

Evidence of relationships between El Niño Southern Oscillation and mule deer harvest in California

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A growing body of research has demonstrated relationships between population dynamics of large herbivores and large-scale climatic phenomena. We investigated gradients in the effects of one such phenomenon, El Niño Southern Oscillation (ENSO), to look for evidence of its influence on mule deer (*Odocoileus hemionus*) harvest. Based on the Southern Oscillation Index (SOI) and reported deer harvest for 55 counties in California, USA, there was evidence that arid and climatically more variable counties to the south and west were more likely to demonstrate a relationship between deer harvest and SOI. Eighteen counties demonstrated a relationship between harvest and SOI, and for 16 of those, harvest was positively related to intensity of ENSO activity. A growing recognition of the role of extrinsic variation, such as that associated with large-scale climate phenomena, means that management of mule deer populations increasingly will have to incorporate an understanding of the mechanisms connecting those phenomena to local weather patterns, forage dynamics, and population dynamics.

Key words: climate, El Niño Southern Oscillation, ENSO, harvest, mule deer, *Odocoileus hemionus*, SOI, Southern Oscillation Index

Evidence from a growing body of research has demonstrated relationships between population dynamics of large herbivores and large-scale climatic phenomena, such as El Niño Southern Oscillation (ENSO; Barber and Chavez 1983) and the North Atlantic Oscillation (NAO; Hurrell 1995). Those phenomena affect terrestrial climate patterns

(Markham and McLain 1977, Goldberg et al. 1987, Hurrell and van Loon 1997) and ultimately, primary and secondary productivity (Post and Stenseth 1999, Holmgren et al. 2001, Jaksic 2001). Both phenomena occur when normally strong prevailing winds relax, causing a reversal in atmospheric pressure differentials (Barber and Chavez 1986, Hurrell and van Loon 1997). The consequence is a modification of ocean currents and ocean temperature patterns that can affect air temperature, precipitation, and biological productivity in terrestrial and aquatic environments (Barber and Chavez 1983, Hurrell 1995, Holmgren et al. 2001, Jaksic 2001, Mysterud et al. 2003). For ENSO, the reversal in the atmospheric pressure differential occurs between the subtropical high-pressure region in the South Pacific Ocean and the equatorial low-pressure region near Indonesia (Gill and Rasmusson 1983). In turn, this causes warm water from the western Pacific to move toward South America, thereby affecting the marine ecosystem but also increasing precipitation in the western Americas (Jaksic 2001).

The effects of large-scale climate phenomena and associated regional weather on population dynamics of large herbivores has been demonstrated to show spatial heterogeneity related to latitude or longitude. Although more commonly seen in small mammals (Hansson and Henttonen 1985, Hanski et al. 1991, Bjornstad et al. 1995), latitude and longitude and their effects on the relationships between climate variation and population dynamics, have been demonstrated recently for pan-Arctic populations of caribou and reindeer (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*; Forchhammer et al. 2002, Post 2005). Populations that are farther north experience more variable climate, more frequent severe weather (e.g., icing of the snowpack), and intermittent, severely food-limited conditions (Solberg et al. 2001). In such populations, NAO as an index of severe winter conditions has a larger effect on dynamics of *Rangifer* populations at more northern latitudes (Post 2005). A similar situation has been described for arid environments where availability of forage for herbivores is a function of primary production determined by variable rainfall (Robertson 1987, Owen-Smith 1990, Marshal et al. 2005) rather than of conditions that limit access to forage (Caughley and Gunn 1993). In both environments, variable conditions result in animal populations that rarely are at equilibrium density with their forage supplies or demonstrate evidence of intraspecific competition; thus, the primary determinant of the dynamics of such populations is more likely to be fluctuating environmental conditions than competition for forage (Crete and Courtois 1997, Choquenot 1998).

Given the role of ENSO in terrestrial plant productivity, the contribution of large-scale climatic phenomena to variability in resources for large herbivores, and the latitudinal and longitudinal effects identified in other systems, our objective was to look for evidence of these relationships in harvest data for mule deer (*Odocoileus hemionus*) in California, USA. Investigation of relationships between large mammal populations and climate patterns requires data of a scope that is broad, both temporally and spatially. We used long-term harvest data because survey data of suitable temporal and spatial scale are scarce for large herbivore populations. California Department of Fish and Game (CDFG) has compiled harvest data by county since 1927 (Mohr and Parker 2007). In addition, mule deer occupy much of California (McLean 1940), where environments range from deserts, characterized by low plant biomass and highly variable precipitation, to temperate rainforest that are characterized by high plant biomass and low variability in precipitation (Munz and Keck 1968). Moreover, ENSO influences climate and ecological systems throughout the state (Markham and McLain 1977, Kurtzman and Scanlon 2007).

Because of the link between precipitation and forage resources for large herbivores (Robertson 1987, Mduma et al. 1999, Marshal et al. 2005), we began by establishing geographic patterns in rainfall and in relationships between ENSO and rainfall. Then, we investigated whether there was evidence of an effect of ENSO on deer populations as revealed through harvest data, an index to population size.

METHODS

Sources of data.—We used reported mule deer harvest data for 55 counties spanning the period 1950-2007. Counties ranged in size from 1,149 km² to 52,376 km², latitudes from 32° N to 42° N, and longitudes from 114° W to 124° W. There was variation in environments within each county, with larger counties tending to have more heterogeneous conditions (vegetation communities, terrain features, climate patterns) than smaller counties. Harvest numbers used in this analysis were for males older than one-year-of-age only. Harvest of females occurred only in a small number of counties, and in those counties harvest was frequently reported as zero. Mule deer harvest in California currently is regulated by a quota system. To investigate whether methods of regulating harvest might influence relationships between harvest and environmental factors, we used linear regression to look for relationships between reported harvest (response variable) and length of hunting season, number of tags available, and number of tags issued to hunters (explanatory variables). These data were not available by county; thus, we used data from 36 general hunt category deer management units (DMU) for years 1998-2007 (Mohr and Parker 2007).

Precipitation was assumed to be the principal environmental factor through which ENSO operated, and that it ultimately influenced deer harvest via primary production and mule deer population responses to forage conditions. We conducted county-specific rainfall analyses to investigate how ENSO-precipitation relationships varied across California. The southern oscillation index (SOI) was used as an index of the intensity of ENSO events and was obtained from the National Oceanographic and Atmospheric Administration Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/data/indices/soi>). The SOI data were available as monthly standardized averages, from which we calculated October-March averages (the period over which ENSO has its strongest effect) to compare to annual rainfall and reported harvest for mule deer.

Annual rainfall totals for weather stations in each county were available from the Western Regional Climate Center (<http://www.wrcc.dri.edu/>). To index forage conditions by county, representative weather stations were chosen from across each county to summarize rainfall. We included stations having ≥ 20 years of data, which affected the exact number of stations available (up to five stations were used to estimate conditions in each county). Once selected, we calculated the coefficient of variation (*CV*) in rainfall for each station. Then we calculated a single county-wide estimate for average annual rainfall and *CV* from individual station averages and *CV*s. Rainfall has been used as an index for forage availability in arid-region large-herbivore studies (e.g., Owen-Smith 1990, Marshal et al. 2002, 2009) and, although less common, fluctuations in rainfall have been shown to be related to resource or habitat conditions in more temperate northern California (e.g., Boroski and Mossman 1998, McCullough 2001).

Statistical analysis.—The objective of our analysis was to look for evidence of county-specific relationships between harvest numbers and SOI. We log-transformed the raw reported harvest data to make them suitable for analysis with linear models (Royama

1992). Reported deer harvest in almost every county showed long-term declines (Mohr and Parker 2007). We assumed that short-term fluctuations in deer harvest were more likely the result of year-to-year variation in precipitation and forage conditions; those short-term fluctuations, rather than the long-term trends, were the focus of our analysis. With this in mind, we used generalized additive models (GAM; Hastie and Tibshirani 1990) to estimate long-term trends in deer harvest for each county, with degrees of freedom for the smoothing function estimated automatically. $\text{Loge}(\text{harvest})$ was the response variable and year was the explanatory variable. The residuals from each GAM analysis (i.e., detrended log-transformed harvest, X_t) should have preserved year-to-year fluctuations that arose from environmental variation; thus, we used the residuals in subsequent analyses to estimate relationships between deer harvest and environmental variables.

We investigated relationships between ENSO and X_t using autoregressive (AR) time-series models that included SOI as a covariate. Doing so allowed us to remove variation in detrended times series that might be explained by an AR process, and to more easily detect relationships with SOI in the residual variation. The methods followed here were based on those developed to study population dynamics of small (Bjornstad et al. 1995) and large (Forchhammer et al. 1998, Post and Forchhammer 2001) mammals. The general form of the AR model used for each county was:

$$X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \beta_2X_{t-2} + \beta_3X_{t-3} + \dots + \beta_dX_{t-d} + \sum_{j=1}^{j=k} \omega_j U_{t-j} + \varepsilon_i, (1)$$

where X_t was the detrended log-transformed harvest for a particular county in year t ; U_t corresponded to the values of the covariate (i.e., SOI); β_0 was the intercept; the coefficients $(1 + \beta_1)$ and $\beta_2 \dots \beta_d$ were the slopes of the relationships between X_t and $X_{t-1} \dots X_{t-d}$; ω_j quantified the direct or delayed relationships with SOI; and ε_i represented remaining variation not explained by the model (for a detailed derivation of this model, see Royama 1992, Bjornstad et al. 1995, Forchhammer et al. 2002).

Equation (1) was used to develop a set of candidate models, from which we selected the most parsimonious AR model for each county. We developed candidate models in two steps. For the first step, we selected from among all AR models containing lags of 0 to 3 years, initially leaving out the SOI covariate (Post 2005); an AR model of lag 0 represented an intercept-only model. Selection of the best model was based on the value of Akaike's Information Criterion, corrected for small-sample bias (AIC_c), where the lowest value was associated with the most parsimonious model of the candidates considered (Burham and Anderson 2002). Then we ranked models according to differences in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c). If more than one model had $\Delta AIC_c < 2$, we used the model with the fewest parameters. For the second step, we developed a second set of candidates containing five models derived from the selected model from step one: four new models, each with SOI as a covariate lagged 0 to 3 years, and the original AR model without the SOI covariate. We judged there to be evidence of an SOI effect if a model with the SOI covariate had an $AIC_c \geq 2$ units smaller than that of the best AR model without a SOI covariate.

Once we selected an AR model for each county, we used logistic regression to investigate the relationship between detection of an effect of ENSO for a county and its environmental characteristics. The response variable was whether an effect of ENSO was detected (0, 1), and the explanatory variables were centroid longitude, centroid latitude, average rainfall, and CV in rainfall. We used the explanatory variables to develop a set of 16 candidate models which we ranked using AIC_c . We conducted all analyses in R (R Development Core Team 2008).

RESULTS

Patterns of rainfall variation.—There were both latitudinal and longitudinal gradients in annual rainfall, *CV* in annual rainfall, and correlation between annual rainfall and SOI (Figure 1a, b, c). The tendency was for more northern and western regions to have higher rainfall, lower *CV*, and weaker correlations with SOI. Among counties, highest average rainfall occurred in Del Norte County (1,700 mm), lowest *CV* occurred in Humboldt County (25%), and highest (i.e., most non-negative) correlation occurred in Trinity County (0.16). All of those counties occurred in the northwestern corner of the state. In contrast, Imperial County, in the southeastern corner of California, had the lowest mean annual rainfall (79 mm) and highest *CV* in rainfall (63%). Imperial County also demonstrated the most strongly negative correlation between rainfall and SOI (-0.51); thus, rainfall was most strongly influenced by intensity of ENSO activity in Imperial County.

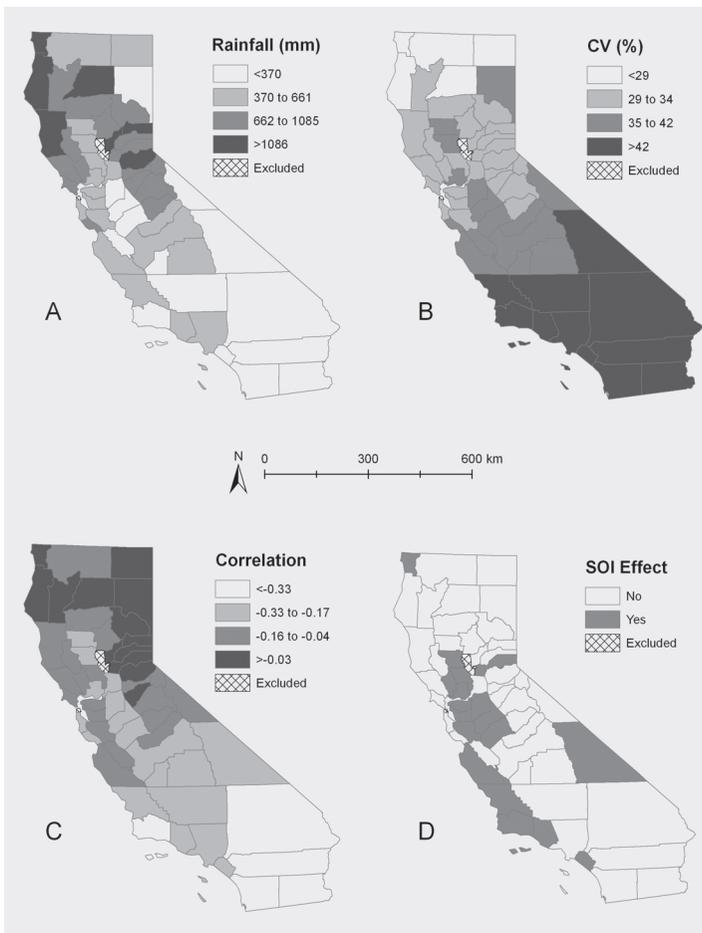


FIGURE 1.—Gradients across California, USA, by county: (A) annual average rainfall; (B) coefficient of variation (*CV*) in annual rainfall; (C) correlation between annual average rainfall and October-March average Southern Oscillation Index (SOI); (D) counties in California demonstrating relationships between SOI and deer harvest.

Evidence of ENSO in deer harvest data.—After accounting for variation explained by long-term trends and AR processes, 18 of 55 counties showed evidence of a relationship between residual harvest and SOI (Figure 1d; Table 1). Of those counties, one demonstrated a positive relationship with the current year's SOI, one a positive relationship with SOI three years previous, 14 a negative relationship with SOI two years previous, and two a negative relationship with SOI three years previous (Table 1). Thus, there were positive relationships (more strongly negative coefficients) between residual variation in \log_e (harvest) and intensity of El Niño activity for 16 of the 18 counties where an effect of ENSO was evident.

TABLE 1.— Relationships between residual deer harvest and the Southern Oscillation Index (SOI) by county for California, USA, 1950-2007.

County	SOI Coefficient	SE	Lag ^a	Rainfall Average (mm)	CV (%)	Correlation ^b	Decimal degrees Longitude	Latitude
Alameda	-0.0555	0.0231	3	436	34.40	-0.13	-121.94	37.65
Alpine	0.0000		0	892	32.46	-0.09	-119.82	38.60
Amador	0.0000		0	919	32.74	-0.06	-120.53	38.46
Butte	0.0000		0	1042	31.58	-0.13	-121.59	39.66
Calaveras	0.0000		0	875	33.16	-0.03	-120.46	38.18
Colusa	-0.0314	0.0193	3	441	38.92	-0.22	-122.25	39.17
Contra Costa	-0.0547	0.0299	4	480	32.31	-0.13	-121.90	37.91
Del Norte	-0.0580	0.0282	3	1700	27.18	0.11	-123.90	41.75
El Dorado	0.0000		0	1151	33.10	0.02	-120.52	38.76
Fresno	0.0000		0	490	36.50	-0.19	-119.66	36.83
Glenn	0.0000		0	511	36.78	-0.24	-122.39	39.59
Humboldt	0.0000		0	1151	25.08	0.04	-123.84	40.74
Imperial	0.0000		0	79	62.96	-0.51	-115.33	33.05
Inyo	-0.0846	0.0308	3	227	46.67	-0.30	-117.31	36.61
Kern	0.0000		0	213	46.10	-0.29	-118.84	35.35
Lake	0.0000		0	907	30.43	-0.09	-122.73	39.10
Lassen	0.0000		0	308	35.74	0.07	-120.63	40.50
Los Angeles	0.0000		0	402	52.19	-0.28	-118.20	34.37
Madera	0.0000		0	457	37.39	-0.15	-119.74	37.32
Marin	0.0000		0	862	32.20	-0.10	-122.72	38.05
Mariposa	0.0000		0	720	31.44	-0.08	-119.87	37.56
Mendocino	0.0000		0	1205	30.17	-0.08	-123.36	39.42
Merced	-0.0773	0.0322	2	278	35.69	-0.17	-120.68	37.20
Modoc	0.0000		0	381	25.42	-0.03	-120.73	41.62
Mono	0.0000		0	302	37.66	-0.14	-118.91	37.93
Monterey	-0.0529	0.0229	3	408	36.34	-0.12	-121.08	36.30
Napa	-0.0468	0.0212	3	854	34.56	-0.12	-122.34	38.48
Nevada	0.0000		0	1085	31.89	-0.03	-120.68	39.32
Orange	0.0991	0.0460	1	347	48.07	-0.33	-117.78	33.68
Placer	0.0631	0.0307	4	972	30.30	0.03	-120.78	39.04
Plumas	0.0000		0	733	32.99	0.04	-120.78	40.03
Riverside	0.0000		0	168	58.23	-0.43	-116.00	33.73
Sacramento	0.0000		0	503	33.85	-0.20	-121.33	38.46
San Benito	0.0000		0	358	36.82	-0.16	-121.08	36.64
San Bernardino	0.0000		0	274	51.43	-0.41	-116.04	34.90
San Diego	0.0000		0	369	44.89	-0.39	-116.76	33.00
San Joaquin	-0.0656	0.0337	3	315	35.68	-0.17	-121.18	38.03
San Luis Obispo	-0.0415	0.0143	3	380	42.26	-0.29	-120.27	35.36
San Mateo	0.0000		0	661	34.05	-0.23	-122.34	37.45
Santa Barbara	-0.0558	0.0197	3	389	45.20	-0.24	-120.05	34.70
Santa Clara	-0.0521	0.0218	3	457	34.95	-0.11	-121.67	37.22
Santa Cruz	0.0000		0	923	35.65	-0.19	-121.98	37.03
Shasta	0.0000		0	1408	26.20	-0.03	-122.15	40.77
Sierra	0.0000		0	1188	34.33	0.00	-120.52	39.59
Siskiyou	0.0000		0	643	28.58	-0.05	-122.57	41.64
Solano	-0.0452	0.0219	3	575	36.15	-0.23	-121.93	38.26
Sonoma	0.0000		0	989	31.00	-0.08	-122.89	38.49
Stanislaus	-0.0896	0.0308	3	303	35.57	-0.19	-121.00	37.52
Tehama	0.0000		0	862	33.77	-0.13	-122.18	40.11
Trinity	0.0000		0	1037	31.75	0.16	-123.15	40.62
Tulare	0.0000		0	521	36.73	-0.17	-118.84	36.26
Tuolumne	0.0000		0	944	32.92	-0.07	-119.93	37.99
Ventura	-0.0471	0.0168	3	459	48.32	-0.29	-119.10	34.47
Yolo	-0.0580	0.0229	3	499	34.21	-0.06	-121.88	38.88
Yuba	0.0000		0	1149	34.66	0.07	-121.31	39.30

^a 0, no effect of SOI; 1, current year; 2, previous year; 3, two years previous; 4, three years previous

^b Pearson's correlation between annual rainfall and October-March average SOI

Based on logistic regression analysis, whether a particular county demonstrated an effect of ENSO on deer harvest was best described by a model containing longitude, latitude, and average annual rainfall (Table 2). After accounting for variation explained by the other variables, the factor by which the odds of detecting a relationship with SOI decreased was 0.9969 (0.9936, 0.9996; back-transformed coefficient and 95% *CI*) for each millimeter increase in average rainfall. For longitude, odds of detecting such a relationship decreased by a factor of 0.41 (0.21, 0.72) for each one-degree change moving eastward. For latitude, odds of detecting a relationship with SOI decreased by a factor of 0.60 (0.33, 0.96) for each one-degree change moving northward. Thus, the likelihood of detecting an effect of ENSO on deer harvest tended to be higher in counties that were more arid, more to the west, and more to the south.

TABLE 2.—Logistic regression model selection to evaluate factors affecting detection of an effect of ENSO in mule deer harvest data by county ($n = 55$), California, USA, 1950-2007.

Model	AIC_c	ΔAIC_c
SOI Effect = Longitude + Latitude + Rainfall Average	64.94	0.00
SOI Effect = Longitude + Rainfall Average	66.94	2.00
SOI Effect = Longitude + Rainfall Average + Rainfall <i>CV</i>	66.98	2.04
SOI Effect = Longitude + Latitude + Rainfall Average + Rainfall <i>CV</i>	67.40	2.46
SOI Effect = Longitude + Latitude	67.45	2.51
SOI Effect = Longitude + Latitude + Rainfall <i>CV</i>	69.22	4.28
SOI Effect = Longitude + Rainfall <i>CV</i>	70.33	5.38
SOI Effect = Rainfall Average	70.49	5.55
SOI Effect = Intercept Only	72.02	7.07
SOI Effect = Rainfall Average + Rainfall <i>CV</i>	72.28	7.34
SOI Effect = Latitude	72.80	7.86
SOI Effect = Latitude + Rainfall Average	72.92	7.97
SOI Effect = Longitude	73.83	8.88
SOI Effect = Rainfall <i>CV</i>	73.84	8.90
SOI Effect = Latitude + Rainfall Average + Rainfall <i>CV</i>	73.86	8.91
SOI Effect = Latitude + Rainfall <i>CV</i>	74.70	9.75

Harvest regulation.—After accounting for variation explained by DMU, there was no evidence of a relationship between $\log_e(\text{season length})$ and $\log_e(\text{reported harvest})$ (slope=0.0001; 95% *CI*: -0.0883, 0.0881). Also, there was no evidence of a relationship between $\log_e(\text{quota})$ and $\log_e(\text{reported harvest})$ (slope=0.0055; -0.0124, 0.0234). Finally, there was no evidence of a relationship between $\log_e(\text{no. tags issued})$ and $\log_e(\text{reported harvest})$ (slope=0.0069; -0.0117, 0.0256). Thus, looking at the evidence across the entire state, there appeared to be no relationship between quota, season length, or number of tags issued and reported harvest within DMU. This finding could have occurred if the actual harvest from a large proportion of DMUs was substantially below that which would be limited by season length, the established quota, or the actual number of permits issued.

DISCUSSION

Patterns of rainfall variation.—The patterns we report for California are consistent with other published accounts of climate variation in western USA for average rainfall (increasing from south to north; Castello and Shelton 2004), variability in rainfall (decreasing with increasing average rainfall; Marshal et al. 2009), and correlation with SOI (increasing from south to north; Redmond and Koch 1991, McCabe and Dettinger 1999). Given the importance of precipitation in the production of forage for large herbivores (Robertson 1987, Marshal et al. 2005, Pettorelli et al. 2005), we expected that these factors would influence the population dynamics of mule deer in California, and that the effect would be apparent from their harvest data.

Latitudinal gradients in the effect of ENSO on precipitation is well-established for Pacific coastal USA (Redmond and Koch 1991, McCabe and Dettinger 1999, Castello and Shelton 2004, Kurtzman and Scanlon 2007). Evidence for a relationship between ENSO and precipitation are apparent only for the southern half of California (McCabe and Dettinger 1999), however, covering semi-arid coastal regions and inland deserts. In the northern half of the state, there is an absence of such evidence; for regions to the north of California, correlation between ENSO and precipitation becomes positive (Redmond and Koch 1991, McCabe and Dettinger 1999). That pattern supports our findings of negative correlations in southern California that increased to approximately zero correlation to the north of 38° N. Climate in California is strongly affected by ENSO, but the Pacific Decadal Oscillation (Kurtzman and Scanlon 2007) and climatic systems originating in the Atlantic Ocean (Hu and Feng 2008) also are associated with regional weather patterns. Future investigations of climate relationships in southwestern USA will have to address those influences to develop a more accurate picture of long-term, large-scale dynamics of large herbivore populations.

Evidence of ENSO in deer harvest data.—An effect of ENSO was evident for less than half of the counties considered. Our analysis indicated that those counties demonstrating such an effect tended to be those with higher *CV* or lower average rainfall in the southern and eastern parts of California. Nevertheless, several highly arid counties (i.e., nearly all covering the desert regions in the southeastern part of the state) showed no evidence of relationships with SOI.

Of the 18 counties for which there was a relationship, 14 demonstrated relationships with SOI two years previous (Table 1). Such a lag would be consistent with a policy where the youngest animals that are harvested are generally two years-of-age. In California, male mule deer must have at least one forked antler to be harvested legally, and most have only spike antlers during the hunting season at the time that they are yearlings. Thus a shorter lag as a consequence of hunting would be unlikely because most yearlings cannot yet be harvested. Factors other than hunting could produce a shorter lag if the effects of those factors influence juvenile or yearling animals, and if they have a larger effect on population dynamics than does harvest on older animals. Where longer lags are apparent, other factors operating over that longer period could influence harvest (e.g., a tendency to harvest older animals would produce longer lags). Lags in general could arise through a chain of influences leading from ENSO through rainfall to forage, body condition of adult females, investment in reproduction, natality and survival of juvenile males, and proportion of males older than two years-of-age in the population that are available for

harvest (Kucera 1991). With the exception of Del Norte, in the far northwestern corner, none of the northern-most counties in California showed evidence of an effect of ENSO (Figure 1), consistent with a finding of no correlation for northern California (McCabe and Dettinger 1999, this study).

Evidence of large-scale gradients in population dynamics is widespread in the ecological literature. Among mammal populations, the clearest relationships between characteristics of fluctuating populations and geographic gradients are latitudinal gradients and small mammal cycles (Hanski et al. 1991, Bjornstad et al. 1995). Latitudinal gradients in small herbivore dynamics appear influenced predominantly by predation, and by interactions among predation, forage, and other characteristics of the environment (Hansson and Henttonen 1985). Large herbivore dynamics, in contrast, appear to be influenced mainly by interactions with forage (Bowyer et al. 2005). Latitudinal and longitudinal gradients in the effect of density-independent factors were evident from pan-Arctic analyses of caribou population dynamics (Post 2005). With increasingly northern populations, the role of intraspecific competition appeared to decrease, and the role of density-independent environmental factors appeared to increase. This pattern was supported by latitudinal gradients in the strength of density feedback that were apparent in caribou populations on Greenland (Forchhammer et al. 2002). Post (2005), however, attributed such latitudinal gradients to spatial variation in the role of abiotic conditions, such as snow cover and icing, in limiting access to forage in more northern populations. Abundance of Svalbard reindeer, for example, commonly fluctuates in response to food limitation caused by ice-covered foraging areas (Aanes et al. 2000, Solberg et al. 2001), and die-offs as a consequence of ice-locked forage are common occurrences in North American high-arctic caribou populations (Caughley and Gunn 1993).

The similarity between arctic ungulate die-offs and responses of large herbivore populations to drought conditions in arid regions was highlighted by Caughley and Gunn (1993), as were the consequences of those die-offs: populations fluctuate in response to varying forage condition with little evidence of intraspecific competition. In such instances, population dynamics should be better predicted by factors contributing to short-term fluctuations (rainfall, ice cover, NAO) in forage availability than by population density. For these reasons, we expected to find strong evidence for ENSO in southern California, where rainfall is more variable and the SOI has a stronger correlation with rainfall.

Why was evidence of ENSO not more apparent?—In our opinion, the interesting question that arises from our results is not, “Why these particular counties?” but, rather, “Why not more southern counties?” We believe the most likely explanation relates to the amount of variation around each relationship considered in this analysis. For example, the finding of no evidence of ENSO in harvest data for Imperial contradicted that reported by Marshal et al. (2002) that, for mule deer in the most arid county (Imperial), ENSO was an important factor influencing deer dynamics. This was particularly puzzling, given that Imperial had both the highest *CV* in rainfall and the strongest correlation with SOI of the counties in California (Table 1). However, Marshal et al. (2002) related ENSO to deer population dynamics through two separate relationships: SOI-rainfall and rainfall-harvest. Those researchers found evidence of both relationships, but did not report a direct relationship between SOI and deer harvest. There was substantial scatter around the fitted models ($R^2=0.38$ for SOI-rainfall; $R^2=0.25$ for rainfall-harvest) such that a direct relationship between SOI and harvest easily could have been obscured by variation in the data. Such variation also could have obscured relationships between SOI and harvest in this analysis.

The use of harvest data rather than estimates of abundance could contribute to that variation. Variation might arise in two forms, in the difference between reported harvest and true harvest and in the difference between true harvest and abundance. Although not ideal for an investigation of population dynamics, harvest records provided data sets with the relatively broad temporal and geographic scope required to address questions involving patterns of climate related to latitude or longitude. Furthermore, use of harvest data as an index to abundance has been used frequently in analyses of population dynamics (Forchhammer et al. 2002, Marshal et al. 2002, Post 2005, Milner et al. 2006, Ranta et al. 2008). Although trends in harvest numbers generally can be expected to follow trends in abundance (Forchhammer et al. 1998), a number of other factors can affect that relationship, including quotas, management strategies, hunting traditions, and time lags in management responses (Milner et al. 2006). Ranta et al. (2008) reported linear relationships between harvest and abundance in three species of upland game birds in Finland; however, analyses of harvest data produced a different picture of spatial and temporal dynamics than did analyses of abundance data. Resulting relationships between harvest and abundance had slopes less than one, CV for harvest was higher than CV for abundance, synchrony in dynamics between regions appeared weaker from harvest data, autocorrelation differed between harvest and abundance, values of the autoregressive coefficients differed, and many of the differences between harvest and abundance depended on the species in question (Ranta et al. 2008). Further differences between abundance and harvest could occur among ungulates, because their populations are strongly age-structured, and harvest of ungulates is commonly age-selective (Caughley 1977). As mentioned in our results, it was unlikely that regulation of harvest had a strong influence on overall patterns of reported harvest across the state. Hunter behavior, independent of regulation, nonetheless could have introduced variation in relationships between reported harvest and actual abundance that would not have been accounted for with even the most accurate reported harvest.

Analysis of the male segment alone could introduce additional variation, because of the differences in dynamics between it and the female segment or the population as a whole (Clutton-Brock et al. 1985). An increase in harvest rate of males is associated with improved reproduction accompanying a reduction of female mule deer, presumably operating through reduction in a competition for forage resources (McCullough 2001); thus, at least at higher densities, abundance of males and females could be negatively related. That pattern was also apparent in an increasing red deer (*Cervus elaphus*) population on Rhum, Scotland (Clutton-Brock and Loneragan 1994), where the number of males was predicted to decrease through emigration and mortality when female abundance became $>60\%$ of their forage-limited maximum density (Clutton-Brock et al. 2002).

Although we demonstrated this for mule deer in only some areas of California, extrinsic sources of variation can strongly influence dynamics of large herbivores (Caughley and Gunn 1993, Choquenot 1998, Marshal et al. 2009), which provides interesting challenges for those attempting to manage such populations. Research of large herbivore ecology that shifts its focus away from classical models of density dependence toward interactive consumer-resource models will help wildlife managers to develop an understanding of mechanisms that link large-scale climate phenomena, local weather patterns, forage dynamics, and ungulate populations.

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