Population dynamics and control of exotic South African oryx in the Chihuahuan Desert, south-central New Mexico

Louis C. Bender, Extension Animal Sciences and Natural Resources, New Mexico State University, P.O. Box 30003, MSC 3AE, Las Cruces, NM 88003, USA *lbender@nmsu.edu*

Patrick C. Morrow, Environmental Stewardship Division, U.S. Army White Sands Missile Range, WSMR, NM 88002, USA

Mara E. Weisenberger, U.S. Fish and Wildlife Service, San Andres National Wildlife Refuge, 5686 Santa Gertrudis Drive, Las Cruces, NM 88012, USA

Bryce Krueger, Department of Fisheries and Wildlife Sciences, New Mexico State University, P.O. Box 30003, MSC 4901, Las Cruces, NM 88003, USA

Abstract: Introductions of exotic species can benefit certain publics but can also have many unanticipated consequences. South African oryx (*Oryx gazella gazella*) were introduced into the Chihuahuan Desert on White Sands Missile Range (WSMR), New Mexico, USA to alleviate a perceived lack of large mammal hunting opportunities. Because of conflicts with oryx as the population increased, we modeled population growth and determined survival of radio-collared oryx to identify rates of population increase, limiting factors to population growth, and levels of harvest necessary to control population growth. Following introductions in 1969–1977, oryx significantly increased their range and showed a rate of increase of approximately $\lambda = 1.22$ through 2000, reaching approximately 3,500 individuals. This rate was marginally positively influenced by total precipitation received the previous year and near the species maximum based on fecundity (approx. $\lambda = 1.26–1.29$). In response to concerns over conflicts with oryx on WSMR, intensive studies of oryx limiting factors, 2001–2003, found annual survival of oryx excluding recovered harvest was ≥0.95 for adults and 1.00 for subadults. Most of the mortality was unrecovered hunting loss, further indicating that oryx had few nonhuman limiting factors. Modeling of the oryx population indicated that adult female harvest must be approximately 0.22–0.25 to control population growth. Intensive harvesting aimed at controlling oryx numbers removed an average of 30 (SE = 2.0)% of the estimated population, 2001–2013, which decreased the population to approximately 1,700 by 2013. Decreased harvest intensity from 2014–2017 to approximately 16 (SE = 1.6)% of the population subsequently allowed oryx to increase again at approximately $\lambda = 1.14$, rebounding to around 2,900 by 2017. Introduction of oryx succeeded in increasing recreational opportunities and revenue for management agencies. However, negative impacts on military missions, vehicle–oryx collisions, possible disease impacts on native ungulates, impacts on protected areas, the logistics of managing hunting programs on a closed military reservation, and optimizing oryx-related revenues continue to be significant management challenges.

Key words: control, dynamics, harvesting, mortality, New Mexico, oryx, *Oryx gazella gazella*

Introductions of exotic species can benefit certain publics but can also have many unanticipated consequences (Edgington 2009). South African oryx (*Oryx gazella gazella*) were introduced onto White Sands Missile Range (WSMR) by the New Mexico Department of Game and Fish (NMDGF) to provide a huntable big game ungulate in an area of New Mexico, USA where hunting opportunities for native ungulates were considered to be limited. Following initial introduction of 7 oryx in October 1969 and an eventual total of 95 oryx by 1977 (Morrison 1981, Edgington 2009), oryx greatly increased their range and population; by 2001, the oryx population numbered about

3,500 in the core range on WSMR (Krueger et al. 2007), and while numbers outside of the core range were uncertain, oryx were common and increasing. The significant increase in population size illustrated how well oryx adapted to habitat conditions of the Chihuahuan Desert, which are similar to their native range in southern Africa (Wood et al. 1970, Walther 1988, Edgington 2009).

With increasing populations came increasing recreation and oryx-related revenues for management agencies. Public hunts for oryx became some of the most valuable and desired recreational opportunities in New Mexico. For example, hunts during the 2000–2013 intensive

control period (see below) sold an average of 1,185 licenses (a high of >1,600) annually at up to $160 (resident) to $1,600 (nonresident) per license as well as an access fee for WSMR, with an average harvest of 989 oryx (P. Morrow, unpublished data). These figures do not include population management hunts on adjacent public lands or hunts on adjacent privately owned lands, which can cost in excess of $3,000 for the latter (Edgington 2009).

Also concurrent with population and range expansion, however, were significant conflicts with oryx (Edgington 2009). On WSMR, oryx–vehicle collisions were a serious safety concern, and oryx posed further conflicts with WSMR's military mission, including presence on warhead impact areas and on runways on the adjacent Holloman Air Force Base. Oryx were also common on the adjacent White Sands National Monument (WSNM) and San Andres National Wildlife Refuge (SANWR), where their potential impacts on native flora and fauna (Edgington 2009) drove significant programs to decrease or eliminate oryx. For example, WSNM constructed a perimeter fence at a cost of >$1 million to exclude oryx and spent an approximated additional $400,000 to remove the oryx that were trapped within the fence (Edgington 2009). On SANWR, staff spent an average of >44 staff-days annually, 2000–2010, escorting oryx hunters on population management hunts to control oryx numbers on the refuge (M. Weisenberger, unpublished data). Moreover, declines in native desert mule deer (*Odocoileus hemionus eremicus*) coincided with increases in oryx numbers (Edgington 2009, Bender et al. 2017). While direct competition was not considered to be an issue (Hoenes and Bender 2010), apparent competition via disease may have been. Oryx introduced exotic diseases that could potentially affect native ungulates (Bender et al. 2003, Li et al. 2003), and oryx can serve as an amplifying host for native diseases (Bender et al. 2003, Li et al. 2003, Bender et al. 2017).

Despite the potential impacts of and conflicts with oryx on the Chihuahuan Desert system, demographics of oryx in New Mexico and other introduction sites (i.e., Texas, USA; Mungall and Sheffield 1994) were poorly understood. Given these conflicts, an understanding of the population dynamics of oryx was necessary to develop sustainable long-term management strategies for oryx, the Chihuahuan Desert system, and WSMRs military mission. Effective management of invasive exotics including ungulates requires information on the ecological interactions of the species, including factors affecting population growth, viability, and survival (Conover 2002). Although harvesting has likely been the most significant limiting factor of oryx on WSMR, very little was known of nonharvest mortality or environmental constraints on oryx dynamics in New Mexico or elsewhere (Nowak 1991, Mungall and Sheffield 1994, Edgington 2009). Thus, our goal was to document population dynamics and limiting factors of oryx in and around WSMR. Our specific objectives included: (1) Determine historical population rates-of-increase of oryx since introduction and how these were affected by environmental factors; (2) estimate survival and nonharvest mortality of subadult and adult oryx on WSMR at the peak of population size and growth; and (3) document effects of intensive harvest on oryx dynamics following the peak of population size driven by management actions designed to significantly reduce oryx numbers on WSMR.

Study area

White Sands Missile Range encompasses about 11,000 km² (approx. 165 km north to south and 64 km east to west) and includes portions of the Jornada del Muerto and Tularosa Basins and several mountain ranges of south-central New Mexico in the Basin and Range physiographical province. The WSMR and surrounding terrain include playas, rugged mountain peaks and canyons, rolling grasslands, sand dunes, lava flows, and scattered springs and ponds. Soils are primarily well drained alluvial deposits (Saiz 1975). Precipitation averages 20–35 cm annually, with the bulk of moisture occurring as short, intense rainstorms from July through September (Kunkel et al. 1990). Snowfall, usually averaging <10 cm, is short lived. Temperatures of the area range from -23–41°C (Kunkel et al. 1990). Three principal seasons occur in the study area: warm-wet (July to October), cool-dry (November to February), and warm-dry (March to June).

Major vegetation communities on WSMR include semidesert grassland, Chihuahuan desertscrub, and Great Basin conifer woodland

(Dick-Peddie 1993). Vegetation is typical of the Chihuahuan Desert shrublands and grasslands with characteristic plant species including grama grasses (*Bouteloua* spp.), dropseeds (*Sporobolus* spp.), bristlegrass (*Setaria leucopila*), soaptree yucca (*Yucca elata*), banana yucca (*Y. baccata*), Mormon tea (*Ephedra* spp.), creosotebush (*Larrea tridentata*), tarbush (*Flourensia cernua*), mesquite (*Prosopis glandulosa*), and fourwing saltbush (*Atriplex canescens*). Pinyon (*Pinus edulis*), juniper (*Juniperus* spp.), and scattered ponderosa pine (*P. ponderosa*) occur in the higher elevations of the San Andres and Oscura Mountains. Potential predators included pumas (*Puma concolor*), coyotes (*Canis latrans*), and a limited number of American black bears (*Ursus americanus*).

Methods

Population trends

The WSMR and NMDGF began consistent aerial minimum count surveys of oryx in 1987. Prior to this, surveys were sporadic and confined primarily to the Rhodes Canyon Range Center (RCRC) and surrounding area, the site of the initial release of oryx. Because of that, our analysis focused on the core range of oryx, which was most consistently surveyed since introduction and included the Rhodes Canyon Range Center, the Stallion Range Center (SRC), and Small Missile Range (SMR) areas of WSMR, which totaled about 4,400 km^2. Surveys occurred throughout the day and covered 100% of count areas thought to be occupied by oryx. In early years, surveys were flown by helicopter, then by fixed-wing aircraft as numbers and range occupied increased. Hence, latter counts were more likely to have missed more oryx than earlier, resulting in potential underestimate of oryx rate-of-increase. Time of survey was found not to significantly influence oryx sightability (Krueger et al. 2007).

We determined mean annual finite rate of population increase (λ) = $(N_{y+n}/N_y)^{1/n}$, where y = year and n = numbers of years in the time series, for 3 distinct periods of oryx population growth on WSMR. First, we used minimum count data to calculate mean annual λ from 1974–2000 when oryx significantly increased both range and numbers on WSMR because harvest was comparatively minor during this period of

rapid population growth and range expansion. Because some harvest occurred during this period, we calculated annual λ correcting for effects of harvest by adding known harvest into population counts. This correction still results in a negatively biased estimate of population growth because the compounding effect of lost reproduction from harvested individuals is not included in estimates. Our goal for this period was to determine growth potential of oryx on WSMR and whether environmental factors (other than harvest) influenced growth of the oryx population (see below).

Second, we determined mean annual λ for the 2001–2013 period, when oryx harvest was substantially increased to control oryx numbers, with significantly increased harvests guided by the development of a sightability-corrected population estimator (Krueger et al. 2007). Last, we calculated mean annual λ for the 2014–2017 period, when harvest was reduced in an attempt to stem or reverse population declines. For these latter 2 periods, we used sightability corrected estimates of population size (Krueger et al. 2007) rather than minimum counts to estimate mean annual λ. We corrected surveys for the effects of group size using Model G3A (Krueger et al. 2007), which incorporated group size and 2 levels of oryx activity in sight-bias correction.

We also determined annual finite rate of population increase using $\lambda = N_{y+1}/N_y$, where y = year. We then modeled factors potentially affecting annual rate of increase during the 1974–2000 period using a modified logistic model (i.e., $r = a + b \times \text{ß}_1 + c \times \text{ß}_2 + \ldots x \times \text{ß}_n$, where r = exponential rate of population increase and ß_{1-n} = environmental factors influencing exponential rate of increase). We included oryx numbers (i.e., density-dependence), delayed density-dependence, annual precipitation during the current year, previous years' precipitation, mean annual temperature, and previous years' mean temperature as environmental covariates. We normalized these covariates to a Z-score using $\text{ß}_Z = (\text{ß}_t - \text{ß}_{mean})/(\text{ß}_{SD})$. We transformed covariates to express the range of each parameter comparably with a mean of 0 and SD of 1 (i.e., so that each annual value represented the number of SDs departure from the mean; Peek et al. 2002). We obtained precipitation and temperature data from 4 weather stations surrounding the core
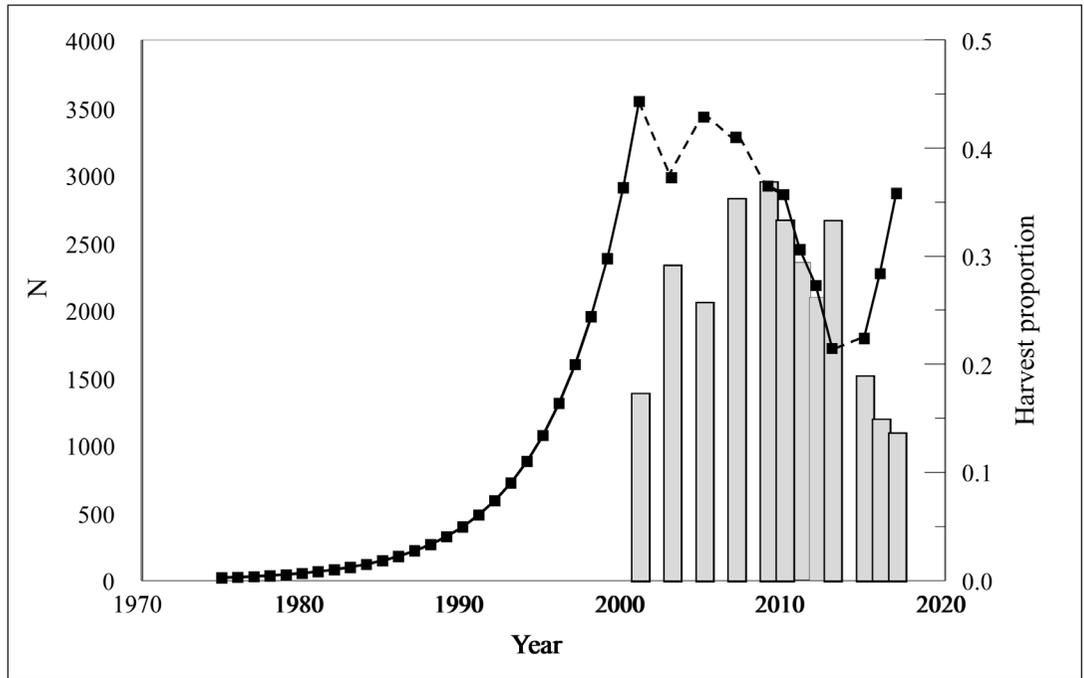
Figure 1. Population trends of oryx (*Oryx gazella gazella*; solid and dashed lines; scaled on left axis) and estimated proportion of the oryx population harvested (bars; scaled on right axis) on White Sands Missile Range, south-central New Mexico, USA. Population counts for 1975–2000 are smoothed and scaled to the 2001 sight-bias population estimate; data from 2001–2017 are sight-bias population estimates. Dashed lines are used to connect estimates for which the intervening year was not surveyed.

oryx range on WSMR and averaged values for which the data were complete (i.e., no missing months). Weather stations included the Ash Canyon station on SANWR, WSNM, and the towns of Bingham and Tularosa. For modeling, current years' values represented January to December totals or means for the count year, while previous years' (or delayed) values represented data recorded January to December of y-1. We used stepwise regression (Zar 1996) to determine the best model because it is more conservative than information-theoretic approaches (Arnold 2010).

Survival and mortality rates

We monitored survival of 101 adult and subadult (excluding calves) oryx that were captured and radio-collared during February to April 2001 (Krueger et al. 2007). We monitored radio-collared oryx for mortality signals during triannual aerial relocation periods and variably from weekly to approximately monthly from the ground, February 2001 to December 2003. When we detected a mortality signal from a radio-collared oryx, we located it from the ground and investigated the cause of mortality as described

in Bender et al. (2012). We excluded mortalities that occurred <30 days post-capture from analysis because capture-related stress may contribute to mortality (Beringer et al. 1996).

We excluded recovered hunter harvest mortalities from survival analyses because we were interested in nonrecovered harvest (hereafter, nonharvest mortality) limiting factors only. Additionally, oryx hunters on WSMR were requested not to harvest radio-collared oryx, so the proportions harvested relative to abundance in the population were likely significantly biased. We estimated annual January to December (February to December for 2001) survival of adults for 2001–2003 and subadults for 2001 using the Kaplan-Meier method (Kaplan and Meier 1958) as modified by Pollock et al. (1989) for staggered entry of study animals. We estimated annual survival rates for subadult oryx for February to December 2001 only, after which we added subadult oryx that survived 2001 into the adult oryx population for survival analysis for 2002–2003. We used the Heisey-Fuller method to calculate annual nonharvest mortality rate (Heisey and Fuller 1985). We made all comparisons of survival and

mortality rates using 2-tailed standard normal *Z* tests (Pollock et al. 1989) at $\alpha = 0.05$.

Potential population dynamics

We estimated maximum potential finite rate of population increase as $\lambda = S_F + \frac{1}{2} \times (J/F)$, where S_F = annual survival rate of adult females and J/F = observed juvenile/female ratio at approximate time of recruitment (White and Bartmann 1998).

Results

Long-term population dynamics

Oryx on WSMR increased at a mean annual rate of $\lambda = 1.22$, 1974–2000 (Figure 1). During this period, harvest percentage was unknown, but low (possibly excepting the last approx. 2 years in the time series). Growth of oryx during this period was best described by the model r = 0.20 (SE = 0.05) + 0.06 (SE = 0.04) × previous years' precipitation, where r = exponential rate of population increase and previous years' precipitation = normalized covariate of total annual precipitation for the previous year ($F_{1,23}$ = 3.3; P = 0.083). This model indicated that oryx showed an average rate of increase of r = 0.20 (approx. $\lambda = 1.22$), which was marginally ($\beta_{90\%CI}$ = 0.00–0.12) positively influenced by above-normal precipitation and slightly depressed by below normal precipitation received the previous year. No other environmental factors were important ($P > 0.155$).

Attempts to control or decrease the oryx population after 2000 increased the mean proportion of the oryx population harvested to 0.296 (SE = 0.020; range = 0.17–0.37) annually, 2001–2013 (P. Morrow, unpublished data). This resulted in a significant decline in the population from around 3,500 to 1,700 at a mean annual rate of $\lambda = 0.94$ (Figure 1). After 2013, harvest proportion decreased to 0.157 (SE = 0.016; range = 0.14–0.19; P. Morrow, unpublished data), which resulted in an increasing trend in the oryx population at a mean annual rate of $\lambda = 1.14$ (Figure 1). Harvest was approximately equal between the sexes for the 2001–2013 period (proportion female = 0.48 [SE = 0.05]), but became increasingly male biased during the 2014–2017 period (proportion female = 0.43 [SE = 0.03]) despite the difficulty differentiating adult oryx by sex for inexperienced observers

(P. Morrow, unpublished data).

Survival

Twenty-one oryx died during 2001–2003. Causes of death included 12 recovered hunter kills and 9 other (i.e., nonharvest) mortalities. Of these 9 other mortalities, at least 7 were oryx that were likely shot during hunts and not recovered based on timing of mortalities during or immediately following hunts in combination with trauma consistent with possible bullet hole(s) in skin and/or bullet impact trauma to scapula, rib, or leg bones on carcasses that were subject only to avian scavenging and showed no indication of trauma to the neck or head area. These remains also were not buried, covered, or disarticulated.

Excluding recovered harvest, annual survival of subadult and adult oryx for 2001–2003 was 1.000 (SE = 0.000, n = 28) and ≥0.95 (n = 67–89), respectively. Non-harvest morality rates were 0.031 (SE = 0.006), 0.034 (SE = 0.005), and 0.051 (SE = 0.008) during 2001–2003, respectively. Annual survival of adult or subadult males and females was similar for nonharvest mortalities ($P > 0.466$).

Potential population dynamics

Fecundity of oryx on WSMR (Roeder 2003; L. Bender, unpublished data) suggested a maximum potential finite rate of population increase of $\lambda = 1.26$–1.29 (= 0.96 + ½ × 0.60–0.65). Given this potential rate of population increase, total annual mortality rates of adult female oryx would need to be around 0.26–0.29 to stabilize population growth of the female segment of oryx on WSMR and maintain population structure (i.e., adult sex ratio [ASR]), assuming minor annual variation in productivity or survival (Bender 2006). Because nonharvest mortality was approximately 4% annually, harvest proportions would thus need to be around 0.22–0.25.

Discussion

South African oryx were highly productive on WSMR (Roeder 2003), and deaths to nonharvest mortality factors were near the species biological minimum due to senescence (see below). Oryx thus have a high growth potential on WSMR, and this was reflected in their population dynamics, as the population

historically increased at rates of about 22% annually with no evidence of any density limitation. How long oryx could have maintained this rate of increase in the absence of aggressive harvesting is unknown. However, density data from Africa (i.e., 1.4 km^2; Nowak 1991) suggest that numbers on our study area could have exceeded 6,000 before density effects limited the population, approximately double the population size that resulted in significant human–oryx conflicts.

Excluding harvest, the observed rate-of-increase was influenced only by precipitation (ß = 0.06 [90% CI = 0.00–0.12]), indicating that oryx had few limiting factors on WSMR (see also Saiz 1975, Edgington 2009). The marginal effect of precipitation was likely primarily related to calf production and survival through effects on forage availability and quality. Drought can limit forage and thereby decrease calf survival of oryx (Nowak 1991, Mungall and Sheffield 1994), similar to native ungulates on WSMR (Bender and Hoenes 2018). Despite the significant adaptations of oryx to arid environments, drought can also result in adult mortality (Nowak 1991).

Excluding recovered harvest, adult oryx on WSMR showed survival rates much higher than the reported average for mature bovid and cervid females (0.895 and 0.855 respectively; Gaillard et al. 2000), which have the highest and most stable survivorship of adult ungulates (Gaillard et al. 2000). Nonharvest mortality rates (0.031–0.051) further highlight that adult oryx have few natural limiting factors on WSMR and that any nonhuman mortality factor (e.g., predation, disease, etc.) is insignificant in oryx population dynamics. If longevity of oryx on WSMR is similar to longevity in the Kalahari (approx. 20 years; Nowak [1991]), then natural mortality of oryx due to senescence alone would average around 5% annually. This is consistent with observed nonharvest mortality rates ($\bar{x}$ = 0.039) on WSMR, as well as the continued presence of our radio-collared oryx on WSMR through at least autumn 2018, >18 years after collaring. Moreover, nonharvest survival estimates are conservative and should be considered minimum survival estimates because most oryx that died of unknown mortality causes (i.e., ≥7 of 9 nonharvest oryx mortalities) were likely shot and not recovered or abandoned by hunters. If

these likely wounding or abandonment losses were included in harvest mortality, then the maximum annual nonharvest mortality rate estimate for oryx on WSMR during this study would be 0.013. Similarly, subadult survival to nonhuman mortality factors on WSMR (1.000) was higher than average survival estimates for yearling bovids (0.829) or cervids (0.929; Gaillard et al. 2000). The only subadult oryx mortality we observed was the result of a recovered hunter harvest.

The above highlight the lack of nonhuman limiting factors on oryx in the Chihuahuan Desert system, supporting previous work. For example, Logan et al. (1996) and Elmer (1997) found that oryx comprised ≤1% of puma prey items. More recently, frequency of oryx in puma scats for the 2000–2005 (16%) and 2006–2010 (3%) periods were no more common than in coyote scats (20% and 4% for the same periods, respectively), indicating that most remains were likely due to scavenging (Bender et al. 2017). Local predators on WSMR certainly have difficulty preying on adult oryx (Edgington 2009), as even African lions (*Panthera leo*) in Botswana's Gemsbok National Park preyed primarily on oryx calves rather than adults (Eloff 1973), and oryx have been reported to kill adult lions (Mungall and Sheffield 1994). However, calves have been reported to be potentially vulnerable to predation on WSMR (Saiz 1975, Edgington 2009). Moreover, the significant unrecovered wounding loss or abandonment provides ample carrion or debilitated oryx for predators, which can be mistaken for actual predation (i.e., predation mistakenly assumed to be the ultimate cause of death, rather than the proximate; Bender 2018). These results reflect oryx vulnerability elsewhere; human exploitation was the primary limiting factor of oryx in Africa, though diseases such a rinderpest can occasionally impact populations significantly (Nowak 1991, Mungall and Sheffield 1994).

Consequently, aggressive hunter harvest or culling is necessary to control oryx populations on WSMR. Because of high elasticity (i.e., a greater effect on population growth per unit of change), adult female survival has the greatest effect on population growth rates (Gaillard et al. 2000). Modeling indicated that total adult female mortality must be approximately 0.26–

0.29 to stop population growth or to initiate population declines. Thus, a management goal for controlling oryx population growth would be an adult female harvest rate of approximately 0.22–0.25, given that nonharvest annual mortality is approximately 0.04 (the latter includes a significant proportion of human-caused mortality likely being unrecovered [i.e., wounding loss or abandonment]).

Management of oryx was intensified given these data and actual population estimates beginning in 2001. Recovered harvest of oryx increased to around 30% per year (approx. 25–26% per year for females based on an ASR of 75–80:100 and harvest sex ratio of 52:48), which resulted in a population decline from approximately 3,500 to 1,700 (annualized λ = 0.94) by 2013 (Figure 1). Thus, harvesting oryx at around 25% per year for females was effective in driving significant population declines, consistent with predictions as this rate was at the high end or greater than that predicted to stabilize the population. In concert with declines in oryx numbers, oryx conflicts on WSMR also significantly decreased. For example, although data were only available starting in 2004, oryx–vehicle collisions dropped from ≥22 annually when population size was >3,000 to <14 annually when population size was <2,000 (P. Morrow, unpublished data). However, the decline from about 3,500 to 1,700 also resulted in decreased recreational opportunities and revenue from oryx licenses. Despite oryx numbers remaining significantly above WSMR goals (management goal of 800–1,200 on WSMR [Burkett 1999]; this goal, however, was based on an assumed population of approximately 2,500, rather than a likely population of around 3,500 in the late 1990s), these declines resulted in lessening of harvest pressure and a reversal in population trend. After harvest percentage was approximately halved from 0.296 to 0.157 after 2013, oryx again began increasing in numbers at approximately λ = 1.14, reaching approximately 2,900 by 2017 (Figure 1).

Management implications

High productivity facilitated by year-round breeding (Roeder 2003), very low nonharvest mortality rates, and minor effects of precipitation result in a high growth potential for oryx on WSMR. Because nonhuman-related mortality of oryx is low and unable to exert any significant regulation or limitation on the oryx population, aggressive harvesting or culling is necessary to control population growth on WSMR and similar hot desert environments, though cold temperatures likely limit any spread of oryx northward into more temperate areas (Mungall and Sheffield 1994). While harvest of female oryx to approximately 25% of the estimated population effectively controlled oryx on WSMR and decreased many oryx-related conflicts, the decreased population also resulted in fewer recreational opportunities and decreased oryx-related revenue. In consequence, harvest pressure was lessened despite a decrease in oryx-related conflicts. Further, trophy quality of oryx harvested, in terms of horn development, also declined as age-structure declined and hunters preferentially harvested symmetrically horned oryx rather than broken or malformed horns (P. Morrow, unpublished data). Thus, while the biological aspects of oryx population control are understood and have been clearly demonstrated on WSMR, sociological concerns continue to complicate management of oryx. Finding an acceptable balance among recreational opportunities, revenues, herd demography, and acceptable levels of impact on the WSMR military mission and the Chihuahuan Desert system remains elusive.

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Associate Editor: Alan Clark

LOUIS C. BENDER (photo unavailable) is a senior research scientist (natural resources) with Extension Animal Sciences and Natural Resources at New Mexico State University.

PATRICK C. MORROW (photo unavailable) is a wildlife biologist with the Department of Army at White Sands Missile Range.

MARA E. WEISENBERGER (photo unavailable) was a refuge wildlife biologist with San Andres National Wildlife Refuge during the oryx project. She is currently the acting monument manager of the Organ Mountains-Desert Peaks and Prehistoric Trackways National Monuments with the Bureau of Land Management.

BRYCE KRUEGER (photo unavailable) was a research assistant with the Department of Fisheries and Wildlife Sciences at New Mexico State University during the oryx project. He is currently a resource conservationist with the National Resource Conservation Service in Washington state.