

Climatic and density influences on recruitment in an irruptive population of Roosevelt elk

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Current paradigms of ungulate population ecology recognize that density-dependent and independent mechanisms are not always mutually exclusive. Long-term data sets are necessary to assess the relative strength of each mechanism, especially when populations display irruptive dynamics. Using an 18-year time series of population abundances of Roosevelt elk (*Cervus elaphus roosevelti*) inhabiting Redwood National Park in northwestern California we assessed the influence of population size and climatic variation on elk recruitment and whether irruptive dynamics occurred. An information-theoretic model selection analysis indicated that abundance lagged 2 years and neither climatic factors nor a mix of abundance and climatic factors influenced elk recruitment. However, density-dependent recruitment differed between when the population was declining and when the population increased and then stabilized at an abundance lower than at the start of the decline. The population displayed irruptive dynamics.

Key words: California, *Cervus elaphus roosevelti*, demography, population dynamics, ungulate, vital rate

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DOI: 10.1644/13-MAMM-A-313

Climatic effects on population dynamics of ungulates are well documented across numerous taxa inhabiting a wide range of environments (Albon et al. 1987; Weladji et al. 2002; Pettorelli et al. 2009; Hamel et al. 2010; Simard et al. 2010; Imperio et al. 2012). Variation in climate can exert particularly strong effects on recruitment by reducing availability of winter forage and taxing thermoregulation of animals living in cold environments. For example, deep winter snow reduced recruitment of elk (*Cervus elaphus*—Garrott et al. 2003) and cold nighttime temperatures combined with high rainfall during parturition negatively affected recruitment of bighorn sheep (*Ovis canadensis nelsoni*—Holl et al. 2004) and black-tailed deer (*Odocoileus hemionus*—Gilbert and Raedeke 2004). Late-winter snowfall led to reduced female body condition and lower probability of parturition for caribou (*Rangifer tarandus*—Adams and Dale 1998). However, the timing of weather events can also positively influence recruitment by enhancing food supplies available to reproductive females, which influence pregnancy rates and offspring survival. For example, time-lagged effects of rainfall during summer correlate positively with recruitment of elk (Coughenour and Singer 1996; Johnson et al. 2013) and plains bison (*Bison bison*—Koons et al. 2012) inhabiting mid-continental climates. Furthermore, precipitation and temperature should have either

a minimal or positive influence on recruitment of ungulates inhabiting milder climates due to the absence of extreme temperatures or extended periods of snow-covered vegetation (Bonenfant et al. 2002). In Mediterranean climates characterized by mild, wet winters and hot, dry summers, there were weak effects of climatic variation on population dynamics of 3 species of cervids (Imperio et al. 2012). However, positive time-lagged effects of precipitation on pregnancy rates and subsequent recruitment were reported for red deer (*C. elaphus*) inhabiting similar climates (Bonenfant et al. 2002; Rodriguez-Hidalgo et al. 2010).

Effects of climate on population dynamics rarely occur in a vacuum. Inverse relations between recruitment and female density are ubiquitous among ungulates, and current paradigms recognize how intrinsic density-dependent mechanisms can strongly interact with density-independent factors like climate (Saether 1997). In addition, ungulate populations can undergo irruptions leading to high-density conditions when released into unoccupied habitats that have minimal top-down influence (Caughley 1970). Hence, variation in climate can exert a



stronger negative impact on recruitment when populations at high density become increasingly food limited (Albon et al. 1987; Rodriguez-Hidalgo et al. 2010; Simard et al. 2010). These density-dependent and independent interactions are especially strong in populations subjected to harsh winter conditions (Hansen et al. 2011), but often more subtle under mild climates (Imperio et al. 2012).

Roosevelt elk (*C. e. roosevelti*) occupying meadows within the redwood forest belt of coastal northern California present a unique opportunity to study interactions between extrinsic climatic factors and intrinsic demographic processes that influence ungulate population dynamics. First, temperatures are mild throughout the year (Harper et al. 1967), so elk in this area do not experience lengthy periods of snow cover and severe cold temperatures during winter like elk from mid-continental climate regions. Second, our study began 6 years after a large area of forage habitat became available to elk, which could set the stage for a 4-stage irruptive population growth curve. After release into a previously unoccupied habitat there is a rapid increase in population abundance (stage 1) that leads to an overshoot of carrying capacity and a peak in abundance (stage 2), followed by a density-dependent decline in abundance (stage 3) and ultimate re-equilibration to a lower carrying capacity (stage 4—Riney 1964; Caughley 1970; Forsyth and Caley 2006; Tyler 2010). The magnitude of the population decline and time to re-equilibrium can be exacerbated, ameliorated, or unaffected by climate severity (Tyler 2010). Therefore, a time series spanning a range of low to high abundances is necessary to critically assess the relative influences of climatic variation and population abundance on recruitment when a population irrupts.

Our objective was to determine how variation in climatic conditions and abundance influenced elk recruitment across a continuous 18-year time series. Given the relatively mild climatic regime and availability of new elk habitat in our study area, we predicted that elk abundance would have a stronger effect than precipitation or temperature on recruitment of Roosevelt elk, and that changes in population size over time would fit a 4-stage model of irruptive growth.

MATERIALS AND METHODS

Study area.—This study was conducted in the Davison Meadows within the lower reach of the Prairie Creek drainage of Redwood National and State parks. The climate is maritime, with cool, foggy summers and rainy winters. Ninety percent of the annual precipitation falls during the rainy season between October and April. Annual precipitation typically averages approximately 150 cm, and snowfall is extremely rare. Mean low temperatures during winter typically remain above freezing (3–5°C) and mean low temperatures during summer rarely exceed 10°C.

The meadows totaled 50 ha and were surrounded by second-growth and old-growth redwood–conifer forests dominated by coast redwood (*Sequoia sempervirens*), Sitka spruce (*Picea sitchensis*), Douglas fir (*Pseudotsuga menziesii*), and western

hemlock (*Tsuga heterophylla*). Meadow vegetation comprised a mix of perennial and annual grasses, e.g., California oat grass (*Danthonia californica*), redtop (*Agrostis alba*), and soft chess (*Bromus hordeaceus*), and forbs (Weckerly et al. 2001). Ostensibly, there has been an increase in reed canary grass (*Phalaris arundinacea*) from 1997 to 2014. The Davison Meadows were historically a fenced cattle pasture unavailable to elk (Harn 1958; Harper et al. 1967). The National Park Service purchased the meadows in 1991 and subsequently removed the fences to allow elk access and to create an elk-viewing area. Elk responded rapidly to fence removal and began frequenting the area shortly thereafter (F.W. Weckerly, pers. obs.). Elk in our study area were nonmigratory and were not legally hunted. Also, female elk in the parks can display strong social bonding, which results in a spatial organization whereby groups comprised of females inhabit forage habitat (meadows) that are rarely or never used by other female groups at the same time (Franklin et al. 1975; Weckerly 1999; Julian et al. 2013).

Data collection.—Population surveys were performed annually during January–February from 1997 through 2013 by driving a predetermined route through the study area (Weckerly et al. 2004). Surveys began at dawn, lasted 1.75 h, and were carried out for 10 mornings per year except in 1998 and 1999 when only 5 surveys were performed. We counted the number of females, juveniles, subadult (1.5-year-old) males, and adult males. Subadult females could not be differentiated from adult females on the basis of external morphology and were combined with counts of adult females. We also pooled juveniles and subadult males with females because they were observed in the same groups more than 99% of the time (Weckerly et al. 2001).

We use female abundance as our measure of population size because recruitment is more strongly tied to variation in female abundance in size-dimorphic ungulates (McCullough 2001). Male and female elk in this population display sexual segregation, with females using meadows more frequently than males (Weckerly 2007). We used the highest count of animals in female groups as our estimate of yearly population size across the time series. A count was considered adequate to estimate abundance because of the high detection probabilities (> 0.9) of females in our study area (Weckerly 2007). Across the 5–10 surveys conducted each year, females likely had a high probability of being detected (e.g., $1 - (1 - 0.9)^5 = 0.999$ —MacKenzie et al. 2006).

Climatic variables (monthly precipitation [sum of precipitation across all days of the month], mean high temperature, and mean low temperature) were obtained from the National Climatic Data Center operated by the National Oceanic and Atmospheric Administration land-based weather stations. Data from Boyes Prairie Station (Station # 046498, 5 km north of the Davison Meadows) most closely represented climatic conditions in our study area but had numerous missing values (27%) across the duration of our time series. We estimated missing values by regressing climate data from Boyes against a complete set of climate data from a station near Crescent City

(Station # 042147), 68 km to the north. Measurements of monthly precipitation and low and high temperatures from Crescent City significantly predicted those from Boyes ($r^2 \geq 0.61$, $P \leq 0.001$). The relationship between the 2 stations was stronger for low temperatures ($r^2 = 0.70$, $P < 0.001$) than for high temperatures ($r^2 = 0.66$, $P < 0.001$), so we used monthly low temperatures in subsequent analyses.

Analyses.—We plotted female abundance (N) against time and the intrinsic rate of population change ($\log_e[N_{t+1}/N_t]$) to examine irruptive dynamics throughout the course of our time series. We expected intrinsic rate of population growth to be near 0 or negative if the female segment of the population was food limited at high density, and greater than 0 when food limitation should be less intense during periods of low density. Since intrinsic rate of population change is also part of N_t we expect a statistically significant relationship. If the relationship is nonsignificant then recruitment could be influenced by density-independent factors, or the relationship to density-dependent recruitment could be more complicated.

We calculated juvenile:female ratios to estimate recruitment. This measure of recruitment has been shown through simulations to be positively related to juvenile survival (Harris et al. 2008) because the variation in juvenile survival is greater than the variation in female survival. Juvenile:female ratios probably reflect fecundity (number of juveniles in a cohort) as well because juvenile survival and fecundity are positively correlated (Noyes et al. 2002; Stewart et al. 2005; Sargeant and Oehler 2007). During times when females in a population are on a high nutritional plane, more females give birth to young that have higher chances of survival.

We built 33 least-squares regression models to examine relationships between precipitation, temperature, female population size (predictors), and juvenile:female ratios (response variable). Models were built to assess the influence of female population size, climatic variables, and both of these factors on juvenile:female ratios. We also built models to assess the possibility of differential influences from irruptive stages 3 and 4 on recruitment. For example, we assessed whether density-dependent influence on elk recruitment differed between the population decline (stage 3) and the re-equilibrium phase (stage 4—Caughley 1970). We created a dummy variable that delineated the data set into years during and before the abundance nadir (i.e., the year with lowest elk abundance) and after the nadir. The irruption stage models allowed us to fit separate linear regressions before and after the abundance nadir (Sokal and Rohlf 2012). We assumed that climatic conditions and recruitment within the same year would be uncorrelated or weakly correlated due to asynchronies between the timing of elk reproductive events and variation in resource availability (Coughenour and Singer 1996). The climate of the study area also had nuances that contributed toward time-lagged effects on elk demography. Unlike mid-continental regions, the mild, maritime climate is associated with higher forage quality in spring compared with the dry summer (Leslie and Starkey 1985; Gogan and Barrett 1994). Precipitation from the previous year, therefore, probably affects forage quantity and quality

utilized by gravid and lactating females, in turn affecting neonatal birth weight and juvenile survival (Albon et al. 1987). Furthermore, precipitation 2 years prior could affect female condition going into the mating season in autumn, thereby affecting pregnancy rates (Noyes et al. 2002). Consequently, each climatic variable was lagged 1 ($t - 1$) and 2 years ($t - 2$) with recruitment. Data points for each climatic variable were grouped into months during the rainy season (October–April) and summer (June–August).

We used model selection statistics calculated for each regression to select the model to summarize our data (Burnham and Anderson 2002; Sokal and Rohlf 2012). For each model we calculated Akaike information criterion corrected for small sample size (AIC_c) and the coefficient of determination (r^2). The “multiple” r^2 was reported for regressions with 1 predictor and “adjusted” r^2 was reported for multiple regressions (Sokal and Rohlf 2012). The delta value (change in AIC_c between a model and the model with the smallest AIC_c) guided our selection of 1 model from the 33 models in our comparison. We constrained models to ≤ 5 parameter estimates because our times series was 18 years (i.e., $n = 18$). The assumptions of normality and homoscedasticity were assessed with plots of residuals (Sokal and Rohlf 2012).

RESULTS

Population size of female elk peaked at a high of 52 animals at the start of the time series before beginning a steady decline that reached a nadir of 17 animals in 2006 (Fig. 1). Thereafter, population size rebounded within a narrow range of 30 and 37 females. Across the 18 years the relationship between abundance and intrinsic rate of population increase was nonsignificant ($r^2 = 0.15$, $F_{1, 14} = 2.57$, $P = 0.131$; Fig. 2). Yet, negative values consistently followed the period of highest female abundance at the beginning of the study and positive values occurred frequently between 2006 (year of the nadir) and 2013.

We selected 1 model that had a much smaller AIC_c (> 8 AIC_c units) relative to the remaining 32 models (Table 1). Our selected model was an irruption stage model that indicated that female abundance lagged 2 years had the strongest relationship with juvenile:female ratios (Fig. 3). Before the nadir in abundance, the model indicated a positive density-dependent relationship with juvenile:female ratios, whereas after the nadir juvenile:female ratios displayed an inverse density-dependent relationship (Table 2).

DISCUSSION

The mild year-round temperatures coupled with the wet conditions in the cooler months of the year are climatic settings that are benign to recruitment of Roosevelt elk in our study. We did, however, observe a complex density-dependent relationship. Density lagged 2 years, not 1 year or both years, appeared to exert the most influence, which suggests that competition for forage or environmental settings that affected

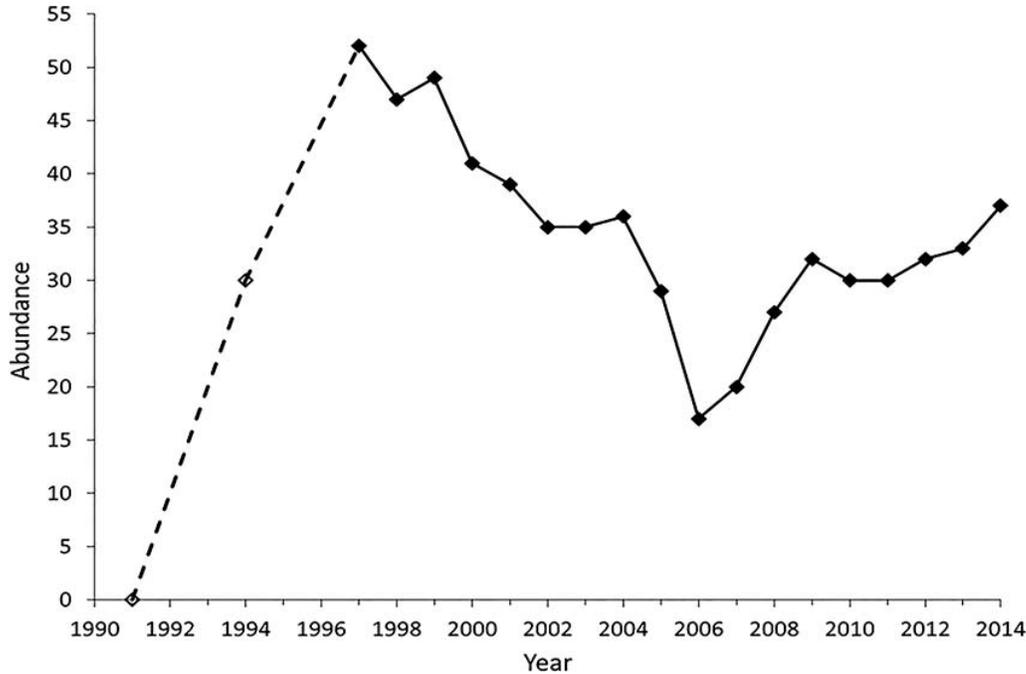


FIG. 1.—Abundance of female Roosevelt elk (*Cervus elaphus roosevelti*) inhabiting the Davison Meadows during January–February, 1997–2013. Systematic surveys of the Davison Meadows using the same protocol were not conducted until 1996 (dashed line, open diamonds). The Davison Meadows became available to elk in 1991, and in 1994 the estimate is based on haphazard counts.

female condition during the time of conception probably wielded the strongest influence on recruitment (Mech et al. 1987; Coughenour and Singer 1996; Noyes et al. 2002). Yet, the nature of the density-dependent relationship differed depending on the stage of the irruptive population growth

curve. Our findings of an inverse density-dependent recruitment after the population decline are consistent with the idea that during the declining stage (stage 3) there was a density-dependent response in recruitment (Caughley 1970). In stage 3 food supplies were probably depleted and females had few

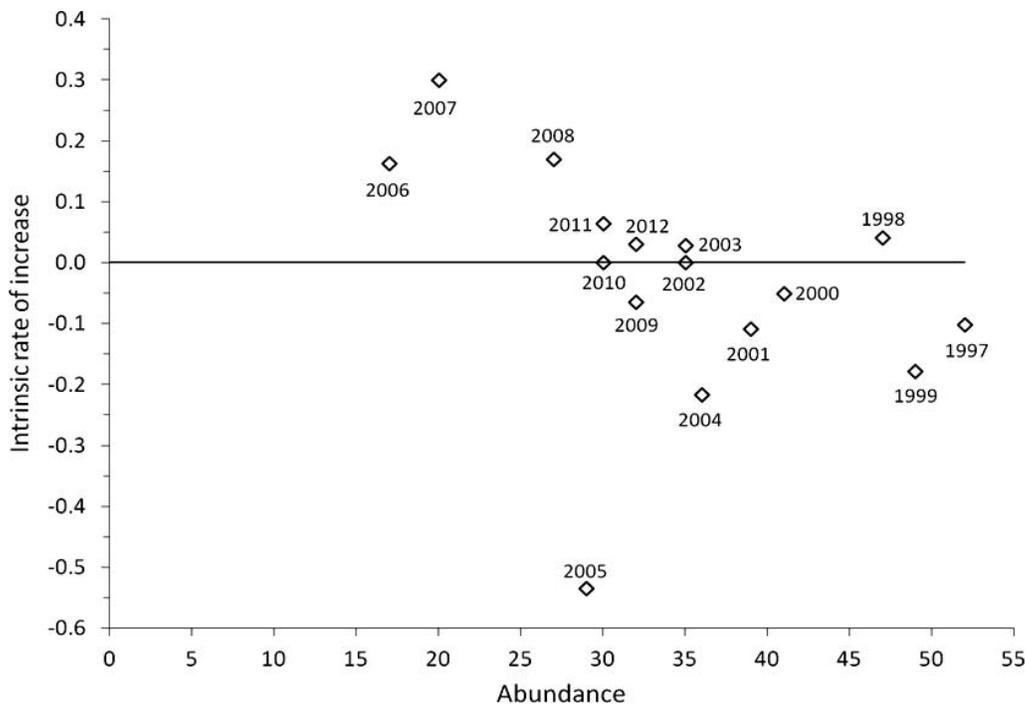


FIG. 2.—Scatter plot of female abundance and intrinsic rate of population increase ($r = \log_e[N_t/N_{t+1}]$) between 1997 and 2012 for Roosevelt elk (*Cervus elaphus roosevelti*) inhabiting the Davison Meadows. The horizontal line denotes no population change ($r = 0$).

TABLE 1.—Model selection summary of 33 least-squares regression models estimating juvenile:female ratios of Roosevelt elk (*Cervus elaphus roosevelti*) considering density, climatic variables, and both density and climatic variables. Fit of models was assessed with Akaike information criterion corrected for small sample size (AIC_c). The model selection summary consists of delta (Δ, difference in AIC_c between model and model with smallest AIC_c), number of parameters estimated in model (nPar), and coefficient of determination (r²). The adjusted r² is reported for models with > 1 predictor and simple r² is presented for models with 1 predictor.

Models ^a	Δ	nPar	r ²
N _{t-1} * nadir	0.00	5	0.71
N _{t-1} * nadir	8.60	5	0.50
N _{t-2}	9.37	3	0.31
N _{t-1}	10.42	3	0.26
PrecipS _{t-1} * nadir	10.43	5	0.44
N _{t-2} + precipR _{t-2}	11.57	4	0.27
N _{t-2} + tempS _{t-2}	12.53	4	0.23
N _{t-1} + N _{t-2}	12.88	4	0.21
N _{t-2} + precipS _{t-2}	12.98	4	0.21
N _{t-2} + tempR _{t-2}	12.99	4	0.21
N _{t-1} + precipS _{t-1}	13.29	4	0.19
N _{t-1} + tempR _{t-1}	13.64	4	0.17
TempR _{t-1}	13.90	3	0.09
N _{t-1} + tempS _{t-1}	13.94	4	0.16
PrecipR _{t-2} * nadir	13.97	5	0.30
N _{t-1} + precipR _{t-1}	14.03	4	0.15
PrecipR _{t-2}	14.18	3	0.07
PrecipS _{t-2}	14.27	3	0.06
TempR _{t-2}	14.67	3	0.04
TempS _{t-1} * nadir	14.72	5	0.27
PrecipR _{t-1}	14.96	3	0.02
TempS _{t-2}	15.05	3	0.02
TempR _{t-2} * nadir	15.32	5	0.24
PrecipS _{t-1}	15.32	3	0.01
TempS _{t-1}	15.34	3	0.01
TempS _{t-2} * nadir	15.85	5	0.22
PrecipS _{t-2} + tempS _{t-2}	16.12	4	0.03
PrecipS _{t-2} * nadir	16.37	5	0.19
TempR _{t-1} * nadir	16.51	5	0.18
PrecipR _{t-1} * nadir	16.65	5	0.18
PrecipR _{t-2} + tempR _{t-2}	16.93	4	0.01
PrecipR _{t-1} + tempR _{t-1}	17.18	4	0.01
PrecipS _{t-1} + tempS _{t-1}	18.94	4	0.01

^a Predictor notation was N for female population size, subscripts are for lags of 1 or 2 years, nadir is a dummy variable that coded a year before or during the lowest abundance (lag 1: 1998–2006, lag 2: 1999–2006) and after the lowest abundance (2007–2014), S is summer (June–August), and R is rainy season (October–April) for precipitation (precip) and low mean temperature (temp). * denotes interaction.

energy and protein reserves to allocate to reproduction. As such, the gradual decline in our time series over 10 years might have been facilitated by recruitment that tended to be low and weakly coupled to abundance.

As expected, precipitation and temperatures during the rainy season or summer appeared to have no influence on recruitment in Roosevelt elk that inhabited Davison Meadows. In contrast, precipitation negatively influenced survival of both adult female and juvenile elk in Wyoming at different times of the year (Sauer and Boyce 1983). In a Mediterranean climate with mild, wet winters and hot, dry summers, precipitation

influenced female body size, which influenced pregnancy rates (Rodriguez-Hidalgo et al. 2010). Snowpack severity and duration adversely affected elk recruitment in Yellowstone National Park (Garrott et al. 2003) and winter snowfall also was negatively correlated with juvenile survival in a population of red deer (Loison and Langvatn 1998). These studies of *C. elaphus* were performed in areas with lengthy periods of snowpack and much colder winter temperatures than in our study area. Indeed, elk in the Davison Meadows were exposed to winter temperatures that were well within the thermal limits of elk (Parker and Robbins 1984).

The population dynamics were consistent with a population irruption. Davison Meadows were grazed by cattle and unavailable to elk before the National Park Service purchased the meadows in 1991. Suddenly a large patch of forage habitat became available to elk in a region dominated by closed coniferous forest. Within months of the purchase by the National Park Service, elk became apparent in Davison Meadows (F. W. Weckerly, pers. obs.). The first robust abundance estimate in the Prairie Creek drainage that occurred in 1996 reflected very high density compared with other Roosevelt elk herds (Weckerly 1996). Two of the co-authors (MAR and FWW) found elk to be ubiquitous during 1994 (haphazard counts of the Davison group between 29 and 32, Fig. 1). Hence, the high-density population likely exhausted the food supply, and the population declined after 1997 and then, seemingly, re-equilibrated at a lower carrying capacity at the end of our time series. During the population decline the density-dependent response in recruitment is consistent with findings from an irruptive bison population (Larter et al. 2000). The observed population dynamics are consistent with stages 1 through 4 of irruptive population models (Caughley 1970).

Between 1991 when Davison Meadows became available to elk and 1997 when our time series began, animals probably moved into the Davison Meadows. It is unlikely, however, that the population irruption in Davison Meadows reflects shifts in distribution of individuals among Davison and nearby meadows across the years of our time series. Strong social bonding and meadow fidelity are characteristics of females inhabiting Davison Meadows since 1997 and in other meadows in the area (Franklin et al. 1975; Weckerly 1999). Furthermore, across the time series reported herein, group size dynamics between the Davison population and nearby populations were not correlated and thus represent distinct geographic units (Julian et al. 2013). The evidence suggests that, across our time series, the individual females that used Davison Meadows constituted a population (Ehrlich and Daily 1993).

Recent investigations of density-dependent and density-independent recruitment have revealed that the 2 mechanisms interact to affect population dynamics (Bonenfant et al. 2002; Garrott et al. 2003). Our findings are novel in 3 respects. First, there are few long-term studies of ungulate recruitment where climate does not appear to be influential (Bonenfant et al. 2002). Elk experienced more abundant, nutritious forage during the cool, not the warmest, time of year, which is contrary to settings in other studies of North American elk in

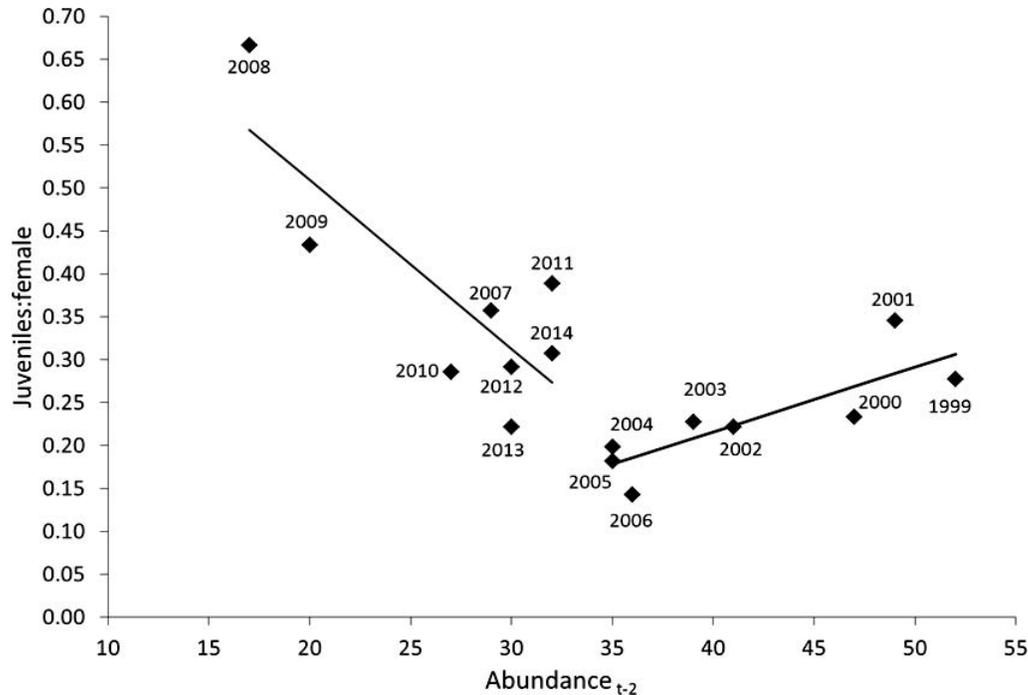


FIG. 3.—Scatter plot of female Roosevelt elk (*Cervus elaphus roosevelti*) abundance (lagged 2 years) and juvenile:female ratios for years before (1999–2006) and after (2007–2014) the nadir in female abundance. Also plotted are the regressions before and after the nadir.

mid-continental climates. Second, irruptive dynamics occurred in a population inhabiting a small area. Irruptive population models were articulated with larger islands (e.g., New Zealand) in mind (Caughley 1970). Third, estimating influences from mild environmental settings on recruitment when European and North American *C. elaphus* ostensibly display irruptive population behavior has, to our knowledge, not been conducted before. Moreover, to our knowledge irruptive population dynamics with empirical population data from all 4 stages have not been documented in *C. elaphus* in North America. The documentation on release, increase, and decline of introduced *C. elaphus* in New Zealand helped to articulate the 4 stages of population irruption (Riney 1964; Caughley 1970; Nugent and Fraser 2005). There are also numerous examples of colonizing or reintroduced elk in North America displaying stage 1 population irruption (Banfield 1949; Gogan and Barrett 1987; Eberhardt et al. 1996; Howell et al. 2002; Larkin et al. 2003; Sargeant and Oehler 2007). Yet, only 1 population was monitored beyond stage 2, and that population was released from culling and was not a colonizing or

reintroduced herd (Coulson et al. 2004). In that population the evidence did not suggest stage 3 or 4 irruptive dynamics but rather an equilibrium population at a size similar to peak abundance (Forsyth and Caley 2006). Results from our study indicate that climatic factors do not strongly influence elk recruitment in a benign climate, but they suggest that stage 1 through 4 irruptive dynamics might occur in colonizing Roosevelt elk populations.

ACKNOWLEDGMENTS

Funding for this long-term research was provided by California Department of Fish and Wildlife, Redwood National Park, Rocky Mountain Elk Foundation, Alamo Safari Club, Granite Bay Safari Club, Houston Safari Club, and Texas State University. We thank Redwood National and State parks for their assistance and cooperation over the years and to the many park biologists that assisted in data collection. R. Keleher, J. Hunt, D. Lancaster, M. Longoria, R. Luna, M. O'Dell, K. Richardson, S. Robinson, S. Shelton, G. Street, and D. Wolcott assisted the authors on counts.

TABLE 2.—Coefficients, SEs, and *t*-tests for the selected model. The reference category for the nadir dummy variable was juvenile : female ratios of Roosevelt elk (*Cervus elaphus roosevelti*) before and during the population decline (1999–2006). The subscript denotes a lag of 2 years and * denotes an interaction.

Coefficient	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	−0.086	0.161	−0.536	0.601
Female abundance _{<i>t</i>−2}	0.007	0.004	1.984	0.071
Nadir	0.988	0.204	4.839	0.004
Female abundance _{<i>t</i>−2} *nadir	−0.027	0.006	−4.576	< 0.001

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Submitted 5 December 2013. Accepted 18 April 2014.

Associate Editor was Christine R. Maher.