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Density dependence and climate effects in Rocky Mountain elk: an application of regression with instrumental variables for population time series with sampling error

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Summary

1. Sampling error in annual estimates of population size creates two widely recognized problems for the analysis of population growth. First, if sampling error is mistakenly treated as process error, one obtains inflated estimates of the variation in true population trajectories (Staples, Taper & Dennis 2004). Second, treating sampling error as process error is thought to overestimate the importance of density dependence in population growth (Viljugrein *et al*. 2005; Dennis *et al*. 2006).

2. In ecology, state-space models are used to account for sampling error when estimating the effects of density and other variables on population growth (Staples *et al*. 2004; Dennis *et al*. 2006). In econometrics, regression with instrumental variables is a well-established method that addresses the problem of correlation between regressors and the error term, but requires fewer assumptions than state-space models (Davidson & MacKinnon 1993; Cameron & Trivedi 2005).

3. We used instrumental variables to account for sampling error and fit a generalized linear model to 472 annual observations of population size for 35 Elk Management Units in Montana, from 1928 to 2004. We compared this model with state-space models fit with the likelihood function of Dennis *et al*. (2006). We discuss the general advantages and disadvantages of each method. Briefly, regression with instrumental variables is valid with fewer distributional assumptions, but state-space models are more efficient when their distributional assumptions are met.

4. Both methods found that population growth was negatively related to population density and winter snow accumulation. Summer rainfall and wolf (*Canis lupus*) presence had much weaker effects on elk (*Cervus elaphus*) dynamics [though limitation by wolves is strong in some elk populations with well-established wolf populations (Creel *et al*. 2007; Creel & Christianson 2008)].

5. Coupled with predictions for Montana from global and regional climate models, our results predict a substantial reduction in the limiting effect of snow accumulation on Montana elk populations in the coming decades. If other limiting factors do not operate with greater force, population growth rates would increase substantially.

Key-words: climate, density dependence, elk, population dynamics, sampling error

In ecology, time-series data are commonly used to estimate the parameters of population growth models. Sampling error in estimates of population size creates two widely recognized problems for the analysis of population growth (Saether *et al*. 2007). First, if sampling error is mistakenly treated as process error, one obtains inflated estimates of the variation in true population trajectories (Staples *et al*. 2004). Second, treating sampling error as process error overestimates the importance of density dependence in population growth (Viljugrein *et al*. 2005; Dennis *et al*. 2006). In ecology, state-space models have emerged as a method to account for sampling error when estimating the effects of density and other variables on population growth (Staples *et al*. 2004; Dennis *et al*. 2006). When population sizes are recorded with error, regression models of the factors affecting population growth that include potential density dependence constitute a special case of the problem of correlation between a regressor (population size, in this case) and the error term. In econometrics, regression with instrumental variables is a well-established method that, like state-space models, addresses

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*Correspondence author. E-mail: screel@montana.edu the problem of correlation between regressors and the error term, but makes fewer assumptions (Durbin 1954; Sargan 1958; Davidson & MacKinnon 1993; Cameron & Trivedi 2005). Nonetheless, ecologists have not made use of regression with instrumental variables in this context. Our intention in this study is not to repeat existing validations of the method itself (Davidson & MacKinnon 1993). Rather we briefly describe regression with instrumental variables, and apply it to the problem of estimating the parameters of a growth model when sampling error is present. We then compare results to those of state-space models fit with the likelihood function of Dennis *et al.* (2006). Because prior studies have discussed the advantages and disadvantages of using maximum likelihood or Bayesian methods to fit state-space models of population growth (Clark & Bjornstad 2004; Staples *et al.* 2004; Dennis *et al.* 2006; Saether *et al.* 2007), we do not address that issue. In our example, we fit population growth models to data on the dynamics of elk in Montana to estimate the effects of density, snow accumulation, rainfall and wolf recolonization.

Regression with instrumental variables

Regression with instrumental variables is a well-described method that addresses correlation between regressors and the error term (Durbin 1954; Sargan 1958; Davidson & MacKinnon 1993; Cameron & Trivedi 2005). In a regression model, an instrument is a variable that is correlated with the regressors but uncorrelated with the errors. For n observations indexed by $t = 1, 2, \ldots, n$ and K regressors, define x_t to be the K-vector that holds the values of the regressors for observation t. Let X be the $n \times K$ matrix obtained by stacking the x_t row-wise. For p instruments, let W be the $n \times p$ matrix that is obtained by organizing the instruments in the same way as the regressors in X. Typically, there are more instruments than regressors ($P > K$), as is true of our analysis (see Material and methods). Then define $\hat{X}$ to be the projection of X on the span of W, that is $\hat{X} = W(W'W)^{-1}W'X$ [the ordinary least-squares (OLS) fit to X obtained by regressing X on W]. Finally, define y to be the vector of observations on the independent variable, and ε to be the vector of errors. The regression model is thus the familiar $y = X\beta + \varepsilon$. The generalized instrumental variables (GIV) estimator of the regression coefficients is given by

$$\hat{\beta}_{\mathrm{GIV}} = (\hat{X}'\hat{X})^{-1}\hat{X}'y$$

and its variance may be estimated as

$$\hat{V}(\hat{\beta}_{\mathrm{GIV}}) = (\hat{X}'\hat{X})^{-1}(\hat{X}'\hat{\Omega}\hat{X})(\hat{X}'\hat{X})^{-1},$$

where

$$\hat{\Omega} = \frac{1}{n}\sum_{t=1}^{n} w_t w_t' \hat{\varepsilon}_t^2$$

and $\hat{\varepsilon}_t = y - X\hat{\beta}_{\mathrm{GIV}}$ (Cameron & Trivedi 2005, pp. 95–111). GIV regression is also known as two-stage least-squares regression: in the first stage, the regressors are regressed on the instruments to estimate $\hat{X}$; and in the second stage, the dependent variable is regressed on $\hat{X}$. If the instruments are not correlated with the errors and the matrix $\frac{X'W}{n}$ converges in probability to a finite matrix with rank K, then the GIV estimator is consistent and asymptotically normally distributed. The formula we give for the estimated variance is valid when the variances of the ε_t are not constant, as is likely to be the case in our application.

Population density, snow and elk dynamics

POPULATION DENSITY

Analyses have long concluded that elk populations are limited (regulated) in a density-dependent manner, although these conclusions were based on methods that did not account for sampling error. Houston (1982) suggested that elk were regulated in a density-dependent manner and stated that ‘changes in the mortality of calves over their first months of life were a strong influence on the density dependence observed’. Singer *et al.* (1997) agreed: ‘Our results corroborate previous conclusions that density-dependent survival of elk calves may limit or regulate the northern Yellowstone elk population’. Taper & Gogan (2002) concurred yet again: ‘Density dependence in both fertility and adult survivorship is strongly suggested’. Although the pattern seems robust, re-examination of these conclusions is of interest, because sampling error can create spurious density dependence (Dennis & Taper 1994).

SNOW

Snowpack is a dominant factor limiting the survival and reproduction of elk in many ecosystems (Post & Stenseth 1999; Taper & Gogan 2002; Garrott *et al.* 2003). The range of elk (*Cervus elaphus*) in western North America is predicted to accumulate substantially less snow in coming decades (Cook *et al.* 2004; Lapp *et al.* 2005; Schindler & Donahue 2006). Global circulation models (e.g. HadCM3) (Johns *et al.* 2003) and regional climate models (e.g. CCCma CGCM1, NCAR RegCM2) (Lapp *et al.* 2002) differ somewhat in their predictions about future precipitation in western North America, but increased winter precipitation is generally predicted. Despite forecasts of increased winter precipitation, climate models concur in forecasts that snowpack in western mountain ranges will decline by 40–70% in the next 20–50 years, mainly due to increased winter rainfall and melting (Bell, Sloan & Snyder 2002; Cook *et al.* 2004; Lapp *et al.* 2005; Schindler & Donahue 2006). These processes are already detectable in the dynamics of glaciers, as many glaciers in western North America have retreated 25% within the last century (Schindler & Donahue 2006).

Elk (Frank & Groffman 1998; Singer *et al.* 1998), like many ungulates (McNaughton 1985; Frank, McNaughton & Tracy 1998), have strong and cascading effects on their communities, so climate-driven ecological release could have appreciable consequences for ecosystem structure and function over a large part of western North America.

Materials and methods

POPULATION GROWTH RATES AND INDEPENDENT VARIABLES AFFECTING GROWTH

The Montana Department of Fish, Wildlife and Parks surveys elk populations annually in 35 Elk Management Units (EMUs). We compiled estimates of elk numbers from 976 aerial surveys published in Montana Fish Wildlife and Park's elk management plan (Hamlin 2004), which provided counts for most of the state's elk over spans as long as 78 years. The population size estimates came from total counts that did not estimate uncertainty, did not correct for variation in counting conditions and did not use systematically stratified sampling methods, so it is reasonable to assume that the population counts include measurement error. Data on precipitation came from NRCS SNOTEL weather stations (http://www.wcc.nrcs.usda.gov/snotel/), using the lowest SNOTEL site in each EMU. For each EMU in each year, we tabulated the cumulative precipitation for October–March (predominantly snow) and April–September (predominantly rain). Data on wolves came from annual reports of the US Fish and Wildlife Service (http://westerngraywolf.fws.gov/) and reports by Montana Fish, Wildlife and Parks (Hamlin 2004). For each EMU in each year, we scored wolves as present, absent or transient (occasionally reported, but no confirmed resident breeding packs).

We extracted 472 population surveys for which all variables were available with lags of 2 years. Lagged variables were used as instruments (see details below). All variables were standardized and normalized prior to the analysis. We tested linear functional forms for all independent variables, because linear effects allowed clear *a priori* expectations (rainfall positive, all others negative), and in empirical tests of the effect of density, linear models usually provide a close approximation of the fit of more complex functional forms (Zeng *et al.* 1998).

Forecasts of future precipitation and snowpack came from published sources cited with results. We downloaded data from GCM model HadCM3 with IS92a conditions, comparing projections for 2070–2100 to observations from 1960–1990 (http://www.metoffice.gov.uk/research/hadleycentre/models/modeldata.html).

STATISTICAL POPULATION GROWTH MODELS

Generalized regression with instrumental variables and state-space models

Population sizes were measured with error (Fig. 1), so a regression model of the factors affecting population growth that includes density dependence is a special case of the problem of correlation between a regressor (population size, in this case) and the error term. State-space models can resolve this problem for time-series models of population size with sampling error. Following Dennis *et al.* (2006), we fit stochastic Gompertz models of population size as a linear state-space models using the Kalman filter (see below), but our primary analyses are based on linear regression using the method of GIV.

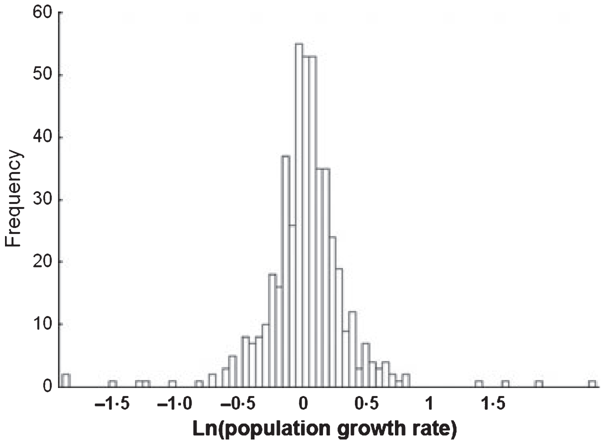

Fig. 1. The distribution of observed population growth rates for Montana elk, 1928–2004. The abscissa plots the intrinsic rate of increase *r*, or ln(λ): λ was measured as N_{t+1}/N_t for each pair of consecutive annual total counts in each of 35 Elk Management Units. These growth rates appear to be affected by measurement error, including some observations that are biologically implausible.

We selected lagged values of rainfall, snowfall and wolf presence as instruments, with time lags of 1 and 2 years (6 instruments), the squares of these variables (6 more instruments), and the interaction between the 1- and 2-year lag for each variable (3 more instruments), plus a vector of ones, for a total of 16 instruments. We then used GNU OCTAVE open-source software (www.octave.org) to fit the model

$$\lambda_{t+1} = a + b * \ln(\text{pop}_t) + c * \text{winSWE}_t + d * \text{sumSWE}_t + e * \text{wolf}_t + \varepsilon,$$

using a heteroscedasticity-consistent variance–covariance estimator (White 1980). In this GLM, λ is the population growth rate, 'pop' is the population count, 'winSWE' is the winter snowfall, 'sumSWE' is the summer rainfall, 'wolf' categorizes wolf presence and *t* subscripts years. Our code for the GIV estimation is available at http://pareto.uab.es/mcreel/Econometrics/MyOctaveFiles/Econometrics/LinearRegression.

State-space models

In GNU OCTAVE, we used the Kalman filter to apply the likelihood function of Dennis *et al.* (2006) and fit a stochastic Gompertz population growth equation as a linear state-space model (Table 2):

$$\text{Pop}_t = a + c * \text{Pop}_{t-1} + E_t$$
$$\text{Count}_t = \text{Pop}_t + F_t$$

Here 'Pop' is the natural logarithm of the unobserved true population size, 'Count' is the natural logarithm of the observed population size, *t* subscripts years, and the error terms *E* and *F* describe process variance (σ^2) and sampling variance (τ^2):

$$E \in \text{normal}(0, \sigma^2)$$
$$F \in \text{normal}(0, \tau^2)$$

We then fit the same state-space model, but allowed the parameter *a* to vary as a function of winter snowfall, summer rainfall and wolf presence (Table 3). Finally, to allow direct comparison of the results from GIV and state-space models, we used GIV to fit the Gompertz growth equation with covariates (Table 4). In the discussion, we will

Table 1. Regression with generalized instrumental variables for effects on elk population growth rate (R^2 = 0·14)

Parameter	Estimate	SE	t	P
Constant	0·024	0·015	1·545	0·123
Population size (t − 1)	−0·078	0·045	−1·732	0·084
Winter precipitation	−0·050	0·019	−2·670	0·008
Summer precipitation	0·011	0·017	0·674	0·518
Wolf presence	−0·009	0·016	−0·566	0·572

Variables standardized and normalized prior to analysis.

Table 2. Results of fitting the stochastic Gompertz equation as a linear state-space model, to 472 estimates of elk population size

Parameter	Estimate	SE	t	P
c	0·986	0·016	60·790	< 0·001
a	0·100	0·122	0·822	0·411
σ^2	0·064	0·011	5·944	< 0·001
τ^2	0·023	0·008	2·987	0·003

Bayesian information criterion: 298·8829; Akaike's information criterion: 282·2550.

Table 3. Results of fitting the stochastic Gompertz equation as a linear state-space model, with environmental covariates, to 472 estimates of elk population size

Parameter	Estimate	SE	t	P
c	0·975	0·012	80·735	< 0·001
a	0·195	0·091	2·146	0·032
σ^2	0·064	0·011	5·758	< 0·001
τ^2	0·022	0·008	2·920	0·004
Winter precipitation	−0·002	0·001	−2·504	0·012
Summer precipitation	0·003	0·002	1·530	0·126
Wolf presence	−0·027	0·022	−1·238	0·216

Bayesian information criterion: 309·4235; Akaike's information criterion: 280·3247.

Table 4. Results of fitting the stochastic Gompertz equation by generalized instrumental variable regression, with environmental covariates, to 472 estimates of elk population size (R^2 = 0·91)

Parameter	Estimate	SE	t	P
Constant	6·835	0·015	444·625	< 0·001
Population size (t − 1)	1·017	0·045	22·484	< 0·001
Winter precipitation	−0·050	0·019	−2·670	0·008
Summer precipitation	0·011	0·017	0·647	0·518
Wolf presence	−0·009	0·016	−0·566	0·572

address the problem of non-stationarity, which arises for these data when fitting a model of population size (Tables 2–4) rather than a model of the population growth rate itself (Table 1).

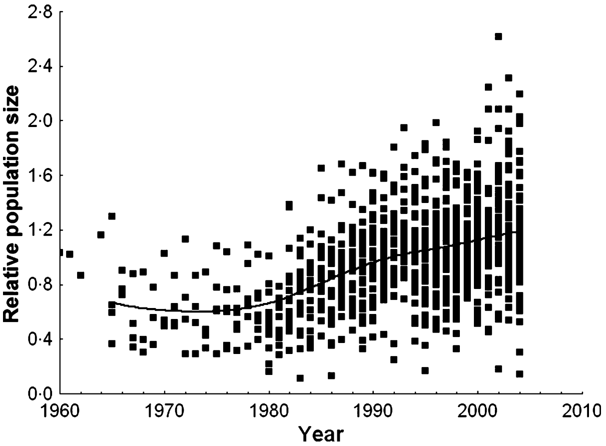

Fig. 2. Trends in population size for all Montana Elk Management Units, 1960–2004. Relative population size is the ratio of current population size to the mean for that Elk Management Unit. As the distribution of growth rates in Fig. 1 implies, elk populations in Montana have generally shown sustained growth (3% annually) over recent decades.

CONVERSION OF PROJECTIONS OF SNOWPACK TO ELK POPULATION GROWTH

For 2021–2050, Lapp *et al.*'s (2005) project that snowpacks in areas that typify elk habitat will decline to 31·6% of recent (1963–1985) levels at elevations of 1400–1600 m, and to 55·6% at elevations of 2000–2200 m. We used these projections, together with the regression coefficient for the effect of snowpack on elk dynamics, to examine what climate models suggest about future elk dynamics. For comparison, we produced a broader but less-detailed estimate of decline in snowpack by comparing annual means of monthly snowpack water equivalents for the periods 1970–1994 and 2039–2063, using Canadian Centre for Climate Modelling and Analysis CRCM3.6 data from CGCM2 with IS92a conditions for the 2·8 million km^2 rectangle between 37·0°–53·5° N and 100·5°–120·6° W (http://www.cccma.ec.gc.ca/data/crcm36/crcm36.shtml, runs aal and aaq). This broader approach predicts a decline (future levels = 43·5% of past levels) in snowpack that falls in the middle of the range predicted by Lapp *et al.* (2005).

Results and discussion

EFFECTS OF POPULATION DENSITY AND SNOW ACCUMULATION ON ELK DYNAMICS

In general, Montana elk populations have grown steadily over recent decades, with geometric mean annual growth (λ) of 1·030 (Figs 1 and 2). Regression with instrumental variables showed that the strongest correlates of population growth were snow accumulation and population density, while summer rainfall and wolf presence had little effect (Table 1). The state-space model without covariates (Table 2) also detected significant density dependence in elk population growth. Sampling error was significant, but small relative to process error. The state-space model with covariates (Table 3) detected a significant negative effect of winter snowpack, negative density dependence, a positive but weak effect of summer rainfall and little effect of wolf presence. Sampling error was again significant, but small relative to process error.

Thus, regression with instrumental variables and the state-space model yielded similar inferences that population density and winter snowpack (Fig. 3) have been the dominant limiting factors for Montana elk dynamics. The results show that both biotic (intraspecific competition) and abiotic (snowpack) factors are important factors limiting the growth of Montana elk populations. These conclusions are broadly supported by prior studies of single populations of Rocky Mountain elk (Houston 1982; Singer *et al.* 1997; Taper & Gogan 2002; Garrott *et al.* 2003) and other temperate ungulates (Coulson *et al.* 2001; Clutton-Brock & Coulson 2002; Saether *et al.* 2007).

Summer precipitation was not a strong predictor of elk dynamics. As expected, the effect of summer rainfall tended to be positive, but this effect was weak in comparison with the negative effect of winter snow accumulation. Because the positive effect of summer rain (which promotes plant growth) is weaker than the negative effect of winter snow (which limits access to grazing and increases the difficulty of movement), recent years of low precipitation in Montana have produced elk numbers that are currently above management goals in most EMUs (Hamlin 2004).

For the state as a whole, the presence of wolves was not a strong predictor of elk dynamics. However, wolves were not present in most EMUs for most of the time span over which these data were collected, and wolves were at relatively low densities in many of the areas that they did occupy. Although wolves had relatively little effect on the dynamics of elk at the scale of the entire state (as of 2003, the last year in these data), recent effects of wolf predation on elk dynamics in the core of the wolf recovery area have been strong (White & Garrott 2005; Creel *et al.* 2007; Creel & Christianson 2008).

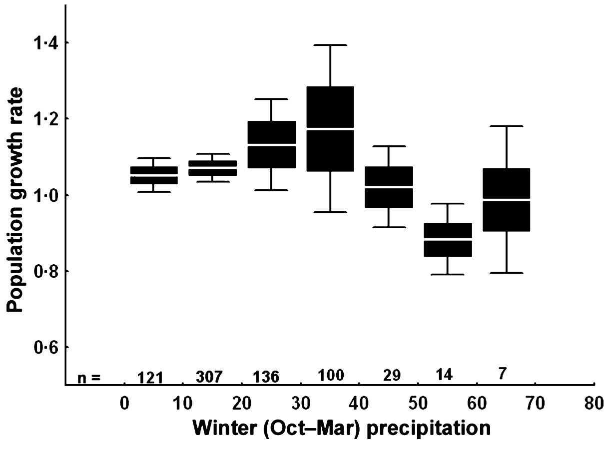

Fig. 3. The relationship of population growth rate (λ) to winter snow accumulation (inches of snow-water equivalent). Central lines show the mean, boxes show 1 SE, and whiskers show 2 SE. Sample sizes (*n*) are given below each bar.

COMPARISON OF METHODS

Inferences from the GIV model (Table 1) and the state-space model (Tables 2 and 3) can be compared, but the GIV model has population growth as its dependent variable, whereas the state-space Gompertz models have population size as the dependent variable. To facilitate comparison, we also fit the Gompertz model using GIV (Table 4). This model has substantially higher R^2 than the GIV model of population growth, but the estimated regression coefficient for population size is > 1, which is evidence that the population size is non-stationary. Non-stationary variables (gross domestic product is a well-known example from econometrics) grow stochastically without bound, and the regression of any non-stationary variable on another non-stationary variable tends to produce a high value of R^2, even if their causal relationship is negligible (Cameron & Trivedi 2005). Consequently, if the data are non-stationary, the reliability of results using estimation methods that ignore the problem is severely in doubt. We used GIV to fit a fifth model, identical to that in Table 1, except that it included the lagged growth rate as a predictor. The regression coefficient for that lagged growth rate (−0·12 ± 0·08, mean ± SEM) was well within the interval (−1,1), which is evidence that the growth *rate* was stationary, even though population size was not. This is a good reason to model the growth rate, as we do with the original GIV model (Table 1), rather than population size (Table 4). Because of non-stationarity, the coefficient of determination for the model of Table 4 is questionable, although basic inferences about the coefficients of the model remained the same.

State-space models using the Kalman filter assume normality of the errors for both process and sampling, and give biased and inconsistent results if these assumptions are violated (Cameron & Trivedi 2005). Moreover, the standard errors estimated by the Kalman filter are also biased, so results can appear more precise than they truly are. Generalized regression with instrumental variables requires no distribution assumptions (White 1980; Davidson & MacKinnon 1993; Cameron & Trivedi 2005). On the other hand, GIV regression is less efficient than state-space models fit by maximum likelihood when the distributional assumptions of the maximum likelihood method are met. The maximum likelihood method loses its efficiency advantage if its distributional assumptions are in error. Finally, GIV regression requires the availability of instruments that are correlated with the regressors but not with the errors. Overall, the GIV approach is more conservative because it is valid under weaker assumptions, but efficiency favours the state-space approach when one has confidence in its distributional assumptions.

For the elk data, standard tests reject the hypothesis that the natural log of population size is normally distributed (Doornik–Hansen test = 7·96, *P* = 0·019; Shapiro–Wilk *W* = 0·98, *P* = 0·000019; Jarque–Barra test = 10·67, *P* = 0·0048). Given these results, it is doubtful that the distribution of ln(population size) conditional on the regressors is normal, which puts the validity of maximum likelihood methods using the Kalman filter in doubt (Cameron & Trivedi 2005).

For GIV regression to be consistent, the instruments must be uncorrelated with the errors. Technically, this assumption is met if the matrix $\frac{X'W}{n}$converges to a finite matrix with rank K, as it did in our application. For reliable inferences with typical sample sizes, it is also necessary to find instruments that are reasonably well correlated with the regressors. In our application, when the $\log_e$ of population size is regressed on the instruments, $R^2 = 0{\cdot}20$, which is large considering the overall noise in these data [$R^2 = 0{\cdot}046$ for the OLS regression of ln(population size) on the regressors].

For some applications, an appealing feature of state-space models is that they give direct estimates of the relative importance of measurement error and process error. If the covariance of the measurement errors is known or consistently estimable, there are other methods available for consistent estimation of regression coefficients, without having to make distributional assumptions, as are needed for maximum likelihood using the Kalman filter (see Cameron and Trivedi 2005, p. 910, equation 26.14). GIV is appropriate when this information is not available. When process error is much more important than measurement error, the OLS estimator will have a slight bias and will be inconsistent, but will converge close to the true value. When measurement error is known to be small and sample size is reasonably large, one could use OLS with a good degree of confidence. One would not need GIV or the state-space methods in this case.

IMPLICATIONS OF FORECAST CLIMATE CHANGE FOR ELK DYNAMICS

Using the coefficient for snowpack from the GIV regression, we converted projections from climate change models into projected effects on elk dynamics. Under both global and regional circulation models, snow accumulation is predicted to decline in western North America, even if winter precipitation increases (Bell *et al.* 2002; Cook *et al.* 2004; Lapp *et al.* 2005; Schindler & Donahue 2006). Increases in melting, sublimation and winter rain are expected to reduce snowpacks to 30–60% of current levels, within 20–50 years. Snowpack at elevations of 1400–1600 m and at 2000–2200 m is predicted to decline to a mean of 32% of recent levels at the lower elevation, and to 56% at the higher elevation (comparisons of 1963–1985 measurements and 2021–2050 projections, using the Canadian Centre for Climate Modelling and Analysis' RCM CGCM1; Lapp *et al.* 2005). These declines align well with a broader estimate (future = 43·5% of past levels; $t_{39} = 9{\cdot}34$, $P < 0{\cdot}001$) obtained by comparing 1970–1994 measurements to 2039–2063 projections for the area 37·0°–53·5° N and 100·5°–120·6° W, which covers 2·9 million km^2 of the northern Rocky Mountains (Canadian Centre for Climate Modelling and Analysis CRCM3.6 data from model CGCM2 with IS92a conditions).

For the Montana elk data, the mean accumulation of winter snow-water equivalents was 0·531 m ($N = 718$ SNOTEL time series). The forecast proportional declines from climate models yield absolute declines of 0·236–0·363 m for snow of this depth. Reductions in snowpack of 0·236–0·363 m convert to increases in annual population growth [$\log_e(\lambda)$] of 0·158–0·242, using the regression coefficient for snowfall from Table 1. Before conversion, the standardized and normalized regression coefficient must be converted from units of standard deviation to units of metres, yielding $\hat{\beta} = 0{\cdot}669$. Thus, *if all else remained the same*, forecast reductions in snow accumulation imply an extremely rapid growth of Montana elk populations ($\lambda = 1{\cdot}195$–$1{\cdot}297$). Contrary to the general effects of climate change on alpine species, our growth models suggest a strongly positive effect of reduced snowpack on the population growth of elk. Population doubling time would drop from its current value 23–29 years to 3–4 years. Such growth is obviously too rapid to be sustained indefinitely, but growth rates higher than this range have been observed in several elk populations (Raedeke, Millspaugh & Clark 2002). It seems likely that other limiting factors will operate with increased force if such changes occurred (for example, increased food limitation or predation), but it is still important to note that projections of reduced snowpack imply ecological release of elk populations from an abiotic factor that has been strongly limiting in the past. Because elk have strong and widespread effects on ecosystem structure and function in the western North America (Hobbs 1996; Frank & Groffman 1998; Frank *et al.* 1998; Frank 2005), climate-driven changes in elk dynamics are likely to have cascading effects.

Conclusion

State-space models provide a method of accounting for sampling error when estimating the parameters of a growth model from a time series. Although this method has been shown to perform well, it relies on the assumption that both sampling and process errors are normally distributed, and that both types of error are present. Generalized regression with instrumental variables is widely recognized in the field of econometrics as a method of accounting for the general problem of correlation between a regressor and the error term, of which this is a special case. Regression with instrumental variables and state-space models produced similar inferences that population density and snow accumulation are important limiting factors for elk dynamics. With either method, the results suggest that forecast reductions in snowpack may release elk from a limiting factor that has been strong in decades past. Wildlife managers should consider this impending issue in plans to manage elk, a species of central importance for the structure and function of many Rocky Mountain ecosystems.

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