Note

Spatial and Temporal Factors Influencing Sightability of Elk

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ABSTRACT Few tracking studies consider seasonal changes in ability to re-sight wildlife, despite potential for biases in sightability to mislead our interpretation of models of movement and abundance. We developed seasonal sightability models based on visual observations of radio-collared elk (*Cervus elaphus*) in Manitoba, Canada, through 6 seasons. We located 377 elk 8,862 times using aerial telemetry from 2002 to 2009. We tested the hypothesis that sites where we were able to visually observe radio-collared elk during aerial telemetry differed from sites where collared elk were known to be present but could not be sighted. Relationships varied with season and elk sightability was influenced by forest type, habitat openness, distance to edge, and time of day. Our results confirm that observers have the highest probability of detecting elk in early and late winter. However, factors such as day length, which increases by 64% during this period, suggest that fewer impediments to detection exist in late winter. Our findings reinforce the need to account for seasonal as well as spatial changes in habitat-specific sightability models. © 2011 The Wildlife Society.

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Calculations of population size and trends, movements, and group size may rely on equations that correct for differences in visual identification of animals under different environmental conditions (Floyd et al. 1979, Samuel et al. 1987, Poole 2007). Where a sample of animals is tracked over time using a mark or radio, unbiased probabilities of visually re-sighting marks may be required. Sighting or re-sighting animals at different times of year may be required for cases such as visually confirming reproductive status or quantifying survival of offspring in spring and summer (e.g., McLoughlin et al. 2002, Brook 2010), assessing reproductive behaviors in autumn (Franklin and Lieb 1979), classified counts of female/offspring or female/male in early winter (Bender et al. 2003, McLoughlin et al. 2003), or estimates of population in late winter (Samuel et al. 1987). The extent to which tracked animals can be located and visually identified is termed sightability. Furthermore, for objectives such as population estimates, choosing the season with the least bias in sightability, or being able to account for likely biases, is critical for obtaining accurate and precise estimates.

Sightability may be influenced by 3 types of factors including: 1) sampling design and objective during a survey (e.g., time of day), 2) biology of surveyed animals (e.g., sex, age, habitat use, group size, animal behavior), and 3) environmental conditions (e.g., canopy cover and habitat type).

These factors interact in complex ways that are poorly understood (Unsworth et al. 1990, McCorquodale 2001, Walsh et al. 2009). Furthermore, factors such as environmental conditions are not static; rather such conditions experience distinct phenology, especially in northern regions. Depending on the objective (e.g., estimating abundance or demography) surveys and studies may be conducted at different times of year. For more flexible objectives, such as population size, it is critical when calculating accurate and precise estimates to select the time of year that offers the highest detectability of elk and the fewest confounding variables.

Only when quantified can biases to sightability be incorporated into analyses relying on visual-re-sight data (Caughley 1974, Samuel et al. 1987, McCorquodale 2001). A sightability model can be developed by comparing attributes at sites where detection variables (e.g., habitat type or canopy cover) are measured for seen and unseen animal groups. We focused primarily on environmental conditions affecting temporal patterns in sightability for a large ungulate, elk (*Cervus elaphus*), based on a large sample of radio-collared animals across 6 seasons. Sightability models for elk have previously been developed for winter (Samuel et al. 1987, McIntosh et al. 2009) and summer (Anderson et al. 1998) conditions; however, no study has yet addressed the seasonality of sightability beyond recognizing that there are differences between summer and winter. We developed sightability models accounting for the effect of season and evaluated the changing influences of environmental conditions (habitat and time of day) during each season. Our objective was to examine the importance of not only

habitat-based biases in sightability, but also how these biases may change with season. We tested the hypothesis that sites where we were able to visually observe radio-collared elk during aerial telemetry would differ from sites where collared elk were known to be present but could not be sighted.

STUDY AREA

Our study area was located in and around Riding Mountain National Park (RMNP) in southwestern Manitoba, Canada (50°51′N, 100°15′W). The region was in transition between the prairies and the northern Boreal Plains ecoregion (Bailey 1968). Riding Mountain National Park is an undisturbed, forested wilderness, 2,974 km² in size. Five major vegetation associations comprise RMNP: northern boreal forest, aspen parkland, bur oak (*Quercus macrocarpa*) savannah, grassland, and eastern deciduous forest (Rowe 1972, Caners and Kenkel 2003). Some important tree species included trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), white (*Picea glauca*) and black spruce (*P. mariana*), and bur oak. The warmest month was July ($\bar{x} = 14°$ C) and January was the coldest month ($\bar{x} = -20°$ C). Snow cover normally lasted from December to March, reaching a cumulative total of 122 cm on average.

METHODS

We captured free ranging elk ($n = 377$; 191 F, 186 M) from 2002 to 2009 using a net-gun fired from a helicopter (Cattet et al. 2004). We equipped each animal with a very high frequency (VHF)-radio collar (Telonics, Mesa, AZ, and SirTrack, Havelock North, New Zealand). We located each animal during daylight hours (usually 0800–1900 hours) 1–16 times every 2 weeks by fixed-wing aircraft (Cessna 172, Wichita, KS). During telemetry flights we located animals either at the point where we observed the animal (visual observation) or where the telemetry receiver operator was confident in being directly overhead of the position based on signal strength (non-visual observation) using standard methods (White and Garrott 1990). In each instance, we recorded locations using a Geographic Positioning System (GPS). We employed only experienced wildlife telemetry pilots with >10,000 hr of flight time and trained VHF receiver operators. As group size has been identified as an important predictor of sightability (Samuel et al. 1987, Anderson et al. 1998, Cogan and Diefenbach 1998) we limited our inferences to observed single elk and unseen elk. Our assumption was that unseen elk were more likely to be solitary than in groups as groups of elk would increase detectability. Thus not detecting elk would be similar to detecting one elk rather than a group of elk. Elk did not respond to approaching fixed-wing aircraft, likely due to the altitude at which relocations occurred and habituation to fixed-wing aircraft, as the RMNP elk population has been intensively tracked since 2002.

We modeled predictability of obtaining visual confirmation during a telemetry observation from temporal and spatial attributes associated with each observation. Temporal attributes included time of day (Table 1) and season. We divided the animal year into 6 periods according to changing environmental conditions (temperature, snow cover, and plant phenology) and elk behavior (calving and mating) after Paquet (1991). We postulated that 6 seasons (Table 2) would be relevant to sighting elk: spring (Mar and Apr); early summer (May and Jun); late summer (Jul and Aug); autumn (Sep and Oct); early winter (Nov and Dec); and late winter (Jan and Feb). We deemed time of day to be important, as light levels in different seasons are known to affect probability of detection (Anderson et al. 1998) and day length in our study area varied from 8.1 hr to 16.4 hr, resulting in dramatic changes in light among seasons.

Table 1. Variables for inclusion in annual and seasonal sightability models, and overall probability of sighting[a] or not sighting,[b] for elk in Riding Mountain National Park, Manitoba, Canada (2002–2008).

Variable[c]	Description[d]	Citations
Conifer	The proportion of conifer forest within a 250-m radius	Samuel et al. (1987), Otten et al. (1993), Cogan and Diefenbach (1998), Anderson et al. (1998), Bleich et al. (2001), McIntosh et al. (2009)
Deciduous	The proportion of deciduous forest within a 250-m radius	Canopy cover: Samuel et al. (1987), Otten et al. (1993), Cogan and Diefenbach (1998), Anderson et al. (1998), Bleich et al. (2001), McIntosh et al. (2009)
Mixedwood	The proportion of mixedwood forest within a 250-m radius	Canopy cover and conifer: Samuel et al. (1987), Otten et al. (1993), Cogan and Diefenbach (1998), Anderson et al. (1998), Bleich et al. (2001), McIntosh et al. (2009)
Marsh and grassland	The proportion of open habitat (e.g., marsh and grasslands) within a 250-m radius	Canopy cover: Samuel et al. (1987), Otten et al. (1993), Cogan and Diefenbach (1998), Anderson et al. (1998), Bleich et al. (2001), McIntosh et al. (2009)
Edge	Minimum distance to hard edge from within a 250-m radius of the relocation	
Time	Time of location	Anderson et al. (1998)

[a] Observed elk $n = 1,056$.
[b] Elk that were not seen $n = 7,626$.
[c] A priori subset of variables: Conifer, Mixed wood, and Deciduous composing 3 classes with different visibilities (i.e., low, medium, and high, respectively); open habitats, for example, marshes and grasslands, are areas where visibility is predicted to be high; edge, that is, contrast between open and forested habitats is predicted to be a factor confounding sightability; time, that is, light levels, is also predicted to affect detection of elk.
[d] Variables extracted from a regional land cover map with 30-m spatial resolution developed using LANDSAT-5 satellite imagery collected in 2002.

Table 2. Rationale for partitioning the year into a priori 6 seasons for elk sightability based on local environmental conditions and elk behavior in Riding Mountain National Park (RMNP).

Season	General environmental conditions in RMNP	Elk behavior
Spring (Mar and Apr)	Snow melts and green-up of sedges and grasses begin in open meadow complexes. Patchwork of snow in different habitats may affect the viewers search image. Day length is variable	Elk aggregate to access grasses and sedges; open areas encourage groupings as an anti-predator response (Creel and Winnie 2005)
Early summer (May and Jun)	Transition of green-up in the deciduous trees and shrubbery potentially decreasing the sightability of elk. Maximum day length and light for observing elk	Calving (Brook 2010) occurs and elk switch to forage in cover rather than grasses and sedges in open habitats (Geist 1982)
Late summer (Jul and Aug)	Trees are in full leaf causing maximum obstruction. Days are long	Transition from a focus on foraging to early mating season for elk and weaning of calves
Autumn (Sep and Oct)	Trees leaves senesce introducing variation in canopy covers. Similarly, meadow complexes become brown resulting in more cryptic background color for detecting elk	Peak mating season for elk (Bowyer 1981, Geist 1982, Wolff and Van Horn 2003)
Early winter (Nov and Dec)	Deciduous canopy is leafless; however, the transition resulting from snow accumulation results in a variable background against which to detect elk. Days become short	Transition from late mating behaviors to feeding and seeking predator refuge for males resulting in spacing out (Geist 1982)
Late winter (Jan and Feb)	Full snow cover, minimal canopy cover, and increasing day length	Elk begin to group up in late winter as susceptibility to predation increases

We included 5 spatial predictors of sightability of elk (Table 1). Increased canopy cover is considered an impediment to animal detection (Samuel et al. 1987, Anderson et al. 1998, McIntosh et al. 2009). For RMNP, Caners and Kenkel (2003) calculated canopy cover for deciduous (45%), mixedwood (51%), and coniferous (56%) forests, whereas marsh and grassland had near 0% canopy cover. We predicted that in habitat with less cover we would have higher probability of detecting elk (e.g., marsh and grasslands). As canopy cover increased from deciduous to mixedwood and coniferous forest, we predicted detection probability would decrease (Samuel et al. 1987, Otten et al. 1993, McIntosh et al. 2009). We included distance to edge (i.e., the linear distance between the relocation point and a contrast between open and forested habitat), which presents the viewer an obvious contrast between habitats, in our analysis as a potential habitat modifier.

Around each telemetry location (both visually confirmed and non-visually confirmed) we created a buffer of 250 m using a Geographic Information System (ARCGIS 9.3 2009, Redlands, CA). We chose this buffer as we estimated spatial error associated with locating VHF collars by aerial telemetry as <250 m (198 m [SE = 17.6, range: 68–381 m] $n = 31$ known location test collars), which we assessed by locating stationary collars placed on the ground at known points. For each location and buffer, we determined the distance to edge and relative proportions of vegetation type (Table 1) using a land cover map with 30-m spatial resolution (LANDSAT-5 satellite imagery collected in 2002).

We screened predictor variables for excessive correlations using a Spearman rank correlation matrix for all possible pairs of independent variables (R Development Core Team 2010). If any 2 variables had an $r_S > 0.7$, we removed the less important variable. We also assessed collinearity using a combination of variance inflation factors (VIF) and variable cluster analysis (Harrell 2001; Design, R package version 2.30, http://CRAN.R-project.org/package=Design), whereby we eliminated variables with VIF > 10.

We modeled probability of sighting elk using binary logistic regression, with the dependent variable being the individual sighting of a radio-collared elk, which was either visually confirmed or not. We first constructed one annual generalized linear model for sightability based on the a priori variables (Table 1), followed by season-specific models. As we limited our inference to a minimum number of variables of importance derived from the literature (Table 1), our set of candidate models consisted of all possible additive combinations of independent variables (Whittingham et al. 2005, Whittingham 2006, Anderson 2008). We determined our most parsimonious model subset from Akaike's Information Criterion difference adjusted for small sample size (ΔAIC_c). We used Akaike weights (w) for multi-model inference (Burnham and Anderson 2002) performed in the R environment for statistical computing (R Version 2.11, www.rproject.org, accessed 03 Mar 2010) with the Multi-Model Inference package (R package, version 0.13.3, http://CRAN.R-project.org/package=MuMIn). Akaike weights provide a normalized comparative score for all models and are interpreted as the probability that each model is the best model of the set of proposed models. Substantial support for a model occurs when $\Delta AIC_c < 2.0$. We averaged all candidate models with $\Delta AIC_c < 2.0$ using the model averaging technique, which calculates averaged β coefficients and unconditional standard errors (Burnham and Anderson 2002). We calculated cumulative AIC_c weights for each independent variable by summing weights of every model containing that variable (Burnham and Anderson 2002). Variables with the highest cumulative AIC_c weights have the greatest influence on elk sightability.

RESULTS

We obtained 8,862 aerial relocations from 2002 to 2009: 1,056 locations were with visual confirmation, and 7,626 locations were at sites where we did not visually observe relocated elk. For overall annual model using all data, 4 candidate models had $\Delta AIC_c < 2.0$. Model-averaged results (Fig. 1) suggest the most important variables driving elk sightability were time of day and proportional availability at a site of deciduous, mixedwood, and open marsh or grassland habitat. These variables were all positively associated with
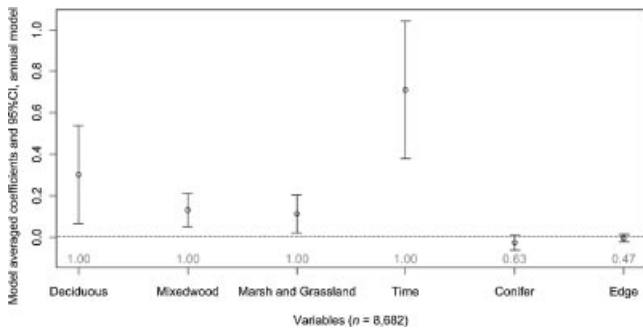
Figure 1. Generalized linear model of annual elk sightability derived from successful or unsuccessful observations of 377 free ranging radio-collared elk taken from fixed-wing aircraft over Riding Mountain National Park, Manitoba, Canada (2002–2009). We derived coefficients and unconditional standard errors from an average of all possible models with change in Akaike value less than 2 (ΔAIC < 2.0). Numbers in gray along the x-axis are cumulative Akaike weights ranging from zero to one that indicate variable importance in the model, with values of one having the greatest importance.

probability of detecting elk. Proportion of conifer and distance to edge at a location both were negatively associated with probability of sighting animals at a relocation event. Overall mean sightability (95% CI) of elk not associated with groups, including all seasons and years, was 0.12 ($\pm$0.003). Lack of goodness of fit in the annual model (Hosmer and Lemeshow Goodness-of-Fit, $P = 0.01$, $\chi^2 = 21.54$) indicated that there was unmodeled heterogeneity in our data: this disappeared once we stratified our analysis by season (Supplementary Table 1).

Probability of visually sighting elk varied among seasons (Fig. 2; probability $\pm$ 95% CI: spring, 0.178 $\pm$ 0.017; early summer, 0.064 $\pm$ 0.011; late summer, 0.021 $\pm$ 0.006; autumn, 0.110 $\pm$ 0.008; early winter, 0.266 $\pm$ 0.035; late winter, 0.253 $\pm$ 0.026). The importance of predictor variables also varied with season (Fig. 3) and was weakest in the transition seasons of early summer and autumn (in these two cases the null model was included in the model average [Supplementary Table 1]). Time of day was a critical variable in spring and late winter but had little importance in summer. The negative effect of coniferous forest on sight-
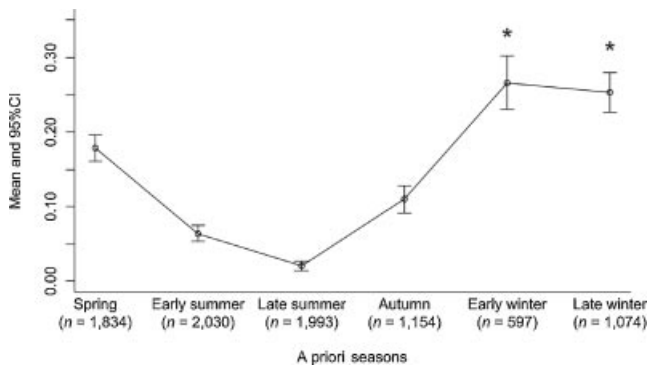

Figure 2. Seasonal trend in elk sightability (2002–2009) derived from successful or unsuccessful observations of 377 free ranging radio-collared elk taken from fixed-wing aircraft over Riding Mountain National Park, Manitoba, Canada. Non-significant differences are indicated by a shared asterisk. We failed to detect a difference between early winter and late winter ($P > 0.05$); however, we detected differences between all other groups ($P < 0.001$).

ability occurred primarily in early and late winter, whereas the negative effect of edge occurred primarily in spring and late winter.

DISCUSSION

Our results demonstrate that accounting for season (Figs. 2 and 3) is imperative to identifying when and where variables influencing sightability are important. For example, the proportion of deciduous forest as a predictor variable was identified as an important variable in our annual model; however, this effect was equivocal (not significantly different from zero) in all seasons except for late winter. Similarly, time of sighting appeared important in the annual model, but by stratifying our analysis by season we saw that it was only important when day length was short (i.e., late winter and spring), when low light and angle of incidence may affect detectability. From the season-pooled model, we expected that locations in marsh and grasslands would always be associated with higher sightability, yet seasonally this association did not increase probability of detection. Conversely edge is equivocal in the annual model but negatively affects probability of detection in late winter and spring. One possible explanation is that late winter–spring is a period of snow loss where snow first melts in open areas, eventually attracting elk to open areas to feed. However, snow cover remains in the adjacent wooded areas, creating a distinct transition that affects animal behavior (e.g., thermoregulation, feeding in the open, bedding in wooded habitat) and detectability (i.e., complex search image required by the observer that simultaneously incorporates open and closed habitats). Edge also creates a contrast between shade and full sunlight, possibly making animals harder to detect.

During seasons with full or partial foliage (i.e., spring–autumn), there was little effect from forest composition until later in the year, when sightability improved in all habitat types. Despite very low sighting rates in early and late summer (6.4% and 2.1%, respectively) few spatial variables contributed significantly to each model, suggesting that vegetation associations were themselves poor predictors of detectability during the growing season. Canopy cover has been found to affect sightability (Anderson et al. 1998). Canopy cover estimates for each specific season were not available, so we chose to use categories (e.g., marsh or grassland to conifer) of increasing canopy cover from which we predicted that increasing canopy cover would be an impediment to detecting elk. Canopy cover was not a universal impediment to sightability, however, conifer negatively affected sightability in winter.

A limitation of our models was that we could only indirectly incorporate effects of behavior. For example, by stratifying by season we may have incorporated effects of temperature on activity levels, as Bleich et al. (2001) found elk were more likely to be observed at temperatures <15° C. However, we were unable to directly incorporate effects of grouping and other behaviors, despite these being shown to affect sightability (Samuel et al. 1987, Anderson et al. 1998, Cogan and Diefenbach 1998, McIntosh et al. 2009). Group size is an important variable to consider where larger groups
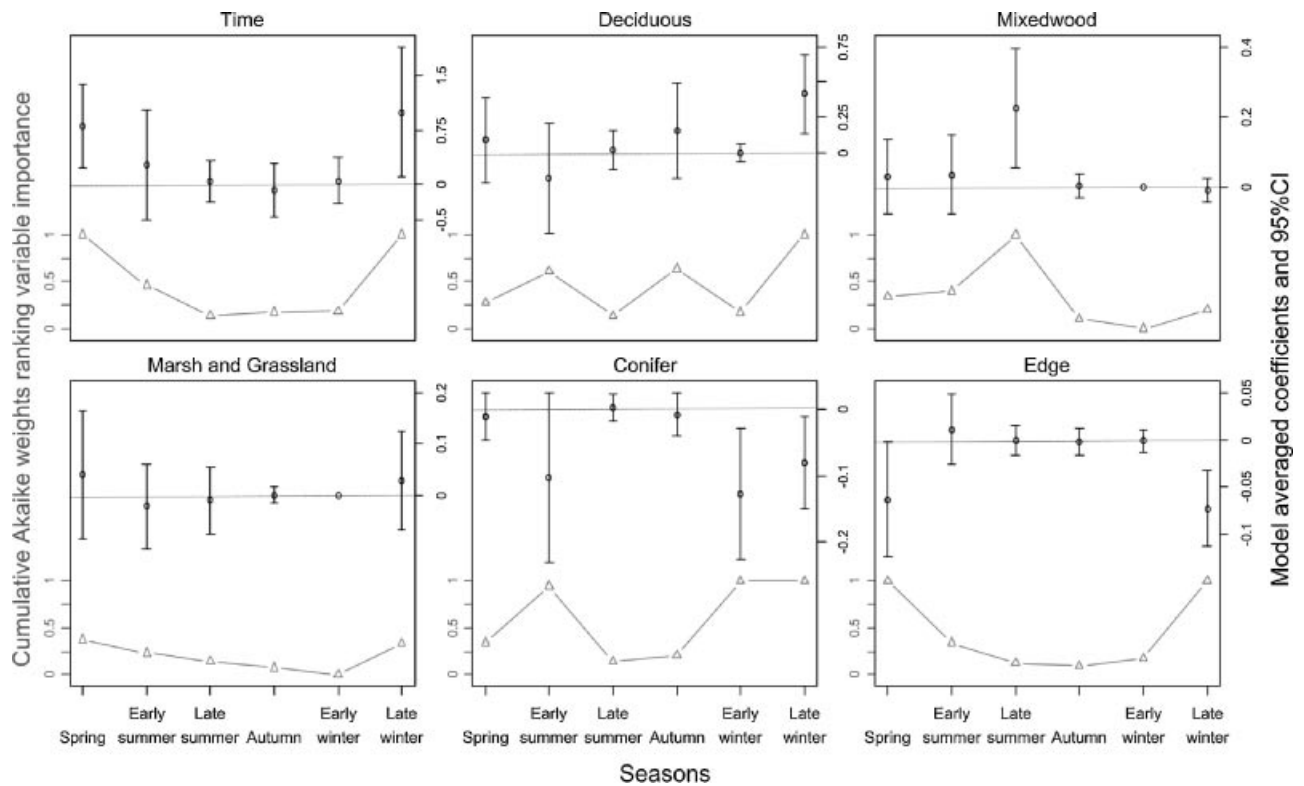
Figure 3. Seasonal comparison of independent variable directionality and importance from generalized linear models of elk sightability (2002–2009). We derived regression models of sightability from successful or unsuccessful observations of 377 free ranging radio-collared elk taken from fixed-wing aircraft over Riding Mountain National Park, Manitoba, Canada within each season. Coefficients and unconditional standard errors are results from each individual season-based average of all possible variable combinations models with a change in Akaike value less than 2 (ΔAIC < 2.0). The scale of right y-axes vary according to coefficient size for each variable. The gray line with triangles tracks the cumulative Akaike weights which rank variable importance in each seasonal model through time.

are easier to detect, thus we assumed that groups that go undetected are likely going to be small or nearly 1, similar to our observed groups of nearly 1. Thus, including groups that are >1 would bias our comparison. Ultimately our design is limited because we cannot compare variables such as group size or activity collected for animals we detected with animals that we failed to detect, as they remained unobserved. Nevertheless, given our large sample size of animals and observations of each animal, we found important relationships among sightability and predictor variables.

Low probability of sighting radio-collared elk demonstrates the potential for imprecise estimates from population surveys. Imprecise estimates will make it difficult to detect changes in population size. Although our objective and technique differed from traditional fixed-wing aerial transect surveys, we failed to detect animals despite knowing where they were, arguably inflating our success of detection rather than impeding it. Our results suggest that uncorrected transect survey techniques at best may produce meaningful indices of population size but are not likely to produce meaningful estimates of population size. This is likely sufficient for management of a hunted population within broad limits; however, in scenarios where wildlife populations host communicable diseases (e.g., chronic wasting disease; brucellosis [*Brucella abortus*]; or, specifically, bovine tuberculosis [*Mycobacterium bovis*], which has infected elk in RMNP [Lees 2004, Nishi et al. 2006]) and specific estimates of

population are sought to make political and scientific decisions about disease management, a reasonably accurate estimate of population size to detect annual changes in population size in response to management interventions requires a more rigorous approach to correcting for sightability bias (Anderson and Lindzey 1996, Bleich et al. 2001, Rosatte et al. 2007).

Management Implications

Our results add to the body of work highlighting the importance of correcting ungulate observation data for variables that affect probability of detecting animals (Samuel et al. 1987, Bleich et al. 2001, McIntosh et al. 2009). In particular, we highlight seasons where elk detection is highest with few factors that confound sightability. Our seasonal models make a case for addressing seasonal changes in sightability. Depending on the objectives of the research (e.g., estimating classified counts, visual detection of calving success, evaluating breeding dynamics, population estimation), developing more than winter and summer sightability models for a region may be required. Furthermore, we reinforce earlier findings that winter is the season where elk detectability is highest; however we introduce covariates within winter (e.g., time of day) that affect detection rates. Although models rarely incorporate time of day, we believe that they should. Ultimately, we demonstrate that seasonality has mixed affects on sightability.

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