Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico

Louis C. Bender and Mara E. Weisenberger

Abstract Understanding the determinants of population size and performance for desert bighorn sheep (*Ovis canadensis mexicana*) is critical to develop effective recovery and management strategies. In arid environments, plant communities and consequently herbivore populations are strongly dependent upon precipitation, which is highly variable seasonally and annually. We conducted a retrospective exploratory analysis of desert bighorn sheep population dynamics on San Andres National Wildlife Refuge (SANWR), New Mexico, 1941–1976, by modeling sheep population size as a function of previous population sizes and precipitation. Population size and trend of desert bighorn were best and well described (R^2=0.89) by a model that included only total annual precipitation as a covariate. Models incorporating density-dependence, delayed density-dependence, and combinations of density and precipitation were less informative than the model containing precipitation alone (ΔAICc=8.5–22.5). Lamb:female ratios were positively related to precipitation (current year: $F_{1,34}$=7.09, P=0.012; previous year: $F_{1,33}$=3.37, P=0.075) but were unrelated to population size (current year: $F_{1,34}$=0.04, P=0.843; previous year: $F_{1,33}$=0.14, P=0.715). Instantaneous population rate of increase (r) was related to population size ($F_{1,33}$=5.55; P=0.025). Precipitation limited populations of desert bighorn sheep on SANWR primarily in a density-independent manner by affecting production or survival of lambs, likely through influences on forage quantity and quality. Habitat evaluations and recovery plans for desert bighorn sheep need to consider fundamental influences on desert bighorn populations such as precipitation and food, rather than focus solely on proximate issues such as security cover, predation, and disease. Moreover, the concept of carrying capacity for desert bighorn sheep may need re-evaluation in respect to highly variable (CV =35.6%) localized precipitation patterns. On SANWR carrying capacity for desert bighorn sheep was zero when total annual precipitation was <28.2 cm.

Key words carrying capacity, density-dependence, density-independence, desert bighorn sheep, *Ovis canadensis mexicana*, precipitation, population regulation

Desert bighorn sheep *(Ovis canadensis mexicana)* are endangered in New Mexico and have declined throughout much of their range in the United States (Krausman et al. 1999, United States Fish and Wildlife Service [USFWS] 2002). Considerable debate exists over the relative importance of factors contributing to declines in bighorn populations and the underlying mechanisms regu-

Address for Louis C. Bender: United States Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit, P.O. Box 30003 MSC 4901, Las Cruces, NM 88003, USA; e-mail: lbender@nmsu.edu. Address for Mara E. Weisenberger: United States Fish and Wildlife Service, San Andres National Wildlife Refuge, P.O. Box 756, Las Cruces, NM 88004, USA.

lating or limiting population size in desert bighorn sheep. For example, desert bighorn populations have been described as being limited by predation (Wehausen 1996, Creeden and Graham 1997, Kamler et al. 2002), precipitation (McKinney et al. 2001), forage quantity and quality (Krausman and Leopold 1986, Krausman et al. 1989, DeYoung et al. 2000), and disease (Gross et al. 1997, Singer et al. 2000*b*), among others. Desert bighorn populations also have been described as regulated by density-dependent recruitment (Douglas and Leslie 1986, Wehausen et al. 1987), and density-dependence has been hypothesized as the principal mechanism influencing dynamics of desert bighorn sheep (Krausman et al. 1999). Identifying factors important in regulation or limitation of sheep numbers is fundamental to developing effective recovery and management programs.

In arid environments, precipitation has important effects on both plant production (Beatley 1969, Noy-Meir 1973, DeYoung et al. 2000) and large-herbivore populations (Wehausen et al. 1987, Cook 1990, Owen-Smith 1990, DeYoung 1997, Marshal et al. 2002). Droughts can result in significant declines of large herbivore populations (Caughley et al. 1985, Fryxell 1987). If precipitation is low, bighorn sheep face poor plant growth, less forage, lower nutritional quality, and increased competition for forage (Wehausen et al. 1987, Wehausen and Hansen 1988, DeYoung et al. 2000, Marshal et al. 2002). As quantity and quality of forage decline, numbers of lambs produced and recruited declines, and consequently so can populations (Wehausen et al. 1987, Wehausen and Hansen 1988, Cook 1990, Douglas 2001). Moreover, declines in body condition due to forage limitations lead to increased vulnerability to most mortality factors (i.e., individual sheep become increasingly predisposed to a variety of proximate mortality causes; Cook 1990, Douglas 2001). Precipitation can therefore influence populations of desert bighorn sheep indirectly through quantity and quality of available forage and subsequent effects on body condition, which in turn affects vulnerability to disease, predation, and competition. Further, desert bighorn generally are considered to require free water (Krausman et al. 1999), especially during dry, hot climatic conditions, which may be more abundant as precipitation increases. However, Krausman et al. (1985) documented desert bighorns not drinking from free-water sources even though available.

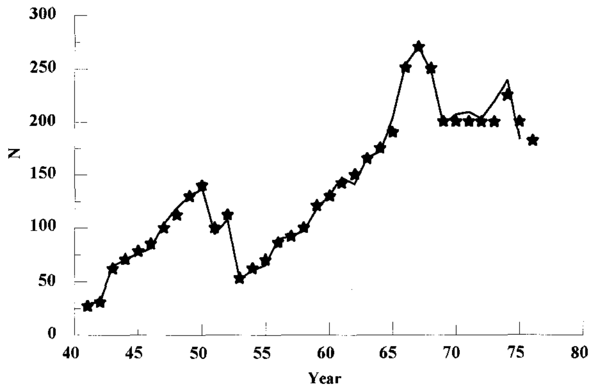

Figure 1. Estimated population size of desert bighorn sheep on San Andres National Wildlife Refuge (★), New Mexico, 1941–1976, and population size as predicted by the model $N_{t+1} = N_t{*}\exp(0.0219 + 0.0354{*}P + 0.0340{*}Z)$, where P = a normalized variate of total annual precipitation and Z = a normal random variate (solid line).

San Andres National Wildlife Refuge (SANWR) was established in 1941, primarily to protect habitat for desert bighorn sheep (Hoban 1990). Populations of desert bighorns have varied over time on SANWR (Figure 1). In the late 1970s, significant human intervention to prevent a downward trend in sheep numbers resulted in capture and removal of 49 desert bighorn sheep to other locations (Hoban 1990). Prior to that, populations were largely unaffected by human intervention, with the exception of limited harvest (4-6 males/year, 1968-1978) and some removals for transplanting elsewhere (8 sheep in both 1972 and 1975), and thus should have equilibrated with environmental conditions. In the late 1970s, a combination of removal, disease, and other factors reduced the SANWR population to <10 individuals (Hoban 1990).

We conducted a retrospective analysis of desert bighorn sheep population dynamics from establishment of SANWR until the population was depleted to remnant status (1941-1976). Our goal was to determine the relative importance of precipitation and density-dependence on population numbers and productivity of desert bighorn sheep on SANWR. We hypothesized that because of the importance of precipitation to plant and herbivore communities in arid environments and the unpredictability of precipitation in the Chihuahuan desert, annual patterns in precipitation would be more important than population density in predicting desert bighorn sheep population trends on SANWR.

Study area

San Andres National Wildlife Refuge (approximately 33°45' N, 106°40' W) was located approximately 48 km northeast of Las Cruces, New Mexico, and was surrounded by White Sands Missile Range. San Andres National Wildlife Refuge covered 23,154 ha, including much of the southern extent of the San Andres Mountains, which was the largest contiguous, relatively undisturbed, Chihuahuan Desert land mass in the United States. The precipitous east escarpment of SANWR rose 1,524 m above the basin to an elevation of 2,510 m above sea level. Precipitation averaged 32.3 cm in the higher-elevation desert bighorn range, with >65% of moisture occurring as short, intense rainstorms from July through October. Snowfall occurred during midwinter, usually averaged <10 cm, and was short-lived. Temperatures of the area ranged from -23° C to 41° C. Three principal seasons occurred in SANWR: warm wet (July-October), cool dry (November-February), and warm dry (March-June). Major vegetation communities on SANWR included semidesert grassland, Chihuahuan desert scrub, and coniferous and mixed woodland (Dick-Peddie 1993). During our period of analysis, permanent water was relatively abundant on SANWR and included a minimum of 30 perennial springs and 2 water developments established in the 1960s.

Methods

Population estimates and population composition (lamb:female) ratio counts for desert bighorns on SANWR were conducted by USFWS and New Mexico Department of Game and Fish (NMDGF) personnel, usually October-December, from 1941-1976 (Sandoval 1979, Hoban 1990). Occasionally, however, surveys were conducted as early as August and as late as the following March or April. Population estimates were attempts to enumerate all individual desert bighorn on SANWR from ground (horseback and foot) surveys that covered the entire area and were occasionally adjusted upward based upon the presence of fresh sign (tracks, etc.) that was found in areas where no bighorns were observed. Thus, population estimates were more correctly viewed as an index. In some later years (1968-1970, 1972, 1976) ground counts were supplemented by aerial counts, which potentially may increase numbers counted but not affect young:female ratios (Bender et al. 2003); however, estimates from these combined counts were similar to ground-only estimates in adjacent years (Figure 1). Lamb:female ratios from this count represent lambs approximately 6-11 months old, as parturition on SANWR peaks late February-April (range: January-June). Numbers of desert bighorn sheep counted ranged from 27-180 (Hoban 1990; San Andres National Wildlife Refuge files), with all classified into sex and age (lamb, adult) classes. Population estimates ranged from 27-270 (Hoban 1990).

We modeled bighorn population dynamics on SANWR using a stochastic model of exponential increase as the base model, then adding covariates to include effects of population size and precipitation on population growth (Dennis and Otten 2000). Thus, the base model was $N_{t+1} = N_t{}^*\exp(a+b^*Z)$, where N_{t+1} = total population in year t+1, N_t = total population in year t, a = the maximum individual survival and recruitment rates at low population density, and Z = a normal random variate (Dennis and Otten 2000). This procedure allows for incorporation of factors assumed to affect population dynamics as additional covariates in the model. For example, the model $N_{t+1} = N_t{}^*\exp(a+b^*Nt+c^*Z)$would incorporate the effects of population density as a modifier of maximum potential growth rate (a), creating a stochastic logistic model with the density effect being either density-dependent (if $b<0$) or inversely density-dependent (if $b>0$).

We defined a series of biologically meaningful alternative models to explore bighorn population dynamics on SANWR. Alternative models included covariates representing density-dependence, delayed-density dependence, total annual precipitation, and combinations of these effects. In model development, density represented the current year's population, and density lagged 1 year represented the previous year's population. We determined a precipitation index for SANWR using a Z-score, where P=(total annual precipitation for year t)-(mean total annual precipitation, 1941-1976) / (SD for total annual precipitation, 1941-1976). We transformed precipitation data to reduce the range of variation to the number of standard deviations from the mean zero for each year's mean precipitation and thus express the range of each parameter in models comparably (Peek et al. 2002). Precipitation data were obtained from USFWS records collected on the desert bighorn range at

SANWR. Four rain gauges were distributed throughout the bighorn sheep range on SANWR, and we used the mean of the gauges for annual precipitation. For modeling, current year's precipitation represented January-December precipitation for the count year and thus covered the late gestation (January-April) and lactation (approximately March-September) period for the lambs counted in late fall-early winter (October-December). Previous years' precipitation was recorded January-December of y-1, when lambs were born in February-April of year y and population composition counts conducted October-December of year y.

We evaluated model performance using an information-theoretic approach with Akaike's Information Criterion, corrected for small samples (AICc; Burnham and Anderson 1998). This allowed biologically meaningful a priori models to be compared, which is analogous to a hypothesis test (Taper and Gogan 2002). We compared performance of alternative models using Akaike differences (ΔAICc; Burnham and Anderson 1998). Because information-theoretic analysis only selects the "best" model from among a suite of candidates and does not indicate whether a selected model actually fits data well, we also used model R^2 to assess overall model fit (Eberhardt 2003).

To explore mechanisms whereby density-dependence and precipitation may affect bighorn sheep dynamics, we calculated the annual instantaneous rate of population increase (r, where r=ln λ and λ=the finite rate of population increase, i.e. N_t / N_{t-1}), for each year, 1941-1976. We then regressed r as a function of population size to detect density-dependence in rate of increase. Because density effects and weather extremes affect juvenile cohorts first (Gaillard et al. 2000), we also regressed observed lamb:female ratios as a function of population size and precipitation. We determined significance of these relations using F-tests (Zar 1996).

Results

A model containing only the current year's precipitation (i.e., precipitation from late gestation through weaning and into the early post-weaning period) provided the greatest information content for dynamics of desert bighorn sheep on SANWR, 1941-1976 (Figure 1). This model, N_{t+1} = N_t*exp(0.021853+0.035404*P+0.034039*Z), fit

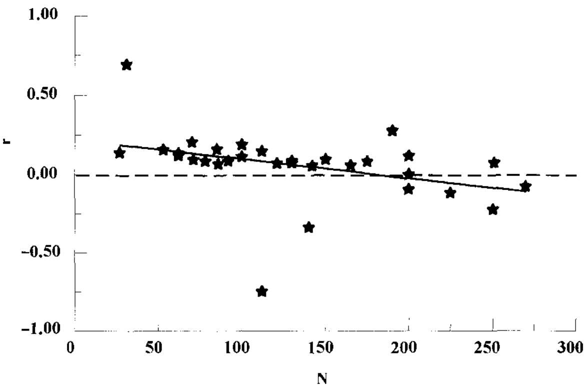

Figure 2. Instantaneous rate of population increase (r) as a function of population size for desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico, 1941–1976 ($F_{1,33}$ = 5.55; P = 0.025).

observed trends in desert bighorn sheep populations well (R^2=0.889; AICc=64.1) and described a low intrinsic potential rate of increase that could be strongly positively influenced by precipitation greater than long-term averages (i.e., normalized covariates >0), but becoming negative with annual precipitation covariates of ≤-0.62, equivalent to precipitation <87% of the long-term mean (28.2 cm v. a mean of 32.3 cm). Models (ΔAICc) including density (8.5), density-lagged (9.4), density and density-lagged (11.8), density-lagged and precipitation (18.8), density and precipitation (18.9), and density, density-lagged, and precipitation (22.5) were inferior to the precipitation-only model.

Although the precipitation-only model best fit trends in desert bighorn sheep populations on SANWR, population rate of increase was also affected ($F_{1,33}$=5.55; P=0.025) by population density (Figure 2). This relationship predicted an ecological carrying capacity (provided annual precipitation was >87% of the long-term mean) of approximately 200 desert bighorns for SANWR (i.e., where the regression of r on N crossed the x-axis; Figure 2). Lamb:female ratios were not related to either the current year's population density ($F_{1,34}$=0.04; P=0.843) or the previous year's population density ($F_{1,33}$ = 0.14; P = 0.715) (Figure 3). However, lamb:female ratios were related to the current year's total annual precipitation ($F_{1,34}$ = 7.09; P= 0.012; R^2=0.18) and weakly to the previous year's total annual precipitation ($F_{1,33}$=3.37; P=0.075; R^2 =0.11) (Figure 4), suggesting that precipitation influenced desert bighorn sheep populations through production or survival of lambs.

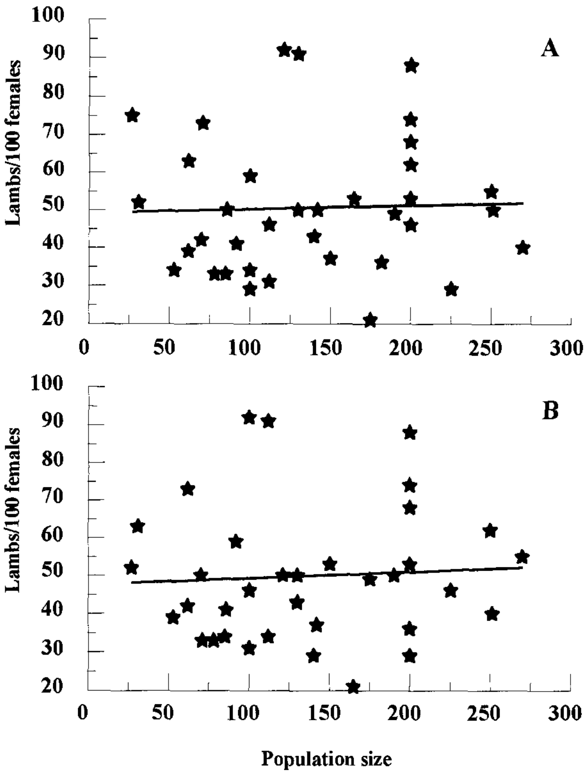

Figure 3. Lamb:female ratios as a function of current (A; $F_{1,34} = 0.04$; $P = 0.843$) and previous years (B; $F_{1,33} = 0.14$; $P = 0.715$) desert bighorn sheep population on San Andres National Wildlife Refuge, New Mexico, 1941–1976.

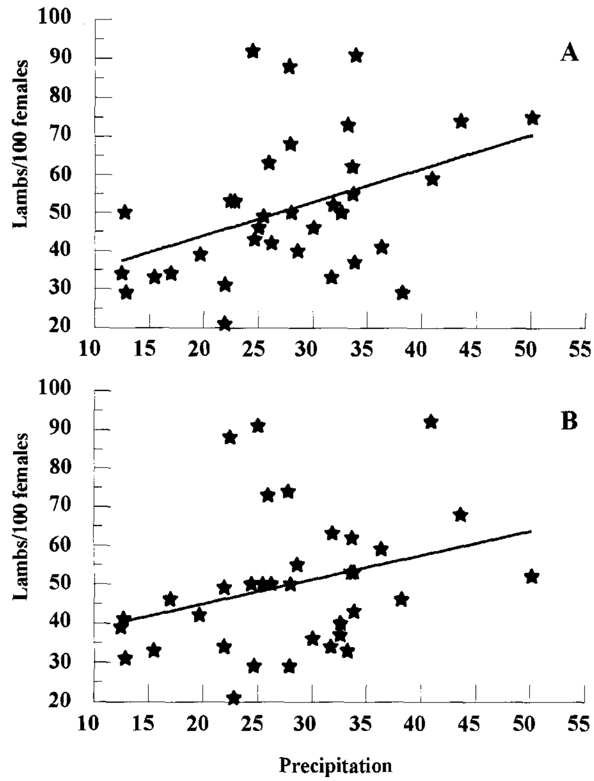

Figure 4. Lamb:female ratios as a function of current (A; $F_{1,34} = 7.09$; $P = 0.012$) and previous years (B; $F_{1,33} = 3.37$; $P = 0.075$) total annual precipitation (cm) recorded on San Andres National Wildlife Refuge, New Mexico, 1941–1976.

Discussion

In arid habitats, both production and nutritional quality of plants are strongly related to precipitation (Beatley 1969, Noy-Meir 1973, DeYoung 1997). Thus, precipitation has important effects on nutritional status of individual herbivores, and nutritional status has been demonstrated to be fundamental to virtually every health, survival, and reproductive process of wild and domestic herbivores (Verme and Ullrey 1984, National Research Council 1985, Sams et al. 1996, Keech et al. 2000, Cook et al. 2004). Consequently, precipitation should relate to both individual (i.e., body condition, body mass) and population performance of desert bighorn sheep, including production and survival of lambs. Several studies have shown these relations for bighorn sheep in arid environments (Berger 1982, Douglas and Leslie 1986, Wehausen et al. 1987, Cook 1990, McKinney et al. 2001), and we found a similar relation using a 36-year dataset for both population trend (Figure 1) and productivity (Figure 4) of desert bighorn sheep on SANWR. Because of the strong relationship between precipitation and forage, and nutrition and individual and population productivity, the most likely mechanism for these relationships was the effect of precipitation on forage quantity and quality. Although precipitation also may have affected desert bighorns on SANWR by increasing the availability of free water, both the abundance of permanent water sites on SANWR and the historic distribution patterns of desert bighorns on SANWR, which indicated selection for succulent vegetation rather than free water per se (Sandoval 1979), argue that the principal effect was through forage.

We also observed evidence for density effects on desert bighorn sheep at SANWR (Figure 2). However, adding density-dependence (or delayed density-dependence) into the model weakened relations to observed desert bighorn population dynamics. Density-dependence frequently is framed in terms of competition for adequate quantity of forage and many historic attempts at predicting carrying capacity of desert bighorn sheep focused on forage quantity (i.e., Mazaika et al. 1992). Plant production is low in Chihuahuan desert habitats, and a minimum level of forage quantity obviously is important for desert bighorn sheep. However, wild herbivores including bighorn sheep face strong foraging constraints relative to forage quality as well (Cook 1990, DeYoung 1997, DeYoung et al. 2000). Thus, the interaction of forage quantity and forage quality is important in determining the level of nutrition of bighorn sheep and consequently population performance potential (Cook 1990, DeYoung et al. 2000). On SANWR, long periods (≥10 y; Figure 1) of adequate precipitation may result in sufficient forage of high nutritional quality to allow desert bighorn to increase to levels where strong density effects associated with large population size stopped population rate of increase (approximately 200 individuals; Figure 2). However, if total precipitation was low (i.e., <87% of historic mean), populations of desert bighorn on SANWR were likely to decline regardless of population density, suggesting that precipitation was acting primarily as a density-independent mechanism limiting desert bighorn on SANWR (although competition, a density effect, may have contributed to these precipitation-induced declines even given very low population size if forage quantity was reduced but forage quality remained adequate). In Texas DeYoung et al. (2000) found that drought-induced declines in forage quality limited habitat capacity for desert bighorn sheep.

Most assessments of bighorn habitat evaluate only the presence of suitable escape cover (Hansen 1980, Holl 1982, Cunningham 1989, Dunn 1996), and many efforts at re-establishing desert bighorn populations include considerable efforts to reduce or eliminate proximate threats to bighorn welfare, such as mountain lions (*Puma concolor*) (Hayes et al. 2000, USFWS 2002). Few efforts evaluate the quantity and especially quality of forage available to sheep (but see DeYoung et al. 2000), despite the wealth of information highlighting the importance of nutrition to survival and productivity of bighorn sheep (Krausman and Leopold 1986, Krausman et al. 1989, Cook 1990, DeYoung 1997, DeYoung et al. 2000). Because our data from SANWR support the importance of precipitation (and consequently forage) for desert bighorn sheep found elsewhere (DeYoung et al. 2000, McKinney et al. 2001), we recommend that the first step in habitat evaluations for desert bighorn sheep restorations be to determine the suitability of forage resources to support sheep populations. If forage is inadequate, such as in periods of below-normal precipitation, then restoration efforts are likely to fail and efforts acting to reduce proximate risks to desert bighorn may yield little benefit to desert bighorn populations.

Lastly, the traditional concept of "carrying capacity" for a large herbivore like desert bighorn sheep needs revision in arid environments. Our data suggested that potential carrying capacity for desert bighorn on SANWR was bifurcated by precipitation; our model indicated that below approximately 28 cm of total annual precipitation (<87% of historic mean), populations were likely to decline regardless of population size, indicating that carrying capacity for desert bighorn sheep was zero under these precipitation conditions. Given adequate precipitation, carrying capacity appeared to be influenced by density effects, as indicated by the response of instantaneous rate of population increase (r) to population size, which declined to $r = 0$ at approximately 200 sheep (Figure 2). It is important to note that expression of density-dependence related to large population size apparently would only occur given extended periods of precipitation near or above long-term averages; such conditions are unlikely to occur for any length of time given the extreme annual fluctuations in precipitation (CV for total annual precipitation on SANWR = 35.6%) and forage quantity and quality in arid environments (Wehausen et al. 1987, Krausman et al. 1999, DeYoung et al. 2000). Estimates of potential populations of desert bighorn sheep that desert habitats can support need to be considered in terms of long-term means and trends in local precipitation patterns.

Management implications

Understanding what regulates or limits wildlife populations is crucial for proper management. With desert bighorn sheep, virtually any proximate mortality factor has been postulated to regulate or limit populations, including predation, disease, precipitation, density-dependence, and competition (Krausman et al. 1999). However, few studies implicating these factors looked at fitness of desert bighorn in a rigorous manner (including our retrospective analysis; i.e. most identified proximate causes of mortality or correlates of population trend without assessing the viability of individual desert bighorn sheep in the population). Cook (1990) demonstrated the importance of differentiating proximate causes of mortality from the underlying factors that were fundamentally responsible for observed mortality in bighorn populations, demonstrating that inadequate nutrition predisposed bighorn sheep to a variety of disease processes as well as accidents. Without clearly demonstrating that individuals can be productive (i.e., individual nutritional condition is good; Clutton-Brock et al. 1982, Verme and Ullrey 1984, National Research Council 1985, Cook et al. 2004), and thus that the population has the potential to increase, management decisions based on these results are tenuous. Although populations in good nutritional condition may still be limited by mortality factors such as predation or density-independent disease, it is important to note that no rigorous data indicate that populations in poor nutritional condition have any potential to be productive and thus increase in numbers. Therefore, more rigor is needed in research designed to elucidate fundamental measures regulating desert bighorn sheep populations. Moreover, priority should be placed on developing measures of absolute body condition of desert bighorn and identifying condition thresholds necessary for fundamental reproductive processes such as conception (i.e., see Cook et al. 2004). Lack of identification of underlying reasons for declines in bighorn sheep populations helps explain the frequent ineffectiveness of actions aimed at addressing proximate causes of mortality, such as providing free-ranging bighorns with medications to treat pasteurellosis (Miller et al. 2000).

Our data indicated that precipitation was able to predict desert bighorn sheep population trend and affected productivity on SANWR, most likely through the well-documented effects of precipitation on forage quantity and quality in arid environments. Thus, on SANWR and likely other Chihuahuan Desert ranges, evaluations of forage quantity and quality, with respect to current and historical precipitation patterns, should be conducted prior to attempts to re-establish desert bighorn populations. Without identifying the underlying ability of ranges to support desert bighorn populations, transplants are likely to continue to show limited success (for bighorn sheep in general, 41% classed as "completely successful," 30% "completely unsuccessful;" Singer et al. 2000*a*) and management prescriptions aimed at limiting the effects of proximate mortality factors (i.e., predator control, disease treatment) will remain controversial.

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Lou Bender is Assistant Unit Leader–Wildlife with the United States Geological Survey's New Mexico Cooperative Fish and Wildlife Research Unit. His previous positions have included elk and deer biologist for Washington Department of Fish and

Wildlife and deer research biologist for Indiana Department of Natural Resources. He received his B.S. in wildlife biology from the University of Montana and M.S. and Ph.D. degrees in wildlife management from Michigan State University. His interests include all aspects of ungulate and carnivore ecology and management. ***Mara Weisenberger*** is a wildlife biologist with the United States Fish and Wildlife Service at the San Andres National Wildlife Refuge, New Mexico. She received Bachelors and Masters degrees from the University of Arizona. Mara previously worked at the Kofa National Wildlife Refuge, Arizona before moving to New Mexico 12 years ago. She has been a member of The Wildlife Society since 1989.

Associate editor: *Krausman*