Commentary

Biological and Statistical Errors Make Inferences Circumspect: Response to Bender and Weisenberger

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ABSTRACT Bender and Weisenberger (2005) reported that desert bighorn sheep (*Ovis canadensis*) on San Andres National Wildlife Refuge (SANWR), New Mexico, USA, were primarily limited by rainfall. However, they failed to mention, or were unaware, that persistent long-term predator control was used to enhance population growth at SANWR. Additionally, lamb:female ratios were collected throughout the year, rather than dates typically associated with assessing recruitment, and therefore influence of precipitation on lamb recruitment was unknown. Finally, model predictions forwarded by Bender and Weisenberger (2005), that carrying capacity of SANWR is zero when annual rainfall is <28.2 cm, were not supported by data, nor were their model results properly interpreted. The coefficient of determination value of 88.9% for the relationship between population size and current year's precipitation was primarily a function of serial correlation between successive years in population data, with current year's precipitation accounting for only 3.8% of this value. This suggests that precipitation was a weak predictor of population increase. These errors in concert make biological inferences reported in Bender and Weisenberger (2005) of limited value. (JOURNAL OF WILDLIFE MANAGEMENT 72(2):580–582; 2008)

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Bender and Weisenberger (2005), using a portion of the modeling procedures originally published by Dennis and Otten (2000), reported results of a retrospective observational analysis of effects of annual precipitation on desert bighorn sheep (*Ovis canadensis*) population dynamics, including population growth and lamb:female ratios on the San Andres National Wildlife Refuge (SANWR), New Mexico, USA. Although errors of omission and interpretation occurred throughout the manuscript, our comments were based on 4 principal flaws.

Incorrect Data Used

We reviewed much of the raw data Bender and Weisenberger (2005) used to calculate lamb:female ratios (Sandoval 1979; E. Rominger, New Mexico Department of Game and Fish, unpublished data). Bender and Weisenberger (2005:958) misinterpreted how lamb:female ratio data were collected by stating that lamb:female ratios were "usually from October–December." In fact, in the raw data we reviewed, lamb:female ratios were a compilation of data collected year-round and never were exclusively October–December data that are considered requisite for estimating recruitment (Remington 1989). Most data were collected outside the October–December period and included spring lamb:female ratios, which often have very little relationship to autumn lamb:female ratios due to a myriad of mortality factors that affect desert bighorn sheep lambs. For example, in 1973 the lamb:female ratio value used by Bender and Weisenberger (2005) was 68:100, whereas actual October–December lamb:female ratio was just 16:100 (E. Rominger, unpublished data). For many years, lamb:female ratios collected between October and December were from one or two observations. These data should not have been interpreted as recruitment ratios, and relationships reported to be derived from October to December data were spurious.

Failure to Report Predator Control

The second major error was one of omission. Bender and Weisenberger (2005:957) stated that desert bighorn sheep populations "...were largely unaffected by human intervention, with the exception of limited harvest...and thus should have equilibrated with environmental conditions." Bender and Weisenberger (2005) failed to mention, or were not aware, that SANWR personnel conducted what was described as "persistent predator control" (Smith 1966:38) from 1940 until at least 1966 to protect and enhance population growth of desert bighorn sheep on SANWR (Kennedy 1957, Munoz 1983). Predator control included the killing of ≥14 mountain lions (*Puma concolor*) by SANWR personnel, and additional mountain lions were killed by sport harvest (Munoz 1983). In addition, predator control included use of the predacides 1080 (sodium monofluoroacetate; Tull Chemical Company, Oxford, AL) and M-44s (sodium cyanide; Pocatello Supply Depot, Pocatello, ID) between 1948 and 1951 (Munoz 1983). These broad-spectrum poisons were used to kill all predators including coyotes (*Canis latrans*), bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), mountain lions, and golden eagles (*Aquila chrysaetos*). In just 3 years, 1948–1950, >570 coyotes were reported to have been killed on or near SANWR (Munoz 1983). These anti-predator management practices, when mountain lion numbers were thought to be extremely low in New Mexico, may have essentially eliminated mountain lions and substantially reduced many other predators in this ecosystem (Berghofer 1967). The SANWR personnel hypothesized that desert bighorn sheep population growth during this period was a function of this

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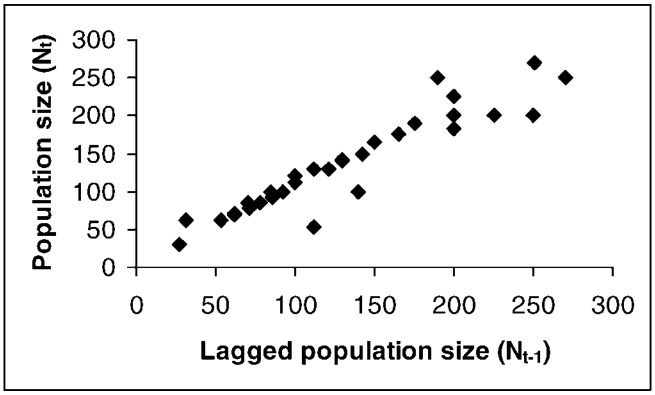

Figure 1. Current year's population size and previous year's population size of desert bighorn sheep on the San Andres National Wildlife Refuge, New Mexico, USA, 1941–1976.

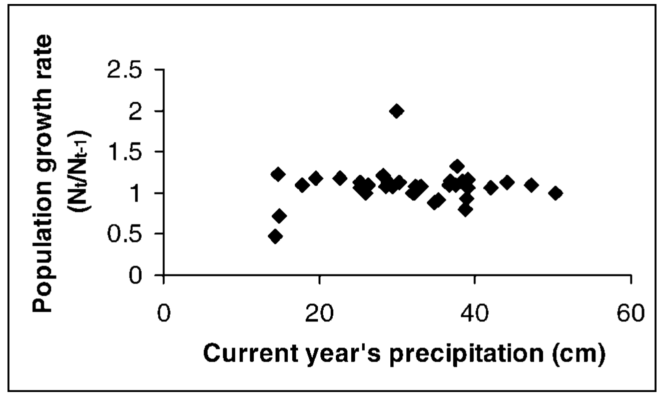

Figure 2. Population growth rate and current year's precipitation on the San Andres National Wildlife Refuge, New Mexico, USA, 1941–1976.

predator control (Kennedy 1957, Smith 1966) and almost certainly contributed to the high density of desert bighorn sheep on SANWR reported by Sandoval (1979).

Considering the profound influence predation can have on desert bighorn sheep population dynamics and on ecosystem function we found it disconcerting that this persistent and long-term management action was not reported (Sinclair and Arcese 1995, Wehausen 1996, Sinclair et al. 1998, Hayes et al. 2000, Kamler et al. 2002). Failure to address the potential effect of this management action on population dynamics of desert bighorn sheep was erroneous in a retrospective analysis.

Model Prediction Contradicts Data

Thirdly, Bender and Weisenberger (2005) stated that carrying capacity of the SANWR was zero when annual rainfall was <28.2 cm. However, the vast majority of desert bighorn sheep populations live in ecosystems where mean annual rainfall is substantially <28.2 cm. For example, mean annual rainfall in Yuma, Arizona, was just 9.0 cm and in Boulder, Nevada, it was 14.8 cm (Russo 1956, Leslie and Douglas 1979). More important to this critique was that model results reported by Bender and Weisenberger (2005) contradicted their own conclusion. The desert bighorn sheep population estimate increased every year between 1953 and 1967 (Sandoval 1979). The Bender and Weisenberger (2005) model output also predicted an increase in the desert bighorn sheep population during this period that mirrors the estimated population increases reported by Sandoval (1979), despite the fact that during 6 of 14 years annual rainfall was <28.2 cm and, thus, population carrying capacity was hypothesized to be zero. Conversely, for the 6 years that the Bender and Weisenberger (2005) model predicted a population decrease, 5 of 6 declines were in years following >28.2 cm of rain. These results were contrary to the assertion by Bender and Weisenberger (2005:956) that "population size and trend of desert bighorn sheep were best and well described by a model that included only total annual precipitation as a covariate."

Statistical Misrepresentation

Fourthly, Bender and Weisenberger (2005) focused their interpretation on the relationship between population size and current year's precipitation using the equation $N_{t+1} = N_t \times \exp^{(a+b+z)}$. Bender and Weisenberger (2005) stated that a significant relationship existed between the natural logarithm of the population rate of increase and population density, but population density was not developed as a component of their model. Because of this apparent relationship, and the lack of discussion by Bender and Weisenberger (2005), we reanalyzed the data. We started by graphing the relationship between current year's population size and previous year's population size (Fig. 1) and the relationship between population growth rate and current year's precipitation (Fig. 2). The equation $N_{t+1} = N_t \times \exp^{(a+b+z)}$ includes last year's population size (N_t) as a fundamental predictor of next year's population size (N_{t+1}). To separate impacts of precipitation from impacts of last year's population size, we performed a natural log transformation of the original equation [$\ln (N_{t+1}/N_t) = a + b + z$]. Just as in Bender and Weisenberger (2005), we used the modeling procedures of Dennis and Otten (2000), but we found that, as a single predictor, current year's precipitation was not statistically related to the natural logarithm of the population rate of increase ($P = 0.261$). However, the previous year's desert bighorn sheep density was significant ($P = 0.025$). As indicated by Dennis and Otten (2000), test statistics provided by regression analysis were not valid for desert bighorn sheep density because desert bighorn sheep density was a random predictor. We, therefore, followed the lead of Dennis and Otten (2000) and bootstrapped test statistics and P-values, and came to the conclusion that when both current year's precipitation and previous year's population size were included as predictors, both factors were statistically related to the natural logarithm of the population rate of increase ($P = 0.012$ and $P = 0.001$, respectively). Therefore, rainfall was only a statistically significant predictor when last year's population size was included in the equation, but not when it was the sole predictor.

The coefficient of determination for the regression of the natural logarithm of the population rate of increase using current year's precipitation alone was just 3.8%. The current year's precipitation had less explanatory power than previous year's desert bighorn sheep density alone (14.4%) and the 2 predictors combined (24.7%). Based on these values, precipitation was a weak predictor of population growth rate (Fig. 2). The generalized coefficient of determination value of 88.9% presented by Bender and Weisenberger (2005) for the relationship between population size and current year's precipitation leads to a false sense of model quality because much of the coefficient of determination value resulted from serial correlation between successive years in the population data (Fig. 1). The first step autocorrelation for the population sequence was 0.894 and indicated a strong serial relationship ($P < 0.001$).

CONCLUSION

Although we appreciate the effort to understand ecological responses via retrospective analyses, errors in Bender and Weisenberger (2005) serve as warning to others that it is imperative to understand and review how historical data were collected. It is equally important to ascertain what other management practices may have influenced those data. A cursory review of model output should have alerted the authors to the spurious relationship in many years. Simply stated, many of these data should not have been used in a statistical model, particularly when conclusions could result in inappropriate management actions. We provide this perspective to caution others to objectively evaluate analyses and interpretations presented by Bender and Weisenberger (2005).

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