Government of
Northwest Territories
Gouvernement des
Territoires du Nord-Ouest

Review of Bison Monitoring Program for the Northwest Territories

John Boulanger[1], Kim Poole[2] and Craig DeMars[3]

[1]Integrated Ecological Research, Nelson, BC
[2]Aurora Wildlife Research, Nelson, BC
[3]Kimberley, BC

2021

Manuscript Report No. 290

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 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. Included in this review is a discussion of 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 abundance should not change dramatically year to year. We propose various improvements for field-based methodologies as well as estimation methods to optimize survey design for monitoring bison populations.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

PART A: APPROACHES FOR MONITORING UNGULATE POPULATIONS: GENERAL LITERATURE REVIEW

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, 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) and are listed as Threatened under the NWT *Species at Risk Act*. The first goal of the *Recovery Strategy for Wood Bison (*Bison bison athabascae*) in the Northwest Territories* 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 (Conference of Management Authorities 2019). 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) primarily aimed at understanding population changes in harvestable species (Moller et al. 2004). As bison have played a central role in Dené culture, and 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 census of all individuals is 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 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 elaphus*; 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). First Nations consider population surveys and monitoring 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

As management actions typically vary relative to estimated population size, effective wildlife management requires reliable estimates. 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 are not independent (Boulanger et al. 2004).

In this section, we review potential methods for estimating population size in ungulates (see also 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 number of marked and unmarked animals is 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 ($\hat{N}$=1,151; 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 ($\hat{N}$=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 <1 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 0), 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. 2004a). 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 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 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 alces*; Peters et al. 2014), Dall's sheep (*Ovis dalli*; Schmidt and Rattenbury 2013), mule deer (Koenen et al. 2002), and blue duiker (*Cephalophus 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 hodgsoni*; 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 Part C 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, Kissel 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 at small spatial scales (Bernatas and Nelson 2004, Carr et al. 2012) and the utility of thermal imaging surveys for estimating population size over wide geographic areas has not been 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 Grevy's zebra (*Equus greyvi*). 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).
Capture-Mark-Recapture (CMR)	Animals are captured, marked and recaptured over multiple sessions to estimate detection probabilities.	Extensive literature support and a wide variety of models are available. Spatially explicit methods (SECR) can	Requires marking of individual animals Necessity of multiple recapture sessions may lead to high relative cost.

Method	**Framework**	**Advantages**	**Disadvantages**
		estimate density.	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 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.

Method	Framework	Advantages	Disadvantages
Remote Camera Trapping	An array or grid of cameras is 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 an increasing population 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. 2004a) 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 of 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 and 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 indicator 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 (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 Data Sources.

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 fecal 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 annually monitored 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-focussed studies (1-2 fixes/day) and will last four to five years (e.g. GlobalStar collars – Vectronics 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 multi-year mark-recapture data are available, immigration and emigration rates can be estimated using robust design models (Pollock 1990).

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 Dené have established zones within which heightened environmental management and monitoring occurs, including community and science-based First Nations 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 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 modelled 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 subregions 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 Section C.

We note that density surface modeling is similar to RSF modeling discussed in RSF 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 spatially explicit capture-recapture (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	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	Requires multiple visits to sites to estimate detection probabilities Estimate is sensitive to size of sample sites and low rates of encounter.

Model	Framework	Advantages	Disadvantages
		detection and occupancy.	
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.
Density surface modeling 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 modeling 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, 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 actions 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 prespecified 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 differences 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.

PART B: 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. 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 stratified random block 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 surveys with 4 strata for strip transect estimates	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	Jul 2011	Aerial mark-resight; 3 resight flights	N/A	~0.07	Yes (paint-ball)		Jung and Egli 2012; Hegel et al.

Jurisdiction	Area; Subspecies	Month Year	Population estimate	Coverage	CV	Sight. Corr.	Composition/ Demography	Reference
								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 2013*b*
	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 and photograph and obtain a count. Coefficient of Variation in all surveys was relatively high (0.25–0.38). The estimate in the 2014 Slave River Lowlands (1,083) was only 7% 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 1, 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 are 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, GNWT 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, GNWT ENR, pers. comm.); 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 2–3 yrs), B2 (subadults: 4–6 yrs), B3 (prime, adult males: 7–12 yrs), and rarely B4 (old bulls ≥10 yrs, with noticeable wear on the horns) (Larter and Allaire 2007; T. Armstrong, pers. comm.). 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 appears 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 (Base Life History 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.

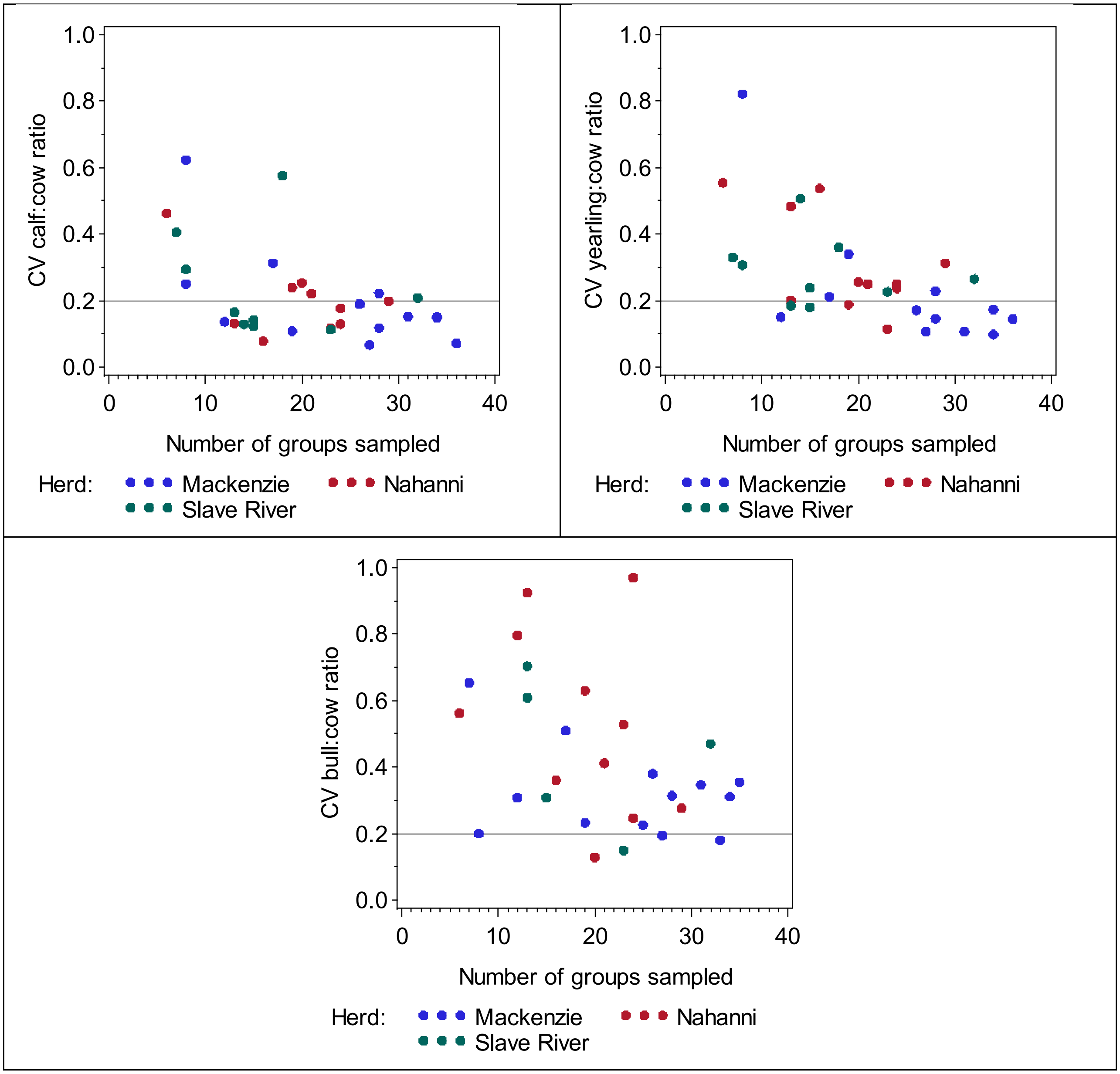

Figure 1. The coefficient of variation (CV) of composition survey estimates as a function of the number of groups sampled for each yearly survey for the three primary NWT survey areas where composition data have been collected.

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. 2008). 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 in Alberta 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). However, no bison from the Ronald Lake herd, found south of WBNP, have tested positive for brucellosis or tuberculosis (Ball et al. 2016). 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 septicaemia 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 Lowlands 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 transect surveys flown twice each year, in February and March (Figure 3). Up to 2020 15 bison have been removed from the Bison Control Area (Species at Risk 2010).

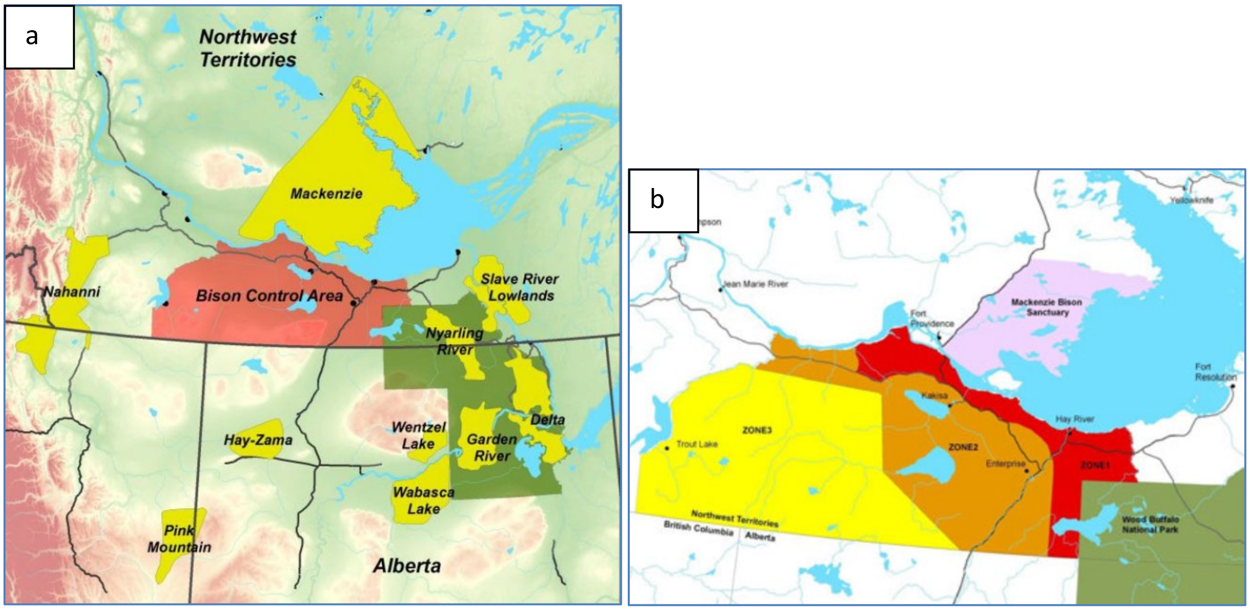

Figure 2. Bison Control Area (Figure 2a) and the three zones (Figure 2b) within the NWT, (Bidwell et al. 2009).

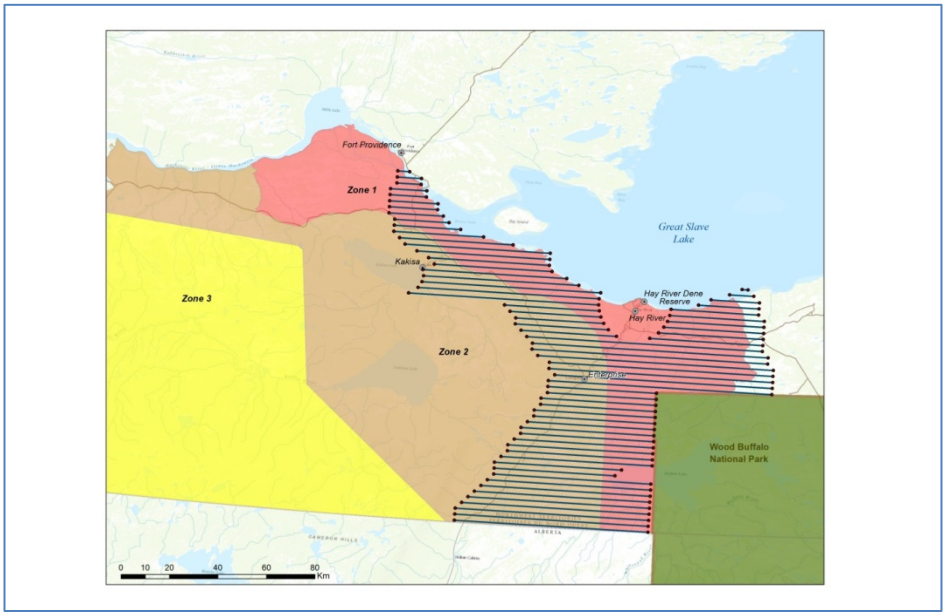

Figure 3. Survey of BCA flown twice per year.

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 restricted to areas of previous outbreaks. Surveillance flights are generally conducted by small fixed-wing aircraft at an altitude of 240-360 m above ground level 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 explore the use of an integrated population model that utilizes data from population surveys and composition surveys to model bison demography in this herd. The main objectives of this exercise were:

- Determine if a population model would work reliably with bison data given the absence of collar-based adult survival estimates;
- Use the population model to explore key strengths and weaknesses of current bison data with resulting recommendations for future field efforts;
- Demonstrate how environmental data might be investigated to examine potential relationships between demographic parameters and environmental covariates;
- Contrast a simpler spreadsheet-based demographic model approach with a Bayesian state space modeling approach.

Data Sources

Demographic Data

The main information about herd status for the Mackenzie comes from sporadic abundance surveys and composition surveys that are conducted annually or bi-annually (T. Armstrong, GNWT ENR, unpublished data). 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 indicating lower values (e.g. 2002 and 2013 for calf:cow ratios). 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.

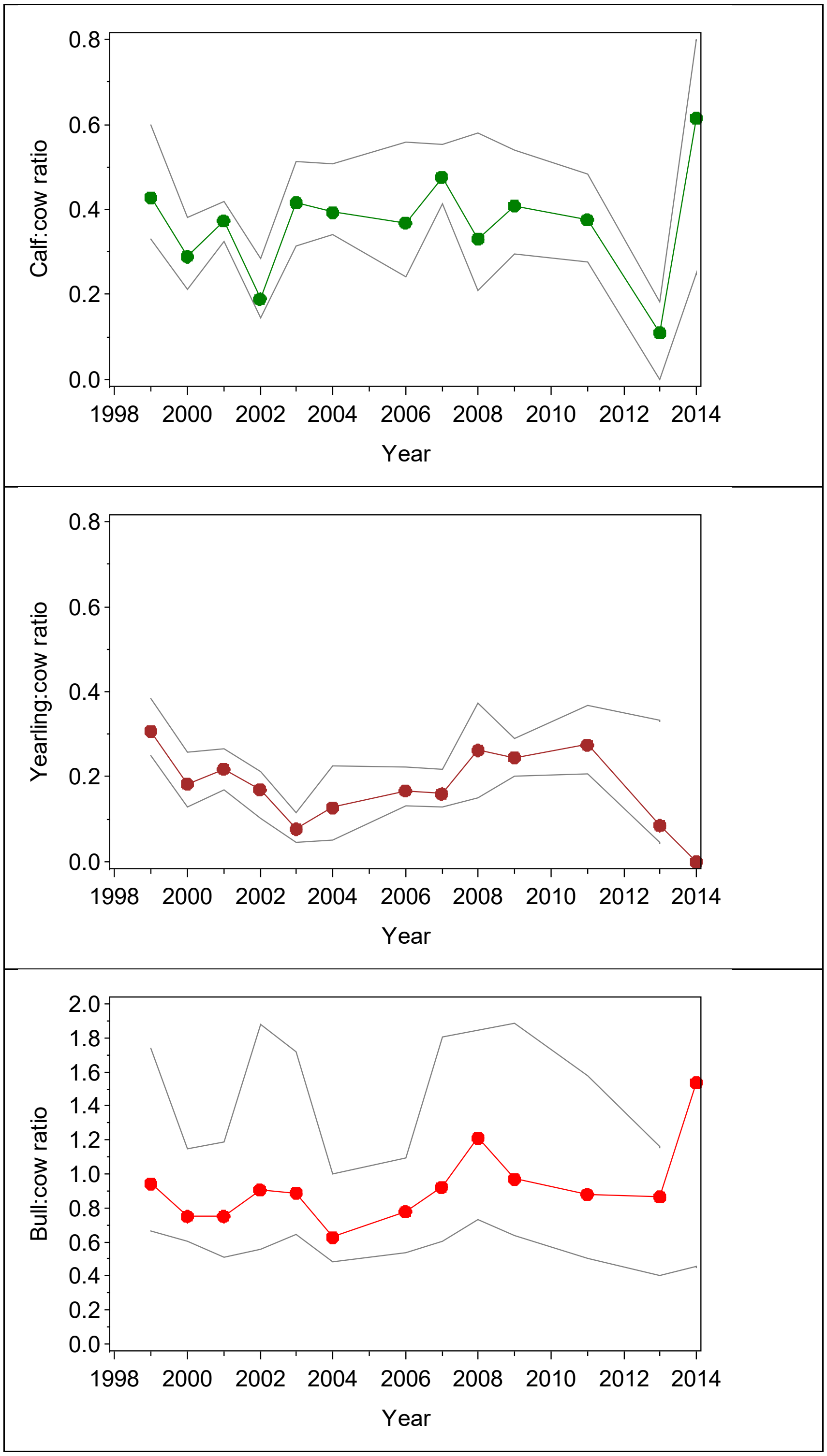

Figure 4. Estimates from composition data for the Mackenzie bison herd with confidence limits estimated using bootstrap percentile methods. Note the different scale on the bull:cow ratio graph. No confidence limits were possible for 2014 for yearlings since none were observed. The upper confidence limits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

Environmental Data

Environmental parameters were derived from Government of the NWT water management stations (snow water equivalent (SWE) for Little Buffalo Tower and Kakisa River; www.enr.gov.nt.ca/programs/water-management/snow-survey-monitoring-network), and from Environment Canada data from the Hay River airport (total snowfall, total rainfall, mean Dec-Mar (winter) temperature, and mean Jun-Jul (summer) temperature; http://climate.weather.gc.ca/). From these data we calculated winter severity index (WSI; calculated after Baccante and Woods 2008, which factors mean monthly temperature with total monthly snowfall), length of winter, and date of last snow >10 cm. Monthly or daily data were used as appropriate. We also examined as a covariate the Pacific Decadal Oscillation (PDO; http://jisao.washington.edu/pdo/PDO.latest). Annual data were summarized from May-April to align with bison year modeling (starting 15 May).

Base Life History Model

The life history 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 third 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 adult females that produced a calf each year was the product of female 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.

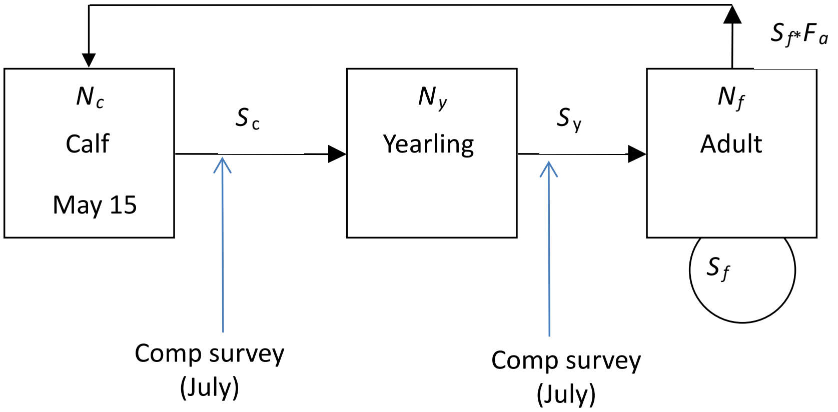

Figure 5. The female life history model used for the bison integrated population model. Male life history was similar (as parameterized by N_m and S_m for adult males) but without the reproductive loop.

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.

The basic process in which an integrated population model works is to estimate each of the demographic parameters so that they best corresponds to each of the field indicators. Intuitively, this could be thought of as subjectively varying each parameter in the model (survival, abundance, fecundity) so that the resulting calf-cow ratios, yearling-cow ratios, and abundance estimates from the model correspond to the field indicators. The actual process of fitting the model is accomplished using statistical programs that efficiently fit the model and provide indicators of how well the model fits the data.

Modeling Strategies

Strength of Field Indicators Guides Modeling Strategies

Inspection of Figure 5 also reveals the main aspects of demography that are directly informed by the field data. Given that birth occurs in May, the calf:cow ratios will indicate variation in yearly fecundity and calf survival from May to July when the composition surveys occur. Yearling:cow ratios will indicate calf survival from the composition survey (July) until the following May when calves become yearlings. After May, yearling:cow ratios will indicate yearling survival up to the July composition survey (i.e., survival from 12-14 months of age). The abundance surveys in March mainly indicate overall trend in herd size including adult survival. However, given that herd size is affected by all cohorts, the link between adult survival and herd size is indirect. Bull:cow ratios will mainly indicate bull survival given that there are no other indicators of bull population size.

Given limitations in field data, model analyses mainly focused on variation in calf survival (Table 4). Variation in adult survival was difficult to assess given that it is only indirectly indicated by field indicators. Variation in yearling survival is mainly indicated by the two month interval between calving (at which time calves of the previous year become yearlings) and the time composition surveys occur. We note that estimation of fecundity is partially confounded with calf survival. For example, a low calf:cow ratio in a given year could be due to low calf survival or low fecundity. The main method the model uses to determine this confounding effect is by considering the yearling:cow ratio in the following year. For example, a scenario in which the calf:cow ratio is lower (0.30) in a given year but the yearling:cow ratio in the next year is similar (0.25) would indicate higher calf survival but lower fecundity. However, this method has the inherent assumption that the calf survival rate is constant across a given year and it also relies on sequential calf:cow and yearling:cow estimates.

Table 4. Summary of demographic parameters for the integrated population model with corresponding strength of estimate based upon related field indicators. Note that the integrated population model uses all the data to estimate each parameter.

Parameter	**Symbol**	**Ages**	**Strength of estimate**	**Primary field indicator(s)**
Adult female survival	S_f	>2	weak	Herd size
Adult male survival	S_m	>2	Very weak	Bull:cow ratio
Fecundity	F_a	>2	weak (confounded with S_c)	Calf:cow ratio
Yearling survival	S_y	1-2	weak	Yearling:cow ratio
Calf survival	S_c	0-1	strong	Yearling:cow ratio and
				Calf:cow ratio

Ranges of Data Considered

We only considered abundance data up to 2012 with the exclusion of the 2013 data that were affected by an 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.

Modeling Approaches Used

Two modeling approaches were used with the bison data. First, a simpler ordinary least squares (OLS) based method (White and Lubow 2002, Boulanger et al. 2011) was used to provide a base assessment of parameter values as well as determine initial feasibility of a modeling approach. This approach can be implemented on a spreadsheet making it useful for management based exercises. However, in its current form it does not provide standard error estimates of model parameters. Second, a Bayesian state-space model (Buckland et al. 2004b, Kery and Schaub 2012) was used for further investigation of temporal variation in parameters and relationships between environmental covariates and parameters. This approach provides a more in-depth method for modeling sampling variation as well as better estimates of parameter precision.

OLS model

The OLS method uses a relatively simple method to assess model fit. 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 $\mathrm{SE}(\hat{\theta})$). 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 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 0-1 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.

Initial analysis revealed that it was not possible for the model to produce reasonable estimates of both yearling survival and adult survival without constraining yearling survival to equal adult survival or calf survival. The reason for this was that there was minimal information to separate adult from yearling survival given the limited field data on either parameter. Moreover, there is little to no information on estimates of yearling survival in the literature (Brodie 2008). The most biologically reasonable constraint was to make yearling equal adult survival and therefore this constraint was applied for model runs.

Model fitting was focused on determining the most parsimonious model to explain variation in productivity (S_c and F_a) given that this was the main data source for the model (from composition surveys). Models with cubic terms for productivity (Table 5: model 5), cubic terms for calf survival (model 1) and combinations of both parameterizations (model 2) were compared to a base model with no trends (model 6). Of these, a model with cubic trends in calf survival was most supported (model 1). A model with trends in adult female survival (model 3) was not supported compared to a model with constant adult female survival.

Table 5. OLS model selection for Mackenzie bison data. Sample-size adjusted Akaike Information Criteria (AIC$_c$), difference in AIC$_c$ between most supported and given model (ΔAIC$_c$), Akaike weight (w_i), the number of parameters (K), and sum of penalties (ΣPen) are displayed. Effective sample size (the number of model and field estimate comparisons used to estimate ΣPen) was 54 for all models.

No	Model	AIC$_c$	ΔAIC$_c$	w$_i$	K	ΣPen
1	$S_f=S_y$, S_m F_a S_c S_c^2 S_c^3	187.50	0.00	0.94	9	165.41
2	$S_f=S_y$, S_m S_c S_c^2 F_a F_a^2	190.77	3.27	0.04	10	165.65
3	$S_f=S_y$, Sm Fa S_c S_c^2 S_c^3 S_f^2	191.04	3.54	0.03	11	162.75
5	$S_f=S_y$, F_a F_a^2 F_a^3	218.00	30.49	0.00	8	198.80
6	$S_f=S_y$, S_c S_m F_a	221.04	33.54	0.00	6	207.26

The most supported population model (Table 5: model 1) estimated cow and yearling survival at 0.90, bull survival at 0.85, and fecundity at 0.41 and mean calf survival of 0.44 (values ranging from 0.05-0.7). 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 0.41 and calf survival is lower. A safer interpretation of model results might be an estimate of productivity as calf survival times fecundity (S_c*F_a) which is displayed in Figure 6. 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 cubic term in calf survival adequately fitting the directional trend in yearling:cow ratios (Figure 6). The directional trend in calf survival marginally affected calf:cow ratios given that calf survival only influenced these ratios for the two month interval between birth and composition surveys. Yearling:cow ratios closely followed productivity as estimated by calf survival and fecundity which illustrates how this ratio is the best indicator of productivity. Estimated trends in abundance fit the limited field data well. Variation in productivity created slight curvilinear trends in herd size. The overall effect of known human-caused mortality levels on herd size was negligible.

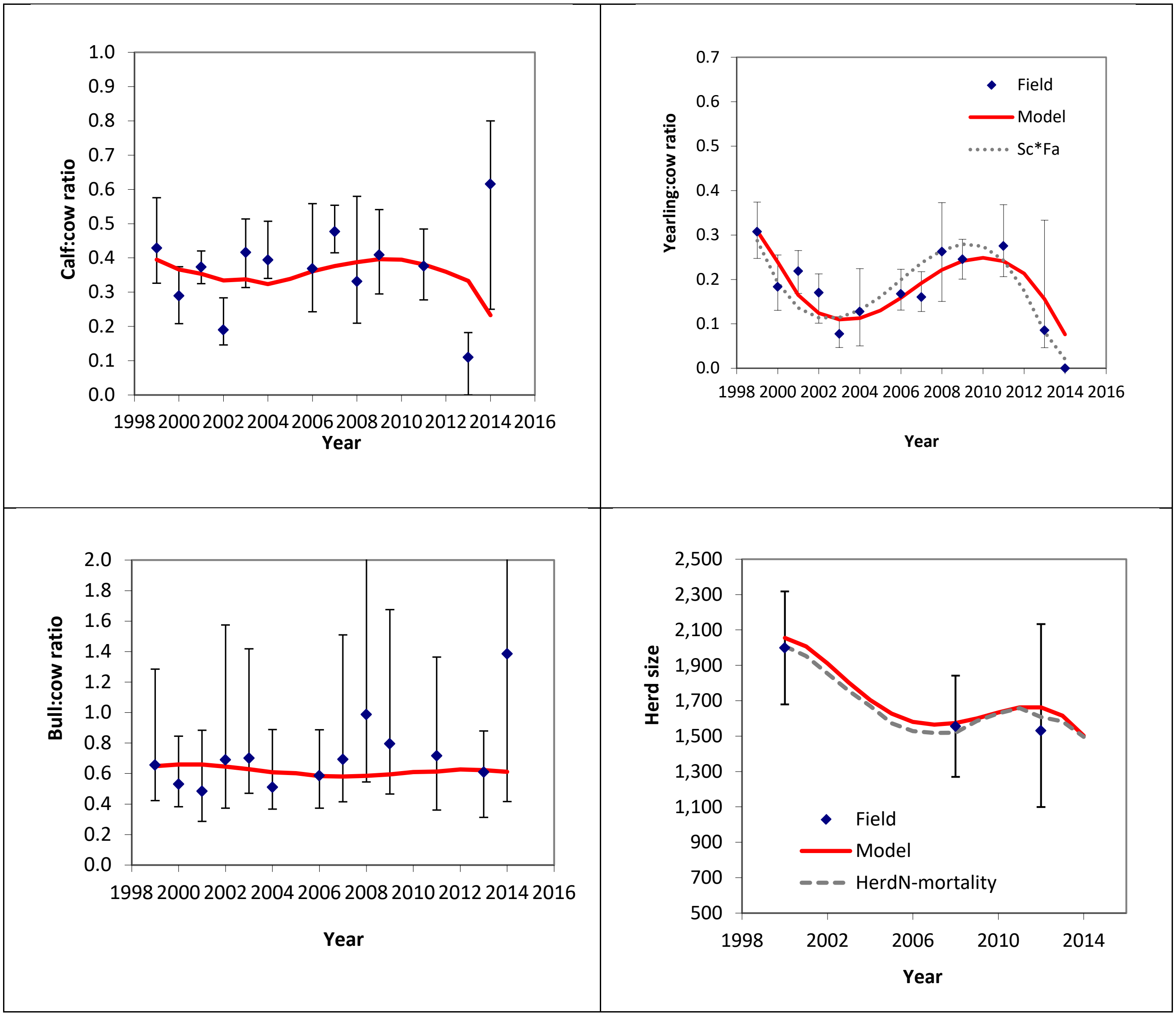

Figure 6. OLS model predictions (red line) compared to field estimates for composition surveys and abundance estimates. Other lines are noted in figure legends.

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

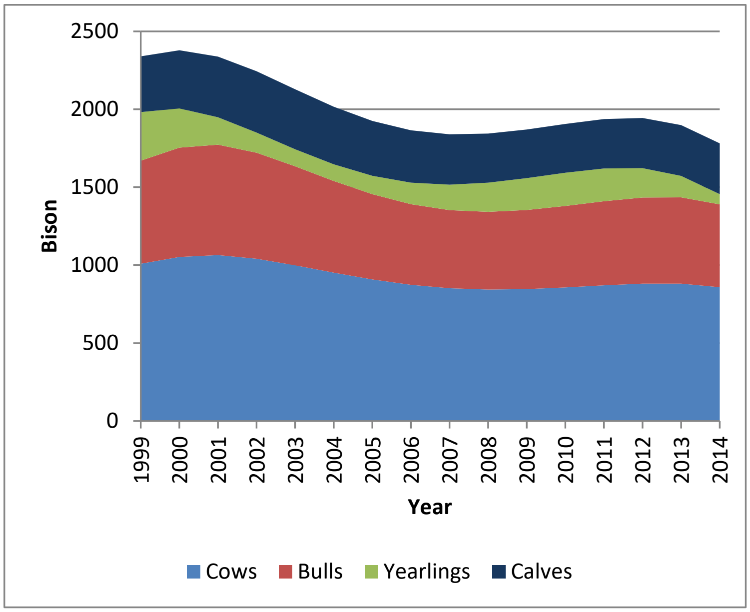

Figure 7. Estimates of overall herd size from the OLS model (Figure 6).

Estimated survival rates for the most supported OLS model included anthropogenic-caused mortalities. We re-ran the model with this mortality subtracted from bull, cow, and yearling N estimates each year to estimate “natural survival rates” under the assumption that all anthropogenic mortality was known. We assumed that all hunting mortality was for male bison, and highway collisions occurred in equal proportions for cows, bulls, and yearlings. These are obviously simplified assumptions that could be eliminated if sex and age of bison were recorded for mortalities. Under this set of assumptions cow survival increased to 0.91 (from 0.90 with human mortality) and bull survival increased to 0.90 (from 0.85 with human mortality). These estimates could be considered the “natural survival rate” needed to produce the observed trends when human-caused mortality is added in.

Bayesian State Space Model

The Bayesian state space analysis was done in collaboration with Joe Thorley of Poisson Consulting Ltd. (Nelson, British Columbia) (Thorley and Boulanger 2015). Details of the state space model analysis can be found in Appendix C. Below we summarize the main results of this exercise.

The objectives of the state space model were to provide estimates of precision for model parameters and to explore potential relationships between demographic parameters and environmental covariates. A side objective of the state space model was to develop “observation models” for the composition survey data that model the statistical distribution of field data. Unlike the OLS approach, the Bayesian state space approach directly models the way data are collected including the fitting of specific probabilistic distributions to field data types. This provides added flexibility in modeling and more flexibility in modeling various sources of variation in the data set.

The Bayesian state space model used the same basic model formulation as the OLS model with some simplifications. The Bayesian model only considered the female segment of the population and therefore bull:cow ratios were not included in modeling efforts. As with the OLS model, yearling and adult survival estimates were set to be equal. In addition, mortality data were not included as an input data source.

For the Bayesian approach, initial values of all parameters including initial population size were defined based upon field parameter estimates and initial values in the OLS model. In general, uninformative prior distributions of parameters were used given minimal information on the distribution of these values. Fitting of composition survey estimates was based upon an assumed over dispersed binomial distribution of calf:cow and yearling:cow ratios. Herd size estimates were assumed to be normally distributed. The basic process of the Bayesian model is to run repeated simulated trajectories of parameters with fitting achieved using a Markov Chain Monte Carlo process. This approach allowed estimates of parameter significance and confidence limits on parameter estimates.

A model with constant adult and yearling survival but time varying calf survival (as a random effect) was used for the main analysis (Table 6) (which was similar to the most supported OLS model: Table 5). Parameter estimates were significant and reasonably precise as determined by narrow widths of confidence limits.

Table 6. Estimate of demographic parameters from the state space model along with confidence limits (Lower, Upper), standard deviation (SD), error (half of the 95% confidence limit as a percent of the point estimate) and significance)

Parameter	Estimate	Lower	Upper	SD	Error	Significance
Adult and yearling survival (S_f and S_y)	0.89	0.86	0.92	0.02	4	0.001
Fecundity (F_a)	0.46	0.41	0.52	0.03	12	0.001
Mean Calf survival (S_c)	0.44	0.32	0.60	0.07	31	0.001
Temporal variation S_c (Random Effect)	0.67	0.33	1.24	0.23	68	0.001
Initial N adults	1780	1273	2303	259.00	29	0.001
Initial N Yearlings	279.70	185.10	381.60	48.40	35	0.001
Dispersion (Calf:cow ratios)	0.75	0.60	0.92	0.08	21	0.001

It is important to note that precision in the context of the state space model can be thought of as “What level of variation in parameter values would create observed trends in the data"? If data are sparse, for example very few herd surveys, then it is likely that there is variation in the data set that may not be detectable. In this case, precision of parameters such as adult survival may be an underestimate of true variation in the population. For example, it is possible that the variance of survival estimates may increase if yearly surveys are conducted which might result in further observed variance in herd size.

Model predictions suggested reasonable fit to the data with time variation in calf survival but with other parameters held at constant levels (Figure 8). Yearling:cow ratios displayed a directional trend which was also indicated in the field data (Figure 4). As with the OLS model, variation in calf survival created only a small amount of variation in overall herd size.

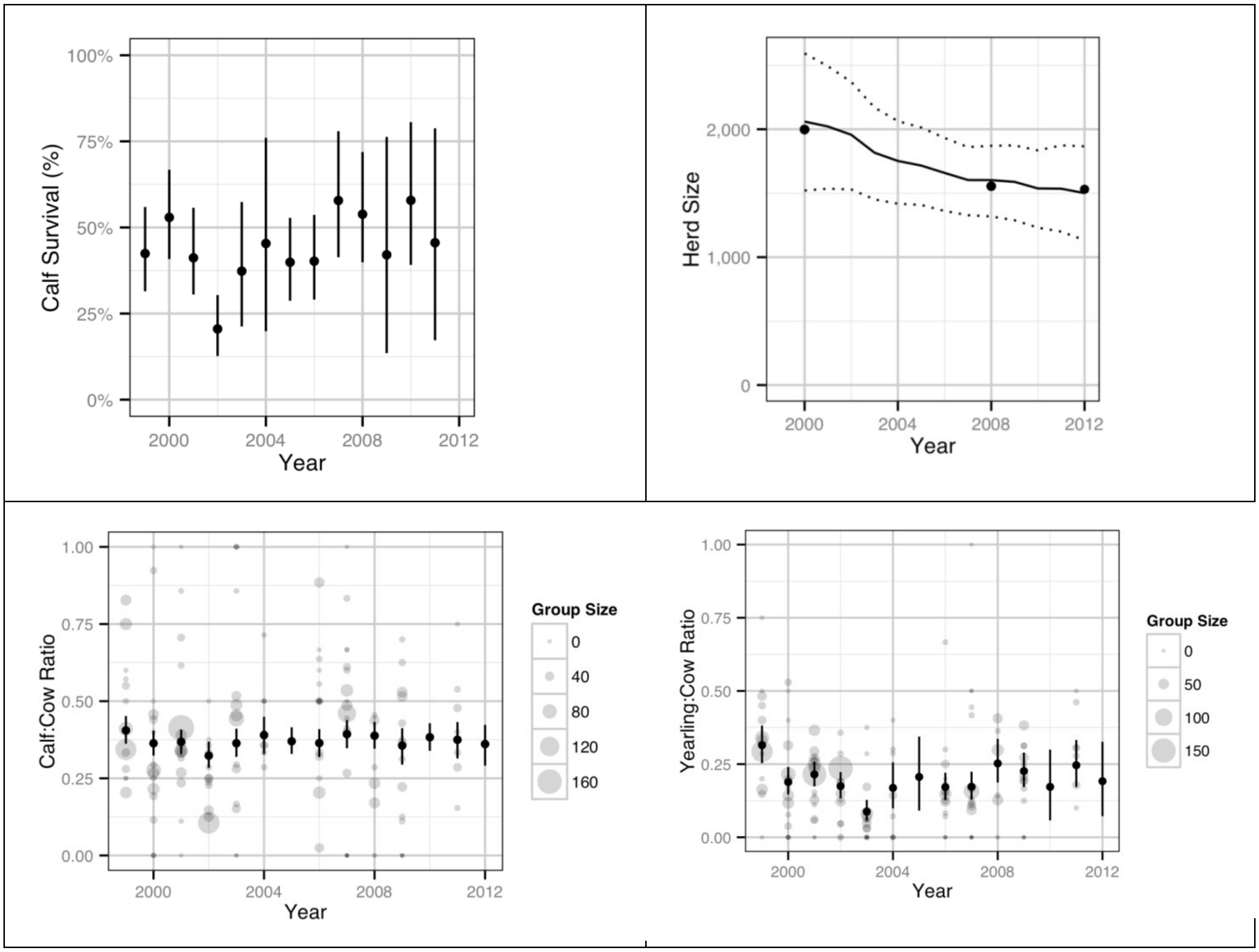

Figure 8. State space estimates of calf survival (upper left) and herd size (upper right) depicted by the solid lines. Error bars are ±95% credible intervals. Comparison of model predictions for calf:cow ratios (lower left) and yearling:cow ratios (lower right) with observations (bubbles proportional to group size for each observation).

A preliminary attempt was made to associate variation in calf survival with environmental indicators. Screening revealed that winter severity index was correlated with most winter indicators (snowfall, winter length). Rainfall and summer air temperature also formed distinct predictors compared to other potential covariates. Prior to model fitting, we standardized all explanatory covariates (Figure 9).

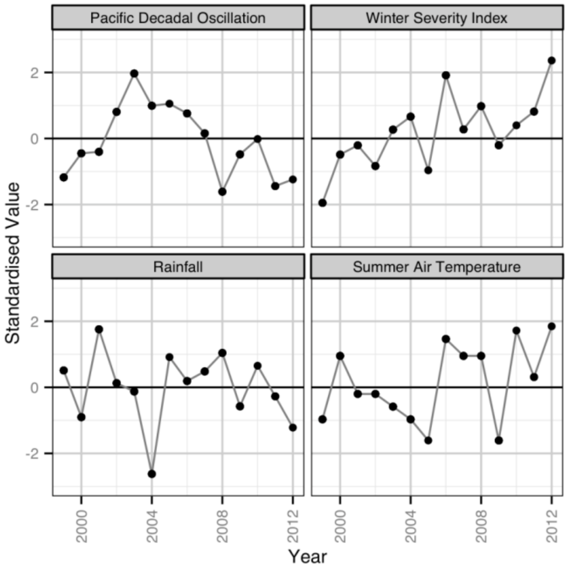

Figure 9. Standardized environmental covariates.

None of the environmental covariates were significant predictors of calf survival at α=0.05. PDO and summer rainfall were marginally significant with p-values of 0.14. In both cases a positive relationship was suggested (higher summer air temperature and rainfall increased calf survival).

We note that this exercise was preliminary and not an exhaustive investigation of environmental factors that influence herd demography. For example, some studies have suggested that there are time lags between the effects of environmental factors and responses in demographic parameters (Brodie 2008). Our investigation did not consider time-lags or the full suite of potential environment covariates.

Conclusions of Modeling Exercises

In summary, this initial test of the OLS and state space integrated population models suggests that working population models of bison demography can be developed even in the absence of survival estimates from collar data. These models provide 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.

Comparison of Estimates with Collar-based Studies

We compared the estimates from models to a review of field studies (Table 7). Estimates of adult survival were slightly lower than many collar-based studies. However, there are some key differences between the parameter estimates from this model and those from collar-based studies. First, estimates of adult survival from the integrated population models represent a mean average across all adult age classes of a given population whereas collar based studies often target older adults. Second, integrated population model estimates may be reduced slightly by lower yearling survival given the assumption that yearling and adult survival rates are equal. Also, adult survival rates from collar-based studies may or may not include anthropogenic mortality and are often of limited sample size. Finally, many of the studies of bison reviewed in Brodie (2008) were for increasing or stable populations, whereas the Mackenzie population was decreasing and therefore survival rates may be lower.

Estimates of calf survival and fecundity from the models are confounded given that there are no direct measurements of fecundity; with the main measurement occurring two months after birthing occurs. This issue, as well as the fact that fecundity is averaged across all age classes (with varying pregnancy rates) make it difficult to compare fecundity estimates with pregnancy rates directly measured in field studies. For example, in some populations, females will only produce calves in alternate years which would effectively half estimated fecundity compared to a biologically-based pregnancy rate (Brodie 2008). Given these issues, the best estimate from modeling efforts may be productivity which is the product of calf survival and fecundity. This basically is a measurement of the proportion of yearling bison produced per adult female in the population.

Table 7. Comparison of OLS, state space model estimates and estimates from a review of studies (Brodie 2008) and a previous study of the Mackenzie bison herd (Larter et al 2000).

Parameter	**Estimates**		**Literature values**	**Comments**
	OLS	**State Space**		
Adult female survival	0.90	0.89 (CI=0.86-0.92)	0.95-0.99[A] 0.75-1.0[B]	
Adult male survival	0.85		0.92-0.96[A] 0.67-1.0[B]	Bulls not considered in state space model
Fecundity	0.41	0.46 (CI=0.41-0.52)	0.37-0.89[A]	Depends on female birthing interval/age structure
Yearling survival	0.90	0.89 (CI=0.86-0.92)	0.55-0.99[A]	Little information in literature
Calf survival	0.44 (range=0.05-0.70)	0.44 (CI=0.32-0.60)	0.25-1.0[A] 0.49-0.63[B]	Variable among populations
Productivity	0.18	0.20		Product of calf survival and fecundity

[A]Brodie 2008

[B]Larter et al. 2000

In summary, estimates from integrated population models should be compared cautiously with traditional collar-based studies given differences in how estimates are derived. A collar-based study may be advantageous to understand individual variation, specific causes of mortality, and drivers of overall demography. An integrated population model avoids collaring, considers all ages in estimation of vital rates, and provides an estimate that is based upon all indicators of herd demography. If collar data are available then it can be added as a data source to the integrated population model, therefore providing a more robust estimate than using each data source separately.

Strengths and Weaknesses of Field Data are Highlighted

This exercise highlights key limitations of data collected for NWT bison herds. First, most information about demography is for productivity and calf survival from yearly composition surveys. Second, limited information on bull and cow survival can be obtained from bull:cow ratios given the lower precision of these indicators due to segregation of bulls and cows during surveys. Finally, herd survey data were too sparse and infrequent to inform the model about trends in herd size beyond simple linear or exponential trends.

The most supported OLS and state space models had temporal variation in calf survival with other parameters held constant. For both OLS and state space models, variation in calf survival did not cause a large degree of variation in overall herd size (Figures 6-8). Interestingly, the variation in adult survival was low (CI=0.86-0.92) from the state space model. We suggest that this result was partially an artifact of sparse data to inform the model about variation in herd size due to variation in adult survival. If an objective of monitoring is to obtain robust estimates of adult survival then we suggest surveys should occur at more frequent intervals (i.e., bi-yearly or tri-yearly). In summary, this modeling exercise suggested the following modifications to field surveys should be considered:

- Conduct biennial or triennial estimates of herd size to better inform models about survival rates and other factors affecting overall herd trend. The model would then be used to fill in information between surveys based on composition and other indicators.
- Composition surveys that occur in early June would provide a better estimate of true fecundity and productivity of the herd.
- To monitor productivity, composition surveys should be conducted annually to allow the most inference on calf survival by the comparison of change in sequential calf:cow and yearling:cow ratios. In addition, this will allow the greatest power to further assess the effect of environmental covariates on herd productivity.
- As discussed in other sections of the report, collection of larger sample sizes from composition surveys would increase the precision and accuracy of bull:cow and other ratios
- Mortality data should be classified by age and sex to allow it to be fully utilized in modeling efforts.

OLS or State Space Model?

We examined both the OLS and state space model results to allow a brief comparison of each of the methods. The strength of the OLS model is its simplicity and ability to efficiently explore dominant trends in parameter variation in the data set using AIC_c model selection. The weakness of this approach is that standard errors of model estimates are not directly obtainable in the present form of the model (but could be obtained using bootstrap resampling) and field data and associated residuals are assumed to be normally distributed. In addition, simplifying assumptions are required for model fitting, such as an initial stable age distribution. Despite these assumptions some authors argue this approach is adequate for management driven modeling exercises (White and Lubow 2002).

The state space approach allows much more flexibility in how data types are modelled as well as various ways to model temporal trends in the data set such as random effects modeling (Kery and Schaub 2012). This allows robust estimates of model parameters as well as methods to deal with specific issues and biases with each of the input data types. The main challenge of this approach is that it involves more complexity in terms of building observation models for each of the data types. An approach where initial models are built with OLS methods followed by more in-depth and comprehensive state space modeling is one way to facilitate model development.

The following refinements should be considered for future modeling efforts:

- The state space model could be developed to further consider bull:cow ratios and observation models for herd surveys.
- The investigation of environmental covariates could be continued with data from other herds considered as well as a larger number of environmental covariates. Further consideration of time-lags in demographic response to environmental conditions should be investigated.
- Data from previous analyses of the Mackenzie herd extending back to 1984 (Larter et al. 2000) would provide a much longer time series as well as radio collared bison data for refined survival rate estimation. Incorporation of these data into the analyses presented in this section would increase the power of the analysis to detect demographic trends as well as potential relationships with environmental covariates.
- Further modeling could be used to assess changes in demography as a result of the recent anthrax outbreak. This work would be most productive if done a few years after the outbreak to allow exploration on the overall impact and likely recovery of the herd.

In conclusion, the choice of modeling method and model formulation will be determined by management objectives and the limitations of field data. Regardless, this approach provides a useful tool to assist in assessment of herd status and interpretation of field data.

PART C: 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 10). 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.

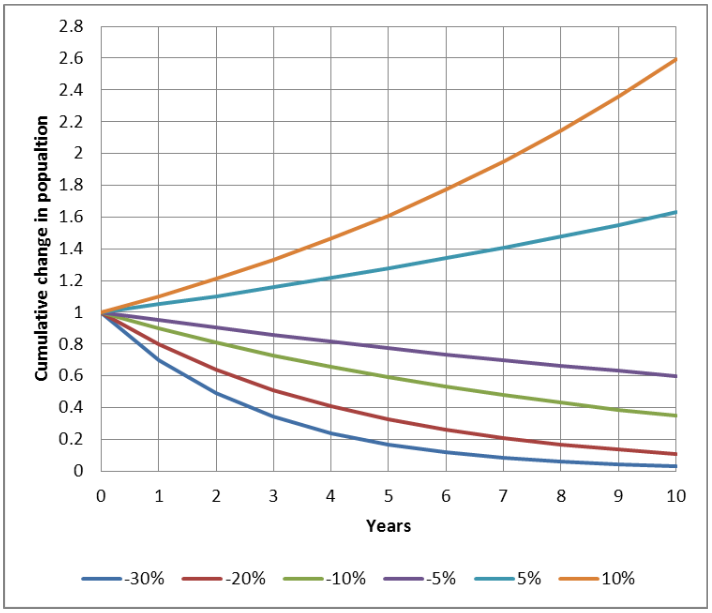

Figure 10. The relationship between annual change and cumulative change in population size as a function of the number of years surveys occur. Each line represents a different level of annual change.

Precision of Bison Abundance Surveys

The most recent estimates from bison surveys have been derived from distance sampling methods (Boulanger and Armstrong 2012, Boulanger and Armstrong 2013, Boulanger and Armstrong 2014). Precision of survey estimates has ranged from 16% for the pooled Mackenzie herd estimates (2012) to 40% for the pooled Slave River Lowlands study (Figure 11). In general the precision of estimates for these two herds 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).

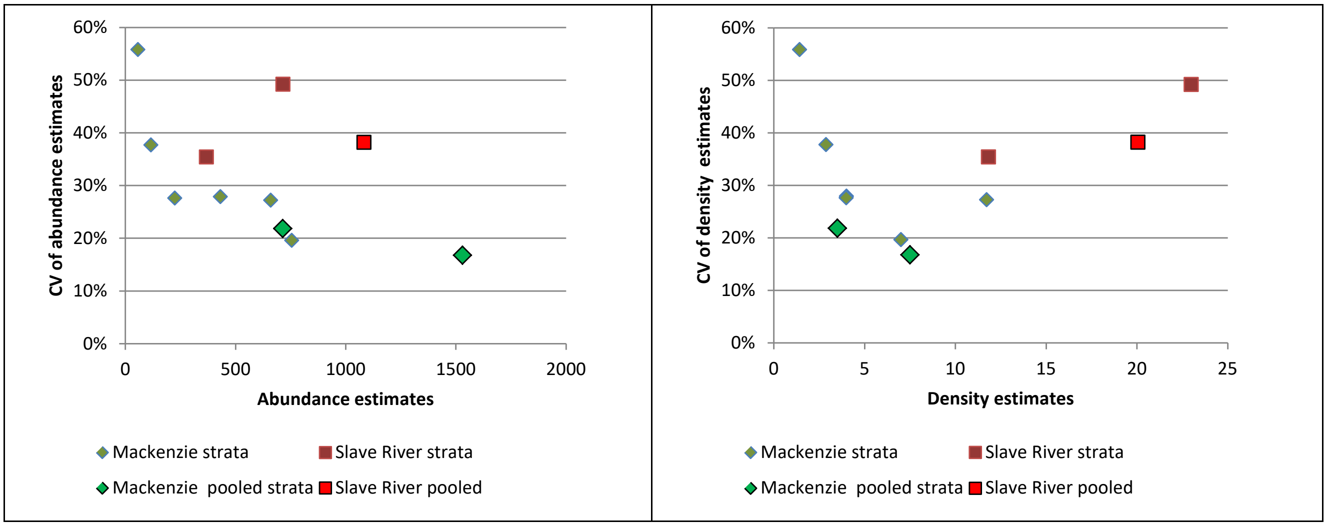

Figure 11. Estimates of precision (CV-coefficient of variation) as related to abundance estimates from the Slave River and Mackenzie bison surveys (Boulanger and Armstrong 2012, Boulanger and Armstrong 2013, Boulanger and Armstrong 2014).

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 and Armstrong 2014), 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 12). 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)).

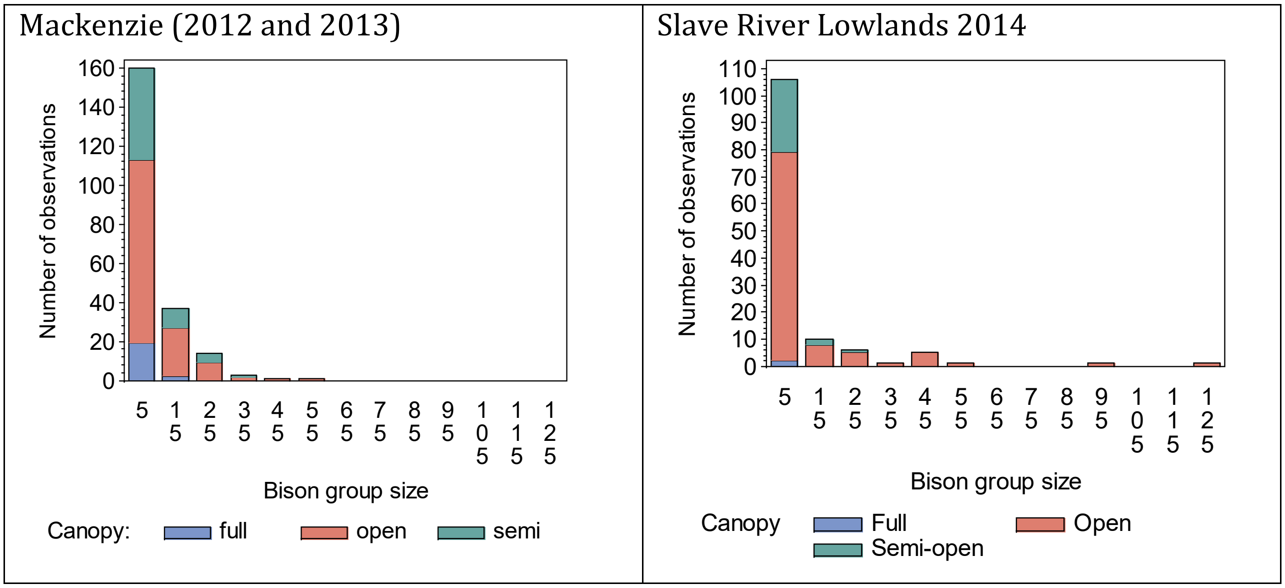

Figure 12. Distribution of group sizes for Mackenzie versus Slave River Lowlands bison surveys.

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 frequent 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. (2004a) 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. (2004a) 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 are required to detect an annual decline of 20% (λ=0.80) if the coefficient of variation is 10% or below (Figure 13). 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.

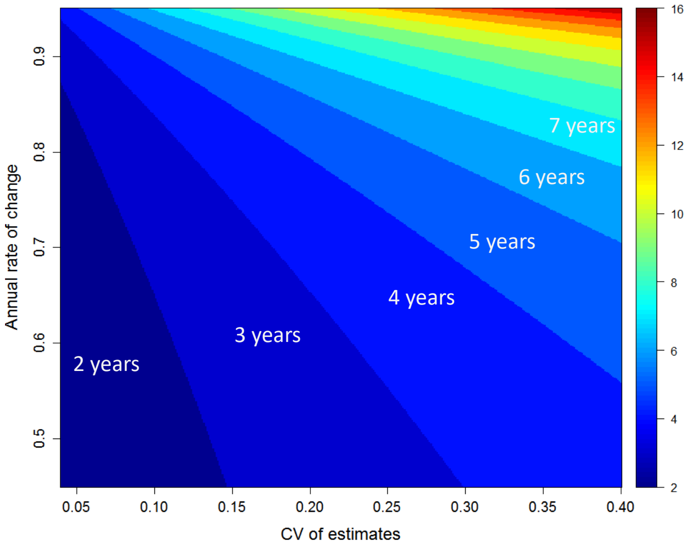

Figure 13. The number of years required to achieve adequate power to detect an annual rate of decline (λ) as a function of the coefficient of variation of annual estimates of abundance.

These results can also be interpreted in terms of percent cumulative change in the population. In Figure 14, 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.

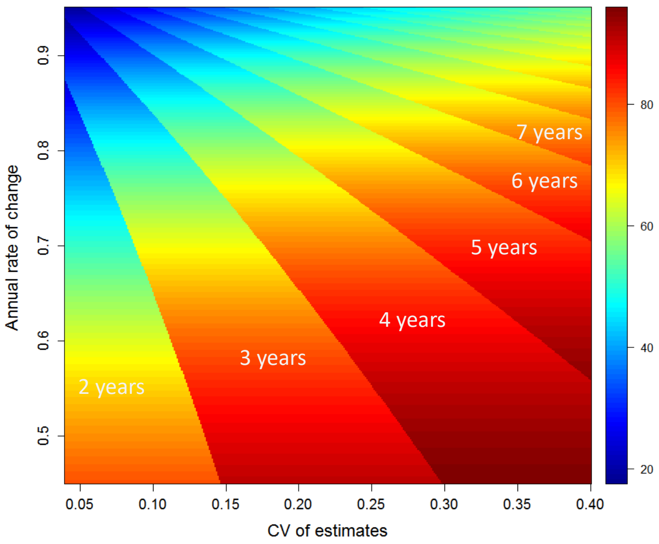

Figure 14. The cumulative percent decrease in population size that would occur when power=0.8 to detect a given trend, as also indicated in Figure 13. Cumulative decrease (i.e., 20% means the population is 20% lower than initial survey) is indicated by the colours and colour legend to the right of the 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 15) suggested relatively similar results as the regression analysis (Figure 14). 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 15) whereas seven years would be required using the regression analysis approach (Figure 14).

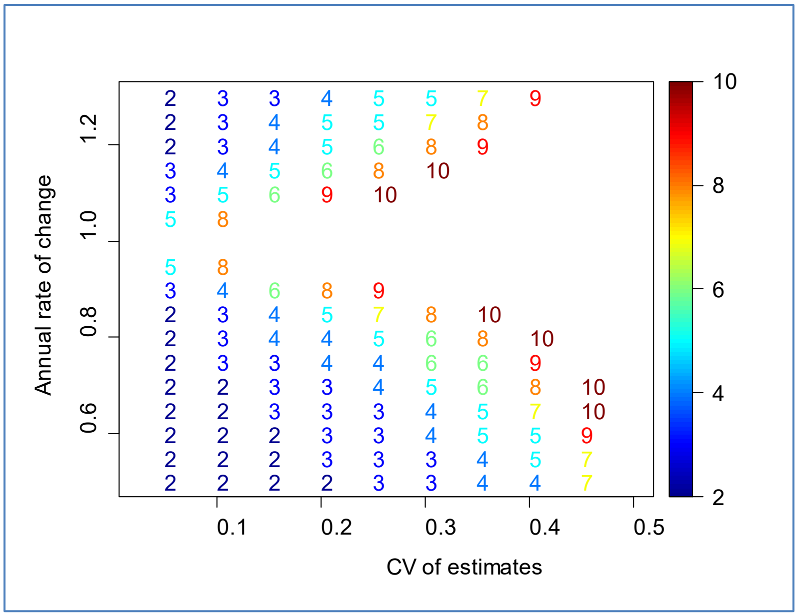

Figure 15. The number of years required to detect a change in abundance using t-tests as a function of CV of estimates and annual rate of change. The numbers in the graph correspond to total years required to detect the change. Only years to detect change that are ten or less are displayed on the graph.

The proportional decrease in population size based on years to detect power suggested that coefficients of variation of 0.15 would be needed to detect a 40% reduction in abundance. A coefficient of variations of 0.20 then would be able to detect a 50% decline in abundance (Figure 16).

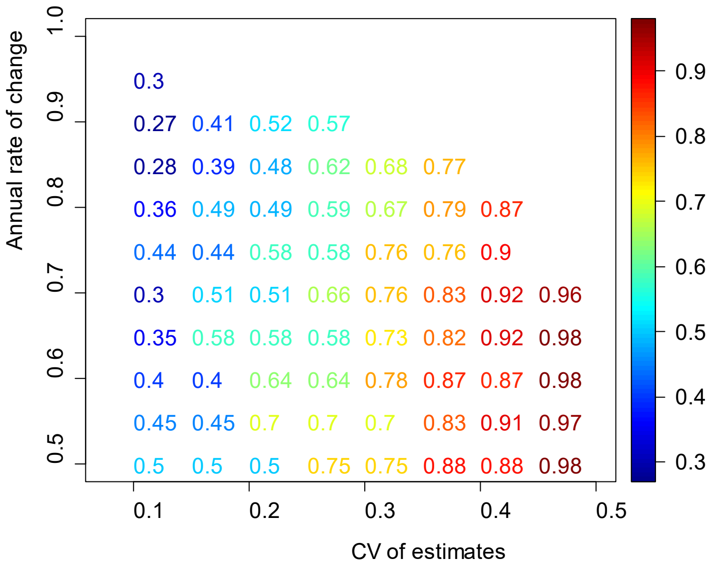

Figure 16. The proportional decrease in population size (numbers in figure) as a function of annual rate of change, CV of estimates to detect the given annual rate of change (Figure 13).

For increasing populations, a coefficient of variation of 0.15 would detect a 60% increase in abundance in two years (Figure 17).

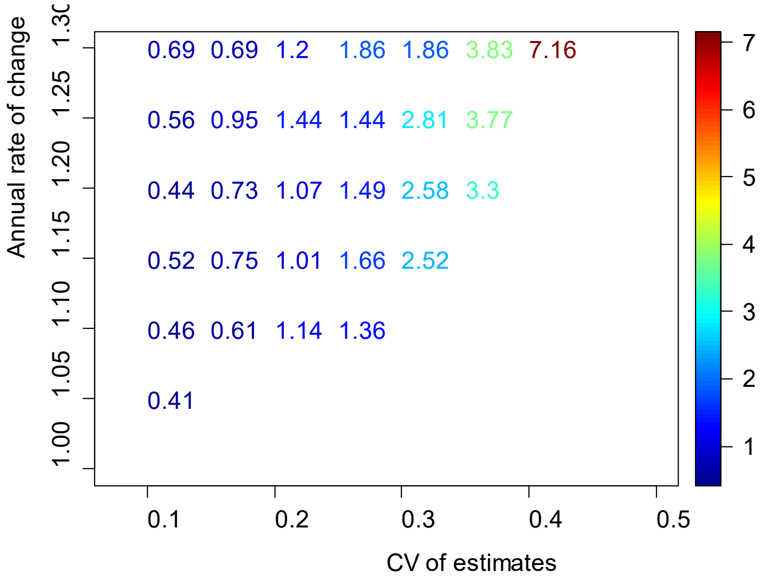

Figure 17. The proportional increase in population size as a function of annual rate of change, CV of estimates, and corresponding years to detect the change as indicated by colour of text (Figure 13).

CV for bison surveys range from 16-40% (Figure 11) 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 coefficient of variation of surveys can be improved to increase power. We suggest that a target coefficient of variation of 15% is optimal with a survey interval of three years. This would detect moderate changes (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 2012-2013. This change would be detected by annual surveys as long as coefficients of variation were less than 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 Base Life History Model 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 18). 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 area is to improve field collection methods as well as consider analyses strategies to increase survey precision rather than increasing survey effort (discussed next).

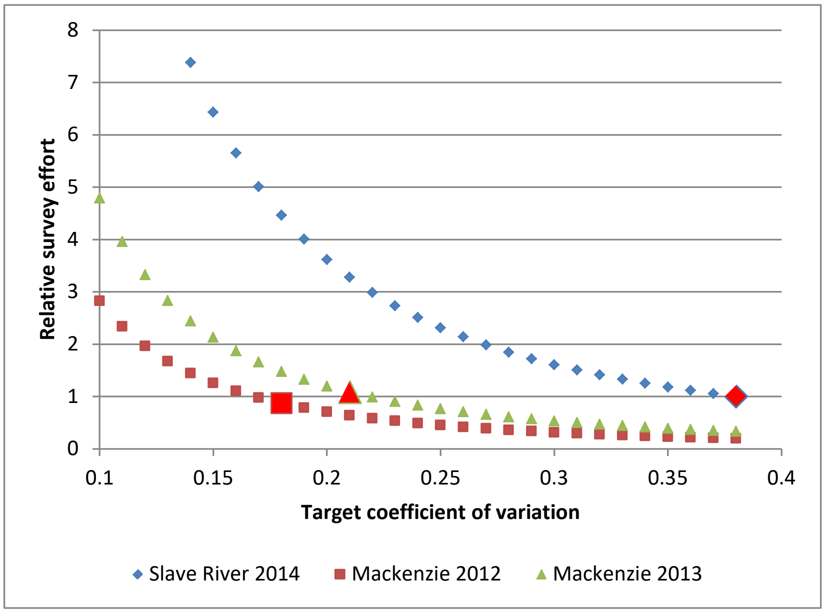

Figure 18. Estimated change in precision due to increasing relative survey effort. The coefficients of variation achieved by each project are denoted by large red symbols. Power analysis suggests that a CV level of 0.15 is optimal.

Stratification and Post-stratification

Stratification can be used to increase survey precision by allocating more effort to strata that have higher densities or have more variability in density. For the recent Mackenzie and Slave River surveys, all strata 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 centres 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 1992, 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 8). 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 8. 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	10763	83	78	66	94%	79%
North	116	43.7	2.89	0.38	4012	75	39	46	52%	61%
West	659	179.3	11.73	0.27	5623	66	94	109	142%	165%
Mackenzie 2013										
East	432	120.49	4.01	0.28	10763	83	103	82	124%	99%
North	57	31.97	1.43	0.56	4012	75	46	49	61%	65%
West	225	61.99	4.00	0.28	5623	66	52	81	79%	123%
Slave River 2014										
East	715	351.9	22.99	0.49	3112	42	55	46	132%	109%
West	368	130.3	11.82	0.35	2290	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 fewer parameters) which will result in a more precise and robust estimate. Some of the main issues with previous surveys are now discussed 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. Distance methods are mainly based upon observers peering out perpendicular to the transect. Therefore, various forms of bias can be introduced if the pilot or navigator see bison and influence the observers. One approach might be to use separate intercoms so the pilot and navigator 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 their 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 modelled efficiently.

Observers Should Only Observe Bison from the Survey Line

Observations for distance sampling should only occur from the sampling transect line. If groups are found when the aircraft is off the transect line such as when taking a waypoint to mark the location of the animal observed 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 from or 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 detection of bison on other lines. This can be challenging if open habitat is being surveyed and line spacing is close 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 0 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 of 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 and Armstrong 2012) which was reduced to 0.167 when the 2013 survey data was added to the analysis (Boulanger and Armstrong 2013). 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 NWT 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 distribution 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 19). 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 centre is often too wet for travel, but the wet centres of meadows are used in the winter when the ground is frozen. Movement through poor habitat is generally rapid as the animals search for favourable habitat.

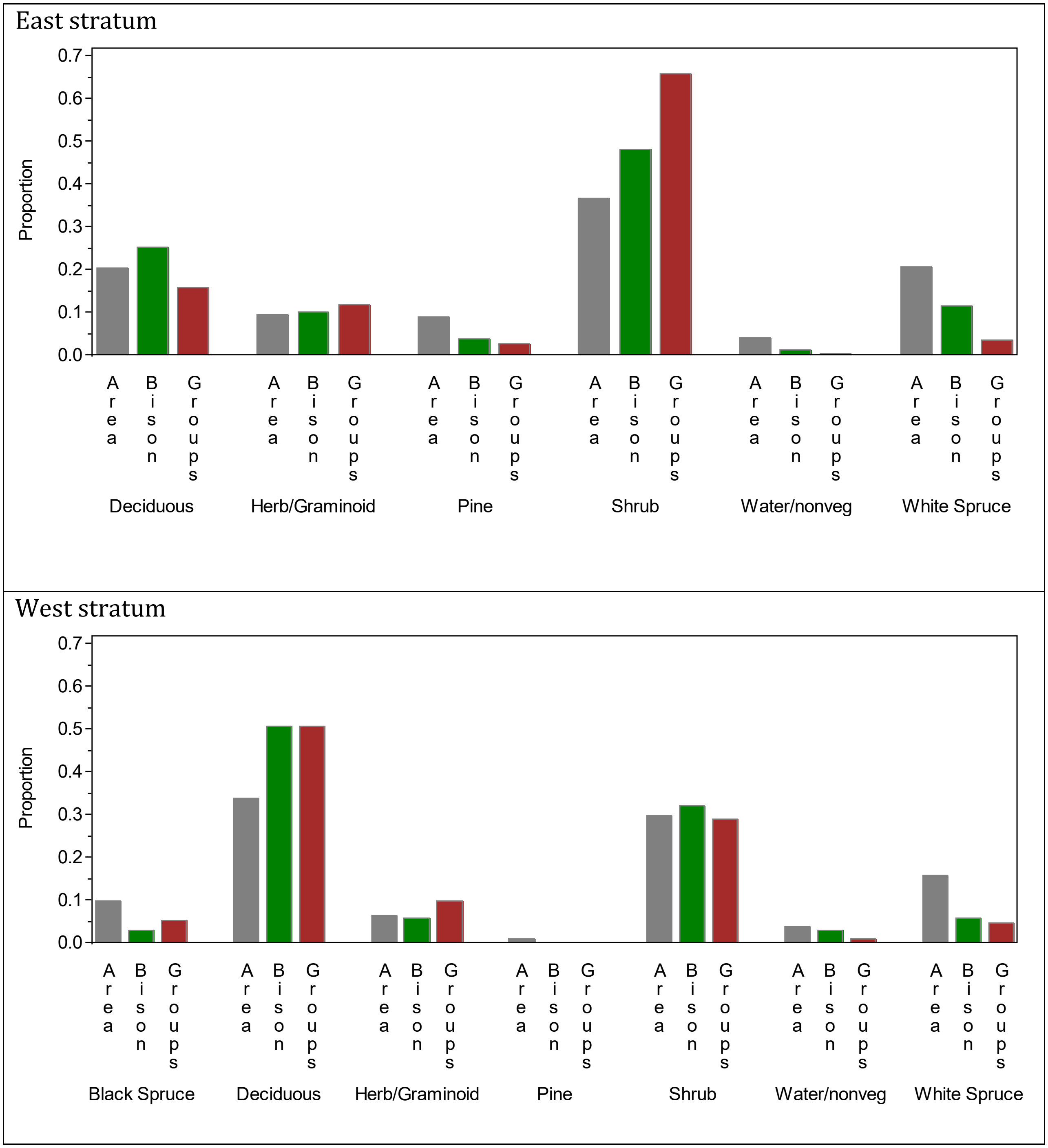

Figure 19. A comparison of the proportion bison groups (*Groups*) or bison counted (*Bison*) occurring in each habitat class compared to the proportion of area (*Area)* in each habitat class in the East and West stratum of the Slave River Lowlands 2014 study area.

SUMMARY

This report provides a set of options for monitoring bison populations in the NWT. We provide a summary of recommendations based on objectives outlined in the original request for proposal in Table 9.

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 the Base Life History Model section of this report. These approaches do not require annual surveys or annual measurements for 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 1 in closed cover habitats. We suggest that density surface modeling may be one approach to improve estimate precision when precision is poor 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 abundance should not change dramatically from 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 a 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 9. A summary of recommendations based on objectives listed in the RFP document (Literature review). *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 3 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 modeling from transect surveys using habitat covariates. • Resource selection function or occupancy modeling 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.

ACKNOWLEDGEMENTS

Terry Armstrong (Environment and Natural Resources, GNWT) provided initial discussion, Department of Environment and Natural Resources documents and feedback, and reviewed this report. Kathleen Groenewegen (Environment and Natural Resources, GNWT) conducted GIS analysis of the Slave River Lowlands data used for the density surface modeling analyses. John Lee skilfully reviewed and compiled literature on traditional knowledge. This report was funded by the Department of Environment and Natural Resources, Government of Northwest Territories.

LITERATURE CITED

Allen, J.R., L.E. Mcinenly, E.H. Merrill and M.S. Boyce. 2008. Using resource selection functions to improve estimation of elk population numbers. The Journal of Wildlife Management 72:1,798–1,804.

Alldredge, M.W., T.R. Simons,and K.H. Pollock. 2007. A field evaluation of distance measurement error in auditory avian point count surveys. Journal of Wildlife Management 71:2,759–2,766.

Anganuzzi, A.A. and S.T. Buckland. 1993. Post-stratification as a bias reduction technique. The Journal of Wildlife Management 57:827.

Armstrong, T. 2014. Slave River Lowlands wood bison population estimate. Unpublished Report. Environment and Natural Resources, Government of the Northwest Territories. 3pp.

Armstrong, T. and K. Cox. 2013. Mackenzie wood bison population estimate. Unpublished Report. Environment and Natural Resources, Government of the Northwest Territories.

Athabasca Chipewyan First Nation. 2012. Níh boghodi: we are stewards of our land. Athabasca Chipewyan First Nation, Fort Chipewyan, AB.

Baccante, N. and R.B. Woods. 2008. Relationship between weather factors and survival of mule deer fawns in the Peace Region of British Columbia. Fish and Wildlife Section, BC Ministry of Environment, Peace Region Technical Report.

Bailey, R.E.,and R.J. Putman. 1981. Estimation of fallow deer (*Dama dama*) populations from faecal accumulation. The Journal of Applied Ecology 18:697.

Bailey, L.L., D.I. MacKenzie and J.D. Nichols. 2014. Advances and applications of occupancy models. Methods in Ecology and Evolution 5:1,269–1,279.

Ball, M.C., T.L. Fulton and G.A. Wilson. 2016. Genetic analyses of wild bison in Alberta, Canada: implications for recovery and disease management. Journal of Mammalogy 97:1,525-1,534

Bårdsen, B.-J.,, and J. L. Fox. 2006. Evaluation of line transect sampling for density estimates of chiru *Pantholops hodgsoni* in the Aru Basin, Tibet. Wildlife Biology 12:89–100.

Barg, J.J., J. Jones and R.J. Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.

Bathurst Caribou Management Planning Committee. 2004. A Management Plan for the Bathurst Caribou Herd. Bathurst Caribou Management Planning Committee Unpublished Report. 51 pp.
[Online] URL: www.nwtwildlife.com/NWTwildlife/caribou/bathurstcoman.htm

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

Bender, L.C. 2006. Uses of herd composition and age ratios in ungulate management. Wildlife Society Bulletin 34:1,225–1,230.

Bender, L.C., W.L. Myers and W.R. Gould. 2003. A comparison of ground and helicopter counts for determining North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus* population composition. Wildlife Biology 9:199–205.

Berkes, F. 2008. Sacred ecology: traditional ecological knowledge and resource management. Taylor & Francis, London, UK.

Berkes, F., J. Colding and C. Folke. 2000. Rediscovery of traditional ecological knowledge as adaptive management. Ecological Applications 10:1,251–1,262.

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

Bidwell, W.A., J.S. Nishi and T.R. Ellsworth. 2009. Bison control area program annual report of survey activities January 2005 – April 2005. Environment and Natural Resources, Government of the Northwest Territories. Manuscript Report No. 196.

Blanc, L., E. Marboutin, S. Gatti and O. Gimenez. 2013. Abundance of rare and elusive species: Empirical investigation of closed versus spatially explicit capture-recapture models with lynx as a case study. Journal of Wildlife Management 77:372–378.

Bonenfant, C., J.-M. Gaillard, F. Klein and J.-L. Hamann. 2005. Can we use the young:female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. Journal of Applied Ecology 42:361–370.

Borchers, D.L., W. Zucchini, and R. M. Fewster. 1998. Mark-recapture models for line transect surveys. Biometrics 54:1207.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1,393–1,405.

Boulanger, J. 2013. Estimates of density and population size for 2012 Mackenzie Bison and Moose survey. Integrated Ecological Research, Nelson, BC. Unpublished report. Draft 25 March 2013.

Boulanger, J. 2014a. Estimates of density and population size for 2012-3 Mackenzie Bison and Moose survey. Integrated Ecological Research, Nelson, BC. Unpublished report. Draft 31 March 2014.

Boulanger, J. 2014b. Estimates of density and population size for 2014 Slave River Lowlands Bison survey. Integrated Ecological Research, Nelson, BC. Unpublished report. Draft 2 July 2014.

Boulanger, J., B.N. McLellan, J.G. Woods, M.F. Proctor and C. Strobeck. 2004. Sampling design and bias in DNA-based capture-mark-recapture population and density estimates of grizzly bears. Journal of Wildlife Management 68:457–469.

Boulanger, J., A. Gunn, J. Adamczewski and B. Croft. 2011. A data-driven demographic model to explore the decline of the Bathurst caribou herd. Journal of Wildlife Management 75:883-896.

Bowden, D.C. and R.C. Kufeld. 1995. Generalized mark–sight population size estimation applied to Colorado moose. Journal of Wildlife Management 59:840–851.

Bradley, M. and J. Wilmshurst. 2005. The fall and rise of bison populations in Wood Buffalo National Park: 1971 to 2003. Canadian Journal of Zoology 83:1,195–1,205.

Boyce, M.S. 1992. Population viability analysis. Annual review of Ecology and Systematics 23:481–506.

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

Brodie, J.F. 2008. A Review of American Bison (*Bos bison*) demography and population dynamics. American Bison Society Working Paper No. 2.

Brown, J.A., M. Salehi, M. Moradi, G. Bell and D.R. Smith. 2008. An adaptive two-stage sequential design for sampling rare and clustered populations. Population Ecology 50:239–245.

Brown, D. and P. Rothery. 1993. Models in biology: Mathematics, statistics, and computing. John Wiley and Sons, New York.

Brown, J.A., M. Salehi, M. Moradi, B. Panahbehagh and D.R. Smith. 2013. Adaptive survey designs for sampling rare and clustered populations. Mathematics and Computers in Simulation 93:108–116.

Buckland, S.T., D.R. Anderson, K.P. Burnham and J.L. Laake. 1993. Distance sampling: estimating abundance of biological populations. First edition. Springer.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, Oxford, United Kingdom.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers and L. Thomas. 2004a. Advanced Distance Sampling - Estimating abundance of biological populations. Oxford Press.

Buckland, S., K. Newman, L. Thomas and N. Koesters. 2004b. State-space models for the dynamics of wild animal populations. Ecological Modeling 171:157-175.

Buckland, S.T., J. Laake and D.L. Borchers. 2010. Double-observer line transect methods: levels of independence. Biometrics 66:169-177.

Burnham, K.P., D.R. Anderson and J.L. Laake. 1985. Efficiency and bias in strip and line transects. Journal of Wildlife Management 49:1,012-1,018.

Burnham, K.P. and D.R. Anderson. 1984. The need for distance data in transect counts. Journal of Wildlife Management 48:1,248-1,254.

Burgman, M.A. and J.C. Fox. 2003. Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. Animal Conservation 6:19–28.

Cameron, R.D. 1994. Reproductive pauses by female caribou. Journal of Mammalogy 75:10-13.

Cameron, R.D., B. Griffith, L.S. Parrett and R.G. White. 2013. Efficacy of calf:cow ratios for estimating calf production of arctic caribou. Rangifer 33:27–34.

Campbell, D., G.M. Swanson and J. Sales. 2004. Comparing the precision and cost-effectiveness of faecal pellet group count methods. Journal of Applied Ecology 41:1,185–1,196.

Carbyn, L.N. 1998. Some aspects regarding wolf predation on bison in Wood Buffalo National Park. International Symposium on Bison Ecology and Management in North America 1997:92–95.

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

Caughley, G. 1974. Interpretation of age ratios. Journal of Wildlife Management 38:557–562.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley, New York, NY

Chandler, R.B. and J.D. Clark. 2014. Spatially explicit integrated population models. Methods in Ecology and Evolution 5: 1,351-1,360.

Christianson, D. and S. Creel. 2014. Ecosystem scale declines in elk recruitment and population growth with wolf colonization: a before-after-control-impact approach. G. Ballard, editor. PLoS ONE 9:e102330.

Cogan, R.D. and D.R. Diefenbach. 1998. Effect of undercounting and model selection on a sightability-adjustment estimator for elk. The Journal of Wildlife Management 62:269.

Conference of Management Authorities. 2019. Recovery Strategy for Wood Bison (*Bison bison athabascae*) in the Northwest Territories. Conference of Management Authorities, Yellowknife, NT, Canada. 45pp.

Conn, P.B., J.L. Laake and D.S. Johnson. 2012. A hierarchical modeling framework for multiple observer transect surveys. PloS one 7:e42294.

Conroy, M.J., J.P. Runge, R.J. Barker, M.R. Schofield and C.J. Fonnesbeck. 2008. Efficient estimation of abundance for patchily distributed populations via two-phase, adaptive sampling. Ecology 89:3362–3370.

Conroy, M.J., R.S. Henry and G. Harris. 2014. Estimation of regional sheep abundance based on group sizes: Aerial Surveys of Bighorn Sheep. The Journal of Wildlife Management 78:904–913.

COSEWIC. 2013. COSEWIC assessment and status report on the Plans Bison *Bison bison bison* and the Wood Bison *Bison bison athabascae* in Canada. Committee on the Status of Endangered Wildlife in Canada. Xv + 109pp.

Coulson, T., J.-M. Gaillard and M. Festa-Bianchet. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology 74:789–801.

Couturier, T., M. Cheylan, A. Bertolero, G. Astruc and A. Besnard. 2013. Estimating abundance and population trends when detection is low and highly variable: A comparison of three methods for the Hermann's tortoise. Journal of Wildlife Management 77:454–462.

Cunningham, J., A.M. Morgan-Davies and C. O'Ryan. 2001. Counting rhinos from dung: estimating the number of animals in a reserve using microsatellite DNA. South African Journal of Science 97:293–294.

Dau, J. 2005. Caribou Management Report 1 July 2002-30 June 2004, Western Arctic Herd. Alaska Department of Fish and Game, Juneau, AK. www.wildlife.alaska.gov/pubs/techpubs/mgt_rpts/ca05_wah.pdf

Dawson, M.J. and J. Hone. 2012. Demography and dynamics of three wild horse populations in the Australian Alps. Austral Ecology 37:97–109.

DeCesare, N.J., M. Hebblewhite, M. Bradley, K.G. Smith, D. Hervieux and L. Neufeld. 2012a. Estimating ungulate recruitment and growth rates using age ratios. Journal of Wildlife Management 76:144–153.

DeCesare, N.J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G.J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K.G. Smith and L.E. Morgantini. 2012b. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1,068–1,083.

DeMars, C.A. and S. Boutin. 2013. Counting ghosts: testing a new aerial survey method for estimating population sizes of boreal caribou. Habitat Conservation Trust Fund, Victoria, BC.

DeMars, C.A., M. Auger-Méthé, U.E. Schlägel and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. Ecology and Evolution 3:4,149–4,160.

Duquette, J.F., J.L. Belant, N.J. Svoboda, D.E. Beyer and C.A. Albright. 2014. Comparison of occupancy modeling and radiotelemetry to estimate ungulate population dynamics. Population Ecology 56:481–492.

Eberhardt, L.L., B.M. Blanchard and R.R. Knight. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Canadian Journal of Zoology 72:360–363.

Efford, M. 2004. Density estimation in live-trapping studies. Oikos 106:598–610.

Efford, M.G. 2011. Estimation of population density by spatially explicit capture-recapture analysis of data from area searches. Ecology 92:2,202–2,207.

Efford, M.G. and D.K. Dawson. 2012. Occupancy in continuous habitat. Ecosphere 3:art32.

Efford, M.G. and R.M. Fewster. 2013. Estimating population size by spatially explicit capture-recapture. Oikos 122:918–928.

Eggert, L.S., J.A. Eggert and D.S. Woodruff. 2003. Estimating population sizes for elusive animals: the forest elephants of Kakum National Park, Ghana. Molecular Ecology 12:1,389–1,402.

Elkin, B., T. Armstrong and T. Ellsworth. 2013. Anthrax Emergency Response Plan (AERP). Government of the Northwest Territories, Department of Environment and Natural Resources, File Report No. 139.

ENR (Environment and Natural Resources). 2013. ENR South Slave Regional Wildlife Workshop Summary Report, October 2013.

Ferguson, T.A. and F. Lavoilotte. 1992. A note on historical mortality in a northern bison population. Arctic 45:47–50.

Fieberg, J. and J. Giudice. 2008. Variance of stratified survey estimators with probability of detection adjustments. Journal of Wildlife Management 72:837–844.

Fisher, J.T., M. Hiltz, L. Nolan and L.D. Roy. 2013. The Alberta boreal deer project: 2012-2013 fiscal year report. Alberta Innovates - Technology Futures, Edmonton, AB.

Forsyth, D.M., R.J. Barker, G. Morriss and M.P. Scroggie. 2007. Modeling the relationship between fecal pellet indices and deer density. Journal of Wildlife Management 71:964–970.

Forsyth, D.M., D.I. MacKenzie and E.F. Wright. 2014. Monitoring ungulates in steep non-forest habitat: a comparison of faecal pellet and helicopter counts. New Zealand Journal of Zoology 41:248–262.

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

Franklin, A.B. 2002. Exploring relationships in survival and estimating rates of population change using Program MARK. Pages 350–356 in R. Fields, editor. Integrating people and wildlife for a sustainable future. Proceedings of the Second International Wildlife Management Congress, Godollo, Hungary. Wildlife Society, Bethesda, MD.

Freeland, W.J. and W.J. Boulton. 1990. Feral water buffalo (*Bubalus bubalis*) in the major floodplains of the 'top end', Northern Territory, Australia: population growth and the brucellosis and tuberculosis eradication campaign. Australian Wildlife Research 17:411–420.

Gaillard, J.-M. and N.G. Yoccoz. 2003. Temporal variation in survivals in mammals: a case of environment canalization? Ecology 84:3,294–3,306.

Gaillard, J.-M., M. Festa-Bainchet and N.G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. TREE 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 367–393.

Gardner, C. and A. DeGange. 2003. A review of information on wood bison in Alaska and adjacent Canada, with particular reference to the Yukon Flats. Appendix A of Joint ADF&G and FWS review of wood bison restoration on Yukon Flats. Fairbanks, AK.

Gasaway, W.C., S.D. DuBois, D.J. Reed and S.J. Harbo. 1986. Estimating moose population parameters from aerial surveys. Biological Papers of the University of Alaska, Institute of Arctic Biology.

Gates, C.C. and J. Wierzchowski. 2003. A landscape evaluation of bison movements and distribution in northern Canada. Addendum to the final report dated December 2001. Axys Environmental Consulting Ltd., Calgary, AB.

Gates, C.C., B. Elkin and D. Dragon. 2001. Anthrax. Pages 396–412 *in* E. Williams and I. Barker (eds.). Infectious diseases of wild mammals. Iowa State University Press, Ames.

Gattone, S.A., M. Esha and J.W. Mwangi. 2013. Application of Adaptive Cluster Sampling with a Data-Driven Stopping Rule to Plant Disease Incidence. Journal of Phytopathology 161:632–641.

Gerrodette, T. 1987. A power analysis for detecting trends. Ecology 68:1,364-1,372.

Gilbert, B.A. and B.J. Moeller. 2008. Modeling elk sightability bias of aerial surveys during winter in the central Cascades. Northwest Science 82:222–228.

Gitzen, R.A., J.J. Millspaugh and B.J. Kernohan. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. Journal of Wildlife Management 70:1,334–1,344.

Gonzalez-Voyer, A., K.G. Smith and M. Festa-Bianchet. 2001. Efficiency of aerial surveys of mountain goats. Wildlife Society Bulletin 29:140–144.

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

Gopalaswamy, A.M., J.A. Royle, M. Delampady, J.D. Nichols, K.U. Karanth and D.W. Macdonald. 2012*b*. Density estimation in tiger populations: combining information for strong inference. Ecology 93:1,741–1,751.

Griffin, P.C., B.C. Lubow, K.J. Jenkins, D.J. Vales, B.J. Moeller, M. Reid, P.J. Happe, S.M. McCorquodale, M.J. Tirhi, J.P. Schaberl and K. Beirne. 2013. A hybrid double observer sightability model for aerial surveys: Hybrid Double-Observer Sightability Model. The Journal of Wildlife Management 77:1,532–1,544.

Gunn, A. and D. Russell (eds.). 2008. Monitoring Rangifer herds (population dynamics) manual. – CircumArctic Rangifer Monitoring and Assessment (CARMA) Network. Available at: www.carmanetwork.com/download/attachments/1114312/demographyþmanual.pdf?version=1

Habib, T.J., D.A. Moore and E.H. Merrill. 2013. Detection and stratification approaches for aerial surveys of deer in prairie parklands. Wildlife Research 39:593.

Haigh, J.C., E.W. Kowal, W. Runge and G. Wobeser. 1982. Pregnancy diagnosis as a management tool for moose. Alces 18:45–53.

Harris, N.C., M.J. Kauffman and L.S. Mills. 2008. Inferences about ungulate population dynamics derived from age ratios. Journal of Wildlife Management 72:1,143–1,151.

Harris, R.B., J. Winnie, S.J. Amish, A. Beja-Pereira, R. Godinho, V. Costa and G. Luikart. 2010. Argali abundance in the Afghan Pamir using capture–recapture modeling from fecal DNA. Journal of Wildlife Management 74:668–677.

Hatter, I.W. and W.A. Bergerud. 1991. Moose recruitment, adult mortality, and rate of change. Alces 27:65–73.

Hatter, I.W. and D.W. Janz. 1994. Apparent demographic changes in black-tailed deer associated with wolf control on northern Vancouver Island. Canadian Journal of Zoology 72:878–884.

Hauser, C.E., A.R. Pople and H.P. Possingham. 2006. Should managed populations be monitored every year? Ecological Applications 16:807–819.

Hayne, D.W. 1949. Calculation of size of home range. Journal of Mammalogy 30:1.

He, F. and K.J. Gaston. 2000. Estimating species abundance from occurrence. The American Naturalist 156:553–559.

Hebblewhite, M., E. Merrill and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141–166.

Hedges, S., A. Johnson, M. Ahlering, M. Tyson and L. S. Eggert. 2013. Accuracy, precision, and cost-effectiveness of conventional dung density and fecal DNA based survey methods to estimate Asian elephant (*Elephas maximus*) population size and structure. Biological Conservation 159:101–108.

Hegel, T.M., K. Russell and T.S. Jung. 2012. Using temporary dye marks to estimate ungulate population abundance in southwest Yukon, Canada. Rangifer, Special Issue No. 20:219–226.

Hemami, M.-R. and M. Momeni. 2013. Estimating abundance of the endangered onager (*Equus hemionus onager*) in Qatruiyeh National Park, Iran. Oryx 47:266–272.

Hervieux, D., M. Hebblewhite, N.J. DeCesare, M. Russell, K. Smith, S. Robertson and S. Boutin. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. Canadian Journal of Zoology 91:872–882.

Hettinga, P.N., A.N. Arnason, M. Manseau, D. Cross, K. Whaley and P.J. Wilson. 2012. Estimating size and trend of the North Interlake woodland caribou population using fecal-DNA and capture-recapture models. The Journal of Wildlife Management 76:1,153–1,164.

Hermanutz, R. and L. Fullerton. 2012. Hay-Zama bison. Pages 21–26. In: M. Ranger and K. Zimmer. Delegated aerial ungulate surveys, 2011/2012 survey season. Data Report, D-2012-00, produced by the Alberta Conservation Association, Sherwood Park, AB.

Hirzel, A.H., J. Hausser, D. Chessel and N. Perrin. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83:2,027–2,036.

Holling, C.S. 1978. Adaptive environmental assessment and management. John Wiley & Sons.

Hood, G.M. 2009. CSIRO, www.cse.csiro.au/poptools, Canberra, Australia.

Hui, C., M.A., McGeoch, B. Reyers, P.C. Roux, M. Greve and S.L. Chown. 2009. Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. Ecological Applications 19:2038–2048.

Humbert, J.Y., L.S. Mills, J.S. Horne and B. Dennis. 2009. A better way to estimate population trends. Oikos 118:1,940-1,946.

Ioannou, C.C., F. Bartumeus, J. Krause and G.D. Ruxton. 2011. Unified effects of aggregation reveal larger prey groups take longer to find. Proceedings of the Royal Society B: Biological Sciences 278:2,985–2,990.

IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. IUCN, Gland, Switzerland and Cambridge, UK.

Ivan, J.S., G.C. White and T.M. Shenk. 2013a. Using auxiliary telemetry information to estimate animal density from capture-recapture data. Ecology 94:809–816.

Ivan, J.S., G.C. White and T.M. Shenk. 2013b. Using simulation to compare methods for estimating density from capture-recapture data. Ecology 94:817–826.

Jacobson, H.A., J.C. Kroll, R.W. Browning, B.H. Koerth and M.H. Conway. 1997. Infrared-triggered cameras for censusing white-tailed deer. Wildlife Society Bulletin 25:547–556.

Jacques, C.N., J.A. Jenks, T.W. Grovenburg, R.W. Klaver and C.S. Deperno. 2014. Incorporating detection probability into northern Great Plains pronghorn population estimates: Pronghorn Detection Probability Model. Journal of Wildlife Management 78:164–174.

Johnson, D.H. 2008. In defense of indices: the case of bird surveys. Journal of Wildlife Management 72:857–868.

Johnson, H.E., L.S. Mills, J.D. Wehausen and T.R. Stephenson. 2010. Combining ground count, telemetry, and mark–resight data to infer population dynamics in an endangered species. Journal of Applied Ecology 47:1,083-1,093.

Jung, T.S. and K. Egli. 2012. Population inventory of the Aishihik wood bison (*Bison bison athabascae*) population in southwestern Yukon, 2011. Yukon Fish and Wildlife Branch Report TR-12-19. Whitehorse, YT.

Karanth, K.U. and J.D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2,852–2,862.

Kelleyhouse, R.A. 2001. Calving ground habitat selection: Teskekpuk Lake and Western Arctic caribou herds. MS thesis, University of Alaska, Fairbanks, AK. 140pp.

Kendall, W.L., J.E. Hines, J.D. Nichols and E.H.C. Grant. 2013. Relaxing the closure assumption in occupancy models: staggered arrival and departure times. Ecology 94:610–617.

Kery, M. and M. Schaub. 2012. Bayesian population analysis using WinBUGS: A hierarchical perspective. Academic Press Waltham, MA.

Khaemba, W.M. and A. Stein. 2002. Improved sampling of wildlife populations using airborne surveys. Wildlife Research 29:269–275.

Khaemba, W.M., A. Stein, D. Rasch, J. De Leeuw and N. Georgiadis. 2001. Empirically simulated study to compare and validate sampling methods used in aerial surveys of wildlife populations. African Journal of Ecology 39:374–382.

Kindopp, R., and M. Vassal. 2010. Wood Buffalo National Park Bison Survey, February 2009. Unpublished Parks Canada Report.

Kissell, R.E. and S.K. Nimmo. 2011. A technique to estimate white-tailed deer *Odocoileus virginianus* density using vertical-looking infrared imagery. Wildlife Biology 17:85–92.

Koenen, K.K.G., S. DeStefano and P.R. Krausman. 2002. Using distance sampling to estimate seasonal densities of desert mule deer in a semidesert grassland. Wildlife Society Bulletin 30:53–63.

Kofinas, G., P. Lyver, D. Russell, R. White, A. Nelson and N. Flanders. 2003. Towards a protocol for community monitoring of caribou body condition. Rangifer 23:43–52.

Kohn, M.H., E.C. York, D.A. Kamradt, G. Haught, R.M. Sauvajot and R.K. Wayne. 1999. Estimating population size by genotyping faeces. Proceedings of the Royal Society of London. Series B: Biological Sciences 266:657–663.

Kolodzinski, J.J., L.V. Tannenbaum, D.A. Osborn, M.C. Conner, W.M. Ford and K.V. Miller. 2010. Effects of GPS sampling intensity on home range analyses. Pages 13–17 *in*. Proc. Annu. Conf. Southeast. Association of Fish and Wildlife Agencies. Volume 64.

Koper, N. and M. Manseau. 2009. Generalized estimating equations and generalized linear mixed-effects models for modeling resource selection. Journal of Applied Ecology 46:590–599.

Krebs, C.J. 1998. Ecological Methodology (Second edition). Benjamin Cummins, Menlo Park, CA.

Krebs, C.J. 2008. Ecology: the experimental analysis of distribution and abundance. Sixth. Benjamin Cummings.

Kumara, H.N., S. Rathnakumar, M.A. Kumar and M. Singh. 2012. Estimating Asian elephant, *Elephas maximus*, density through distance sampling in the tropical forests of Biligiri Rangaswamy Temple Tiger Reserve, India. Tropical Conservation Science 5:163–172.

Kunkel, K. and D.H. Pletscher. 1999. Species-specific population dynamics of cervids in a multipredator ecosystem. Journal of Wildlife Management 63:1,082.

Laake, J., M.J. Dawson and J. Hone. 2008. Visibility bias in aerial survey: mark–recapture, line-transect or both? Wildlife Research 35:299.

Laake, J., R.J. Guenzel, J.L. Bengtson, P. Boveng, M. Cameron and M.B. Hanson. 2008. Coping with variation in aerial survey protocol for line-transect sampling. Wildlife Research 35:289-298.

Lammers, D.K. Ogorzalek, T. Olson, J. Flocchini, S. Forrest, B. Anderson, A. Grajal, D. Jorgensen, C. Kremer, T. LeFaive, J. Majerus, D. Montanye, D. O'Brien, S. Sarver and J. Stone. 2013. Bison Conservation Management: Guidelines for Herd Managers. September 2013. World Wildlife Fund, Inc.

Lampa, S., K. Henle, R. Klenke, M. Hoehn and B. Gruber. 2013. How to overcome genotyping errors in non-invasive genetic mark-recapture population size estimation-A review of available methods illustrated by a case study: Genotyping Errors in CMR-A Review. Journal of Wildlife Management 77:1,490–1,511.

Larter, N.C. and D.G. Allaire. 2007. History and current status of the Nahanni wood bison population. Environment and Natural Resources, Government of the Northwest Territories. File Report No. 136.

Larter, N.C. and D.G. Allaire. 2013a. Dehcho boreal caribou study progress report, April 2013. Environment and Natural Resources, Government of the Northwest Territories.

Larter, N.C. and D.G. Allaire. 2013b. Population Survey of the Nahanni Wood Bison Population, March 2011. Environment and Natural Resources, Government of the Northwest Territories. Manuscript Report No. 229.

Larter, N.C., A.R.E. Sinclair, T. Ellsworth, J. Nishi and C.C. Gates. 2000. Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. Animal Conservation 4:299-309.

Latham, M.C., A.D.M. Latham, N.F. Webb, N.A. Mccutchen and S. Boutin. 2014. Can occupancy–abundance models be used to monitor wolf abundance? D. Russo, editor. PLoS ONE 9:e102982.

Lele, S.R., E.H. Merrill, J. Keim and M.S. Boyce. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. F. Huettmann, editor. Journal of Animal Ecology 82:1,183–1,191.

Lohr, S.L. 1999. Sampling: design and analysis. Duxbury Press.

Long, R.A., P. MacKay, W.J. Zielinski and J.C. Ray. 2008. Noninvasive survey methods for carnivores. Island Press.

Lukacs, P.M. and K.P. Burnham. 2005. Estimating population size from DNA-based closed capture-recapture data incorporating genotyping error. Journal of Wildlife Management 69:396–403.

MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J. Andrew Royle and C.A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2,248–2,255.

MacKenzie, D.I., J.D. Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey and J.E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press.

MacKenzie, D.I. and J.A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1,105–1,114.

Mahoney, S.P., J.A. Virgl, D.A. Fong, A.A. MacCharles and M. McGrath. 1998. Evaluation of a mark-resighting technique for woodland caribou in Newfoundland. Journal of Wildlife Management 62:1,227–1,265.

Manly, B.F.J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology, 2nd edition. Chapman and Hall. London, UK.

Manly, B.F.J., L. McDonald, D. Thomas, T.L. McDonald and W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second. Kluwere Academic Publishers.

Marques, T.A., M. Andersen, S. Christensen-Dalsgaard, S. Belikov, A. Boltunov, Ø. Wiig, S.T. Buckland and J. Aars. 2006. The use of global positioning systems to record distances in a helicopter line-transect survey. Wildlife Society Bulletin 34:759–763.

Marzluff, J.M., J.J. Millspaugh, P. Hurvitz and M.S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85:1,411–1,427.

Mathewson, H.A., J.E. Groce, T.M. Mcfarland, M.L. Morrison, J.C. Newnam, R.T. Snelgrove, B.A. Collier and R.N. Wilkins. 2012. Estimating breeding season abundance of golden-cheeked warblers in Texas, USA. Journal of Wildlife Management 76:1,117–1,128.

McClintock, B.T. and G.C. White. 2009. A less field-intensive robust design for estimating demographic parameters with mark-resight data. Ecology 90:313–320.

McClintock, B.T. and G.C. White. 2010. From NOREMARK to MARK: software for estimating demographic parameters using mark-resight methodology. Journal of Ornithology.

McCullough, D.R. 1994. What do herd composition counts tell us? Wildlife Society Bulletin 22:295–300.

McCullough, P. and J.A. Nelder. 1989. Generalized Linear Models. Volume 2.Chapman and Hall, New York, NY.

McCorquodale, S.M., S.M. Knapp, M.A. Davison, J.S. Bohannon, C.D. Danilson and W.C. Madsen. 2013. Mark-resight and sightability modeling of a western Washington elk population. Journal of Wildlife Management 77:359–371.

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

McLellan, B.N., R. Serrouya, H.U. Wittmer and S. Boutin. 2010. Predator-mediated Allee effects in multiprey systems. Ecology 91:286–292.

McMahon, C.R., BW. Brook, D.M.J.S. Bowman, G.J. Williamson and C.J.A. Bradshaw. 2011. Fertility partially drives the relative success of two introduced bovines (*Bubalus bubalis* and *Bos javanicus*) in the Australian tropics. Wildlife Research 38:386–395.

Merkle, J.A. and D. Fortin. 2014. Likelihood-based photograph identification: Application with photographs of free-ranging bison. Wildlife Society Bulletin 38: 196–204.

Merz, G. 1986. Counting elephants (*Loxodonta africana cyclotis*) in tropical rain forests with particular reference to the Tai National Park, Ivory Coast. African Journal of Ecology 24:61–68.

Millspaugh, J.J., R.M. Nielson, L. McDonald, J.M. Marzluff, R.A. Gitzen, C.D. Rittenhouse, M.W. Hubbard and S.L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70:384–395.

Miller, D.L., M.L. Burt, E.A. Rexstad and L. Thomas. 2013. Spatial models for distance sampling data: recent developments and future directions. Methods in Ecology and Evolution doi: 10.1111/2041-210X.12105.

Minta, S. and M. Mangel. 1989. A simple population estimate based on simulation for capture-recapture and capture-resight data. Ecology 70:1,738–1,751.

Mitchell, J.A. 2002. A landscape evaluation of bison movements and distribution in northern Canada. M.E. Des. Thesis. University of Calgary, Calgary, AB. 135pp.

Moesker, M. 2004. An annotated bibliography of traditional ecological knowledge and wood bison; an overview of research projects, literature and people. Vrije Universiteit, Amsterdam, The Netherlands, and the Institute of the Environment, University of Ottawa, Ottawa, ON.

Moller, H., F. Berkes, P.O. Lyver and M. Kislalioglu. 2004. Combining science and traditional ecological knowledge: monitoring populations for co-management. Ecology and Society 9: 2. [online] URL: www.ecologyandsociety.org/vol9/iss3/art2/

Morden, C.-J.C., R.B. Weladji, E. Ropstad, E. Dahl, Ø. Holand, G. Mastromonaco and M. Nieminen. 2011. Fecal hormones as a non-invasive population monitoring method for reindeer. Journal of Wildlife Management 75:1,426–1,435.

Morris, W.F. and D.F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Inc., Sunderland, MA.

Mysterud, A. and R.A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1,435–1,441.

Neal, A.K., G.C. White, R.B. Gill, D.F. Reed and J.H. Olterman. 1993. Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. Journal of Wildlife Management 436–450.

Neff, D. J. 1968. The pellet-group count technique for big game trend, census, and distribution: a review. The Journal of Wildlife Management 32:597.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. The Auk 117:393.

Nilsen, E.B., S. Pedersen and J.D.C. Linnell. 2008. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecological Research 23:635–639.

Nishi, J.S., T.R. Ellsworth, N. Lee, D. Dewar, B.T. Elkin and D.C. Dragon. 2007. An outbreak of anthrax (*Bacillus anthracis*) in free-roaming bison in the Northwest Territories, June–July 2006. Canadian Veterinary Journal 48:37–38.

Noon, B.R., N.M. Ishwar and K. Vasudevan. 2006. Efficiency of Adaptive Cluster and Random Sampling in Detecting Terrestrial Herpetofauna in a Tropical Rainforest. Wildlife Society Bulletin 34:59–68.

Ogutu, J.O., N. Bhola, H.-P. Piepho and R. Reid. 2006. Efficiency of strip- and line-transect surveys of African savanna mammals. Journal of Zoology 269:149–160.

Otis, D.L., K.P. Burnham, G.C. White and D.R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:3–135.

Ottichilo, W., J. de Leeuw and H. HT Prins. 2001. Population trends of resident wildebeest [*Connochaetes taurinus hecki* (Neumann)] and factors influencing them in the Masai Mara ecosystem, Kenya. Biological Conservation 97:271–282.

Pacifici, K., R.M. Dorazio and M.J. Conroy. 2012. A two-phase sampling design for increasing detections of rare species in occupancy surveys: Two-phase sampling design for rare species. Methods in Ecology and Evolution 3:721–730.

Parks Canada. 2010. Wood Buffalo National Park of Canada management plan. Wood Buffalo National Park of Canada Headquarters, Fort Smith, NWT.

Parlee, B.L., E. Goddard, Ł.K.D. First Nation and M. Smith. 2014. Tracking change: traditional knowledge and monitoring of wildlife health in northern Canada. Human Dimensions of Wildlife, 19, 47–61.

Peters, W., M. Hebblewhite, K.G. Smith, S.M. Webb, N. Webb, M. Russell, C. Stambaugh and R.B. Anderson. 2014. Contrasting aerial moose population estimation methods and evaluating sightability in west-central Alberta, Canada: Distance Sampling for Moose Population Estimation. Wildlife Society Bulletin 38:639–649.

Phillips, S.J., R.P. Anderson and R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling 190:231–259.

Plhal, R., J. Kamler, M. Homolka and Z. Adamec. 2011. An assessment of the applicability of photo trapping to estimate wild boar population density in a forest environment. Folia Zoologica 60:237–246.

Poley, L.G., B.A. Pond, J.A. Schaefer, G.S. Brown, J.C. Ray and D.S. Johnson. 2014. Occupancy patterns of large mammals in the Far North of Ontario under imperfect detection and spatial autocorrelation. W. D. Kissling, editor. Journal of Biogeography 41:122–132.

Polfus, J.L., K. Heinemeyer, M. Hebblewhite and Taku River Tlingit First Nation. 2014. Comparing traditional ecological knowledge and western science woodland caribou habitat models: TEK Caribou Habitat Models. The Journal of Wildlife Management 78:112–121

Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. The Journal of Wildlife Management 46:752–757.

Pollock, K.H., J.D. Nichols, C. Brownie and J.E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:1–97.

Pollock, K.H., S.R. Winterstein, C.M. Bunck and P.D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.

Poole, K.G., D.M. Reynolds, G. Mowat and D. Paetkau. 2011. Estimating mountain goat abundance using DNA from fecal pellets. The Journal of Wildlife Management 75:1,527–1,534.

Poole, K.G., C. Cuyler and J. Nymand. 2013. Evaluation of caribou *Rangifer tarandus groenlandicus* survey methodology in West Greenland. Wildlife Biology 19:225-239.

Pradel, R. 1996. Utilization of mark–recapture for the study of recruitment and population growth. Biometrics 52:703–709.

R Development Core Team. 2009. R Foundation for Statistical Computing, Vienna, Austria.

Rachlow, J.L. and L.K. Svancara. 2006. Prioritizing habitat for surveys of an uncommon mammal: a modeling approach applied to pygmy rabbits. Journal of Mammalogy 87:827–833.

Rasiulis, A.L., M. Festa-Bianchet, S. Couturier and S.D. Côté. 2014. The effect of radio-collar weight on survival of migratory caribou. The Journal of Wildlife Management 78:953–956.

Rees, S.G., A.E. Goodenough, A.G. Hart and R. Stafford. 2011. Testing the effectiveness of capture mark recapture population estimation techniques using a computer simulation with known population size. Ecological Modeling 222:3,291–3,294.

Rice, C.G., K.J. Jenkins and W.-Y. Chang. 2009. A sightability model for mountain goats. Journal of Wildlife Management 73:468–478.

Rovero, F. and A.R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology 46:1,011–1,017.

Rowcliffe, J.M., J. Field, S.T. Turvey and C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. Journal of Applied Ecology 45:1,228–1,236.

Rowe, M. 2006. 2006 Halfway-Sikanni plains bison inventory. British Columbia Ministry of Environment, Peace Region.

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

Royle, J.A. 2008. Hierarchical modeling of cluster size in wildlife surveys. Journal of Agricultural Biological and Environmental Statistics 13:23-36.

Royle, J.A., R.B. Chandler, C.C. Sun and A.K. Fuller. 2013. Integrating resource selection information with spatial capture-recapture. D. Warton, editor. Methods in Ecology and Evolution 4:520–530.

Salb, A., C. Stephen, C. Ribble and B. Elkin. 2014. Descriptive epidemiology of detected anthrax outbreaks in wild wood bison (*Bison bison athabascae*) in northern Canada, 1962–2008. Journal of Wildlife Diseases 50:459–468

Samuel, M.D., E.O. Garton, M.W. Schlegel and R.G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. The Journal of wildlife management 622–630.

Schaefer, J.A. 2003. Long-Term Range Recession and the Persistence of Caribou in the Taiga. Conservation Biology 17:1,435–1,439.

Schmidt, J.H. and K.L. Rattenbury. 2013. Reducing effort while improving inference: Estimating Dall's sheep abundance and composition in small areas: abundance and composition with small samples. The Journal of Wildlife Management 77:1,048–1,058.

Schramm, T. 2002. Caribou Mountains critical ungulate habitat and Traditional Ecological Knowledge study, a GIS analysis. Department of Renewable Resources, University of Alberta, Edmonton, AB.

Schwarz, C.J. 2001. The Jolly-Seber model: More than just abundance. Journal of Agricultural, Biological, and Environmental Statistics 6:195-205.

Seddon, P.J., K. Ismail, M. Shobrak, S. Ostrowski and C. Magin. 2003. A comparison of derived population estimate, mark-resighting and distance sampling methods to determine the population size of a desert ungulate, the Arabian oryx. Oryx 37: 286-294.

Shury, T.K., D. Frandsen and L. O'Brodovich. 2008. Anthrax in free-ranging bison in the Prince Albert National Park area of Saskatchewan in 2008. Canadian Veterinary Journal 50:152–154.

Silver, S.C., L.E.T. Ostro, L.K. Marsh, L. Maffei, A.J. Noss, M.J. Kelly, R.B. Wallace, H. Gómez and G. Ayala. 2004. The use of camera traps for estimating jaguar (*Panthera onca*) abundance and density using capture/recapture analysis. Oryx 38: 148-154.

Sinclair, A.R.E., J.M. Fryxell and G. Caughley. 2006. Wildlife ecology, conservation, and management, second edition. Wiley-Blackwell.

Skalski, J.R., J.J. Millspaugh and R.D. Spencer. 2005a. Population estimation and biases in paintball, mark-resight surveys of elk. Hudson, editor. Journal of Wildlife Management 69:1043–1052.

Skalski, J.R., K.E. Ryding and J.J. Millspaugh. 2005b. Wildlife demography: analysis of sex, age, and count data. Elsevier Academic Press, Amsterdam.

Skogland, T. 1984. The effects of food and maternal conditions in fetal growth and size in wild reindeer. Rangifer 4:39–46.

Smith, D.R., M.J. Conroy and D.H. Brakhage. 1995. Efficiency of adaptive cluster sampling for estimating density of wintering waterfowl. Biometrics 51:777.

Smith, D.R., R.F. Villella and D.P. Lemarié. 2003. Application of adaptive cluster sampling to low-density populations of freshwater mussels. Environmental and Ecological Statistics 10:7–15.

Soetart, K. 2014. Plotting multi-dimensional data (plot3d) for program R. in /R-Forge/Project: plot3d. Sollmann, R., B. Gardner, A.W. Parsons, J.J. Stocking, B.T. McClintock, T.R. Simons, K.H. Pollock and A.F. O'Connell. 2013. A spatial mark-resight model augmented with telemetry data. Ecology 94:553–559.

Sollmann, R., B. Gardner, A.W. Parsons, J.J. Stocking, B.T. McClintock, T.R. Simons, K.H. Pollock and A.F. O'Connell. 2013. A spatial mark-resight model augmented with telemetry data. Ecology 94:553–559.

Species at Risk. 2010. Wood Bison Management Strategy for the Northwest Territories. NWT Species at Risk. Environment and Natural Resources, Government of the Northwest Territories.

Steinhorst, R.K. and M.D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 415–425.

Sullivan, W.P., B.J. Morrison and F.W.H. Beamish. 2008. Adaptive Cluster Sampling: Estimating Density of Spatially Autocorrelated Larvae of the Sea Lamprey with Improved Precision. Journal of Great Lakes Research 34:86–97.

Swenson, J.E., K. Wallin, G. Ericsson, G. Cederlund and F. Sandegren. 1999. Effects of ear-tagging with radiotransmitters on survival of moose calves. The Journal of Wildlife Management 63:354.

Tessaro, S.V. 1989. Review of the disease, parasites, and miscellaneous pathological conditions of North American bison. Canadian Veterinary Journal 31:174–180.

Testa, J.W., E.F. Becker and G.R. Lee. 2000. Movements of female moose in relation to birth and death of calves. Alces 36:155–162.

Thiessen, C. 2012. Peace Wood Bison: Annual Report 2011/12. British Columbia Ministry of Forests, Lands, and Natural Resource Operations, Fort St. John.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R.B. Bishop, T.A. Marques and K.P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Thompson, S. K. 1990. Adaptive cluster sampling. Journal of the American Statistical Association 85:1050.

Thompson, S.K. 2012. Sampling. Third. Wiley, New York, NY.

Thompson, S.K. 2013. Adaptive web sampling in ecology. Statistical Methods & Applications 22:33–43.

Thompson, W.L. 2004. Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters. Island Press.

Thompson, W.L., G.C. White and C. Gowan. 1998. Monitoring Vertebrate Populations. Academic Press, San Diego, CA.

Thorley, J.L. and Boulanger, J. 2015. Mackenzie Wood Bison Population Dynamics Analysis 2015. A Poisson Consulting Analysis Report.
URL: www.poissonconsulting.ca/f/164478860.

Thurmond, M.C. 2003. Conceptual foundations for infectious disease surveillance. Journal of Veterinary Diagnostic Investigation 15:501–514.

Tobler, M.W., S.E. Carrillo-Percastegui and G. Powell. 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. Journal of Tropical Ecology 25:261.

Turechek, W.W. and L.V. Madden. 1999. Spatial pattern analysis and sequential sampling for the incidence of leaf spot on strawberry in Ohio. Plant disease 83:992–1,000.

Valkenburg, P., M.A. Keech, R.A. Sellers, R.W. Tobey and B.W. Dale. 2002. Investigations of regulating and limiting factors in the Delta caribou herd. Research Final Report. Federal Aid in Wildlife Restoration, Projects W-24-5, W-27-1-5, Study 3.42. Alaska Department of Fish and Game, Juneau, AK.

Vander Wal, E., P.D. McLoughlin and R.K. Brook. 2011. Spatial and temporal factors influencing sightability of elk. The Journal of Wildlife Management 75:1,521–1,526.

Vore, J.M. and E.M. Schmidt. 2001. Movements of female elk during calving season in northwest Montana. Wildlife Society Bulletin 29:720–725.

Walsh, D.P., H. Campa, D.E. Beyer and S.R. Winterstein. 2011. Measurement error and survey design in sightability model development. The Journal of Wildlife Management 75:1,228–1,235.

Walsh, D.P., ed. 2012. Enhanced surveillance strategies for detecting and monitoring chronic wasting disease in free-ranging cervids. U.S. Geological Survey Open-File Report 2012–1036. 42pp.

Walsh, D.P., C.F. Page, H. Campa, S.R. Winterstein and D.E. Beyer. 2009. Incorporating estimates of group size in sightability models for wildlife. Journal of Wildlife Management 73:136–143.

Waltert, M., S. Heber, S. Riedelbauch, J.L. Lien and M. Muhlenberg. 2006. Estimates of blue duiker (*Cephalophus monticola*) densities from diurnal and nocturnal line transects in the Korup region, south-western Cameroon. African Journal of Ecology 44:290–292.

Wasser, S.K., J.L. Keim, M.L. Taper and S.R. Lele. 2012. To kill or not kill - that is the question. Frontiers in Ecology and the Environment 10:67–68.

Watson, R.M., I.S.C. Parker and T. Allan. 1969. A census of elephant and other large mammals in the Mkomazi region of northern Tanzania and southern Kenya. East African Wildlife Journal 7:11–26.

Weaver, S.P. and F.W. Weckerly. 2011. Sex ratio estimates of Roosevelt elk using counts and Bowden's estimator. California Fish and Game 97:130–137.

Wegge, P. and T. Storaas. 2009. Sampling tiger ungulate prey by the distance method: lessons learned in Bardia National Park, Nepal. Animal Conservation 12:78–84.

White, G.C. 1996. NOREMARK: Population estimation from mark-resight surveys. Wildlife Society Bulletin 24:50–52.

White, G.C., D.J. Freddy, R.B. Gill and J.H. Ellenberger. 2001. Effect of adult sex ratio on mule deer and elk productivity in Colorado. Journal of Wildlife Management 65:543–551.

White, G.C. and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study Supplement 46:120-138.

White, G.C. and B. Lubow. 2002. Fitting population models to multiple sources of observed data. Journal of Wildlife Management 66:300-309.

White, G.C., K.P. Burnham and D.R. Anderson. 2002. Advanced features of program MARK. Pages 368-377 in R. Fields, R.J. Warren, H. Okarma and P.R. Seivert, editors. Integrating People and Wildlife for a Sustainable Future: Proceedings of the Second International Wildlife Management Congress. Gödölló, Hungary.

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

Williams, R. and L. Thomas. 2009. Cost-effective abundance estimation of rare animals: Testing performance of small-boat surveys for killer whales in British Columbia. Biological Conservation 142:1,542–1,547.

Wittmer, H.U., R.N.M. Ahrens and B.N. McLellan. 2010. Viability of mountain caribou in British Columbia, Canada: Effects of habitat change and population density. Biological Conservation 143:86–93.

Wittmer, H.U., B.N. McLellan, D.R. Seip, J.A. Young, T.A. Kinley, G.S. Watts and D. Hamilton. 2005. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. Canadian Journal of Zoology 83:407–418.

Woolley, T. and F.G. Lindzey. 1997. Relative precision and sources of bias in pronghorn sex and age composition surveys. Journal of Wildlife Management 61:57-63.

Worton, B.J. 1987. A review of models of home range for animal movement. Ecological Modeling 38:277–298.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164.

Wray, K. and B. Parlee. 2013. Ways we respect caribou: Teetl'it Gwich'in rules. Arctic 66:68–78.

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

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 Assoc 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.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
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

APPENDIX C: MACKENZIE WOOD BISON POPULATION DYNAMICS ANALYSIS 2015

Draft: 11 May 2015

Suggested Citation: Thorley, J.L. and J. Boulanger. 2015. Mackenzie Wood Bison Population Dynamics Analysis 2015. A Poisson Consulting Analysis Report.
URL: www.poissonconsulting.ca/f/164478860.

The source code is available on GitHub.

Background

The Mackenzie wood bison (*Bison bison athabascae*) herd abundance has been estimated in four years since 1999 while herd composition data have been collected in all but three years. The herd composition data are collected in July while the abundance estimates are from March.

The primary questions this analysis attempts to answer are:

- What is the survival of calves, yearlings and adult in the Mackenzie herd?
- Is survival of calves in the Mackenzie herd driven by climatic conditions?

Methods

Data Preparation

The data were provided by the Government of the Northwest Territories.

In 2012 the herd experienced high mortality due to an anthrax outbreak. Consequently, the 2013 and 2014 data were excluded.

Statistical Analysis

Hierarchical Bayesian models were fitted to the data using R version 3.2.0 (Team 2013) and JAGS 3.4.0 (Plummer 2012) which interfaced with each other via jaggernaut 2.2.10 (Thorley 2013). For additional information on hierarchical Bayesian modeling in the BUGS language, of which JAGS uses a dialect, the reader is referred to Kery and Schaub (2011, 41–44).

Unless specified, the models assumed vague (low information) prior distributions (Kery and Schaub 2011, 36). The posterior distributions were estimated from a minimum of 1,000 Markov Chain Monte Carlo (MCMC) samples thinned from the second halves of three chains (Kery and Schaub 2011, 38–40). Model convergence was confirmed by ensuring that Rhat (Kery and Schaub 2011, 40) was less than 1.1 for each of the parameters in the model (Kery and Schaub 2011, 61). Model adequacy was confirmed by examination of residual plots.

The posterior distributions of the *fixed* (Kery and Schaub 2011, 75) parameters are summarised in terms of a *point* estimate (mean), *lower* and *upper* 95% credible limits (2.5th and 97.5th percentiles), the standard deviation (*SD*), percent relative *error* (half the 95% credible interval as a percent of the point estimate) and *significance* (Kery and Schaub 2011, 37, 42).

Variable selection was achieved by dropping *insignificant* (Kery and Schaub 2011, 37, 42) fixed (Kery and Schaub 2011, 77–82) variables and *uninformative* random variables. A fixed variable was considered to be insignificant if its significance was ≥ 0.05 while a random variable was considered to be uninformative if it's percent relative error was ≥ 80%.

The results are displayed graphically by plotting the modeled relationships between particular variables and the response with 95% credible intervals (CRIs) with the remaining variables held constant. In general, continuous and discrete fixed variables are held constant at their mean and first level values respectively while random variables are held constant at their typical values (expected values of the underlying hyperdistributions) (Kery and Schaub 2011, 77–82). Where informative the influence of particular variables is expressed in terms of the *effect size* (i.e., percent change in the response variable) with 95% CRIs (Bradford, Korman, and Higgins 2005).

Model Description

The following model description observes several conventions.

The survival between life stages was estimated using a hierarchical Bayesian population dynamic state-space model (Kery and Schaub 2011). Key assumptions of the population dynamic model include:

- A 50:50 sex ratio.
- Constant probability of a female adult calving.
- Annually varying calf survival.
- Calf survival is able to vary with the Pacific Decadal Oscillation Index.
- Constant and identical yearling and adult survival.
- Clustering of cows with and without calves.
- Each year runs from May 15 to May 15.
- Survival does not vary seasonally.

In addition the effect of various environmental variables on calf survival was tested by adding a standardised covariate to the population dynamic model.

Model Code

The JAGS model code, which uses a series of naming conventions, is presented below.

Population Dynamic

Variable/Parameter	**Description**
bAdults[i]	Number of adults at the start of the ith year
bAdults1	Number of adults at the start of the first year
bCalves[i]	Number of calves at the start of the ith year
Bison[i]	The ith herd size estimate
bProductivity	Probability of a female adult calving
bSurvivalAdult	Adult and yearling survival
bSurvivalCalf	Calf survival
bYearlings[i]	Number of yearlings at the start of the ith year
bYearlings1	Number of yearlings at the start of the first year
Calves[i]	Number of calves in the ith composition observation
Cows[i]	Number of cows in the ith composition observation
Dayte[i]	Day of the year of the ith composition observation
eCorrection	Survival correction for the timing of the herd size estimates
eProportionCalves[i]	Expected proportion of cows with a calf in the ith composition observation
eProportionCowsYearlings[i]	Expected proportion of cows and yearlings that are cows in the ith composition observation
eSurvivalCalfYear[i]	Calf survival from the ith to i+1th year
sDispersionCalves	SD of the extra-binomial variation in cow with calf clustering
sSurvivalCalfYear	SD of the effect of year on bSurvivalCalf
YearBison[i]	The year of the ith herd size estimate
YearlingsCows[i]	Number of yearlings and cows in the ith composition observation

Population Dynamic - Model1

```
model{

 bProductivity ~ dunif(0, 1)
 bSurvivalAdult ~ dunif(0, 1)
 bSurvivalCalf ~ dunif(0, 1)

 sSurvivalCalfYear ~ dunif(0, 2)
```

```
  for(i in 1:nYear){
    bSurvivalCalfYear[i] ~ dnorm(0, sSurvivalCalfYear^-2)
    logit(eSurvivalCalfYear[i]) <- logit(bSurvivalCalf) + bSurvivalCalfYear[i]
  }

  bYearlings1 ~ dunif(0, 500)
  bAdults1 ~ dunif(0, 4000)

  bCalves[1] <- bAdults1 / 2 * bProductivity
  bYearlings[1] <- bYearlings1
  bAdults[1] <- bAdults1

  for(i in 2:nYear){
    bCalves[i] <- bAdults[i-1] / 2 * bSurvivalAdult * bProductivity
    bYearlings[i] <- bCalves[i-1] * eSurvivalCalfYear[i-1]
    bAdults[i] <- (bYearlings[i-1] + bAdults[i-1]) * bSurvivalAdult
  }

  eCorrection <- 308/365
  for(i in 1:length(YearBison)) {
    eCalves[i] <- bCalves[YearBison[i]] * eSurvivalCalfYear[YearBison[i]]^eCorrection
    eYearlings[i] <- bYearlings[YearBison[i]] * bSurvivalAdult^eCorrection
    eAdults[i] <- bAdults[YearBison[i]] * bSurvivalAdult^eCorrection

    eBison[i] <- eCalves[i] + eYearlings[i] + eAdults[i]
    Bison[i] ~ dnorm(eBison[i], 250^-2)
  }

  sDispersionCalves ~ dunif(0, 2)
  for(i in 1:length(Year)) {
    eCorComp[i] <- ((Dayte[i] - 135) / 365)
    eCalvesComp[i] <- bCalves[Year[i]] * eSurvivalCalfYear[Year[i]]^eCorComp[i]
    eYearlingsComp[i] <- bYearlings[Year[i]] * bSurvivalAdult^eCorComp[i]
    eAdultsComp[i] <- bAdults[Year[i]] * bSurvivalAdult^eCorComp[i]

    eCowsComp[i] <- eAdultsComp[i] / 2

    eDispersionCalves[i] ~ dnorm(0, sDispersionCalves^-2)
    logit(eProportionCalves[i]) <- logit(eCalvesComp[i] / eCowsComp[i]) + eDispersionCalves[i]
```

```
  eProportionCowsYearlings[i] <- eCowsComp[i] / (eYearlingsComp[i] + eCowsComp[i])

  Calves[i] ~ dbin(eProportionCalves[i], Cows[i])
  Cows[i] ~ dbin(eProportionCowsYearlings[i], YearlingsCows[i])
 }
}
```

Environmental

Variable/Parameter	Description
bSurvivalCalfEnv	Effect of the environmental variable on bSurvivalCalf

Environmental - Model1

```
model{

 bProductivity ~ dunif(0, 1)
 bSurvivalAdult ~ dunif(0, 1)
 bSurvivalCalf ~ dunif(0, 1)

 bSurvivalCalfEnv ~ dnorm(0, 2^-2)
 sSurvivalCalfYear ~ dunif(0, 2)
 for(i in 1:nYear){
  bSurvivalCalfYear[i] ~ dnorm(0, sSurvivalCalfYear^-2)
  logit(eSurvivalCalfYear[i]) <- logit(bSurvivalCalf) + bSurvivalCalfEnv * Env[i] + bSurvival
CalfYear[i]
 }

 bYearlings1 ~ dunif(0, 500)
 bAdults1 ~ dunif(0, 4000)

 bCalves[1] <- bAdults1 / 2 * bProductivity
 bYearlings[1] <- bYearlings1
 bAdults[1] <- bAdults1

 for(i in 2:nYear){
  bCalves[i] <- bAdults[i-1] / 2 * bSurvivalAdult * bProductivity
  bYearlings[i] <- bCalves[i-1] * eSurvivalCalfYear[i-1]
  bAdults[i] <- (bYearlings[i-1] + bAdults[i-1]) * bSurvivalAdult
 }

 eCorrection <- 308/365
```

```
 for(i in 1:length(YearBison)) {
  eCalves[i] <- bCalves[YearBison[i]] * eSurvivalCalfYear[YearBison[i]]^eCorrection
  eYearlings[i] <- bYearlings[YearBison[i]] * bSurvivalAdult^eCorrection
  eAdults[i] <- bAdults[YearBison[i]] * bSurvivalAdult^eCorrection

  eBison[i] <- eCalves[i] + eYearlings[i] + eAdults[i]
  Bison[i] ~ dnorm(eBison[i], 250^-2)
 }

 sDispersionCalves ~ dunif(0, 2)
 for(i in 1:length(Year)) {
  eCorComp[i] <- ((Dayte[i] - 135) / 365)
  eCalvesComp[i] <- bCalves[Year[i]] * eSurvivalCalfYear[Year[i]]^eCorComp[i]
  eYearlingsComp[i] <- bYearlings[Year[i]] * bSurvivalAdult^eCorComp[i]
  eAdultsComp[i] <- bAdults[Year[i]] * bSurvivalAdult^eCorComp[i]

  eCowsComp[i] <- eAdultsComp[i] / 2

  eDispersionCalves[i] ~ dnorm(0, sDispersionCalves^-2)
  logit(eProportionCalves[i]) <- logit(eCalvesComp[i] / eCowsComp[i]) + eDispersionCalve
s[i]
  eProportionCowsYearlings[i] <- eCowsComp[i] / (eYearlingsComp[i] + eCowsComp[i])

  Calves[i] ~ dbin(eProportionCalves[i], Cows[i])
  Cows[i] ~ dbin(eProportionCowsYearlings[i], YearlingsCows[i])
 }
}
```

Results

Model Parameters

The posterior distributions for the *fixed* (Kery and Schaub 2011, 75) parameters in each model are summarised below.

Population Dynamic

Parameter	Estimate	Lower	Upper	SD	Error	Significance
bAdults1	1780.00000	1273.00000	2303.00000	259.00000	29	0.001
bProductivity	0.45970	0.40530	0.51670	0.02960	12	0.001
bSurvivalAdult	0.88991	0.85823	0.92207	0.01622	4	0.001
bSurvivalCalf	0.44130	0.32300	0.60060	0.07020	31	0.001
bYearlings1	279.70000	185.10000	381.60000	48.40000	35	0.001
sDispersionCalves	0.74820	0.60320	0.91880	0.08010	21	0.001
sSurvivalCalfYear	0.66580	0.33460	1.23600	0.23260	68	0.001

Convergence	Iterations
1.01	1e+05

Environmental - Pacific Decadal Oscillation

Parameter	Estimate	Lower	Upper	SD	Error	Significance
bAdults1	1763.0000	1283.00000	2290.00000	261.00000	29	0.0010
bProductivity	0.4550	0.40150	0.51470	0.02940	12	0.0010
bSurvivalAdult	0.8910	0.86025	0.92222	0.01589	3	0.0010
bSurvivalCalf	0.4459	0.33070	0.57910	0.06430	28	0.0010
bSurvivalCalfEnv	-0.3077	-0.73910	0.13260	0.22140	140	0.1378
bYearlings1	277.6000	191.50000	379.90000	47.70000	34	0.0010
sDispersionCalves	0.7528	0.60290	0.93010	0.08200	22	0.0010
sSurvivalCalfYear	0.6090	0.24400	1.28700	0.25900	86	0.0010

Convergence	Iterations
1.01	1e+05

Environmental - Winter Severity Index

Parameter	Estimate	Lower	Upper	SD	Error	Significance
bAdults1	1768.00000	1293.00000	2306.00000	260.00000	29	0.0010
bProductivity	0.45660	0.40040	0.51560	0.02950	13	0.0010
bSurvivalAdult	0.88925	0.85634	0.92127	0.01612	4	0.0010
bSurvivalCalf	0.44660	0.31550	0.59530	0.07000	31	0.0010
bSurvivalCalfEnv	0.17980	-0.28890	0.67070	0.24050	270	0.3893
bYearlings1	276.70000	189.90000	374.20000	48.80000	33	0.0010
sDispersionCalves	0.74890	0.59600	0.91360	0.08140	21	0.0010
sSurvivalCalfYear	0.69000	0.32500	1.34500	0.25000	74	0.0010

Convergence	Iterations
1.01	1e+05

Environmental - Rainfall

Parameter	Estimate	Lower	Upper	SD	Error	Significance
bAdults1	1785.50000	1294.10000	2285.60000	256.10000	28	0.0010
bProductivity	0.46020	0.40370	0.52020	0.02970	13	0.0010
bSurvivalAdult	0.88934	0.85726	0.92169	0.01665	4	0.0010
bSurvivalCalf	0.44340	0.30310	0.61400	0.07660	35	0.0010
bSurvivalCalfEnv	-0.00900	-0.60000	0.56900	0.29700	6700	0.9781
bYearlings1	281.70000	189.90000	387.00000	50.00000	35	0.0010
sDispersionCalves	0.74970	0.59400	0.92190	0.07990	22	0.0010
sSurvivalCalfYear	0.71800	0.35500	1.37300	0.26000	71	0.0010

Convergence	Iterations
1.01	1e+05

Environmental - Summer Air Temperature

Parameter	Estimate	Lower	Upper	SD	Error	Significance
bAdults1	1771.20000	1301.40000	2269.50000	252.70000	27	0.0010
bProductivity	0.45900	0.40270	0.51810	0.02970	13	0.0010
bSurvivalAdult	0.89212	0.86129	0.92205	0.01558	3	0.0010
bSurvivalCalf	0.42610	0.30690	0.57820	0.06710	32	0.0010
bSurvivalCalfEnv	0.31410	-0.12770	0.75160	0.21490	140	0.1378
bYearlings1	277.30000	197.10000	377.40000	46.40000	33	0.0010
sDispersionCalves	0.74130	0.59450	0.91120	0.08130	21	0.0010
sSurvivalCalfYear	0.60890	0.28370	1.12560	0.22700	69	0.0010

Convergence	Iterations
1.01	1e+05

Figures

Population Dynamic

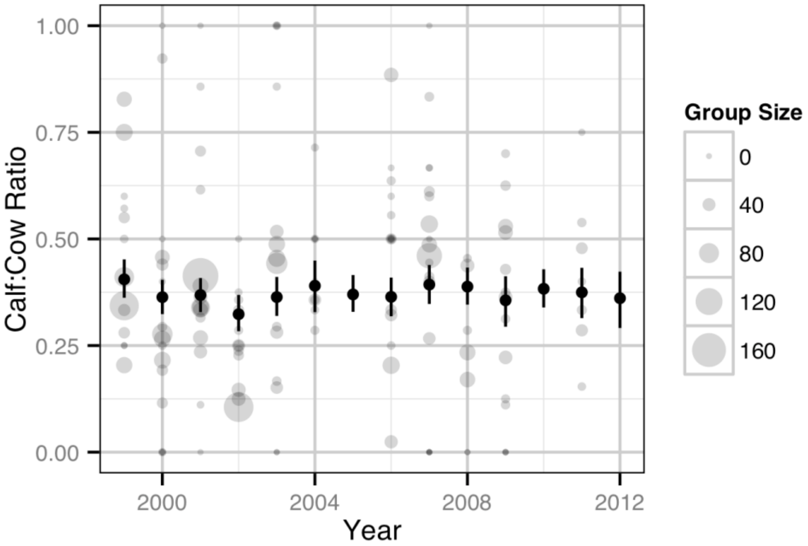

Figure 1. The predicted calf:cow ratio (black symbols ±95% credible intervals) and field composition data by year.

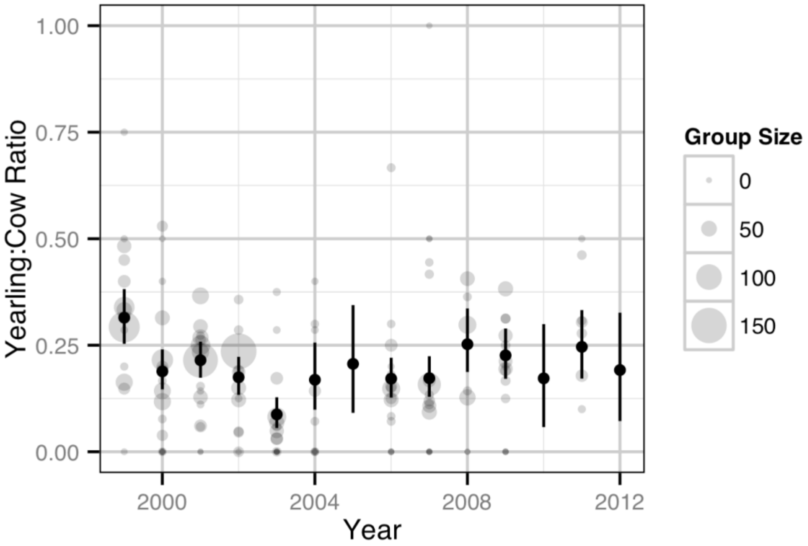

Figure 2. The predicted yearling:cow ratio (±95% credible intervals) and field composition data by year.

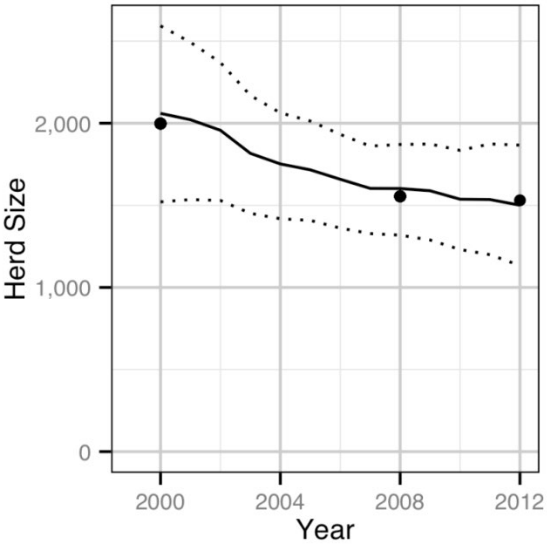

Figure 3. The predicted herd size (±95% credible intervals) in March by year.

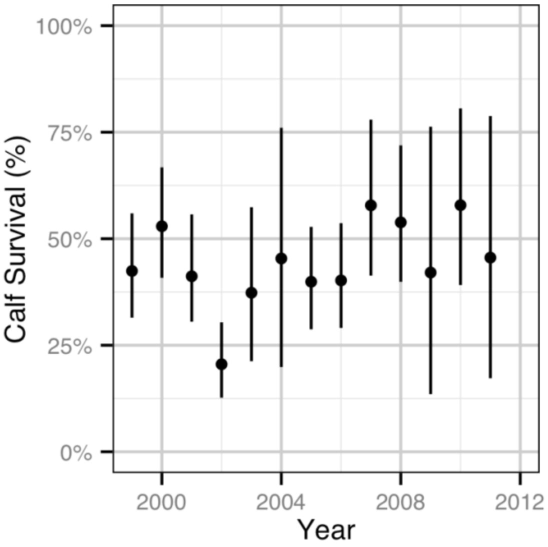

Figure 4. The predicted calf survival (±95% credible intervals) by year.

Environmental

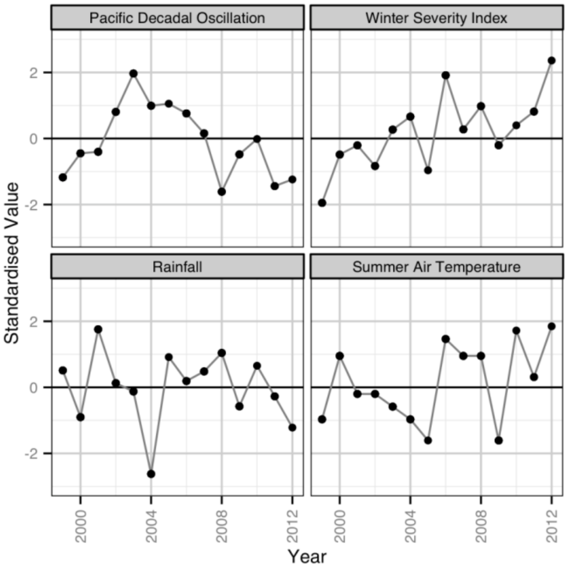

Figure 5. Standardized environmental variables by year.

Acknowledgements

The organizations and individuals whose contributions have made this analysis report possible include:

- Aurora Wildlife Research
    - Kim Poole
- University of Alberta
    - Craig Demars
- Government of the Northwest Territories
    - Terry Armstrong
- Poisson Consulting
    - Robyn Irvine

References

Bradford, M.J., J. Korman and P.S Higgins. 2005. Using confidence intervals to estimate the response of salmon populations (*Oncorhynchus Spp.*) to experimental habitat alterations. Canadian Journal of Fisheries and Aquatic Sciences 62 (12): 2716–26. doi:10.1139/f05-179.

Kery, M. and M.Schaub. 2011. Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective. Boston: Academic Press.

Plummer, M. 2012. JAGS Version 3.3.0 User Manual. http://sourceforge.net/projects/mcmc-jags/files/Manuals/3.x/.

R Core Development Team. 2013. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. www.R-project.org.

Thorley, J.L. 2013. Jaggernaut: An R Package to Facilitate Bayesian Analyses Using JAGS (Just Another Gibbs Sampler). Nelson, B.C.: Poisson Consulting Ltd.