RAINFALL, EL NIÑO, AND DYNAMICS OF MULE DEER IN THE SONORAN DESERT, CALIFORNIA

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Abstract: We used long-term El Niño southern oscillation (ENSO), rainfall, and deer harvest records to investigate effects of ENSO and rainfall on mule deer (*Odocoileus hemionus*) population trends in the Sonoran Desert, southeastern California, USA. We found significant relationships between the southern oscillation index and rainfall ($R^2 = 0.38$, $P \leq 0.001$), and between rainfall and annual deer harvest ($R^2 = 0.25$, $P \leq 0.001$). We also found that deer harvest (i.e., an index of deer abundance) in any year was related to accumulations of rainfall >5 years before that hunting season ($R^2 = 0.34$), whereas the change in harvest between years (i.e., an index of rate of population change) was most related to rainfall the year immediately prior to that hunting season ($R^2 = 0.15$). Fluctuations in deer populations in the deserts of California ultimately may be caused by ENSO events.

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Rainfall patterns are the primary factor driving system dynamics in arid regions. Close relationships exist between amount of rainfall and plant growth in arid regions (Beatley 1969, Noy-Meir 1973, Robertson 1987, Polis et al. 1997). Herbivores also respond to changes in rainfall and plant biomass (Caughley et al. 1985, Fryxell 1987, Rautenstrauch and Krausman 1989, Owen-Smith 1990, Choquenot 1998). When precipitation is variable from year to year, years of abundant rainfall provide abundant forage for large herbivores. During those times, reproduction and survival are high, mortality is low, and populations increase. Periods of low rainfall result in poor plant growth, less forage production, and increased competition for forage. During extreme droughts, large-scale die-offs and declines in populations of herbivores may occur as reproduction and survival decrease and mortality increases (Caughley et al. 1985, Fryxell 1987).

The El Niño southern oscillation occurs when warm water pools in the western Pacific because of the weakening of trade winds that usually keep Pacific ocean water circulating (Cane 1983). The result is a change in sea-level atmospheric pressure caused by warmer-than-usual surface ocean temperatures. This change affects large-scale air movement over the Pacific and affects the climate in nearby terrestrial areas (Barber and Chavez 1983). The El Niño southern oscillation has considerable impacts on rainfall and climate over arid environments (Polis et al. 1997). In years when El Niño occurs, rainfall may increase productivity of desert ecosystems (Polis et al. 1997), with resultant increases in biomass. Increased rainfall caused by ENSO events has been proposed to cause irruptions of rodent populations (Lima and Jaksic 1998, 1999), and subsequent increases in their predators (foxes, owls, and hawks) in semiarid regions of Chile (Jaksic et al. 1997). Increased rainfall caused by ENSO events also has affected reproduction in Darwin's finches (*Geospiza* spp.) on the Galápagos Islands (Grant et al. 2000).

Rainfall is suspected to have an important influence on mule deer populations in the inland deserts of southern California. Despite the importance of mule deer as a game species, biologists have only recently begun to look at their population dynamics in that region. Because precipitation is linked to ENSO events, we hypothesize that ENSO drives population dynamics and causes fluctuations in mule deer numbers. If correct, we predict that the amount of rainfall in California deserts was directly related to intensity of ENSO, and that mule deer abundance and rate of increase would be directly related to amount of rainfall. Our objective was to test these predic-

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tions using long-term southern oscillation, deer harvest, and rainfall data.

STUDY AREA

We investigated relationships between ENSO, rainfall, and deer population trends in the Sonoran desert of southeastern California (33°00'N, 114°45'W). The climate was arid, with hot summer temperatures (daytime highs >45 °C) and low annual rainfall (averaging 70 mm in Imperial County, California; Imperial Irrigation District, unpublished data). Plant species found in this area were common to the Lower Colorado River Valley Desert subdivision of the Sonoran Desert. Upland areas included creosote bush (*Larrea tridentata*), burro bush (*Ambrosia dumosa*), and ocotillo (*Fouquieria splendens*). Areas adjacent to the Colorado River contained salt cedar (*Tamarix* spp.), cattail (*Typha domingensis*), and arrowweed (*Pluchea sericea*). In washes, palo verde (*Cercidium floridum*), ironwood (*Olneya tesota*), catclaw (*Acacia greggii*), mesquite (*Prosopis glandulosa*), and cheese bush (*Hymenoclea salsola*) were common. Other ungulates occurring in the area included bighorn sheep (*Ovis canadensis*) and feral burros (*Equus asinus*). Potential predators of mule deer included mountain lion (*Puma concolor*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and golden eagle (*Aquila chrysaetos*; Andrew et al. 1997). The area contained 29 water sources in addition to the Colorado River, and most were ephemeral. Seasons were hot-dry (Apr–Jun), hot-moist (Jul–Sep), and cool (Oct–Mar). Andrew et al. (1999) described the area in detail.

METHODS

We used the southern oscillation index (SOI) as a measure of intensity of ENSO events. The SOI was based on differences in sea-level atmospheric pressure between Darwin, Australia, and Tahiti. An El Niño year was defined as a year during which, for 4 months, the monthly average of the SOI was >2 standard deviations below the 1950–1980 base period average. A strong negative deviation in SOI indicated an El Niño (warm-water) event, whereas a strong positive deviation indicated a La Niña (cold-water) event (Boersma 1998). We used annual averages of monthly SOI data during 1951–1998 from the National Centers for Environmental Prediction, National Oceanographic and Atmospheric Administration (ftp://ftp.ncep.noaa.gov/pub/cpc/wd52dg/data/indices/soi). We used monthly rainfall (R) data for Imperial County, California, 1940–1998 (Imperial Irrigation District, unpublished data). We analyzed relationships between SOI and R with least-squares linear regression.

We used deer harvest data reported to the California Department of Fish and Game (CDFG) for Imperial County, 1948–1998, as an index of deer abundance. Deer harvest seasons occurred every year in November. Harvest data until 1990 was based on report-card returns by successful deer hunters. Beginning in 1990, the report-card returns were supplemented with information gathered by CDFG wildlife officers from interviews with hunters during hunting season. We performed a log-transform on deer harvest numbers to stabilize variance. Because we suspected annual changes in deer harvest would more accurately track changes in resource abundance (Caughley 1987), we determined this annual change by subtracting the log-transformed deer harvest of 1 year from that of the previous year. We used least-squares regression to analyze relationships between R and transformed deer harvest (H), R and change in transformed deer harvest (ΔH), and H and ΔH to look for density dependence in deer population growth. We tested for a nonlinear relationship using regression with a second-order polynomial; we concluded nonlinearity when the squared term differed significantly from zero.

We compared H or ΔH for each year to amount of rainfall over periods of differing lengths immediately prior to each year's hunting season. We used the coefficient of multiple determination (R^2) to compare ability of each period length to explain variation in H. The intervals were 1 month prior to hunting season, and then 3–90 months prior to hunting season at 3-month intervals.

RESULTS

The long-term average in annual SOI was –0.31 ± 0.16 SE (n = 48). Southern oscillation index tended to show a long-term decrease ($R^2 = 0.08$, $F_{1,46} = 3.94$, $P = 0.053$; Fig. 1a), suggesting an increasing intensity of the ENSO since 1951. A long-term trend also was evident in deer harvest ($R^2 = 0.48$, $F_{1,49} = 45.25$, $P \leq 0.001$; Fig. 1c). There was no single long-term trend in R ($R^2 = 0.02$, $F_{1,57} = 1.16$, $P = 0.287$; Fig. 1b); however, this was the only data set for which we had values before 1948. Long-term annual averages in R and deer harvest were 70 ± 5 mm (n = 59) and 24 ± 2 deer (n = 51), respectively.

We found a negative relationship between SOI and R for years 1951–1998 (R = 62.64 –

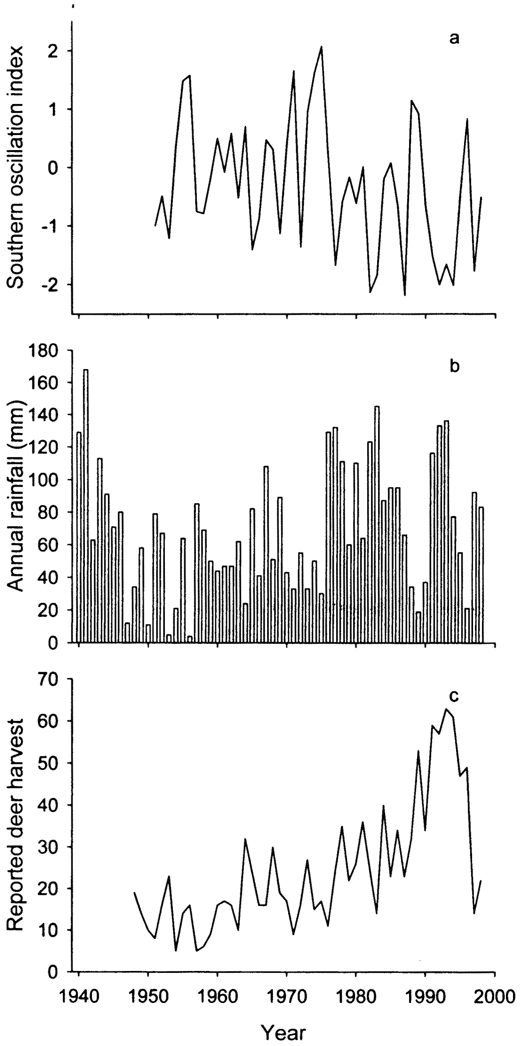

Fig. 1. Time series of (a) southern oscillation index values for 1951–1998, (b) annual rainfall totals for Imperial County, California, 1940–1998, and (c) reported mule deer harvest for Imperial County, California, USA, 1948–1998.

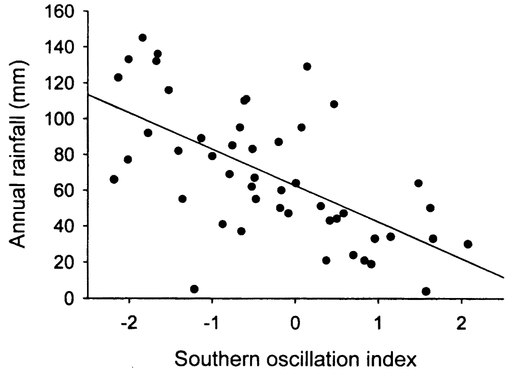

Fig. 2. Relationship between rainfall and southern oscillation index in Imperial County, California, USA, 1951–1998 (R^2 = 0.38, $P \le 0.001$).

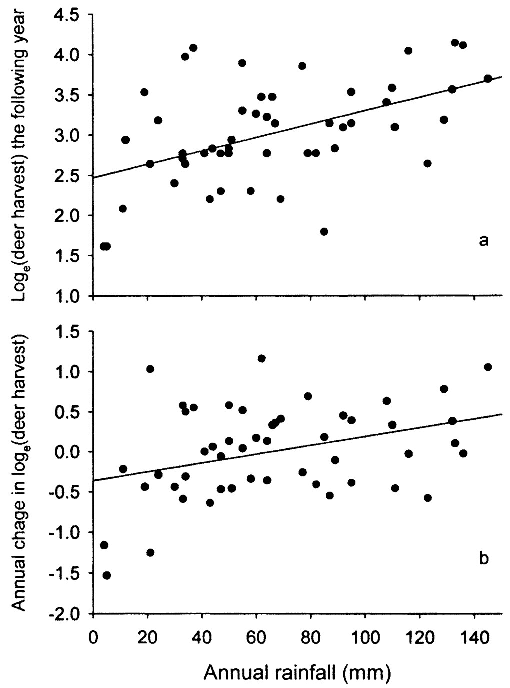

Fig. 3. Relationships between (a) log$_e$(deer harvest) 1948–1998 and rainfall the previous year (R^2 = 0.25, $P \le$ 0.001) and (b) annual change in log$_e$(deer harvest) and rainfall the previous year in Imperial County, California, USA, 1948–1998 (R^2 = 0.13, P = 0.011).

20.17[SOI]; $R^2 = 0.38$, $F_{1,46} = 28.50$, $P \le 0.001$; Fig. 2), indicating that rainfall in southeastern California during these years was affected by ENSO events. We found a positive relationship between H in 1 year (i.e., in Nov) and R the previous year (i.e., Jan–Dec for the year ending 10 months earlier; H = 2.47 + 0.0083R; R^2 = 0.25, $F_{1,49}$ = 16.07, $P \le 0.001$; Fig. 3a). Although the overall curvilinear relationship was significant for R and H (P = 0.001), the second-order term did not differ significantly from zero (P = 0.815); hence, we rejected the curvilinear model. A plot of H against R suggested a curvilinear pattern also, but the second-order term did not differ significantly from zero (P = 0.125). The linear relationship fitted to these data was ΔH = –0.36 + 0.0055R (R^2 = 0.13, $F_{1,48}$ = 7.00, P = 0.011; Fig. 3b).

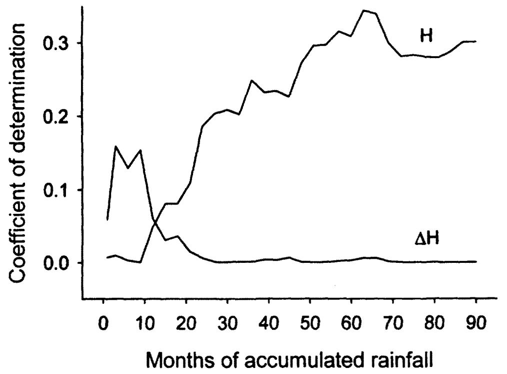

Fig. 4. Effect of differing periods of rainfall accumulation before each year's hunting season on variation explained in $\log_e$(deer harvest) (H) and annual change in $\log_e$(deer harvest) (ΔH) in Imperial County, California, USA, 1948–1998.

The largest amount of variation in H was explained by accumulated rainfall (AR) over the previous 63 months (Fig. 4). Coefficients of multiple determination increased from accumulations over 1 month to accumulations over 63 months ($R^2 = 0.34$), and then remained approximately 0.30 for accumulations over 66–90 months. We found a curvilinear relationship ($R^2 = 0.43$, $F_{2,48} = 18.46$, $P \leq 0.001$), but the constant did not differ significantly from zero ($P = 0.760$). The fitted model without the constant was $H = 0.014(AR_{63}) - 0.000015(AR_{63})^2$ (Fig. 5a).

Variation in ΔH was best explained by accumulated rainfall over the previous 3–9 months (Fig. 4). Coefficients of multiple determination decreased from 0.15 at 9 months' accumulation, to near 0 after 12 months' accumulation. We used accumulation over 9 months and H to look for density dependence in ΔH. The fitted relationship was $H = 0.89 + 0.0081(AR_9) - 0.41H$ ($R^2 = 0.36$, $F_{2,44} = 13.00$, $P \leq 0.001$). We removed variation in ΔH explained by H to show effects of rainfall independent of the effects of H; the residuals showed an increasing pattern with increasing amounts of 9 months' rainfall accumulation (Fig. 5b). Next, we removed variation in ΔH explained by rainfall to show effects of H independent of rainfall (i.e., density dependence in ΔH); the residuals showed a decreasing pattern with increasing H (Fig. 5c). We tested for nonlinearity by fitting curvilinear models to 2 data sets, each consisting of 1 independent variable and the residual variation in ΔH left from the other independent variable. For both data sets, the overall curvilinear relationships were significant, but second-order terms were not ($P \geq 0.152$).

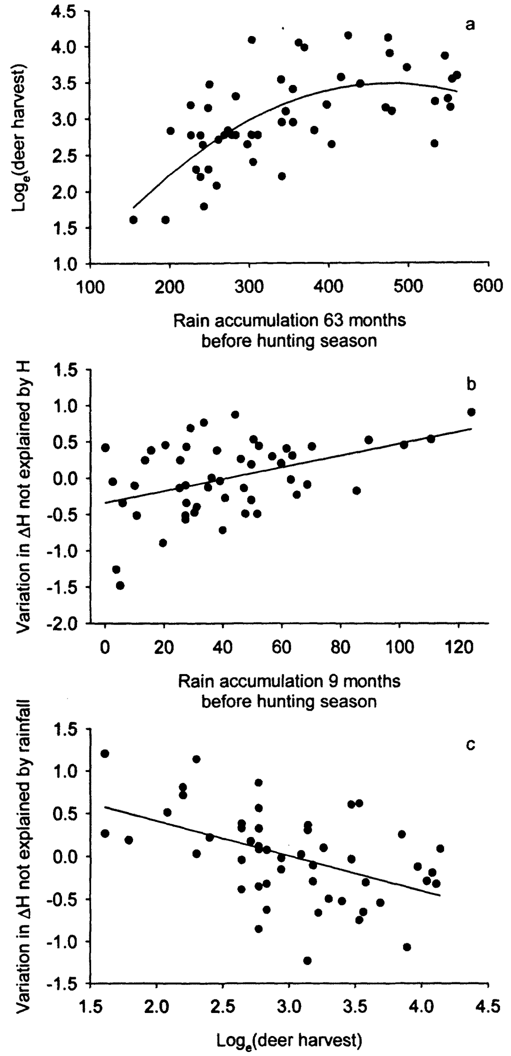

Fig. 5. Relationships between (a) accumulated rainfall 63 months before each hunting season and $\log_e$(deer harvest) ($R^2 = 0.43$, $P \leq 0.001$), (b) accumulated rainfall 9 months before each hunting season and the residuals from a linear regression between $\log_e$(deer harvest) (H) and change in $\log_e$(deer harvest) (ΔH; $R^2 = 0.19$, $P = 0.001$), and (c) $\log_e$(deer harvest) and the residuals from a regression between accumulated rainfall 9 months before each hunting season and change in $\log_e$(deer harvest) (ΔH; $R^2 = 0.24$, $P \leq 0.001$) in Imperial County, California, USA, 1948–1998.

DISCUSSION

Resource availability is 1 of the most important factors affecting abundance of large mammals (Caughley 1970; Skogland 1983, 1985; Sinclair et al. 1985; Fryxell 1987). In systems with highly variable environmental influences, density-independent factors, such as precipitation, can cause variation in food supply that have large effects on dynamics of large herbivores (Caughley 1987, Choquenot 1998). Forage resources in deserts are affected primarily by rainfall and, as demonstrated by our results, rainfall is highly variable from year to year. As a result, resource availability and its influence on deer populations is highly variable from year to year. In this manner, dynamics of mule deer in southern California likely are driven by the density-independent fluctuations in rainfall caused by ENSO events. The study of a highly labile system was ideal for understanding interactions between deer populations and their resources (Caughley and Gunn 1993). High annual variation in our study area provided a wide range in rainfall (i.e., an index of resource abundance) and deer abundance. Under less variable conditions, such relationships would have been difficult to detect.

The largest source of error in our analysis may have been the reported deer harvest. There were 2 potential problems with the quality of the harvest data. First, harvest numbers until 1990 depended on reporting by hunters, and not all hunters reported their harvest. There have been efforts to estimate the reporting rate and accuracy of harvest estimates (R. C. Mohr, CDFG, personal communication). California Department of Fish and Game currently adjusts reported harvest numbers with hunting-zone-specific correction factors based on reported kill and records from area meat-processing facilities. The correction factor for the hunting zone that includes Imperial County is 1.62 (Mohr 2000), meaning a reporting rate of 62%. However, because this is a recently derived estimate of reporting rate (i.e., since 1994), we used uncorrected reported harvest for this analysis so that biases in reporting rate would have similar effects over all years. This reporting rate estimate provided an idea of accuracy in the reported deer harvest; however, it did not indicate how accurately harvest reflected deer abundance in Imperial County. We assumed a direct relationship between deer harvest and deer abundance, an assumption made by some state wildlife agencies that use harvest information to estimate trends in deer populations and to establish harvest regulations (Rupp et al. 2000).

The second potential problem was that harvest data collection methods changed in 1990. The recent involvement of wildlife officers in collecting harvest data likely has increased the accuracy of the harvest data. We believe that this had the effect of increasing the amplitude of fluctuations in our data, but not the pattern of fluctuations with respect to rainfall. We adjusted the change in amplitude by log-transforming the harvest data, but the apparent responses to rainfall remained in the transformed data. Despite reporting accuracy and changes in data collection methods, deer harvest tracked rainfall with reasonable accuracy. With a continued effort to collect harvest information, further analyses of this type will provide more accurate relationships between this deer population and its forage resources.

The relationship between R and ΔH (Figs. 3b, 5b) appeared curvilinear, although our analysis did not support this. A curvilinear relationship would make sense, because it is essentially a numerical response relationship, with ΔH an index of exponential rate of population change (r) and rainfall an index of forage biomass. Caughley and Gunn (1993) described a theoretical relationship for the numerical response of a population to a change in its resources (i.e., between r and forage biomass). Between zero and low resource abundance, r increases rapidly and changes from a negative to positive rate of increase at some threshold of forage biomass. As forage increases, r becomes constant because animals reach maximum rates of reproduction and survival.

There is continued research about the relative importance of density-dependent and density-independent factors in driving population dynamics (Choquenot 1998, Lima et al. 1999). Although we found clear relationships between rainfall and H, we also found evidence for density dependence in ΔH (Fig. 5c). As H in any year increased, ΔH from that year to the next decreased, a pattern consistent with increasing intraspecific competition for forage at high animal density (Sinclair et al. 1985).

Other studies have demonstrated density dependence in demographic parameters in populations strongly affected by ENSO precipitation. The number and proportion of pregnant and lactating females in populations of leaf-eared mouse (*Phyllotis darwini*) were positively affected by rainfall, and rainfall was an important density-independent factor in the demography of these animals (Lima and Jaksic 1998). However, the proportion of pregnant and lactating females was affected by density the previous year (Lima and Jaksic 1998). Furthermore, reproductive rate (log[no. juveniles/no. adult females]), and reproductive index ([pregnant and lactating females + juveniles]/total population density) were related to density the previous year, but not to rainfall (Lima and Jaksic 1998). Lima et al. (1999) simulated population dynamics of rodents responding to rainfall in semiarid Chile, and found they were unable to produce realistic results unless both rainfall and density-dependent effects were included in the model. They found further support for the importance of density dependence in that ENSO-driven rainfall disturbances affected a large area of Chile, that outbreaks were localized, and that there was large variation from site to site affected in large part by past population dynamics at those sites. The combination of endogenous factors, manifested via density-dependent effects on reproduction and survival, and exogenous factors, manifested via density-independent effects of rainfall and food supply, explained variation in outbreaks of rodents in South America (Lima et al. 1999).

That ΔH decreased with increasing H may indicate a feedback mechanism between deer abundance and forage abundance, and that dynamics of deer in this area are not driven entirely by fluctuations in rainfall and forage. Feedback between an herbivore and forage occurs via the functional response (Caughley and Gunn 1993). Because of this feedback, one could argue that the dynamics of mule deer exhibit density dependence. The problem is that this term implies a direct causal relationship between deer density at some point in time and rate of increase at the same time (Caughley 1987). Because we are working in a highly variable system, the approach of relating r to population density is inappropriate; it assumes carrying capacity (i.e., *K* carrying capacity; sensu Macnab 1985) to be relatively constant (Caughley 1976, Sinclair 1989). Therefore, the mechanisms involved in the interactions between population and food supply must be considered explicitly. Because we lack data on the functional response of deer to forage in this area, or effects of off-take by deer on forage abundance, we must be satisfied with an understanding of this system that is equivalent to a single-species population model that lacks the causal links between forage abundance and deer demography.

The number of deer harvested during 1 year was influenced by rainfall accumulated over several years. Change in deer harvest, however, seemed to be influenced by rainfall accumulated over only 1 year. If we assumed that ΔH was an accurate index to r for this mule deer herd, then our findings support the idea that r more accurately reflects changes in resource abundance than does deer abundance. Caughley (1987) reached a similar conclusion about kangaroos (*Macropus* spp.): abundance in any year was a reflection of the dynamics of resources over several previous years; whereas, rate of population change was a reflection of resources at that moment or in the very recent past. For kangaroos, there was little lag between a change in resources and a population response, because they immediately capitalized on increased forage with increased reproduction, and there was a rapid decrease in reproduction, or increased mortality, during times of scarcity (Caughley 1987). For mule deer, there is likely some lag in increase because they reproduce only annually at a fixed time of year, and some lag in decrease because adult females are able to survive stressful periods (Bartmann et al. 1992). Despite these lags, our results demonstrate a short-term response to forage in the rate of population change coupled with a longer-term response in deer abundance.

A numerical response type of relationship may become clearer with more data. The curvilinear relationship was most noticeable because of 3 values in the lower-left region (Figs. 3b, 5b). Those data suggested a rapid decrease in deer abundance because of low rainfall and resource abundance. Although not ideal from the perspective of managing deer for hunting opportunities, periods of drought that cause decreases in deer numbers provide important data in this region of low H, and a clearer relationship between resource availability and deer population dynamics.

MANAGEMENT IMPLICATIONS

The relationships reported here provide an understanding of how an important factor affects mule deer dynamics in 1 region of California. Ideally, the next step would be to use these relationships to predict future deer population abundance and harvest. With enough data, short-term predictions may be possible, but with questionable accuracy. The El Niño southern oscillation is unpredictable, only becoming apparent shortly before a particular hunting season. Also, the intensity of an ENSO and its effect on rainfall and forage production are highly variable. Knowledge of an imminent ENSO event might allow a wildlife manager to predict a high-rainfall or low-rainfall year with reasonable accuracy, but that knowledge cannot provide enough information to predict a suitable harvest quota. Maynard Smith (1974) distinguished between highly detailed, practical models for making predictions about a population and more theoretical models for understanding general ecological principles. Both types of models have their roles in resource management (May 1974). Because of the nature of these data and the remaining gaps in our understanding of mule deer dynamics, the relationships presented should remain at present within the realm of understanding models.

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LITERATURE CITED

Andrew, N. G., V. C. Bleich, and P. V. August. 1999. Habitat selection by mountain sheep in the Sonoran desert: implications for conservation in the United States and Mexico. California Wildlife Conservation Bulletin 12.

———, ———, ———, and S. G. Torres. 1997. Demography of mountain sheep in the east Chocolate Mountains, California. California Fish and Game 83:68–77.

Barber, R. T., and F. P. Chavez. 1983. Biological consequences of El Niño. Science 222:1203–1210.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121.

Beatley, J. C. 1969. Biomass of desert winter annual plant populations in southern Nevada. Oikos 20:261–273.

Boersma, P. D. 1998. Population trends of the Galápagos penguin: impacts of El Niño and La Niña. Condor 100:245–253.

Cane, M. A. 1983. Oceanographic events during El Niño. Science 222:1189–1195.

Caughley, G. 1970. Eruption of ungulate populations with emphasis on Himalayan thar in New Zealand. Ecology 51:54–72.

———. 1976. Wildlife management and the dynamics of ungulate populations. Pages 183–246 *in* T. H. Coaker, editor. Applied biology. Volume 1. Academic Press, London, United Kingdom.

———. 1987. Ecological relationships. Pages 159–187 *in* G. Caughley, N. Shepherd, and J. Short, editors. Kangaroos, their ecology and management in the sheep rangelands of Australia. Cambridge University Press, Cambridge, United Kingdom.

———, G. C. Grigg, and L. Smith. 1985. The effect of drought on kangaroo populations. Journal of Wildlife Management 49:679–685.

———, and A. Gunn. 1993. Dynamics of large herbivores in deserts: kangaroo and caribou. Oikos 67:47–55.

Choquenot, D. 1998. Testing the relative influence of intrinsic and extrinsic variation in food availability on feral pig populations in Australia's rangelands. Journal of Animal Ecology 67:887–907.

Fryxell, J. M. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. Oecologia 72:83–91.

Grant, P. R., B. R. Grant, L. F. Keller, and K. Petren. 2000. Effects of El Niño events on Darwin's finch productivity. Ecology 81:2442–2457.

Jaksic, F. M., S. I. Silva, P. L. Meserve, and J. R. Gutiérrez. 1997. A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. Oikos 78:341–354.

Lima, M., and F. M. Jaksic. 1998. Delayed density-dependent and rainfall effects of an irruptive rodent in semiarid Chile. Acta Theriologica 43:225–234.

———, and ———. 1999. Survival, recruitment and immigration processes in four subpopulations of the leaf-eared mouse in semiarid Chile. Oikos 85:343–355.

———, J. E. Keymer, and F. M. Jaksic. 1999. El Niño–southern oscilliation-driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics. American Naturalist 153:476–491.

Macnab, J. 1985. Carrying capacity and related slippery shibboleths. Wildlife Society Bulletin 13:403–410.

May, R. M. 1974. Stability and complexity in model ecosystems. Second edition. Princeton University Press, New Jersey, USA.

Maynard Smith, J. 1974. Models in ecology. Cambridge University Press, Cambridge, United Kingdom.

Mohr, R. C. 2000. 1999 California deer kill report. California Department of Fish and Game, Sacramento, USA.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Owen-Smith, N. 1990. Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. Journal of Animal Ecology 59:893–913.

Polis, G. A., S. D. Hurd, C. T. Jackson, and F. S. Piñero. 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. Ecology 78:1884–1897.

Rautenstrauch, K. R., and P. R. Krausman. 1989. Influence of water availability and rainfall on movements of desert mule deer. Journal of Mammalogy 70:197–201.

Robertson, G. 1987. Effect of drought and high summer rainfall on biomass and composition of grazed pastures in western New South Wales. Australian Rangelands Journal 9:79–85.

Rupp, S. P., W. B. Ballard, and M. C. Wallace. 2000. A nationwide evaluation of deer hunter harvest survey techniques. Wildlife Society Bulletin 28:570–578.

Sinclair, A. R. E. 1989. Population regulation in animals. Pages 197–241 *in* J. M. Cherret, editor. Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell Scientific Publications, Oxford, United Kingdom.

———, H. Dublin, and M. Borner. 1985. Population regulation of Serengeti wildebeest: a test of the food hypothesis. Oecologia 65:266–268.

Skogland, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. Oecologia 60:156–168.

———. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology 54:359–374.

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