ESTIMATING MOOSE ABUNDANCE AND TRENDS IN NORTHEASTERN WASHINGTON STATE: INDEX COUNTS, SIGHTABILITY MODELS, AND REDUCING UNCERTAINTY

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ABSTRACT: The state of Washington was historically considered to be unoccupied by moose (*Alces alces*) with initial colonization in the 1920s primarily in the northeastern quarter of the state. All evidence indicates a steadily increasing population since, with moose and moose hunting now firmly established. Given the expectation that Washington's moose population will face increasing challenges in the coming decades, our monitoring objective is to move from index-counts to valid estimates of abundance. We documented environmental covariates as an adjunct to simple counts from annual helicopter-based surveys in 2002–2012, and examined the performance of existing moose sightability models on these data. While acknowledging our inability to compare modeled estimates with actual abundance, we reasoned that if existing models converged on similar results, this would suggest that moose sightability is a sufficiently general phenomenon that the cost of developing a specific local model might not be justified. However, despite using similar covariates, the sightability models applied to our data produced widely disparate abundances and estimates with poor precision. Specifically, where coniferous forest cover renders expected detection probability low, sightability models tend to behave erratically. We also used covariate data bearing on sampling variation to refine our estimate of population trend. Multiple regression analyses revised the linear rate of increase associated with the raw counts of the instantaneous rate of growth, $r = 0.084$ (SE = 0.019) to an adjusted estimate of $r = 0.077$ (SE = 0.075). While incapable of transforming an index into a population estimate, accounting for variables likely to affect raw counts may be useful to refine estimates of trend. The use of an approach that avoids the autocorrelation inherent in a simple regression of counts on time better reflects true uncertainty.

Moose (*Alces alces*) are generally considered to have colonized the northeastern portion of the U.S. state of Washington in the 1920s, but did not become well established until the 1970s (Base et al. 2006). The population evidently increased in the latter part of the 20th century, with limited-entry hunting initiated by the then Washington Department of Game in 1977, and increasing to approximately 130 permits drawn annually in 2012 (WDFW 2013). Evidence available from hunters suggests that moose have increased since 2001, at least within areas open to hunting. The mean annual number of moose observed/day/hunter (as documented via a mandatory, web-based reporting system) increased from 2001 to 2012 (linear regression of raw counts on time: $\beta = 0.086$, SE = 0.034, n = 11, $t = 2.57$, $P = 0.030$; marginal decline in days required/successful hunt: $\beta = -0.295$, SE = 0.164, n = 11, $t = -1.8$, $P = 0.102$) at the same time that hunter success rate (average = 93%) increased ($\beta = 0.009$, SE = 0.001,

n = 11, t = 4.27, P = 0.002). However, with the decline of many moose populations in adjacent jurisdictions due to forest maturation, increases in parasites, increases in predators, and the effects of climate change, the status of Washington's moose population has elicited increased concern among the public.

The problem of estimating abundance and trends of moose populations has vexed biologists and managers (e.g., Gasaway et al. 1985), just as surely as the public at large – and hunters in particular – have expressed the expectation that such figures be available. As an often solitary, generally forest-dwelling and invariable shy animal that eschews large aggregations, moose share with white-tailed deer (*Odocoileus virginianus*) characteristics that make it among the more difficult of North American ungulates to survey. Due to the logistical challenges of estimating abundance over large areas, surveys from fixed- or rotary-wing aircraft have become the staple among North American wildlife management agencies (Timmermann 1993, although see Rönnegård et al. 2008, Månsson et al. 2011, and Boyce et al. 2012 for alternatives to aerial survey). But, it has long been recognized that even raw counts of animals from aerial surveys are often insufficient to estimate either abundance or trends. Among approaches used to move from raw index counts of moose to population estimates are double-sampling (Gasaway et al. 1986), conventional distance sampling (Dalton 1990), sightability models (i.e., logistic regression based upon detectability of marked animals; Anderson and Lindzey 1996, Drummer and Aho 1998, Quayle et al. 2001, Guidice et al. 2012), application of infra-red thermal imagery to doubly-sampled units (Bontaites et al. 2000), mark-recapture distance sampling (Nielson et al. 2006), and independent double-observer surveys (Cumberland 2012).

Since 2002, the Washington Department of Fish and Wildlife (WDFW) has conducted standardized moose surveys from helicopters in both the Colville and Spokane districts to produce indices of population abundance. Although referenced when devising hunting seasons and harvest limits, these surveys have not been used to estimate abundance. Rather, management has been based on informal evaluation of these surveys in combination with hunting statistics, implicitly assuming that these indices track population abundance. Over the years, the number and distribution of survey units flown has varied, as have biological and environmental attributes (documented elsewhere) that influence detection probability. In short, understanding the various environmental factors that interfere with a simple equating of animals observed to animals present has become indispensable to our understanding of the count data.

Sightability models (Samuel and Pollock 1981) have been used for a variety of hunted ungulate species in western North America (e.g., elk [*Cervus elaphus*; Samuel et al. 1987, Gilbert and Moeller 2008] and mule deer [*Odocoileus hemionus*; Ackerman 1988]), and have been the focus of considerable efforts by WDFW (McCorquodale 2001, Rice et al. 2009). Biologists in the WDFW Spokane district have gathered physical attribute data commonly assumed to affect detection of moose. Although not collected for application to a specific sightability model, these covariate data allowed us to apply existing sightability models retrospectively.

A number of situation-specific sightability models for moose have been developed, including those in Wyoming (Anderson and Lindzey 1996), Michigan (Drummer and Aho 1998), British Columbia (Quayle et al. 2001), Alberta (Peters 2010), interior Alaska (Christ 2011), Minnesota (Guidice et al. 2012), and coastal Alaska (Oehlers et al.

2012). Although differing in details, these models are all notable in their common finding that vegetative cover (typically, coniferous forest) was the most important, and in some cases, the only covariate affecting detection probability of moose groups. Other putative variables bearing on detection probability (e.g., snow cover, group size, weather conditions, individual observers) were generally unimportant.

Thus, we were motivated by the following notion: given the similarity of covariates shown to be predictive of detection in sightability models, might it be the case that "moose detectability" is a general-enough phenomenon that existing models can be applied in northeastern Washington to estimate abundance, obviating the need to develop a local model? We did not attempt to validate or recalibrate any one model, but reasoned that a first approximation to answering the question of generalizability would result from comparing the performance of alternative models on an identical data set. If they generated similar results, this would suggest that the probability of moose detection is a generalizable phenomenon. If results diverged widely, it would suggest that moose detection is situation-specific, and that a novel sightability model would be required for site-specific and survey-specific data. Additionally, if our analysis suggested that adopting an existing sightability model in eastern Washington was unwarranted, we wondered if covariate data could refine our estimates of population trend.

METHODS

Aerial winter surveys (December-February) of moose using a helicopter have been conducted annually by WDFW staff in the Spokane district since 2002. These surveys were not designed to generate population estimates, but rather were considered as index counts that correlated positively with true abundance. We identified 51 survey blocks based on field landmarks; average block size was 13.5 km^2 ranging from 9.0–17.8 km^2. Prior to each annual survey, each block was categorized into 1 of 3 population density strata (low, medium, high) based on the previous years' survey, or if lacking, general field knowledge. The annual selection of blocks followed a stratified random design: all high density blocks were surveyed each year, whereas a random selection of medium and low density blocks was flown, depending on available funding. Survey coverage (i.e., proportion of all mapped survey blocks included within that year's survey) averaged 33% ranging from 18–44%. Flight lines within blocks were not mapped prior to the survey, nor were they strictly controlled. Rather, flight paths were designed to maximize coverage within each block, reflecting the shape and topographic features within, and were generally ~400 m apart. Flight lines and locations of each moose group were recorded using hand-held GPS units.

All surveys were conducted with a Robinson R-44 helicopter; typically 2 experienced observers were used (front left, rear right), and observations by the helicopter pilot were also counted. Surveys were timed to coincide with good weather occurring shortly after a snowfall to the extent practical, avoiding patchy snow cover, and occurred as early as 8 December and as late as 3 February. Surveys generally occurred over 3–6 days each winter in response to weather conditions. Although never applied formally in a model setting, covariates hypothesized to influence detection of moose groups were collected in the same manner and with the same definitions each year (Samuel et al. 1987). In addition to group size (and sex/age composition), these were activity (bedded, standing, moving), percent snow cover, percent obstructing vegetative cover (visually estimated to

nearest 5%), and an index of terrain type (flat or hilly).

To assess the behavior of existing sightability models when applied to these data, we programmed the Sightability Model Package (Fieberg 2012) in R 3.1.1 (R Development Core Team 2011) to replicate the models developed in the 3 closest geographic regions to eastern Washington: Wyoming (Anderson and Lindzey 1996), British Columbia (Quayle et al. 2001), and Minnesota (Guidice et al. 2012). In addition, we obtained the parameters for an additional model produced for a different geographic region of British Columbia, but not published at the time (J. Quayle, British Columbia Ministry of Environment, Victoria, British Columbia, pers. comm.). These 4 models, hereafter referred to as "Wyoming", "BC", "BC-2", and "Minnesota", defined and categorized vegetative cover slightly differently; therefore, we binned our continuous data into the categories needed for each of the 4 models. We summarized data using JMP v. 11.1 (SAS Institute, Cary, North Carolina, USA).

We further explored our covariate information to determine if it could improve our estimate of the rate of change of the moose population, even if it failed to find application in existing sightability models. A simple regression of the natural logarithm of raw index counts on time would ignore the effects of environmental variation on detection completely, as well as the existence of temporal correlation in population indices, thereby under-estimating true process variance and creating a sense of false precision. Thus, we adopted the approach suggested by Dennis et al. (1991:120; see also Morris and Doak 2002:68 and Mills 2007:109) in which natural logarithms of the ratios of successive raw counts are regressed on the intervals between surveys, forced through the origin.

We added to the basic regression model a suite of covariates hypothesized to affect detection probability or reflect survey effort, and thereby influence population trend estimates. We took as covariates the percent forest cover information used in the sightability models above (in this case, using the mean annual percent cover for all observed moose, weighted by moose group size). We further added other covariate data collected during 2002–2012 that did not enter into the top sightability models. These were the weighted mean annual percent snow cover recorded at each moose observation, the weighted mean annual index of moose activity of each observed moose group (1 = sitting, 2 = standing, 3 = moving), and the number of survey units entering the survey in each year (Table 1). Each of these varied annually and was a plausible candidate as a covariate that affected our interpretation of index counts.

Because the response variable in each case was the ratio of the natural logarithm of raw counts in successive years, we used as independent variables the ratios of the natural logarithms of the putative explanatory variables in those same 2 years. Thus, our models took the form:

$$Y = \alpha + \beta_1 x_1 + \quad \ldots \quad + \beta_4 x_4 + e \quad (1)$$

where:

Y = ln (count $(t+1)$ / count (t)), the index counts of moose counted in each year (t),

α = the intrinsic, annual growth rate (because the interval between successive counts were all 1 year in our case),

β = coefficients to be estimated from data for each covariate hypothesized to affect sightability,

x_1 = ln(percent forest cover $(t+1)$ / percent forest cover (t)),

x_2 = ln(percent snow cover $(t+1)$ / percent snow cover (t)),

x_3 = ln(activity index $(t+1)$ / activity index (t)),

x_4 = ln(units surveyed $(t+1)$ / units surveyed (t)), and

e = error, assumed normally distributed with constant variance.

We then assessed the strength of evidence for each of the 16 possible additive models (all possible combinations, plus a null model with no covariates) using AIC$_c$. In testing for significant pairwise correlations ($P = 0.05$), we did not detect any evidence of collinearity in the above set of predictors. Our best estimate of the rate of growth during the time period was the model averaged estimate, $\hat{\alpha}$.

RESULTS

The number of moose observed annually ranged from 81 (2002) to 185 (2012). In total, 810 moose groups were observed in the 11 years, with a mean group size of 1.69 (SD = 0.98, range = 1–10). Snow cover was generally high, and percent vegetative cover at observation sites ranged from 0–100% (annual range = 23–52%) (Table 1).

As expected, the 4 models generated point estimates of more moose than observed as raw counts, both because of imperfect detection and incomplete sample coverage.

However, the 4 abundance estimates using identical data sets varied considerably within each year (Fig. 1). Point estimates produced by the Wyoming model averaged 5.6x higher (range = 3.2–6.9) than those produced by the Minnesota model. Point estimates produced by the 2 BC models produced similar results ('BC-2' model not shown for clarity), and were generally closer to the Wyoming than Minnesota model. There was considerable annual fluctuation in abundance estimated by these models; in some cases, annual increases far exceeded the biological capability of even the most productive moose population (e.g., more than doubling between 2006 and 2007 in all 4 models). In addition, most abundance estimates had wide confidence intervals, especially the Wyoming and BC models. The annual confidence intervals expressed as a % of the point estimates averaged 157% for the Minnesota model, 356% for the Wyoming model, and 368% for the BC model. The proportion of total variance due to the

Table 1. Basic data used in application of ancillary data to refine trend estimates of moose abundance, Spokane district in northeastern Washington, winters 2002–2012. Shown are number of moose seen during annual helicopter flights; number of survey units flown each year; the mean activity index of observed moose (weighted by group size) where 1 = bedded, 2 = standing, 3 = moving; weighted mean percent snow cover near observed moose, and weighted mean percent vegetation cover near observed moose.

| Year	Raw count (moose observed)	Number of units surveyed	Mean moose activity index	Mean percent snow cover	Mean percent vegetation cover
2002	81	12	1.91	78.56	51.57
2003	59	17	1.69	84.07	35.85
2004	114	16	1.71	99.84	23.46
2005	74	9	1.54	76.42	50.88
2006	94	18	1.45	83.24	28.46
2007	112	13	1.42	100.00	49.46
2008	116	20	1.41	100.00	42.33
2009	124	20	1.45	95.56	48.02
2010	168	20	1.64	99.58	51.01
2011	117	20	1.55	70.09	45.81
2012	185	22	1.49	96.73	44.41
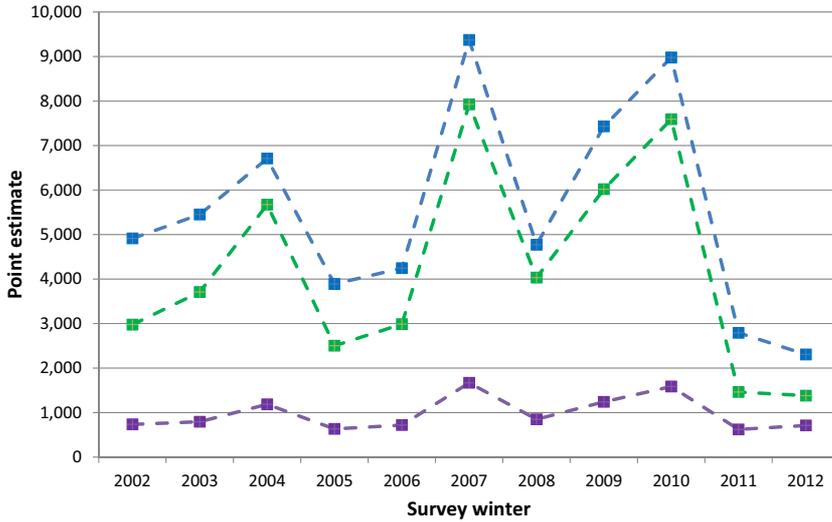
Fig. 1. Population trends of moose in northeastern Washington (2002–2012) based on application of 3 moose sightability models. Shown are point estimates produced by identical data sets each year by each model. Purple triangles and dashed lines = Minnesota model; green diamonds and dashed lines = BC model; blue squares and dashed line = Wyoming model.

model itself was much lower in the Minnesota model than the other 3 models (Table 2), whereas the proportion associated with incomplete sampling was much higher. Examined over the 11-year time period, even the coarse population trends implied by application of the 4 sightability models were inconsistent.

Why did the Wyoming and BC models project so many more moose than the Minnesota model, given that they used a similarly defined covariate and an identical data set? Graphical illustration of the core relationships underlying the 3 models (Fig. 2) revealed the influence that a seemingly minor difference in the regression coefficient associated with detection probability relative to vegetative cover translated upon the estimates. When visual obstruction (forest canopy cover) is ~30%, the models behave similarly; however, when visual obstruction approaches ≥50% the model estimates diverge (Fig. 3). For example, Figure 3 reconfigures the sightability curves in terms

Table 2. Point estimates, upper and lower 95% confidence bounds, variance components (sampling, sightability, model) from application of 4 moose sightability models to observation data from helicopter-based moose surveys, Spokane district, northeastern Washington, winters 2002–2012.

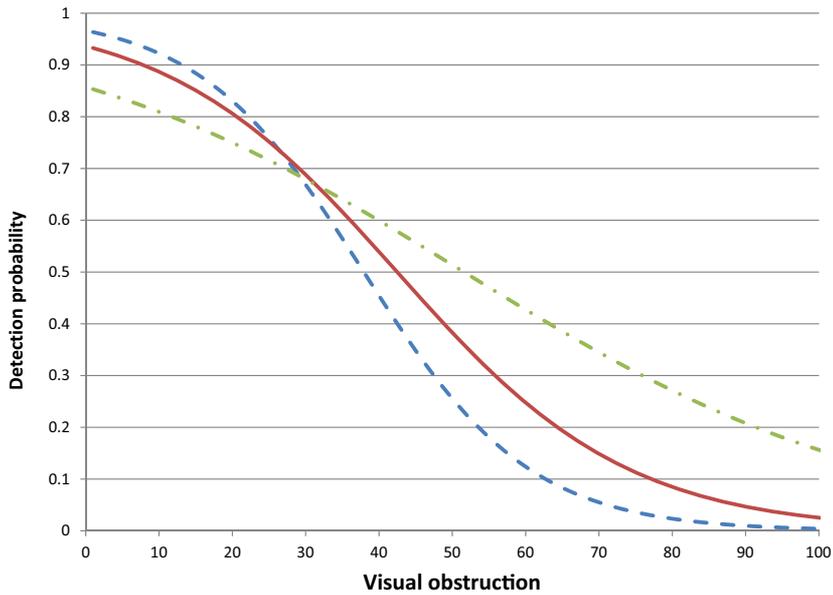| Model	Wyoming	BC	BC-2	Minnesota
Point Estimate	2,488	1,323	1,866	558
Lower 95%	985	574	746	353
Upper 95%	9,479	4,597	7,283	1,049
Sampling variance	0.07	0.12	0.07	0.64
Sightability variance	0.10	0.11	0.12	0.16
Model variance	0.83	0.77	0.81	0.20

Fig. 2. Smoothed representations of functions relating the probability of detecting a moose group given that it is present (vertical axis) to the percent vegetation capable of obstructing observation from a helicopter (horizontal axis). The lines were generated using sightability models developed in Wyoming (Anderson and Lindzey 1996; dashed blue line), British Columbia (Qualye et al. 2001; solid red line), and Minnesota (Guidice et al. 2012; dot-dash green line).
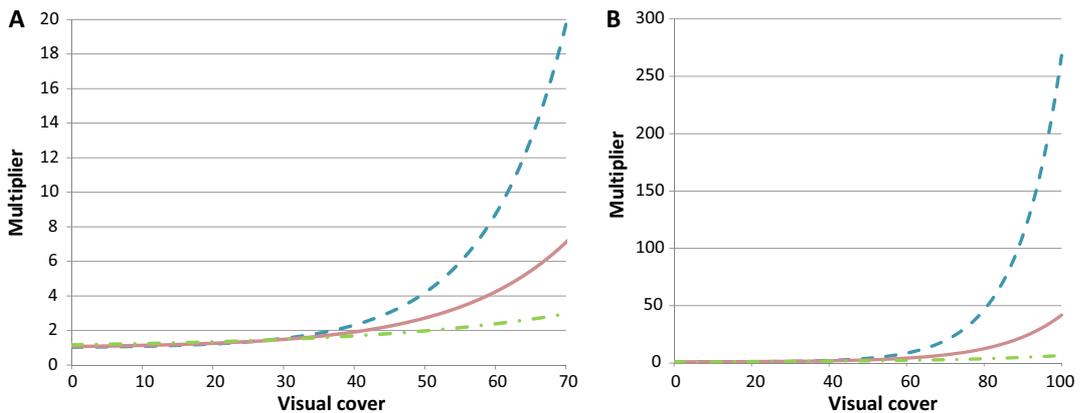

Fig. 3. Smoothed representations of mean expansion factors applied to each moose group observed based on the percent vegetation capable of obstructing observation from a helicopter (horizontal axis); shown are A) visual cover up to 70%, and B) visual cover up to 100%. The lines were generated using sightability models developed in Wyoming (Anderson and Lindzey 1996; dashed blue line), British Columbia (Qualye et al. 2001; solid red line), and Minnesota (Guidice et al. 2012; dot-dash green line).

of the 'expansion factor' or 'multiplier' applied to each moose from each of the models. At 50% cover, the Minnesota model projects ~2 moose for each observed, whereas the Wyoming model projects ~4 (Fig. 3a). With visual cover >60%, differences in multipliers applied to individual observations increasingly diverge (Fig. 3b); for example, in the Wyoming model at 80% cover, a single moose projects to about 50 and a cow-calf pair to 100 moose. Figure 3b illustrates that under dense canopy, minor fluctuations in how field investigators code this covariate can produce substantial differences in detection probability, and ultimately the estimated abundance.

Regression of the natural logarithm of raw counts on time yielded a naïve estimate of the intrinsic growth rate (r) of 0.084 (SE = 0.019), suggesting an average annual discrete growth rate (λ) of ~1.09. The top-ranked regression model incorporating co-variates and accounting for autocorrelation contained mean percent snow cover only (Table 3). The model including the mean activity index and snow cover had similar support (Δ AIC$_c$ = 1.12), and together, these 2 models absorbed most (86%) of the Akaike weight (Table 3). The model averaged slope, accounting for all possible models and representing the estimate instantaneous growth rate r was 0.077 (approximate SE = 0.075),

Table 3. Competing models of the effects of annual covariates hypothesized to influence detection of moose observed during helicopter surveys, Spokane district in northeastern Washington, winters 2002–2012. All models are of the form shown in Equation 1. Shown are the point estimate of the intrinsic growth rate r, its standard error (SE), the number of parameters in the model (K), ΔAIC$_c$, and the AIC$_c$ weight. Variables: snow = weighted mean percent snow cover near observed moose; activity = mean activity index of observed moose weighted by group size where 1 = bedded, 2 = standing, 3 = moving; units = number of survey units flown each year; and vegetation = weighted mean percent vegetation cover near observed moose.

Model	Predictors	r	SE	K	ΔAIC$_c$	AIC$_c$ weight
1	intercept + snow	0.053	0.074	3	0.000	0.547
2	intercept + snow + activity	0.112	0.063	4	1.117	0.313
3	intercept only	0.084	0.114	2	4.489	0.058
4	intercept + activity	0.158	0.105	3	5.753	0.031
5	intercept + snow + vegetation	0.054	0.078	4	6.909	0.017
6	intercept + snow + units	0.055	0.080	4	7.291	0.014
7	intercept + vegetation	0.078	0.114	3	8.648	0.007
8	intercept + units	0.072	0.121	3	9.621	0.004
9	intercept + snow + vegetation + activity	0.113	0.064	5	10.370	0.003
10	intercept + activity + vegetation	0.154	0.101	4	11.019	0.002
11	intercept + snow + units + activity	0.112	0.068	5	11.654	0.002
12	intercept + units + activity	0.147	0.110	4	12.419	0.001
13	intercept + snow + units + vegetation	0.078	0.077	5	15.151	0.000
14	intercept + units + vegetation	0.010	0.122	4	15.365	0.000
15	intercept + units + vegetation + activity	0.169	0.109	5	20.918	0.000
16	intercept + snow + units + vegetation + activity	0.131	0.060	6	23.599	0.000
Mean		0.077	0.075			

slightly lower than the 0.084 with raw counts unadjusted for covariates and auto-correlation. That is, our best estimate of population trend (λ) that incorporated auto-correlation, our suite of visibility covariates, and model uncertainty was ~1.08 during the 2002–2012 time period. However, none of the top-ranking regression models, nor the modeled averaged estimate (Table 3) provided evidence that would reject the conventional null hypothesis that $r = 0$ at the customary Type I error rate of $\alpha = 0.05$.

Our data seemed to suggest a constant rate of growth throughout the time period. However, various alternative shapes may enjoy greater support than a linear trend.

For example, the Wyoming or BC models could arguably support a concave down function rather than a constant growth rate with high variance. To examine this alternative, we modeled a simple quadratic regression, using year and year^2 as predictors in addition to the top covariates, allowing for a curving of the previously straight line (Fig. 4). As suggested by Harris et al. (2007), we assessed the strength of evidence for these 2 competing models using AIC_c, the AIC_c weight, and the significance of the quadratic term. Models including the quadratic term were invariably less parsimonious than simple linear models, and quadratic terms were not significant (Table 4). Thus,
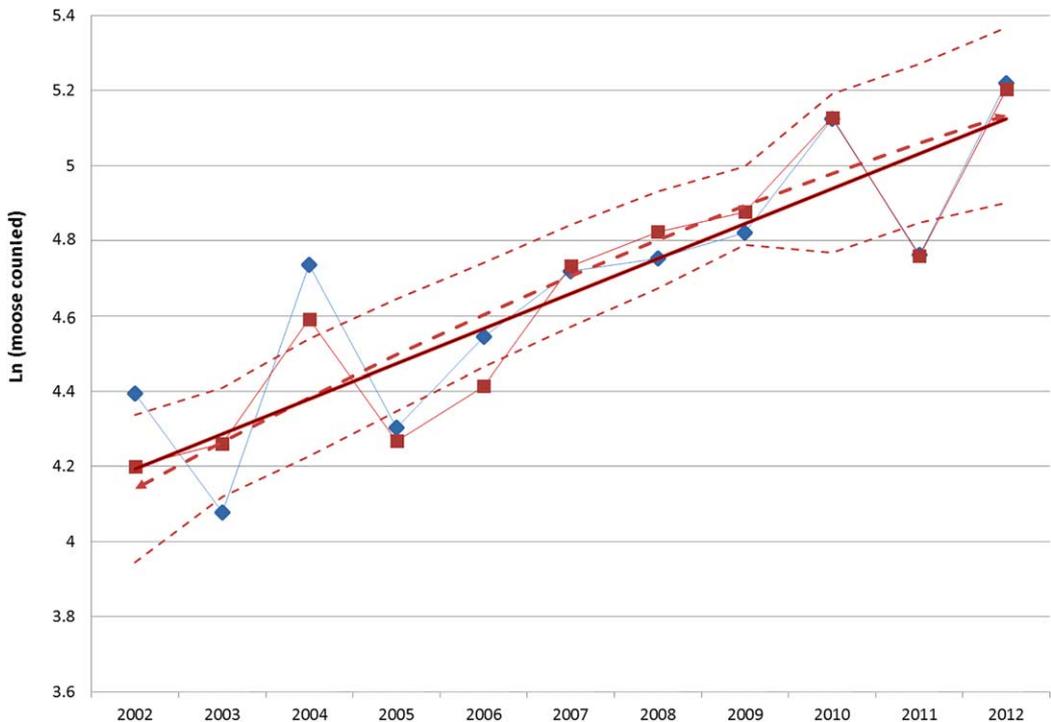

Fig. 4. Trend of moose over time in northeastern Washington (2002–2012) illustrating the effects of accounting for sightability covariates in a regression context, and of using a quadratic term. Blue diamond symbols = natural logarithm of raw index counts of moose, 2002–2012; red square symbols = index counts predicted by top-ranked model accounting for mean annual moose activity and mean annual snow cover; bold solid red line = linear prediction from best model; bold dashed red line = quadratic prediction from best model; AIC supports the linear over the quadratic. Approximate 95% confidence limits surrounding quadratic prediction are shown in light dashed lines.

Table 4. Traditional models regressing ln(counts) on time, using the top ranking suite of covariates from Table 3, comparing the fits of linear and quadratic relationships with time. Support for the quadratic over the linear model would suggest that r, the intrinsic rate of growth, increased or decreased during the period.

Predictors	Time	year	SE	t	P	year^2	SE	t	P	AIC$_c$	AIC$_c$ weight
intercept + snow	linear	0.075	0.015	5.05	0.001					0.722	0.902
	quadratic	0.073	0.014	5.25	<0.001	0.007	0.013	1.45	0.190	5.164	0.098
intercept + snow + activity	linear	0.095	0.014	6.72	0.002					1.148	0.995
	quadratic	0.099	0.020	4.98		−0.003	0.007	−0.36	0.7289	11.909	0.005
intercept only	linear	0.084	0.018	4.50	0.001					2.661	0.928
	quadratic	0.084	0.020	4.26	0.003	0.002	0.007	0.30	0.775	7.780	0.072
intercept + activity	linear	0.099	0.023	4.22	0.003					6.541	0.958
	quadratic	0.115	0.031	3.74	0.007	−0.010	0.012	−0.85	0.423	12.789	0.042

although the quadratic model will always be disadvantaged when compared with the linear model (by virtue of having an extra parameter), these results suggest that through 2012, counts provided no evidence of any moderation in the population growth rate.

DISCUSSION

Most authors describing the development of sightability models caution about extrapolating coefficients beyond the conditions under which they were developed, and we concur. Although all 4 sightability models used very similar covariates, subtle differences in their coefficients led to dramatically disparate estimates when identical data sets were applied to them. Although sightability modeling is a well-explored and valid approach to estimating detection probability, it is vulnerable to extrapolation beyond site-specific conditions. We have concluded that should we wish to employ a valid sightability model for moose in northeastern Washington, we have little choice but to develop one *de novo* using radio-collared animals. Even then, the relatively dense conifer cover that characterizes most moose habitat in northeastern Washington

may, at best, yield a sightability model sensitive to errors in assigning covariate scores and have low precision.

When we accounted for detection-related covariates and autocorrelation of counts, our best estimate of the rate of population growth was lowered slightly, but this also clarified that simple linear regression provided a misleading assessment of precision. Although available evidence from both approaches suggested a positive trend, the addition of plausible sightability covariates (Dennis et al. 1991) showed that data were not yet sufficiently precise or abundant to rule out an unchanging (or even negative) trend with time. The fact that the standard error of r ($ln \lambda$) exceeded its point estimate under the model lacking any sightability covariates (Model 3, Table 3) suggests that most of the difference in analyses came from accounting for autocorrelation rather than adding covariates. The estimates of r (i.e., $ln \lambda$) were identical (0.084), but the SE in the Dennis et al. (1991) regression approach (0.115) was much higher than the 0.019 returned by the simple linear regression model. However, by examining the suite of

models incorporating the sightability covariates, we gained insight into the potential that annual variation of one or another was the true driver underlying the apparent trend. Rather than choosing only a single "best" model, our model averaging embraced and accounted for uncertainty while making use of the less-informative covariates. That said, its ambition was modest; it attempted to correct a trend index rather than to estimate true abundance. It did not provide a basis for scaling our estimated population increase in real numbers of moose, and provided only a relative, not an absolute measure of detectability. Without the latter, we remain unable to estimate moose abundance.

One surprising finding in our use of ancillary data to refine our estimate of population trend was that models incorporating vegetation cover, invariably identified as the most important covariate in sightability models (Anderson and Lindzey 1996, Drummer and Aho 1998, Quayle et al. 2001, Guidice et al. 2012, Oehlers et al. 2012), were not ranked highly (Table 3). One possible reason is that in this analysis, unlike with sightability models, we were not assessing the influence of vegetation cover ability to prevent detection, but rather its relationship with animals *already* detected. Our regression approach was limited to data from animals that were observed. Also, our regression analysis necessarily used the means of all covariates assessed across all animals observed in each year, in contrast to their use in sightability models where they are assessed from observations of each animal group.

Our regression approach could have been biased by covariates that were not quantified and/or included in our models. First, our annual selection of survey blocks may have been subconsciously biased to increasingly favor those with higher moose density as we gained experience in survey

techniques and increased our qualitative understanding of moose distribution. We find such a bias unlikely because, except for the ∼1/3 of blocks categorized as "high density" (always surveyed), medium and low density blocks were selected on the basis of a random algorithm. Secondly, we might imagine that observer expertise increased with time, such that moose detection increased independently of environmental covariates; if so, our estimate of population trend would be biased high. Lacking marked animals and/or double-observer "mark-recapture" data, an assessment of this source of bias was not possible. Thirdly, we cannot rule out the possibility that unknown covariates affected detection probability. If so, and if these exhibit a trend with time, the resultant trend estimate could be biased. We quantified, but did not include in regression models, the group size of observed moose. Although often an important predictor of elk sightability, group size in moose rarely exceeds 3 (usually 1 or 2) and has never been identified as an important predictor of detection.

We are hardly plowing new ground by reiterating that models are only as useful as the reliability with which their assumptions align with intended use. We provide no basis for doubting the usefulness and accuracy of sightability models as a whole, but interpret our exercise as a sensitivity analysis applied to a similar (not identical) situation in which these models were developed. In this context, we find the divergence in estimates compelling evidence that extrapolation beyond their intended use or without proper and tested re-calibration is unwarranted. That said, the time and effort to collect ancillary data likely to be relevant to detection probability may be worthwhile. In our case, we used ancillary data in a regression environment to provide additional assurance that population trends suggested by raw index counts were unlikely to have been solely

artifacts of varying environmental or sampling conditions. In so doing, we clarified that even with 11 years of data and ancillary data related to sightability, aerial surveys if interpreted in isolation, were not capable of removing uncertainty about the actual population trend during the decade-long study period.

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