded beyond the traditional sampling grid area by sampling sub grids or using two stage sampling approaches where "core areas" with higher coverage are sampled to estimate population size and density and secondary areas are sampled to assess distribution and broader-scale density (Conroy et al. 2008, Efford and Fewster 2013). This approach allows for an assessment of distribution which is similar to occupancy, but without the subjectivity and potential issues with defining plot sizes in occupancy models (Efford and Dawson 2012). The main advantage of SECR models in this context is that scale of movement and detection probabilities are estimated directly from the underlying mark-recapture data as opposed to occupancy where only detection is estimated. If habitat covariates exist it is also possible to develop RSF-type models that model density surfaces to therefore assess factors that might influence distribution and densities of the target species within survey extents (Miller et al. 2013, Royle et al. 2013). Because the development of SECR methods is relatively recent, we note that there are no published studies of its use with ungulates although it has been used extensively with carnivores and other species. For ungulates, capture-recapture data would likely be derived from fecal DNA-based methods or mark-resight methods (Sollmann et al. 2013). These data collection methods may result in SECR having higher costs than the other approaches reviewed here for evaluating and monitoring species distribution.

Table 2: Comparison of six approaches for evaluating species distribution and habitat associations.

Model	Framework	Advantages	Disadvantages
Minimum Convex Polygon	Estimates range size by constructing the smallest polygon that encompasses observed animal locations.	Conceptually easy to construct.	Requires collared bison or presence only data. Potentially biased by small sample sizes and animal location error. Can include large areas that may be unsuitable habitat. Limited value in predicting wildlife-habitat relationships.
Utilization Distribution	Estimates a probability surface describing the relative intensity of animal use.	Less biased by sample size and likely provides a more accurate estimate of range size for non-territorial species than MCP. Intensity of use can be linked to environmental covariates allowing explicit predictions of space use across the study area.	Requires collared bison or presence only data. Does not take into account resource availability.
Occupancy	Study area is partitioned into sample sites which are repeatedly surveyed to estimate detection probability and occupancy.	Explicitly models imperfect detection. Incorporates 'absence' data which yields a more straightforward interpretation of species occurrence within the study area. Environmental covariates can be included to account for heterogeneity in detection and occupancy.	Requires multiple visits to sites to estimate detection probabilities. Estimate is sensitive to size of sample sites and low rates of encounter.
Resource Selection Function	Compares the distribution of animal locations to the distribution of available locations within the study area.	Can use aerial survey or telemetry data. Yields fine-scale, spatially explicit evaluation of wildlife-habitat relationships.	Non-probabilistic sampling framework and lack of absence data inhibits strong inference on species occurrence.

Model	Framework	Advantages	Disadvantages
Density surface modelling Aerial transect distance surveys.	Uses data from distance surveys to estimate spatial extent of sampling and probability of detection of bison. Divides transects into segments that are summarized in terms of habitat.	Estimates detection of animals and incorporates this into estimates of association between habitat and density. Provides a direct assessment of density.	Requires distance sampling data with associated sample size requirements.
Density surface modelling Spatially Explicit Capture-Recapture	Estimates a surface of animal densities across the study area using a two-stage approach.	Sample plot size is estimated empirically. Environmental covariates can be included to model density and distribution.	Requires individually marked bison. For fecal-DNA approaches, may be labour intensive more costly than other approaches. No empirical tests on ungulates.

Detecting Mortality Events and Disease Outbreaks

Bison in the NWT are affected by three diseases, but it is primarily anthrax that can cause rapid mortality to a sizable portion of the population under relatively specific environmental conditions (reviewed in NWT disease in Detecting Disease Outbreaks in the NWT). Our focus in this section is not on the epidemiology or surveillance for incidence of diseases in NWT bison populations, but on detection of major mortality events (e.g. disease, drowning, or starvation) that could affect a large enough portion of a population to change management strategies for the herd. However, principals from disease surveillance – "an active, on-going, formal, and systematic process aimed at early detection of a specific disease or agent in a population, or early prediction of elevated risk of a population acquiring an infectious disease, with a pre-specified action that would follow the detection of disease" (Thurmond, 2003) – could be applied to detection of mortality events. Disease-surveillance programs employ "proportional risk sampling" or "weighted sampling" to enhance the ability to detect the disease of interest by focusing surveillance efforts on areas and individuals with the highest probability of being infected or, in other words, those at the greatest disease risk (Thurmond 2003, Walsh 2012).

Oral history has been used to identify historical die-offs in what is now the WBNP area that resemble features of anthrax mortality that occurred among bison in the same area more recently (Ferguson and Laviolette 1992). Local knowledge by community members can aid in understanding of bison habitat selection, movement patterns, water crossing locations, and distribution as they relate to disease risk management measures (Mitchell 2002).

In Prince Albert National Park anthrax was initially not known to occur when first detected by hikers (Shury et al. 2008). Rapid testing followed by four helicopter surveys detected a total of 28 bison killed, mostly adults.

In WBNP and the Slave River Lowlands, the length of an outbreak was not a determinant of the number of dead bison found, but outbreaks starting in July had more deaths than those staring in June (Salb et al. 2014). This study concluded that males were more likely to be detected in an outbreak, outbreaks were likely not random events, and there was no relationship between outbreak size or length and location. The authors concluded that surveillance activities may benefit from targeting bulls.

As noted, anthrax in NWT bison generally occurs under specific environmental conditions – in summer, generally during hot dry conditions following very wet springs (Gates et al. 2001). Large-scale mortality events are generally clustered (e.g. a group of bison breaking through ice on one of the main lakes or rivers; anthrax outbreaks) and highly clustered dispersion of samples reduces the probability of detecting at least one event (Walsh 2012). However, large-scale mortality events often will cause large difference in population estimates and therefore may be more detectible than usual fluctuations in abundance. Collection of weather covariates that might create conditions favourable to anthrax could be used to help determine the best strategy to detect disease events. Retrospective analysis of historic survey and composition data could be used to test whether historic anthrax events are correlated with weather or other environmental variables.

OVERVIEW OF OPTIONS FOR MONITORING BISON IN THE NWT

Here we provide an overview of bison monitoring across northwestern Canada, and use data from the Mackenzie bison herd to evaluate the efficiency of composition surveys and explore the use of an integrated population model.

Review of Bison Monitoring in the NWT and Other Canadian Jurisdictions

Population Monitoring

Recent bison survey methods in jurisdictions in western and northern Canada outside of the NWT vary from roadside counts and spaghetti-type aerial surveys to transect surveys and mark-resight surveys (Table 3). Survey effort varies from periodically to infrequently. Several studies provide minimum counts with no associated variance. Survey design for the Aishihik herd in the Yukon used arguably invasive paint-balling of 8% of the herd followed by three resight sessions; the CV of the estimate was a tight 0.06 (Jung and Egli 2012). Strip transects of herds in WBNP provided 30% coverage in some areas and full coverage in others, and also resulted in tight confidence around the estimate (CV = 0.09; Kindopp and Vassal 2010). Mark-resight using photographic identification provided relatively tight estimates, but is likely most appropriate for smaller, more easily accessible populations (Merkle and Fortin 2014). With the exception of the Yukon and Prince Albert National Park surveys, no other areas address a sightability correction factor.

Table 3. Most recent bison survey parameters gathered by herd/jurisdiction in western and northern Canada. N/A = not applicable.

Jurisdiction	Area; Subspecies	Month Year	Population estimate	Coverage	CV	Sight. Corr.	Composition/ Demography	Reference
British Columbia	Pink Mt; Plains	Feb. 2006	Aerial SRB sampling (Gasaway); 2 strata	N/A	-	No	Aerial surveys	Rowe 2006
	Nordquist, Etthithun; Wood	2012, year-round	Minimum road counts; opportunistic aerial count	N/A	-	No	Road-based transects	Thiessen 2012
Alberta	Hay-Zama; Wood	Mar. 2012	Strata flight, chopper count	Unknown	-	No	Aerial surveys	Hermanutz and Fullerton 2012
Wood Buffalo National Park	WBNP; Wood	Feb.-Mar. 2009 (2014)	2 x 500 m strip transect; 4 strata (Jolly II)	40-100%	0.09	No	Aerial surveys	Kindopp and Vassal 2010
Saskatchewan	Prince Albert NP (Sturgeon R); Plains	Mar. 2011-12	Photograph mark-resight; 10 sampling events; (minimum count strip survey)	N/A	0.12-0.14	Yes (MARK)	Adults only	Merkle and Fortin 2014
Yukon	Aishihik; Wood	July 2011	Aerial mark-resight; 3 resight flights	N/A	~0.07	Yes (paint-ball)		Jung and Egli 2012, Hegel et al. 2012
NWT	Nahanni; Wood	Mar. 2011	2 x 500 m strip transect; (Jolly II)	23%	0.25	Yes (7 collars)	Separate surveys	Larter and Allaire 2013b
	Mackenzie; Wood	Mar. 2012-13	2 x 500 m strip transect and Distance sampling; 3 strata	40%; 2.5 km transect spacing	0.22	Yes (Distance)		Armstrong and Cox 2013, Boulanger 2104a
	Slave R Lowlands; Wood	Feb. 2014	Line transect; Distance sampling; 2 strata	2.5 km transect spacing	0.38	Yes (Distance)		Armstrong 2014, Boulanger 2104b

Recent surveys of the three NWT bison herds have used strip transects (with sightability correction assessed using collared individuals) and distance sampling (Table 3). If large groups are observed, the survey aircraft leaves the transect to circle each group to photograph and obtain a count. CV in all surveys was relatively high (0.25–0.38). The estimate in the 2014 Slave River Lowlands (1,083) was only seven percent higher than the number of bison counted on transect (1,013) due to double counting of bison from adjacent transect lines (Boulanger 2014b; unpublished data). We note that double counting of bison from adjacent lines does not bias distance sampling estimates.

Pellet-based, DNA-based, or remote camera methods, are probably too labour intensive given that the sightability of bison is relatively high and therefore it is not cost-effective to genotype DNA from pellets unless further inference on genetic variability is an objective. Beyond higher cost, the main disadvantage of DNA methods is the longer time period required for genotyping of pellet data and subsequent difficulties in obtaining timely estimates for management.

Radio collaring bison for mark-resight methods and survival rate estimation may be useful in smaller areas but is less likely to be cost-efficient for all bison herds. Collaring would be most beneficial for areas that have higher forest cover to allow a secondary estimate of sightability using mark-resight methods or sightability models. However, use of mark-resight methods, which require suitable sample sizes of collared bison, is not efficient for herds that are primarily in open areas where distance sampling methods can be efficiently employed to estimate detection rates.

Of methods that are available we suggest that distance sampling methods provide the most inference and robust estimates and are likely the most cost-effective. Distance sampling allows the data from all observations to be used (as opposed to only observations within the 400 m survey strip for strip transects) and is therefore more efficient than strip transects. The main constraint for the use of distance sampling is appropriate collection of sighting data to allow simpler detection function models to be used. In addition, sightability near the plane is assumed to be close to one, an assumption that can be further tested using double observer/distance sampling methods. We provide suggestions for enhancement of distance sampling methods in Modeling Ungulate Population Dynamics: A Case Study Using Wood Bison.

Composition Monitoring

Classification of bison during aerial surveys is generally limited to calves, possibly yearlings and adults ≥2 years (e.g. Hermanutz and Fuller 2012, Jung and Egli 2012, Larter and Allaire 2013b). Multiple age and both sex classes can be discerned, but this requires viewing from close range on the ground (Carbyn 1998).

Surveys to determine herd composition in the Mackenzie, Slave River Lowlands and WBNP are usually conducted in June to mid-July, where a helicopter is used to locate bison by searching open habitats known to be inhabited at that time of the year (as in non-systematic sampling) (Bradley and Wilmshurst 2005, T. Armstrong, Environment and Natural Resources (ENR), unpublished data). Surveys are timed for after most of the calves are born, but early enough that none have started to lose their reddish coat which facilitates detection. With this timing there will have been some calf mortality. Small groups are classified from the air, either by using binoculars during hover or by pushing animals and classifying by naked eye during a fly-by. For large herds a location is chosen where the pilot can put observers on the ground then push the animals toward them, with classification conducted as they go by. Success of this method is highly variable (T. Armstrong, ENR, personal communication); it works well if the location is appropriate, the animals remain calm, and the pilot reads the herd behaviour correctly. If not, only animals on the near side of the herd may be classified as they stampede past on a hard run.

Composition surveys for the Nahanni herd are conducted by boat in mid- to late July to allow the Liard and Nahanni river levels to drop and expose the sand bars which bison utilize in the summer, likely areas that provide relief from heat and insects, and relatively easy access to high-quality forage (Larter and Allaire 2007). A similar approach to group size is used as for aerial surveys; small groups are classified from the boat, and larger groups are classified with binoculars from shore. One or two large mixed sex/age groups and few mature bulls groups are usually classified each year (Larter and Allaire 2007). For the Nahanni herd about 130-170 individuals generally are classified out of a population of about 400-430 animals, perhaps 30-40% of the population. Observations of calves (20-57:100 cows) and yearlings (10-31:100 cows) vary widely among years, but only two population estimate data points are available (2004 and 2011) that produced similar estimates (see Larter and Allaire 2007).

Bison are classified into the following age and sex categories: calves, yearlings, cows and bulls classified by horn morphology as B1 (juveniles: estimated age two to three years), B2 (subadults: four to six years), B3 (prime, adult males: seven to 12 years), and rarely B4 (old bulls ≥10 years, with noticeable wear on the horns) (Larter and Allaire 2007; T. Armstrong, ENR, personal communication.). Calves and yearlings are not classified by sex. Juvenile survival can be determined by comparing the ratio of yearlings/100 cows to calves/100 cows (Larter and Allaire 2007), and appear to be strong indicator of population trend (Bradley and Wilmshurst 2005). However, comparison of recruitment from annual calf/cow or yearling/cow ratios assumes a similar adult survival rate. An integrated population model (Integrated Population Model) provides a way to estimate calf survival rate and recruitment while accounting for adult female survival.

Estimates of the Precision from NWT Composition Data

We suggest that composition survey analyses should always be accompanied by estimates of standard error and confidence limits to determine the contribution of sampling variance to observed population trends. We used bootstrap methods (Manly 1997) to estimate standard error and confidence limits on composition data from the Mackenzie, Slave River and Nahanni herds. For this procedure data sets were randomly resampled for 500 iterations with confidence limits defined by the 2.5th and 97.5th percentile of resampled estimates and standard error estimated by the standard deviation of resampled estimates. We then graphically analyzed trend and empirically assessed sample sizes needed to obtain adequate precision of estimates.

We note that this exercise mainly considers estimate precision as opposed to bias. One assumption of estimates is that the herd is sampled representatively so that the actual proportions observed in groups will indicate actual composition of the entire herd. Factors such as segregation of sex or age groups can challenge this assumption especially if some sex and age groups occur in smaller groups that are not as easily observed. For this reason we suggest a systematic approach to composition survey design that samples groups in proportion to abundance. Of methods employed an aerial survey approach provides the best method to obtain a representative sample.

One of the main reasons for reduced precision is low sample sizes of groups encountered during the composition survey. A comparison of the CV of estimates versus the number of groups for all composition data suggests that at least 25 (calf:cow ratios) to 30 (yearling:cow ratios) groups need to be sampled for the CV of composition estimates to be less than 0.20 (Figure 1). The precision of bull:cow ratios was lower than yearling:cow and calf:cow ratios. This is presumably due to a large degree of variation in the numbers of bulls in groups encountered which is potentially due to segregation of bull and cow bison. In this case most estimates were imprecise even when sample sizes were larger.

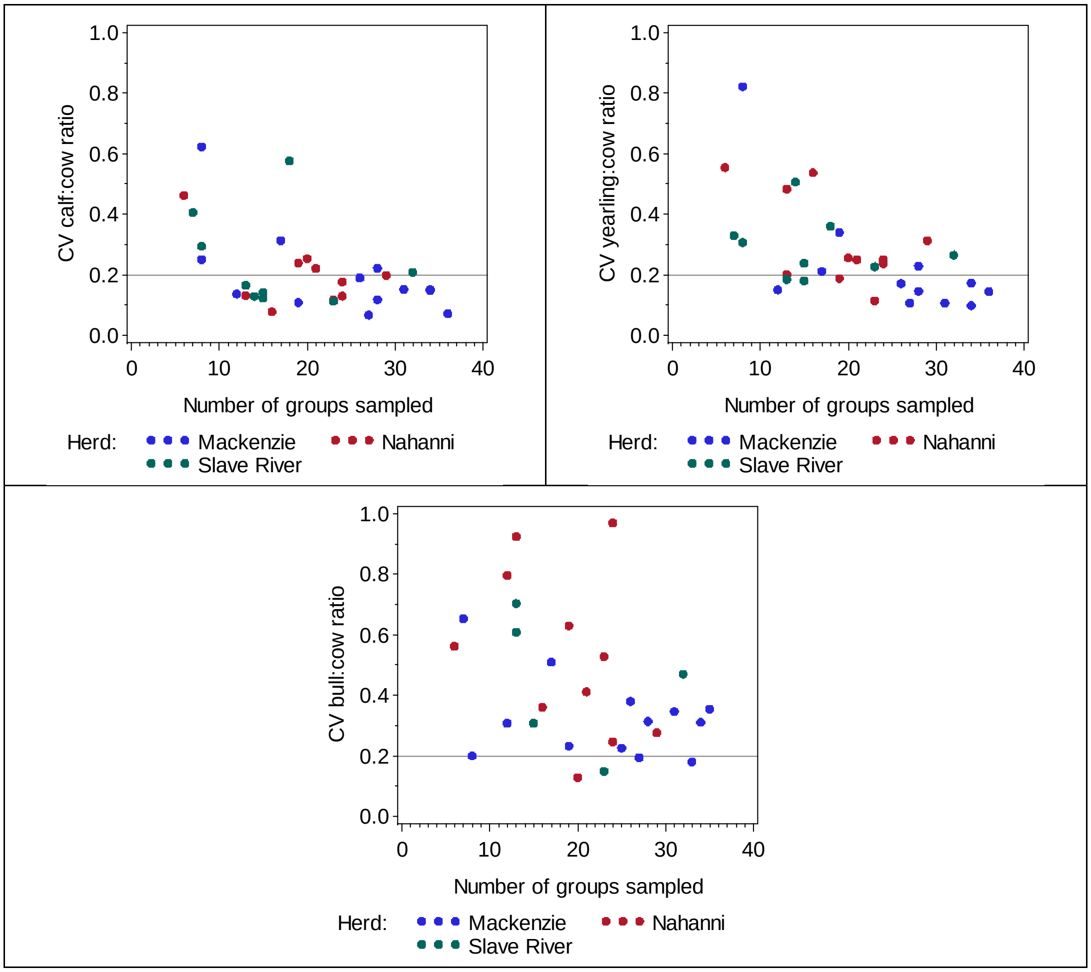


Figure 1: The CV of composition survey estimates as a function of the number of groups sampled for each yearly survey for the three primary NWT survey areas where composition data have been collected.

The main conclusion from this analysis is that threshold sample sizes of groups (>30) need to be obtained to allow reasonable precision for composition survey estimates. Otherwise, it may be difficult to separate variation in composition due to sampling variation from actual biological variation in productivity or adult sex ratio. We speculate that determination of bull:cow ratios may require greater sampling intensity that attempts to better sample groups of bulls that are segregated from other groups. We provide the composition estimates from Figure 1 with associated standard errors in Appendix B of this report.

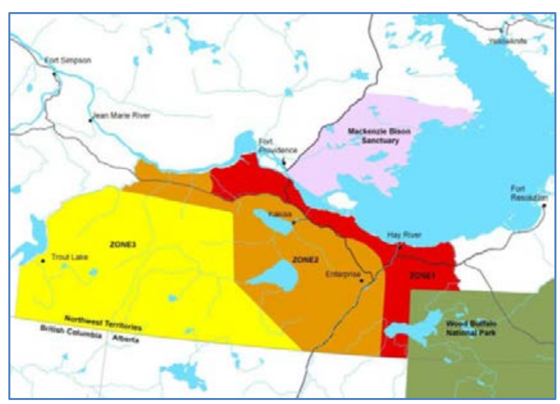
We also suggest that composition surveys are most valuable if viewed in the context of overall population demography through the use of an integrated population model. If this approach is used it is possible to estimate calf survival, yearling survival, adult survival as well as overall productivity through the integration of composition survey data and repeated abundance surveys. Using this approach potentially protects against bias caused by differential trends in survival rates of age and sex classes (Boulanger et al. 2011, Harris et al. 2011). It also allows the test of association of demographic parameters with environmental or other covariates. We provide a case study of this approach with the Mackenzie bison composition and abundance data in Modeling Ungulate Population Dynamics: A Case Study Using Wood Bison.

Detecting Disease Outbreaks in the NWT

Wood bison in WBNP, the Slave River Lowlands, and surrounding areas and in Alberta and the NWT are affected by two cattle diseases, bovine brucellosis (caused by the bacterium *Brucella abortus*) and tuberculosis (caused by the bacterium *Mycobacterium tuberculosis*), and anthrax (COSEWIC 2013). Brucellosis causes reduced fecundity largely through infertility and increased incidence of abortion, and tuberculosis is a respiratory disease which impacts fecundity and survival (Tessaro 1989). Anthrax is a naturally occurring infectious disease caused by the endospore-forming bacterium *Bacillus anthracis* (Gates et al. 2001). Spores can remain dormant in the soil for decades; disease outbreaks in the WBNP area may have occurred nearly two centuries ago (Ferguson and Laviolette 1992). Anthrax outbreaks emerge in certain environmental conditions – in summer, generally during hot dry conditions following very wet springs – with rapid mortality a result of toxins in the bloodstream causing septicemia and death (Gates et al. 2001). Disease outbreaks can severely affect subpopulations, as shown by the 53% reduction in the Mackenzie herd between 2012 and 2013 as a result of an anthrax-caused die-off (Boulanger 2014a). Seven documented anthrax outbreaks were documented in the Slave River Lowland between 1963 and 2001, killing at least 950 bison (Nishi et al. 2007). In WBNP and the Slave River Lowlands the length of an outbreak was not a determinant of the number of dead bison found, but outbreaks starting in July had more deaths than those staring in June (Salb et al. 2014).

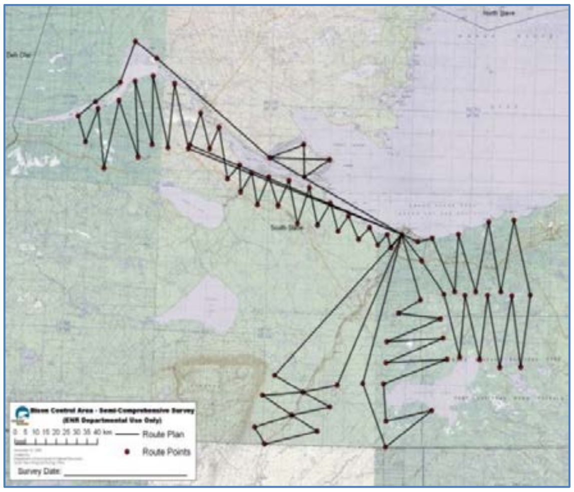
The NWT is faced with two tasks related to disease: ensuring that bison from the Greater WBNP meta-population infected with either brucellosis or tuberculosis do not come in contact with bison from the Mackenzie and Nahanni subpopulations, and detecting anthrax outbreaks in a timely manner to allow management responses to minimize spread of the disease. To address the first task, the NWT Bison Control Area was created in 1987 and covers much of the NWT west of the Park and south of Great Slave Lake and the Mackenzie River (Bidwell et al. 2009; Figure 2). The area is currently patrolled using aerial shoreline patrols flown weekly from December to March along western Great Slave Lake and the Mackenzie River to Mills Lake, and transects surveys within three zones. Surveys are flown in mid-February using a zigzag flight pattern in Zone 1 (semi-comprehensive survey; Figure 2a), followed by a more extensive transect survey in late March covering Zones 1 and 2 (comprehensive survey; Figure 3b). Up until 2010, 14 bison have been removed from the Bison Control Area (Species at Risk 2010).

2a



2b

Figure 2. Bison Control Area (Figure 2a) and the three zones (Figure 2b) within the NWT, (Bidwell et al. 2009).

3a 

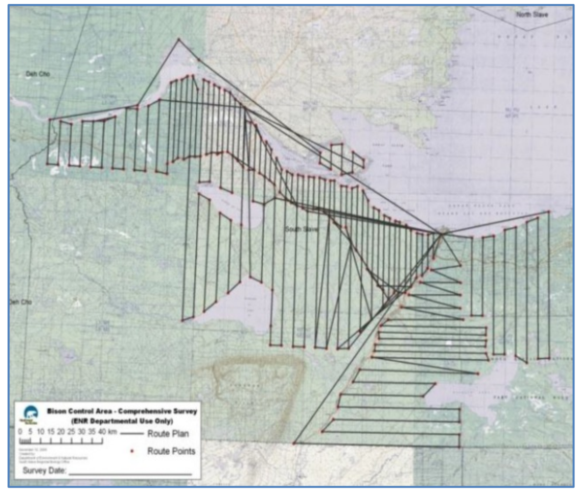
3b 

Figure 3. Semi-comprehensive survey flown in mid-February (Figure 3a) and comprehensive survey flown in late March (Figure 3b) within the Bison Control Area (Bidwell et al. 2009).

Anthrax surveillance surveys are conducted bi-weekly, generally between mid-June and mid-August, within the core of the Slave River Lowlands and Mackenzie herd ranges (Elkin et al. 2013). An increase in aerial surveillance also occurs if anthrax is suspected or detected (e.g. Nishi et al. 2007). Surveillance flights are conducted over large open areas, low marshy areas and water edges, and major bison concentrations within the normal bison range, emphasizing but not be restricted to areas of previous outbreaks. Surveillance flights are generally conducted by small fixed-wing aircraft at an altitude of 240-360 m AGL and an air speed of approximately 100-120 knots.

Further Refinement of Prediction of Disease Outbreaks

It may be possible to use weather data to predict likely occurrences of disease. As noted, anthrax in NWT bison generally occurs under specific environmental conditions – in summer, generally during hot dry conditions following very wet springs (Gates et al. 2001).

Further Refinement of Surveillance Efforts

We note that data from distance surveys could be analyzed to determine detection probabilities of bison during aerial surveys and from this simulation methods could be used to assess survey effort needed to detect threshold densities of bison in control areas. In detail, distance sampling methods estimate probability of detection of bison within a specified "effective sampling area", the encounter rate of observers with bison (which will be proportional to density), and the average group size of bison encountered (Buckland et al. 1993). Each of these parameters can be varied in a simulation study to determine optimal sampling effort to ensure detection of at least one bison group given an assumed density of bison and group size. This analysis would require that a threshold density as well as study extent be defined for the surveillance areas. Previous simulation studies (Gates and Wierzchowski 2003) of bison movement between populations could be used to further allocate surveys to areas that bison may occur within the surveillance zones.

Modeling Ungulate Population Dynamics: A Case Study Using Wood Bison

In this section we use data from the Mackenzie bison herd to evaluate the efficiency of composition surveys and explore the use of an integrated population model that utilizes data from population surveys and composition surveys to model bison demography in this herd.

Composition Surveys

The main information about herd status for the Mackenzie comes from sporadic abundance surveys and composition surveys that are conducted annually or bi-annually. Composition estimates with associated confidence limits show that some of the annual variation in composition could be due to sampling variation (Figure 4). For example, when precision is considered it becomes evident that many of the yearly differences in ratios could be attributed to sampling variation with some years (2002 and 2013 for calf:cow ratios) indicating lower values. The challenge with composition data is determining how it relates or predicts overall population trends and demography which is where an integrated population model can be useful.

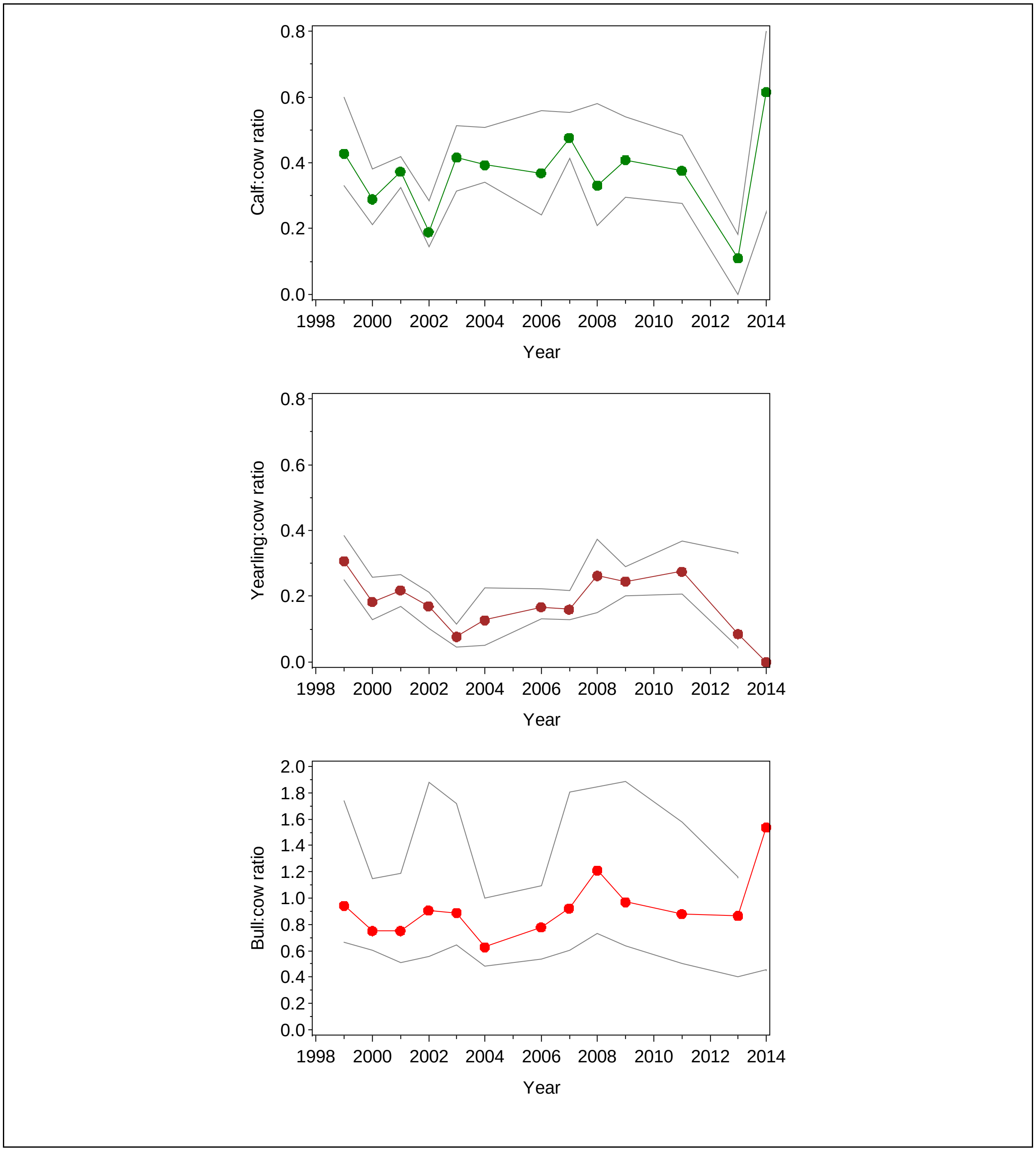


Figure 4. Estimates from composition data for the Mackenzie bison herd with confidence limits estimated using bootstrap percentile methods. Note the different scale on the bull:cow ratio graph. No confidence limits were possible for 2014 for yearlings since none were observed. The upper confidence limits for bull:cow ratio for 2014 was five (off the graph).

Integrated Population Model

We used the population survey and composition data to test the application of an integrated population model for the Mackenzie bison herd. One of the main questions was whether this type of model would work reliably with bison data given the absence of collar-based adult survival estimates.

Development of Model

The model was based on a caribou demographic model (Boulanger et al. 2011) with some changes to accommodate bison life history and survey methods (Figure 5). For this model we assumed a three stage population model with each year defined by the approximate time (May 15) in which bison calves are born. For this model, the proportion of calves that survived to become a yearling was estimated as calf survival (S_c), the proportion of yearlings that became adults as yearling survival (S_y) and the proportion of adults that survived each year as S_f (females) and S_m(males). A female bison did not breed until its 3rd breeding season (aged two years, five months during the fall breeding season) and therefore could produce a calf when it turned three years old. The proportion of calves produced by females was estimated as fecundity F_a. The actual proportion of calves produced by adult females each year was the product of their survival through the winter and fecundity. An even sex ratio at birth was assumed so that half the calves produced were male and half were female.

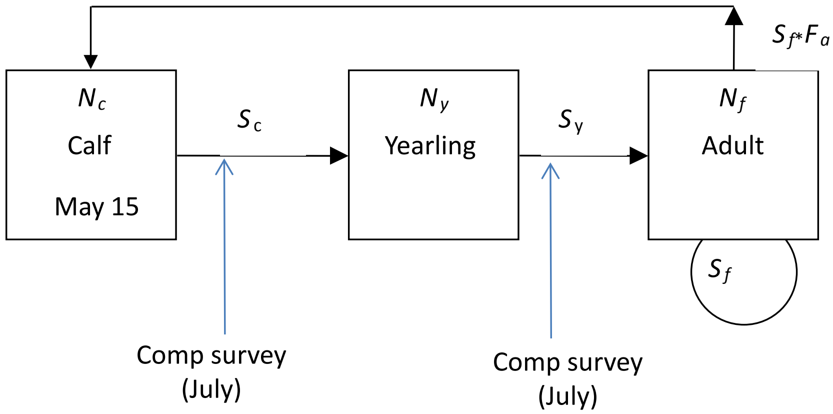


Figure 5: The female life history model used for the bison integrated population model. Male life history was similar (as parameterized by N_m and S_m for adult males) but without the reproductive loop.

Model parameters were estimated from composition surveys that usually occurred in July and abundance surveys that occurred in February and March. For composition surveys each measurement was parameterized dependent on assumptions about bison life history and the timing of the survey. Calf:cow ratios were estimated as $(F_a S_c^{(t/365)})/S_f^{(t/365)}$ where t was the interval in days between the birth of the calf (May 15) and the composition survey therefore scaling survival rates for the appropriate interval. Yearling:cow ratios were estimated as $(N_y S_y^{(t/365)})/(N_f S_f^{(t/365)})$ and bull:cow ratios were estimated as $(N_m S_m^{(t/365)})/(N_f S_f^{(t/365)})$. Bison abundance during March surveys was estimated as $N_c S_c^{(t/365)} + N_y S_y^{(t/365)} + N_f S_f^{(t/365)} + N_m S_m^{(t/365)}$ where t was the interval between May 15 of the previous year and the survey that usually occurred in February or March of the following year. Each model prediction *(θ)* was compared to a corresponding field estimate ($\hat{\theta}$), using the penalty term (ε) where. $\epsilon = [(\theta - \hat{\theta})/SE(\hat{\theta})]^2$. The penalty term considered the agreement between model predictions (θ) and field estimates ($\hat{\theta}$) in the units of the precision of the field estimate (as estimated by SE($\hat{\theta}$). For example, a large difference between a model prediction and a field estimate might not result in a large penalty if the standard error of the field estimate was large. White and Lubow (2002) further showed that the penalty terms were proportional to the log-likelihood of the model and therefore could be used instead of log-likelihood values to assess model fit.

The basic objective of modeling was to maximize agreement between field data and model parameters. To accomplish this, the parameters were iteratively varied (using the SOLVER optimization algorithm in Excel (Microsoft Corporation, Redmond, Washington, USA) to minimize the sum of penalties for a given set of parameters and model formulation, which is termed the Ordinary Least Squares (OLS) estimator of model parameters. Survival and fecundity terms were logit-transformed (McCullough and Nelder 1989) to ensure that the resulting estimate was in the zero to one interval. An initial stable age distribution was assumed to minimize variability in parameters caused by initial state conditions. PopTools (Hood 2009) add-in was used to estimate the stable age distribution.

The main objective of this modeling effort was to determine the initial feasibility of this approach given the limited sources of field data. We therefore fit a simple intercept model that assumed all parameters were constant over time. It is possible to add extra slope terms to explore other trends in parameters as well as add temporal covariates (i.e., weather, traditional ecological knowledge) to further elaborate and refine the population model which we suggest should be undertaken after initial discussion and refinement of the population model.

We only considered abundance data up to 2012 with the exclusion of the 2013 data that was affected by the anthrax outbreak. The 2013 data point created extra variation in the data that was not typical of previous years. We suggest that future efforts could consider these data and subsequent changes in parameters caused by the anthrax outbreak.

Preliminary Results

The constant parameter population model estimated cow survival at 0.93, bull survival at 0.89, yearling and calf survival at 0.51, and fecundity at 0.39. These estimates seem plausible and could be compared to estimates from collared data. The fecundity estimate is probably the least reliable estimate since it is partially confounded with calf survival and includes young bison (aged three) that may have a lower chance of producing a calf. For example, it is possible that fecundity is higher than 0.39 and calf survival is lower. A safer interpretation of model results might be an estimate of productivity as calf survival times fecundity (0.2) which would mean that of cows in the population in a given year, 20% will produce calves that survival to the following year. A survey of calf:cow ratios in mid- to late June after peak of calving could provide additional information that would refine fecundity and calf survival estimates in this context by providing an initial estimate of the proportion of cows that gave birth to calves.

Plots of model predictions for each field measurement revealed reasonable fit across the duration of the data with the exception of some temporal trends in yearling and calf:cow ratios not being captured by the constant parameter model (Figure 6). For example, the downward trend in yearling:cow ratios from 1999 to 2004 followed by an increase was not captured by the constant parameter models. In this case, weather covariates or traditional knowledge covariates about range condition may provide a way to describe this variation. Polynomial non-linear terms could be used to further refine the model fit but this approach does not inform about mechanisms (compared to the use of covariates). Estimated trends in abundance fit the limited field data well. This suggests that the observed trends in abundance could be explained by a relatively simple population model; however, it is also possible that more pronounced changes in abundance occurred but were not captured by the limited abundance data.

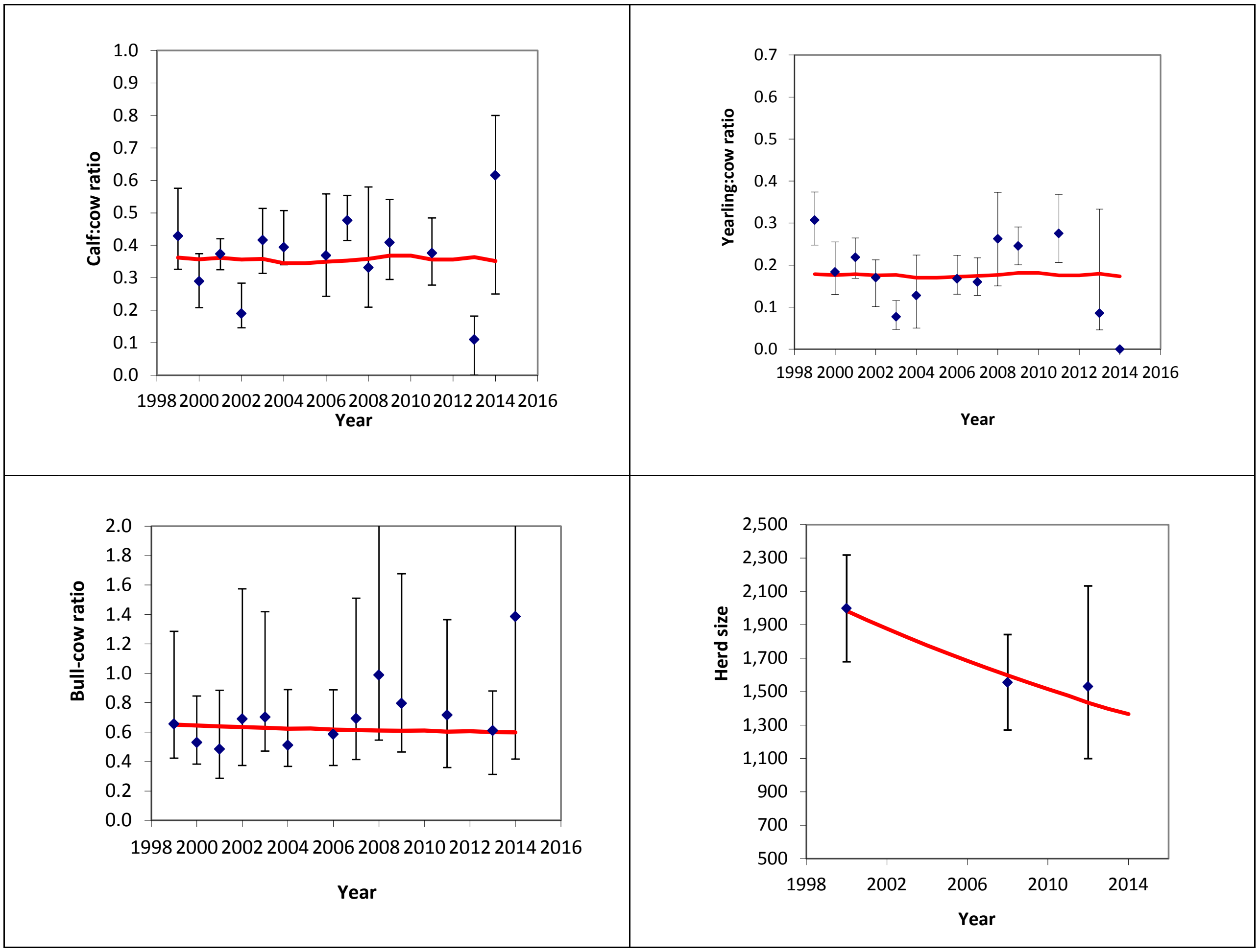


Figure 6: OLS model predictions (red line) compared to field estimates for composition surveys and abundance estimates.

Estimates of overall estimated abundance are given in Figure 6 which suggests a slow decline of each cohort over time (Figure 7).

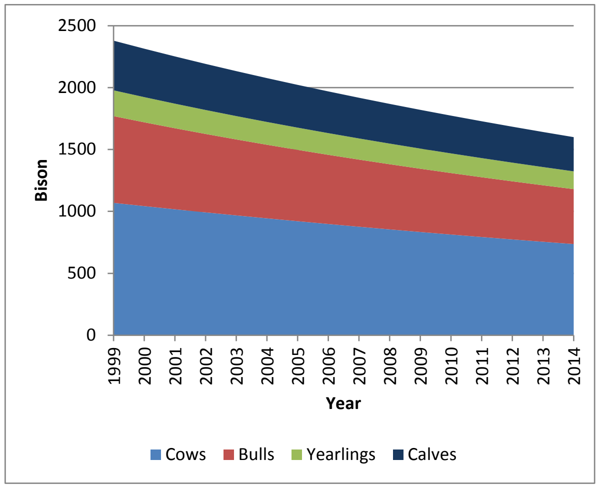


Figure 7: Estimates of overall herd size from the OLS model (Figure 6).

Further Refinement of Model

In summary, this initial test of an integrated population model suggests that a working population model of bison demography can be derived even in the absence of survival estimates from collar data. This model provides a method to better understand how composition survey estimates relate to overall herd size as well as estimates of survival rate and productivity for each age and sex class.

We note that a model that estimates temporal trends in parameters will provide further inference on how composition surveys relate to overall trend. One obvious refinement of the model would be incorporation of harvest level which will allow a better estimate of natural survival rate. In addition, models that consider temporal variation in calf survival and yearling survival could be used to explore changes in herd size not detected by the sparse abundance data. Temporal trends can be modeled using polynomial non-linear model terms however this approach does not provide explanation for the trends. Use of covariates that correspond to field conditions is the best method to explore variation in survival if these covariates are available. A temporal covariate can be derived from any indicator that is collected consistently on a yearly basis. For example, the relationship between population trend (r) and dry season rainfall provides an adequate approximation for modeling temporal changes in the size of populations of feral Asian swamp buffalo

(*Bubalus bubalis*) in Australia (Freeland and Boulton 1990). If a relationship exists for bison then it would be possible to constrain the model so that variation in survival rates is proportional to dry rainfall or other climatic variables. This approach would efficiently model temporal variation and also aid the model in prediction of trends based on current climatic conditions. Other temporal covariates based on traditional knowledge, disease outbreak, or other factors that potentially relate to demography could also be tested under the model framework.

Finally, this base model could be further evolved to produce standard error estimates of parameters through Bayesian state-space modeling (Buckland et al 2004, Johnson et al. 2010). In addition, this approach provides additional options for modeling temporal trends through covariates or random effects models. This enhancement was beyond the initial scope of this exercise but could be efficiently undertaken now that a base model is formulated.

POWER ANALYSES OF ABUNDANCE SURVEYS

This section provides further analysis and discussion about optimal monitoring strategies for bison with a focus on study design issues and associated power to detect change in population over time. We use results of past bison inventories to estimate power to detect population change as well as methods to increase power by study design, field implementation, and analysis methods. For this section it is assumed that distance sampling methods will be used for surveys.

In terms of population demography we often quantify change in terms of annual change in population size. The actual ability of power to detect change in population size often takes years of time and with annual change being compounded yearly to produce a larger net change. For example, a population declining at 10% per year will be at 60% of its size in five years (Figure 8). In this context risk and associated sampling intensity to detect a decline would be based on current status of the population and the target level of decline that managers would like to detect.

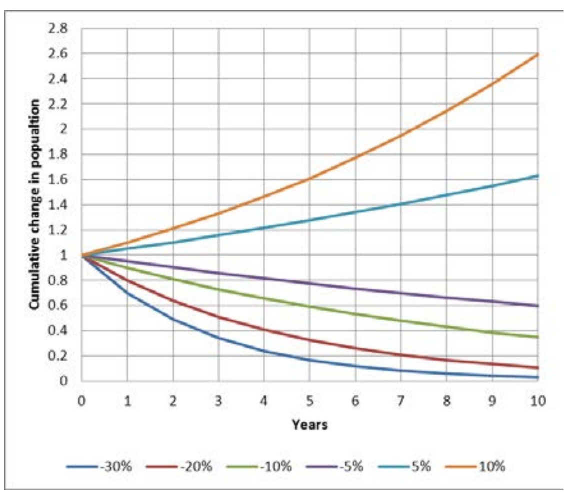


Figure 8: The relationship between annual change and cumulative change in population size as a function of the number of years surveys occur. Each line represents a different level of annual change.

Precision of Bison Abundance Surveys

The most recent estimates from bison surveys have been produced using distance sampling methods Boulanger 2014a, b). Precision of surveys has ranged from 16% for the pooled Mackenzie herd estimates (2012) to 40% for the pooled Slave River Lowlands study (Figure 9). In general the precision of estimates as indicated by the coefficient of variation is not proportional to abundance which is usually the case for distance sampling projects (Burnham et al. 1985, Gerrodette 1987).

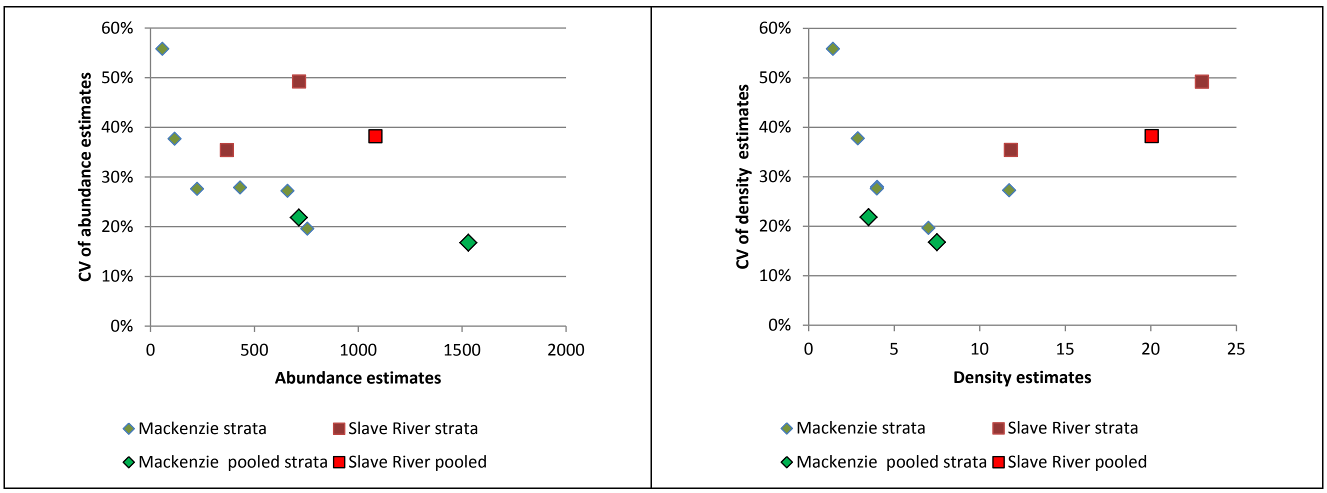


Figure 9: Estimates of precision [coefficient of variation (CV)] as related to abundance estimates from the Slave River Lowlands and Mackenzie bison surveys (Boulanger 2014a, b).

The difference in precision of estimates between the Slave River Lowlands and Mackenzie herds is non-intuitive given similarities in sampling effort and higher densities of bison estimated from the Slave River study. As discussed in Boulanger (2014b), low precision for the Slave River study was due to bison being observed sporadically in very large groups (>50 bison) which created a large degree of between-transect variation in densities as well as other challenges in fitting detection functions (Figure 10). In addition, the number of lines surveyed for the Slave River study area (55) was lower than the number of lines surveyed for the Mackenzie study area (135; Boulanger 2014a).

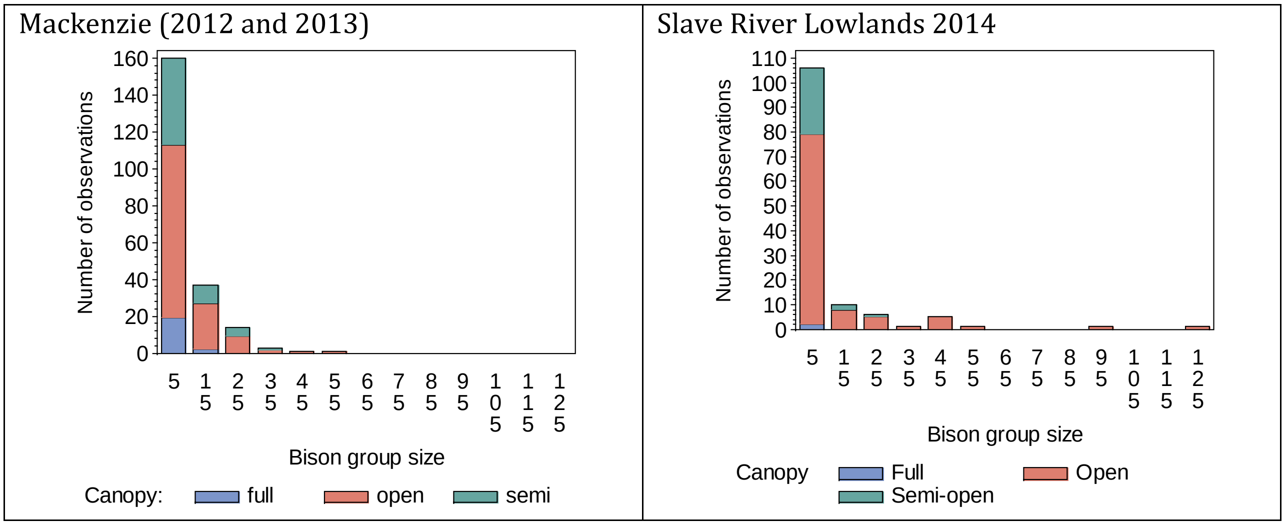


Figure 10: Distribution of group sizes for Mackenzie versus Slave River Lowlands bison surveys.

Power Analyses of Abundance Surveys

Power analyses were conducted for a design which involved annual surveys and a design which used *t*-tests to determine if there was a change in estimates between two surveys. The first approach would be most useful for a population that is at lower abundance and therefore required periodic monitoring. The second approach would be useful for initial years of a survey or for populations that were infrequently monitored.

The key question asked for both approaches is the number of years required to detect a change (for annual surveys) or the number of years in which change would be detected under assumed rates of change in the population. For both these approaches it is assumed that management would be interested in detecting a given annual rate of change. For example, for general monitoring a reduction of 10-20% annually may be the threshold for management actions. For monitoring of diseases, the threshold may be larger.

For annual surveys the power analysis formulas from Buckland et al. (2004) were used to estimate power under a range of survey precision levels (CV) and annual rates of change

($\lambda = N_{t+1}/N_t$). CV was assumed to be equal across different levels of abundance and therefore abundance was not explicitly simulated. The alpha level to detect a change was set at 0.2 and a power level of 0.8 was considered adequate for monitoring purposes. The underlying population trend was assumed to be log-linear. Two types of trend models were considered. The number of years to obtain adequate power, and the resulting cumulative change in the population was estimated for each combination of CV and λ. Analyses were conducted in R (R Development Core Team 2009) using base scripts developed by Len Thomas (Centre for Research into Ecological and Environmental Modeling and School of Mathematics and Statistics, University of St. Andrews, The Observatory, St. Andrews, Scotland). R package plot3d (Soetart 2014) was used to plot and summarize the power analysis data.

For the sequential *t*-tests, a simulation method was used which simulated estimates from surveys under varying levels of CV, survey interval, and annual rates of change between surveys. The proportion of surveys in which a change was detected was used to estimate power. The degrees of freedom for *t*-tests were based on the Mackenzie bison survey assuming similar designs for each year. The number of years to obtain adequate power, and the resulting cumulative change in the population was estimated for each combination of CV and λ. Analyses were conducted using SAS statistical software with graphical summaries of the data plotted in R.

Regression Analysis of Annual Surveys

The formulas of Buckland et al. (2004) mainly consider precision of the slope parameter in a regression equation with an underlying log-linear trend model. Two underlying error models were considered. First, a model that assumed fixed population sizes (no variation in lambda) was used for the primary analysis. This approach applies best to shorter-terms data sets. Second, a model that assumed an additional process variance component or random variation in lambda was used to assess how this additional source of variation affected power.

Power analysis suggested that at least three years of data is required to detect an annual decline of 20% (λ=0.80) if the coefficient of variation is 10% or below (Figure 11). With the general range of bison surveys (CV=20%) then at least four to five years of annual surveys would be required. For plausible CV levels (≥15%) then at least three years of data are needed to detect declines in bison populations.

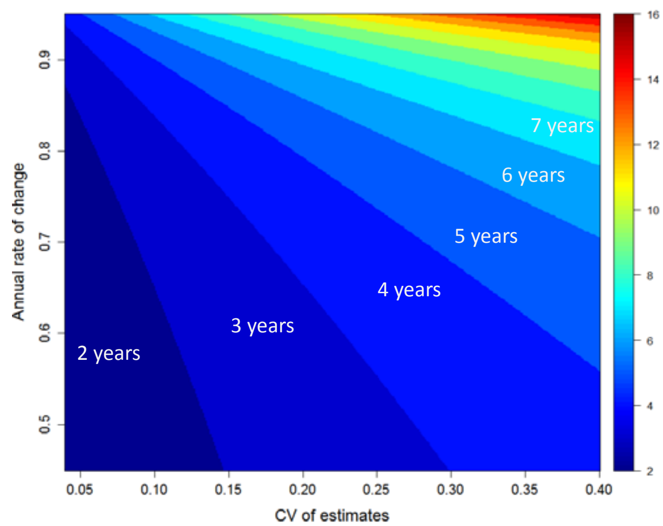


Figure 11: The number of years required to achieve adequate power to detect an annual rate of decline (λ) as a function of the CV of annual estimates of abundance.

These results can also be interpreted in terms of percent cumulative change in the population. In Figure 12, the percent change is represented by colour bands. From this it can be seen that CV levels of 0.15 are needed to detect small to moderate changes in abundance. Higher levels of CV require a longer time span of monitoring (>4 years) with resulting larger changes in population size.

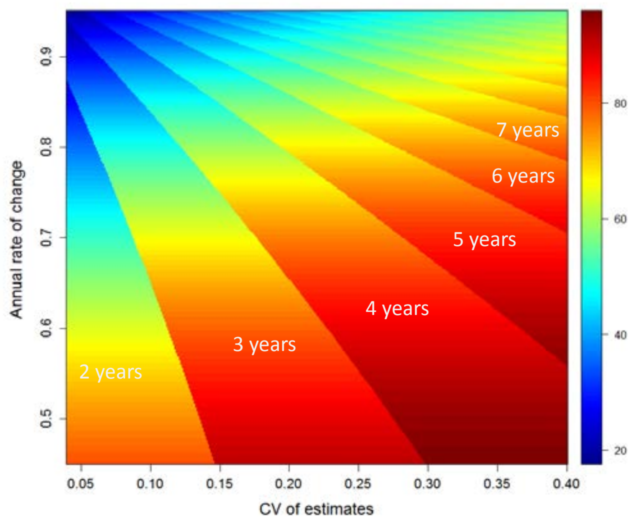


Figure 12: The cumulative percent decrease in population size that would occur when power=0.8 to detect a given trend, as also indicated in Figure 8. Cumulative decrease (i.e., 20% means the population is 20% lower than initial survey) is indicated by the colours and colour legend to the right of the graph. A small change of <30% is represented by blue, a moderate change of 30-50% is represent by light blue, a large change of 50-70% is represented by yellow, and very large change of >70% is represented by orange and red.

Using *t*-tests of Successive Surveys

Simulations of comparison of successive surveys using *t*-tests (Figure 13) suggested relatively similar results as the regression analysis (Figure 12). In general, power was similar as regression analyses for cases in which the interval between surveys was low. If surveys were imprecise (CV>40%) then power was reduced compared to regression approaches. For example, if CV=40% and the annual rate of decline was 0.8, then ten years would be required to detect a change in population size (Figure 13) whereas seven years would be required using the regression analysis approach (Figure 12).

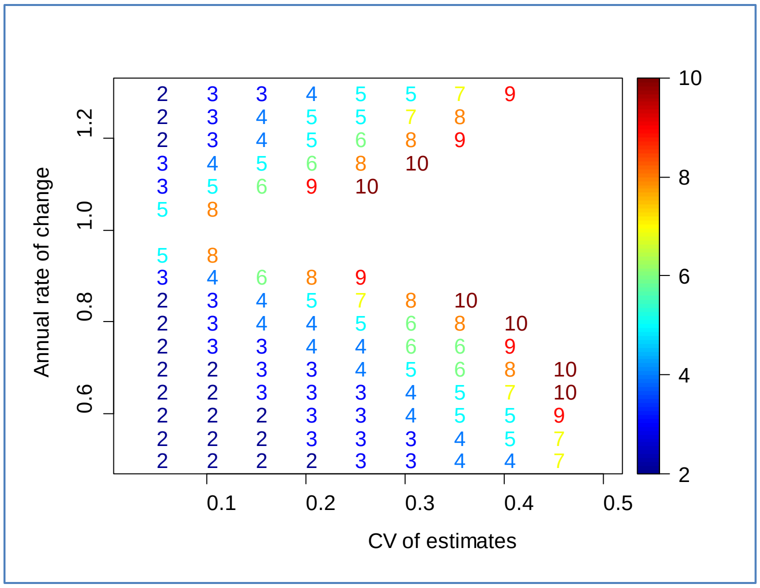


Figure 13: The number of years required to detect a change in abundance as a function of CV of estimates and annual rate of change. The numbers in the graph correspond to total years required to detect the change. Only years to detect change that are ten or less are displayed on the graph.

The proportional decrease in population size based on years to detect power suggested that CV of 0.15 would be needed to detect a 40% reduction in abundance. A CV of 0.20 then would be able to detect a 50% decline in abundance (Figure 14).

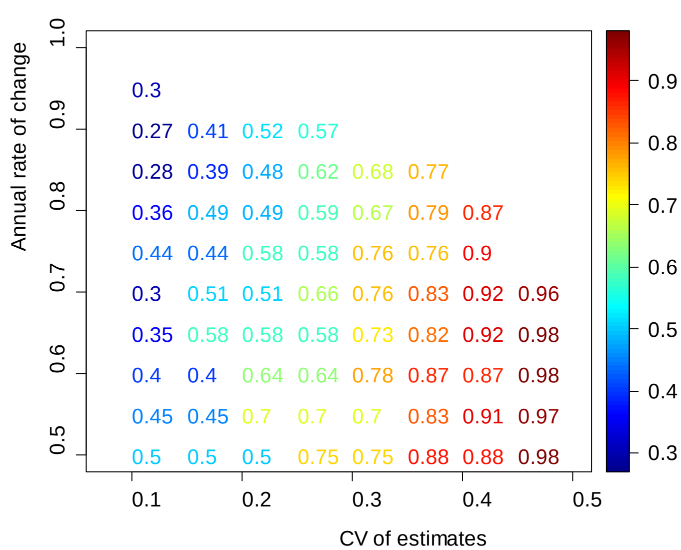


Figure 14: The proportional decrease in population size as a function of annual rate of change, CV of estimates, and corresponding years to detect the change (Figure 13).

For increasing populations, a CV of 0.15 would detect a 60% increase in abundance (Figure 15).

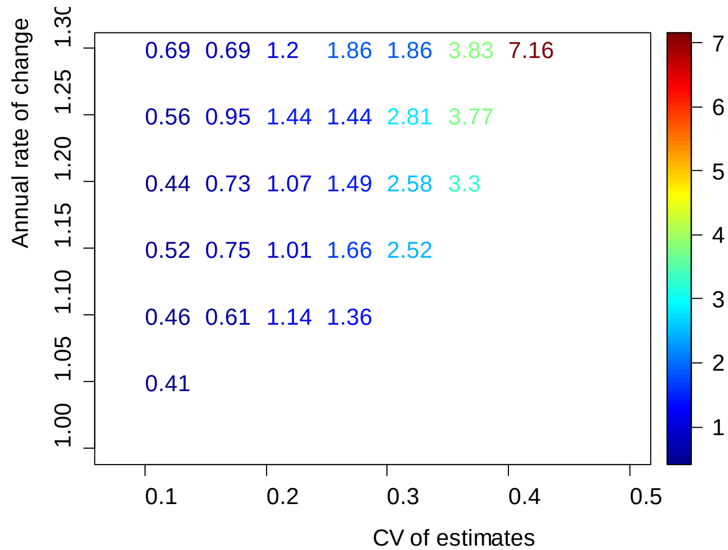


Figure 15: The proportional increase in population size as a function of annual rate of change, CV of estimates, and corresponding years to detect the change (Figure 13).

CV for bison surveys range from 16-40% (Figure 9) suggesting that large changes in abundance would occur before they are detected statistically. The optimal survey interval will therefore depend on what change would cause a management action and if the CV of surveys can be improved to allow higher power. We suggest that a target CV of 15% is optimal with a survey interval of three years. This would detect moderate (20% annual change) in abundances. The similarity in power between regression and sequential *t*-tests for shorter time intervals also suggests that the increase in power from annual surveys may not be worth the extra survey effort.

Power analyses also suggest that large-scale changes (40% reduction) in population size caused by disease outbreaks would be detected in short intervals. For example, the Mackenzie anthrax outbreak caused an annual rate of change of 0.46 (or a 54% reduction in population size) from 2012 to 2013. This change would be detected by annual surveys as long as CV were <0.20 (Figure 14).

We note that power analysis results suggest that just monitoring abundance may not provide enough feedback on population size and demography, and therefore a strategy that considers multiple sources of indicators should be considered as discussed in Integrated Population Model section of this report.

Recommendations to Increase Survey Power and Precision.

The main methodology used for recent surveys in the Mackenzie and Slave River Lowland herds has been distance sampling. This approach provides the best estimates of methods available if it can be assumed that sightability near the aircraft is one and field sampling is conducted properly. There are various ways this method can be enhanced to allow estimates of higher precision which are detailed below.

Design-based Improvements

Increasing Survey Effort

One method to increase survey precision is to simply fly more survey lines by decreasing the transect spacing and increasing kilometers flown. Buckland et al. (1993) provides formulas to determine the potential increase in precision by increasing the relative survey effort of total kilometers flown. The equation that is used considers the total kilometers flown in the current survey effort, the CV of density achieved, the mean and standard deviation of group size, and the total numbers of groups observed. From this it is possible to determine the approximate amount of effort required to increase precision.

Results from the Mackenzie 2012 and 2013 surveys indicate that if a target level of precision (CV) is 15% then survey effort would need to be 1.25 and 2.12 times greater for the 2012 and 2013 Mackenzie herd surveys (Figure 16). Effort would need to be 6.42 times greater for the Slave River Lowlands study which is clearly not possible within a single survey. Basically, the low precision of the Slave River survey which was partially caused by difficulty in fitting detection functions is difficult to overcome just by increasing survey effort. Therefore, the best strategy for the Slave River study is to improve field collection methods as well as consider analyses strategies to increase survey precision rather than increasing survey effort (discussed next).

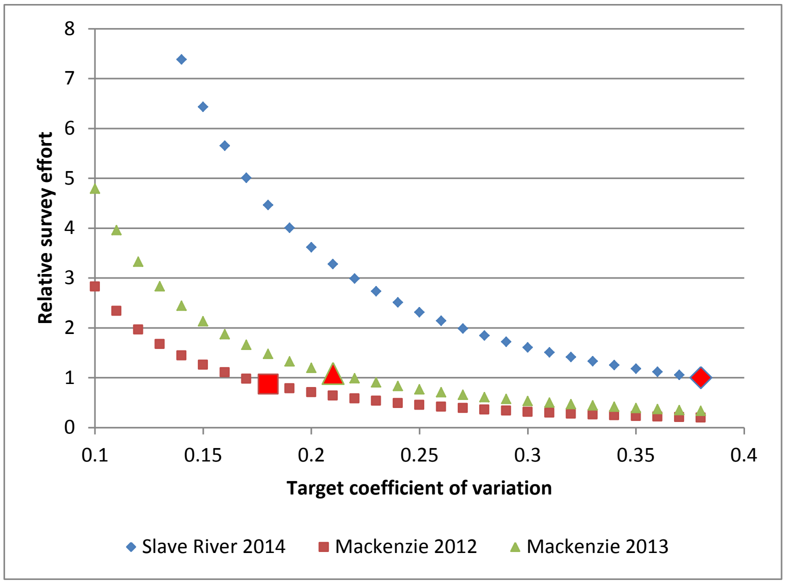


Figure 16: Estimated change in precision due to increasing relative survey effort. The CV achieved by each project is denoted by large red symbols. Power analysis suggests that a CV level of 0.15 is optimal.

Stratification and Post-stratification

Stratification can be used to increase survey precision by allocating more effort to stratum that have higher densities or have more variability in density. For the recent Mackenzie and Slave River surveys, all stratums received similar sampling effort regardless of density. Bison distribution is not uniform across the landscape, and traditional and local knowledge can help inform bison distribution regarding habitat selection, movement corridors, and centers of activity (Mitchell 2002). To determine potential gains due to stratification we used estimates from existing surveys to perform optimal allocation of survey effort. Optimal allocation estimates the best allocation of survey effort to maximize overall estimate precision. We then evaluated the relative increase or decrease in sampling effort for consistency across years and strata. We used allocation formulas based on density and standard error of estimates (Thompson 2012, Krebs 1998) from past aerial surveys.

Results suggested that effort could be reduced in the North stratum for the Mackenzie 2012 and 2013 surveys with allocation using density and standard error of the estimates (Table 4). However, there was less of a consistent result for East and West strata with higher and lower levels of effort suggested for each stratum and year combination. Therefore, it can be concluded that effort should not be changed for these strata given the degree of yearly variation in densities and distribution.

For the Slave River survey, an increase in effort was suggested for the East stratum compared to the West stratum given the higher densities and lower precision of the East estimates. This result was possibly due to the large degree of variation in cluster size for the East stratum.

Table 4: Results of allocation exercise on survey results. The estimates of abundance (N), Density, and CV for each survey, and strata area and number of transects surveyed is compared to that based upon allocation using abundance (N) and survey precision (SE). The percent difference for SE and number of transects (D) between allocation and actual transects surveyed is given.

Survey statistics							Allocation			
		Estimates			Sampling effort		Transects		% difference	
Strata	N	SE(N)	Density	CV	Area (km^2)	No. transects	SE	D	SE	D
Mackenzie 2012										
East	755	148.3	7.02	0.20	1,0763	83	78	66	94%	79%
North	116	43.7	2.89	0.38	4,012	75	39	46	52%	61%
West	659	179.3	11.73	0.27	5,623	66	94	109	142%	165%
Mackenzie 2013										
East	432	120.49	4.01	0.28	10,763	83	103	82	124%	99%
North	57	31.97	1.43	0.56	4,012	75	46	49	61%	65%
West	225	61.99	4.00	0.28	5,623	66	52	81	79%	123%
Slave River 2014										
East	715	351.9	22.99	0.49	3,112	42	55	46	132%	109%
West	368	130.3	11.82	0.35	2,290	41	23	36	56%	88%

Field-based Improvements

Distance sampling methods are potentially sensitive to deviations from survey protocol which can result in sighting distributions which are not easily described by detection functions and associated covariates. Therefore, proper training of observers and recorders as well as pilots of aircraft is essential to ensure reliable estimates. If this is done then a simpler detection model can be used (with less parameters) which will result in a more precise and robust estimate. Some of the main issues with previous surveys are now covered with recommendations for improvement.

Observer, Pilots, and Recorders Should Go Through a Distance Sampling Training Session before Survey

The level of precision for distance sampling is directly related to the complexity of models needed to fit detection functions to the data. Some factors such as canopy closure and bison group size are hard to control. Other factors, such as observer attentiveness to areas near to the plane can be optimized so that a simpler detection function model can be used which will result in higher estimate precision. A brief, possibly online tutorial should be given to familiarize the observers with the fundamentals of distance sampling and appropriate observation methods. This will ensure that additional/unnecessary variance is not introduced into the data set.

If data are recorded using tablet computers it would also be possible for results to be evaluated after each day of the survey. Even a plot of a basic histogram of detections can be used to diagnose potential issues and provide feedback to observers during the survey.

The Pilot and Recorder Should be Independent of the Observers

The pilot and navigator have different views than observers from the side of the airplane. Distance methods are mainly based upon an observer peering out from a perpendicular distance to the transect. Therefore, various forms of bias can be introduced if the pilot or navigator saw bison and influence the observers. One approach might be to use separate intercoms for observers and the pilot/navigator so that they do not influence the observers. Alternatively, the navigator/data recorder could simply not call out observations until the group has past. This would then allow collection of a double-observer data set that could be used to model detection probabilities close to the line (Borchers et al. 1998, Laake et al. 2008, Buckland et al. 2010, Boulanger et al. 2014). In general, pilots are less trained than other observers and will have a field of vision that is (or should be) influenced by the area in front of the plane. This does not correspond well to distance sampling. Therefore, it may make sense to not include the pilot and navigator/data recorder in the survey or record his observations separately.

Observations should be assigned to Only One Observer

Observations should be assigned to the primary observers that are situated on each side of the plane. If the bison groups are also seen by the pilot and observer then they can be assigned as a secondary observation. This ensures that differences in primary observers are modeled efficiently.

Observers Should Only Observe Bison from the Survey Line not While Way Pointing Groups

Observations for distance sampling should only occur from the sampling transect line. If groups are found during way pointing then biases, such as elongated tails of the distribution of sightings can occur. We suggest that observers be told to "take a break" during way pointing so that they do not look for bison further along the transect line.

Field Methods Should Ensure that Observations are Independent

Transect sampling could be conceptualized as taking a snapshot of each line in a similar way as quadrat sampling. Therefore, detection of bison or counting of bison on one line should not influence the counting or detection of bison on other lines. This can be challenging if open habitat is being surveyed and line spacing is closed together. As shown in the Slave River report (Boulanger 2014b), it is completely possible that a group of bison may be seen on two adjacent lines. This will not cause bias as long as the sighting on one line does not influence the sighting on the other line. Furthermore, recorders should always record observations even if the bison were seen previously. The best way to ensure independence is to survey every other line while flying away from the survey base and then survey the other lines on the way back to the survey base. This will reduce the chance that observers and recorders remember bison groups from adjacent lines.

Sightability Close to the Plane Should be Tested Especially for Closed Canopy Habitats

A fundamental assumption of distance methods is that sightability on the line is equal to one. If it is not close to one then estimates may be biased as well as less precise. We suggest that a plane capable of seating two observers on each side be used for a trial survey to estimate sightability on the survey line. This approach would use double observers to call out bison groups before the plane flies to waypoint the groups. An analysis would then be used to estimate sightability on the line as a function of habitat type and other factors.

If a larger proportion of habitat in the survey area is closed canopy, such as within the Nahanni herd range (Larter and Allaire 2013b), then it is possible that some bison will have very low or zero sighting probabilities due to forest cover. In this case double-observer methods may not accurately estimate detection probabilities since it is assumed that all bison have a non-zero probability of detection. The best method to estimate detection in this case is mark-resight or sightability models which use collared or marked bison (i.e., paintballs) to estimate proportion of bison not observed. Peters et al. (2014) used sightability models to estimate sighting probabilities of moose near the survey plane and then applied the sightability estimate to scale the distance sampling detection function. This approach does require a suitable sample of marked bison. We note that mark-resight methods with covariates (McClintock and White 2010) can be used to efficiently estimate detection rates of bison in forested habitats. Simulations can be used to assess sample sizes of bison needed to estimate detection rates.

Analysis Improvements

Use of Covariates to Describe Variation in Detection

Factors such as observer, weather conditions, vegetation cover, and snow cover can all affect sightability of bison. Noting of each factor for bison observations allows the testing and modeling of factors that influence sightability. As noted previously, data recorders should attempt to make sure that each factor is recorded consistently within each survey and between surveys so that this information can be used to its fullest extent in the analysis.

Meta-analyses of Data from Different Studies

One of the main limiting factors to distance sampling is obtaining large enough sample sizes to model detection functions, especially for areas where bison density is lower. One approach to confront this challenge is pooling data sets across surveys to increase sample sizes with resulting increases in precision. For example, the original Mackenzie density estimate from 2012 had a CV of 0.199 (Boulanger 2013) which was reduced to 0.167 when the 2013 survey data was added to the analysis (Boulanger 2014a). Combining data sets will not cause bias in estimates as long as the primary differences in sightability between surveys are accounted for in the analysis. Therefore the success of this approach will be determined by how well survey methods are standardized and how well factors that influence sightability are recorded during surveys.

We note that the meta-analysis modeling methodology explicitly tests for differences in sightability between surveys as part of the modeling process. For example, the fit of models that assume unique detection function shapes for each project is compared to a model with pooled detection functions and covariate models. Therefore, this method can account for differences between surveys (i.e., a survey area with more open habitat) while helping confront issues with low sample sizes from individual projects.

Density Surface Modeling

Density surface modeling (Miller et al. 2013) can increase estimate precision as well as explain observed patterns of distribution within the study area. A density surface model attempts to explain variation in density of bison observed with habitat and other spatial covariates obtained by GIS analysis of the data set. By using this approach it is possible to account for or explain variation in distribution within the study area, therefore decreasing variance compared to non-spatial analyses that assume constant density within the study area. In addition, density surface model maps, which show estimates of density within the study area, can identify areas of high use and habitat value which can be useful for delineation of conservation areas.

One initial question was whether bison distribution was associated with forest cover classes in bison study areas. To initially test this assumption the Government of the Northwest Territories (GNWT) categorized the habitat class that bison were observed in during aerial transect for the Slave River study and also estimated the area of each habitat class within the Slave River study area. The proportion of observations and the proportion of bison counted in each habitat class were then compared to the proportional area of each class. If bison were occurring randomly or with no selection it would be expected that these proportions would be similar. If not then it is likely that bison were selecting for or against habitat classes. These distributions shifts could be described with density surface modeling.

Graphical analysis suggested that larger proportions of bison groups or individual bison were higher in shrub and lower for white spruce and pine compared to proportional area for the East stratum. For the West stratum, counts of individual bison and bison groups were higher in deciduous and lower for white spruce compared to proportion of area (Figure 17). Without a statistical analysis it is hard to determine the significance of these proportions. However, these preliminary results support the application of a density surface model to better explain variation in distribution and potentially reduce the variance of overall density estimates.

Comparable data on habitat selection can be obtained from local knowledge. In the Greater WBNP Ecosystem community members indicated that bison rapidly establish trails along the most direct and practical route between favoured habitat patches, prefer graminoid meadows, have an affinity for burned areas, and typically avoid muskeg, dense forest, and steep terrain (Mitchell 2002). The edges of large meadows are used in summer because the center is often too wet for travel, but the wet centers of meadows are used in the winter when the ground is frozen. Movements through poor habitat are generally conducted rapidly as the animals search for favourable habitat.

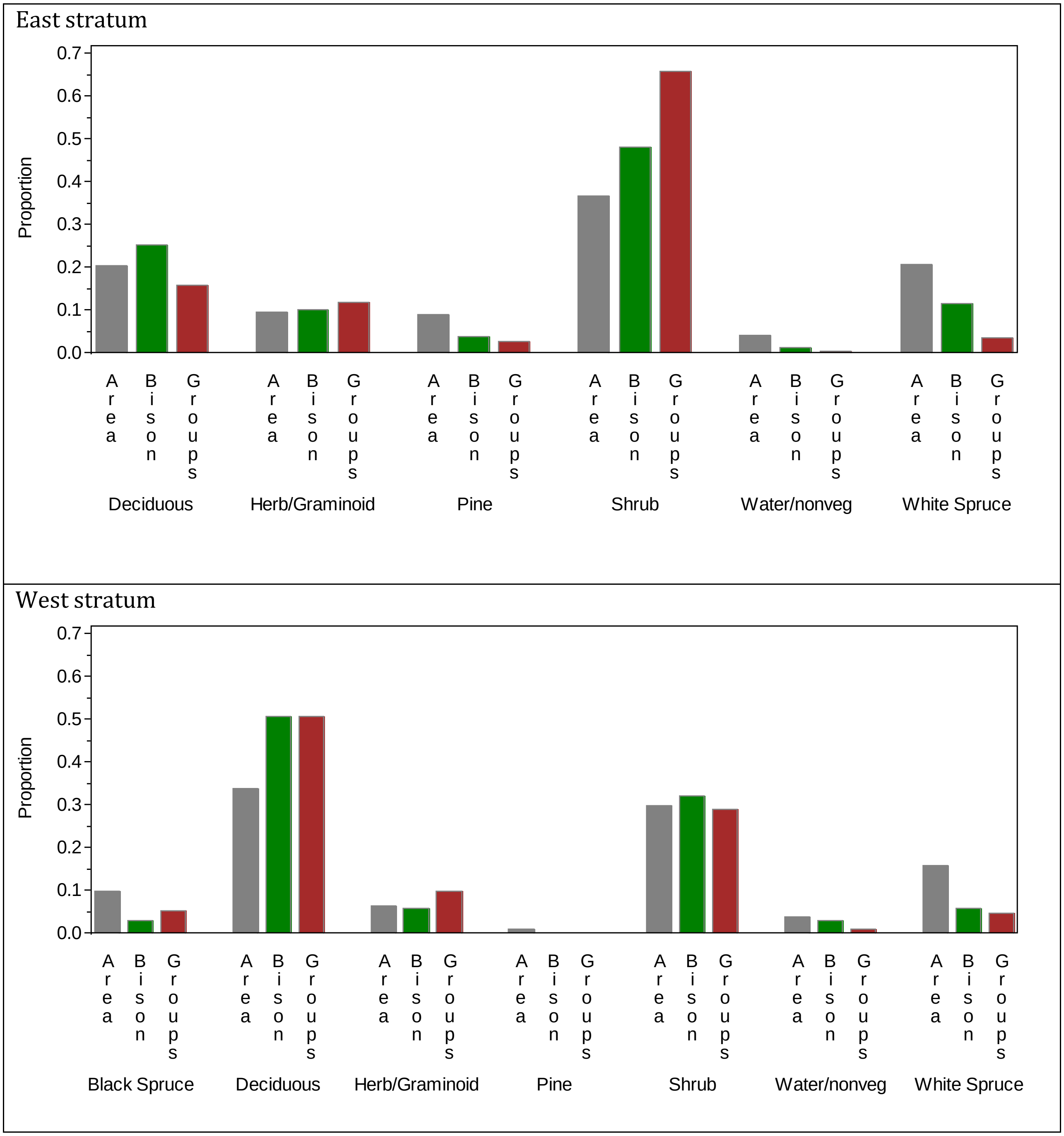


Figure 17: A comparison of the proportion bison groups (Groups) or bison counted (Bison) occurring in each habitat class compared to the proportion of area (Area*)* in each habitat class in the East and West stratum of the Slave River Lowlands 2014 study area.

SUMMARY

This report provides a set of options for monitoring of bison populations in NWT. We also provide a summary of recommendations in Table 5.

One of our main conclusions is that management should be based on use of all population indictors. If there are estimates of population size, survival estimates, and recruitment rates then it is possible to fit multiple-data source models to further model demography and population trends (Buckland et al. 2004, Johnson et al. 2010, Boulanger et al. 2011) as demonstrated in Integrated Population Model. These approaches do not require annual surveys or annual measurements from any of the demographic indicators. They can accommodate sample biases with indicators, such as the effects of differential survival of calves and cows on calf:cow ratios, and can also incorporate harvest data (Boulanger et al. 2011). This approach utilizes all the data sources in a unified analysis therefore maximizing inference when compared to stand-alone interpretation of single data sources. This approach is most powerful if temporal covariates that relate to demography can be collected and used to describe temporal variation in model parameters.

A variety of methods are available to estimate abundance and density of bison. Of these, distance sampling is most advantageous because it does not involve marking individual bison but still allows an estimate of detection probability needed to ensure robust estimates. It also allows further modeling of density within the survey area using density surface modeling. The main challenge for distance sampling is collection of field data that meets distance sampling assumptions as well as confronting variation in density due to aggregation of bison into larger groups. We provide a set of recommendations to improve field collection methods including the use of double-observer methods on a trial basis to test whether sightability near the plane is equal to one in closed cover habitats. We suggest

that density surface modeling may be one approach to reduce lowered estimate precision due to uneven density of bison in sampling areas.

Hauser et al. (2006) suggested that annual surveys of abundance are only needed if the results of the survey will directly affect management actions or if populations are near critical status thresholds, and they recommended the use of population models as a secondary means to evaluate status. Power analyses suggest that annual abundance surveys are unlikely to detect year-to-year changes in population size. Anthrax outbreaks (detected by summer surveillance flights) will trigger the need for more intensive monitoring, but otherwise herd abundance should not change dramatically year to year (one exception may be starvation due to severe winter/spring weather). Given likely rates of change and levels of survey precision, we suggest that a three year sampling interval be used for surveys. Intervals for abundance surveys could vary with population size; less often at higher numbers, more often at lower numbers (similar principle to monitoring for the Bathurst caribou herd; Bathurst Caribou Management Planning Committee 2004). As noted above, composition surveys, surveillance flights to detect anthrax outbreaks, and multiple-data source models can be used to infer likely population status in years between abundance surveys. Exceptions to this pattern would occur if population size is low which would suggest that population viability could be impacted by stochastic events or adversely affected by typical mortality sources.

Composition surveys are useful indicators but they require suitable sampling design to ensure a random or representative sample of herd structure. Results from bootstrap resampling of composition data suggests that at least 30 groups should be sampled to obtain adequate precision of composition survey data. It is also suggested that the composition data be combined with other data in an integrated population model which should allow better inference on actual trends in demography.

Table 5: A summary of recommendations based on objective listed in the RFP document (Literature review B). *Hyperlinks* to applicable sections in the report can be followed by pressing the control button while selecting each link.

Objective	Recommended Methodology
Detect changes in population size	Aerial transect distance sampling methods. Supplement distance sampling with sightability models or mark resight methods if canopy closure obscures a high proportion of bison. Analyze trend with regression methods, or t-tests of successive surveys. Survey interval of three years if survey precision can be improved to a CV of 15%. Infer trend between abundance surveys using an integrated population model with covariates.
Estimate age and sex-specific survival and productivity	Composition surveys with estimates of precision to estimate productivity, age class and adult bison survival through an integrated population model. Composition surveys need to sample at least 30 groups to ensure adequate precision of estimates. Estimates of productivity could be enhanced by composition surveys after the peak of calving (most likely in late June) to assess proportion of calves produced each year for the integrated population model.
Monitor movements, range, and habitat selection	Density surface modelling from transect surveys using habitat covariates. Resource selection function or occupancy modelling for broad scale shifts in distribution.
Detect mortality events especially anthrax outbreaks	Power analyses suggest that large changes in population size can be detected within the recommended three year survey interval. Covariates such as weather may help predict likely conditions for disease outbreaks. The integrated population model estimates calf and yearling survival from composition surveys therefore detecting potential decreases in calf or yearling survival if surveys are conducted annually.
Estimate probabilities of detection on aerial surveys	Aerial transect distance sampling methods estimates detection probabilities, encounter rates, and group sizes. Supplement with sightability models or mark resight methods if canopy closure obscures a high proportion of bison. A simulation study could be used to estimate survey effort needed to ensure detection of individuals in surveillance areas.

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APPENDIX A. TRADITIONAL KNOWLEDGE SOURCES ACCESSED FOR NORTHERN BISON REVIEW

Note: Annotated bison traditional knowledge literature review list available from authors.

In addition to those sites listed below the Yellowknife Public Library and the ENR-ITI Shared Library were visited.	
The Arctic Institute of North America, The Arctic Science and Technology Information System (ASTIS) database (www.aina.ucalgary.ca/astis/)	1
Anthropological Papers of the American Museum of Natural History (http://digitallibrary.amnh.org/dspace/handle/2246/6)	2
AUSPACE Athabasca university (http://auspace.athabascau.ca/handle/2149/1528)	3
Elder Interviews Golder Associates 2008 (www.total-ep-canada.com/upstream/documents/Additional_Information/AIR_July2010/Appendix_A_Wood_Buffalo.pdf)	4
Wood Buffalo National Park Management Plan 2010 (www.pc.gc.ca/eng/pn-np/nt/woodbuffalo/plan/plan1.aspx)	5
Aurora Research Institutes NWT Research Database (http://nwtresearch.com/licensing-research/nwt-research-database)	6
Yellowknife Public Library (all NWT libraries) (www.yellowknife.ca/en/living-here/public-library.asp)	7
The Canadian Association of Geographers (www.cag-acg.ca/files/pdf/agm/2012_AGM_program.pdf)	8
GNWT Department of Environment and Natural Resources (www.enr.gov.nt.ca; www.env.gov.yk.ca/publications-maps/plansreports.php; http://www.enr.gov.nt.ca/sites/enr/files/reports/bison_movements_distribution.pdf)	9
Bison Producers of Alberta resource library (www.bisoncentre.com)	10
Athabasca Cree First Nations (www.acfn.com)	11
University of Ottawa (www.uottawa.ca/ie/English/Research/IE-bison%20summary_e.pdf)	12
www.wildlifecollisions.ca/woodbisonresources.htm	13
Mountain Forum (www.mtnforum.org/sites/default/files/publication/files/1418.pdf)	14
ENR-ITI Shared Services Library (http://g92011.eos-intl.net/G92011/OPAC/Index.aspx)	15

APPENDIX B: COMPOSITION ESTIMATES WITH CONFIDENCE LIMITS

Composition estimates with standard error (SE) and confidence limits (low, high) from bootstrap resampling. The number of groups sampled each year (n) is given also.

Year	n	Calf:cow				Yearling:cow				Bull:cow			
		CC	SE	low	high	YC	SE	low	high	BC	SE	low	high
Mackenzie herd													
1999	31	0.43	0.07	0.33	0.60	0.31	0.03	0.25	0.38	0.94	0.33	0.67	1.74
2000	34	0.29	0.04	0.21	0.38	0.18	0.03	0.13	0.26	0.75	0.14	0.60	1.15
2001	27	0.37	0.03	0.32	0.42	0.22	0.02	0.17	0.26	0.75	0.17	0.51	1.19
2002	26	0.19	0.04	0.15	0.28	0.17	0.03	0.10	0.21	0.91	0.35	0.56	1.88
2003	28	0.42	0.05	0.31	0.51	0.08	0.02	0.05	0.12	0.89	0.28	0.65	1.72
2004	19	0.39	0.04	0.34	0.51	0.13	0.04	0.05	0.22	0.63	0.15	0.48	1.00
2006	28	0.37	0.08	0.24	0.56	0.17	0.02	0.13	0.22	0.78	0.15	0.54	1.10
2007	36	0.48	0.03	0.41	0.55	0.16	0.02	0.13	0.22	0.92	0.33	0.60	1.80
2008	17	0.33	0.10	0.21	0.58	0.26	0.06	0.15	0.37	1.21	0.62	0.73	2.37
2009	34	0.41	0.06	0.29	0.54	0.25	0.02	0.20	0.29	0.97	0.30	0.63	1.89
2011	12	0.38	0.05	0.28	0.48	0.28	0.04	0.21	0.37	0.88	0.27	0.50	1.58
2013	8	0.11	0.07	0.00	0.18	0.09	0.07	0.05	0.33	0.87	0.17	0.40	1.16
2014	8	0.62	0.15	0.25	0.80	0.00	0.00	0.00	0.00	1.54	1.01	0.46	5.00
Nahanni													
1999	6	0.25	0.12	0.00	0.43	0.11	0.06	0.02	0.24	0.64	0.36	0.49	1.44
2002	13	0.14	0.18	0.00	1.00	0.14	0.07	0.00	0.24	1.14	0.90	0.65	3.29
2003	16	0.56	0.04	0.50	0.68	0.10	0.05	0.00	0.21	0.82	0.30	0.56	1.69
2004	13	0.42	0.06	0.29	0.50	0.31	0.06	0.14	0.39	0.76	0.71	0.56	2.07
2005	21	0.28	0.06	0.13	0.38	0.26	0.07	0.11	0.38	1.02	0.42	0.67	1.85
2006	24	0.47	0.08	0.24	0.58	0.25	0.06	0.11	0.34	1.21	1.17	0.81	3.00
2007	20	0.41	0.10	0.27	0.67	0.20	0.05	0.13	0.31	0.95	0.12	0.73	1.24
2008	24	0.39	0.05	0.27	0.48	0.28	0.07	0.12	0.39	0.84	0.21	0.60	1.31
2009	19	0.43	0.10	0.23	0.65	0.27	0.05	0.15	0.35	0.86	0.54	0.68	1.60
2010	23	0.36	0.04	0.26	0.44	0.29	0.03	0.22	0.35	1.09	0.58	0.78	2.54
2011	29	0.42	0.08	0.28	0.61	0.18	0.06	0.04	0.25	0.65	0.18	0.52	1.12
Slave River Lowlands													
1999	18	0.15	0.09	0.00	0.21	0.19	0.07	0.00	0.21	3.74	12.84	1.54	49.00
2000	8	0.37	0.11	0.00	0.38	0.15	0.05	0.00	0.17	0.52	5.52	0.40	24.00
2002	7	0.41	0.17	0.25	0.91	0.18	0.06	0.00	0.23	0.63	3.49	0.33	4.00
2003	15	0.54	0.07	0.38	0.64	0.31	0.06	0.24	0.46	0.99	2.94	0.54	3.88
2004	15	0.64	0.09	0.42	0.76	0.28	0.07	0.16	0.41	0.66	0.20	0.46	1.29
2008	23	0.30	0.03	0.23	0.36	0.11	0.03	0.06	0.16	0.62	0.09	0.47	0.82
2009	32	0.31	0.06	0.18	0.43	0.21	0.06	0.09	0.32	0.86	0.40	0.43	1.95

Year	n	Calf:cow				Yearling:cow				Bull:cow			
		CC	SE	low	high	YC	SE	low	high	BC	SE	low	high
2011	14	0.28	0.04	0.25	0.39	0.11	0.06	0.06	0.25	0.98	0.69	0.77	2.72
2014	13	0.27	0.05	0.19	0.36	0.12	0.02	0.07	0.15	1.49	0.91	0.86	3.83