The Fourth California Islands Symposium: Update on the Status of Resources Edited by W. L. Halvorson and G. J. Maender. 1994. Santa Barbara Museum of Natural History, Santa Barbara, CA.

- Bratton, S. 1975. The effect of European wild boar (Sus scrofa) on gray beech forest in the Great Smokey Mountains. Ecology 56:1356-66.
- Brumbaugh, R. 1980. Recent geomorphic and vegetation dynamics on Santa Cruz Island. In: California Channel Islands (edited by D. Power), Santa Barbara, California, Santa Barbara Museum of Natural History, pp. 139–158.
- Callaway, R., and C. D'Antonio. 1991. Shrub facilitation of coast live oak establishment in Central California. Madrono 38(3):158-169.
- Carey, V. 1991. C implementation of gee for S. Computer code obtained through STATLIB at Carnegie Mellon.
- Carlquist, S. 1974. Island biology. Columbia University Press, New York. 660 pp.
- Chipping, D. 1993. Impacts of wild pigs on native vegetation. In: The Wild Pig in California Oak Woodland: Ecology and Economics (edited by W. Tietie and R. Barrett), San Luis Obispo, California, Integrated Hardwood Range Management Program, Department of Forestry and Resource Management, University of California, Berkeley, p. 4.
- Collins, P. 1987. A review of the population status of the Santa Cruz Island harvest mouse (Reithrodontontoyys megalotis santacruzae), with emphasis on their distribution and status in the Prisoners Harbor area. Report prepared for The Nature Conservancy, Santa Barbara, California. 19 pp.
- Daily, M. 1987. California's Channel Islands: 1001 questions answered. McNally and Loftin, Santa Barbara, California. 284 pp.
- Daubenmire, R. 1968. Plant communities textbook of plant synecology. Harper and Row, New York. 410
- De Nevers, G. 1993. What is feral pig damage? In: The Wild Pig in California Oak Woodland: Ecology and Economics (edited by W. Tietje and R. Barrett), San Luis Obispo, California, Integrated Hardwood Range Management Program, Department of Forestry and Resource Management, University of California, Berkeley, pp. 9-10.
- Griffin, J. 1976. Regeneration in Quercus lobata savannas, Santa Lucia Mountains, California. American Midland Naturalist 95:422-435.
- Hochberg, M., S. Junak, and R. Philbrick. 1980. Botanical study of Santa Cruz Island for The Nature Conservancy. Santa Barbara Botanic Garden, Santa Barbara, California. 10 pp.

- Lindsey, J. 1993. Models for repeated measurements. Clarendon Press, Oxford. 342 pp.
- Mayer, J., and I. Brisbin, Jr. 1991. Wild pigs of the United States: their history, morphology, and current status. University of Georgia Press, Athens. 313 pp.
- Muick, P., and J. Bartolome. 1987. Factors associated with oak regeneration in California (General Technical Report PSW-100). U.S. Department of Agriculture Forest Service, Pacific Southwest Forest and Range Research Station.
- Peart, D. 1993. Impact of feral pig activity on vegetation composition associated with Quercus agrifolia on Santa Cruz Island, California. In: The Wild Pig in California Oak Woodland: Ecology and Economics (edited by W. Tietje and R. Barrett), San Luis Obispo, California, Integrated Hardwood Range Management Program, Department of Forestry and Resource Management, University of California, Berkeley, pp. 12-13.
- Philbrick, R., and J. Haller. 1977. The California Islands. In: Terrestrial Vegetation of California (edited by G. Barbour and J. Major), John Wiley and Sons, New York, pp. 893-906.
- Schofield, E. 1989. Effects of introduced plants and animals on island vegetation: examples from the Galapagos archipelago. Conservation Biology 3(3):227-238.
- Schuyler, P. 1988. Feral pigs (Sus scrofa) on Santa Cruz Island; the need for a removal program. The Nature Conservancy, Santa Barbara, California. 24 pp.
- Sterner, J. 1990. Population characteristics, home range, and habitat use of feral pigs on Santa Cruz Island, California. MS Thesis, University of California at Berkeley. 104 pp.
- Stromberg, M. 1993. Pers. comm., Hastings Reserve, UCNRS, Carmel Valley, California.
- Thorne, R. 1969. The California Islands. Annals of the Missouri Botanical Garden 56:391-408.
- Tietje, W., and R. Barrett (editors). 1993. The Wild Pig in California Oak Woodland: Ecology and Economics. San Luis Obispo, California, Integrated Hardwood Range Management Program, Department of Forestry and Resource Management, University of California, Berkeley. 45 pp.
- Van Vuren, D. 1984. Diurnal activity and habitat use by feral pigs on Santa Cruz Island, California. California Fish and Game 70:140-144.

Ecology of Feral Goats Eradicated on San Clemente Island, California

Dawn R. Keegan,¹ Bruce E. Coblentz,² and Clark S. Winchell³

¹Department of Fisheries and Wildlife, Nash 104, Oregon State University, Corvallis, OR 97331 ¹CH2M HILL, 825 N.E. Multnomah, Suite 1300, Portland, OR 97232-2146 Tel. (503) 235-5000; Fax (503) 235-2445 ²Department of Fisheries and Wildlife, Nash 104, Oregon State University, Corvallis, OR 97331 Tel. (503) 737-1959; Fax (503) 737-3590 ³Natural Resource Office, Code 18N2, P.O. Box 357040, NAS North Island, San Diego, CA 92135-7040 Tel. (619) 545-4743; Fax (619) 545-1101

Abstract. Feral goats (Capra hircus) severely degraded endemic biota on San Clemente Island, resulting in the listing of 4 plants, 2 birds, and 1 reptile as threatened or endangered. The U.S. Navy instituted an intensive feral goat eradication program in 1972. After 17 yr, remnant groups of feral goats were still present and the "Judas" goat technique, exploiting the gregarious nature of the goats, was implemented in June 1989. Between June 1989 and April 1991, 263 feral goats had been killed on San Clemente Island. Natality, survivorship, and physiological condition of San Clemente Island goats were higher and mortality rates lower than other feral goat populations, presumably because of the unusually low density of goats on San Clemente Island. This feral goat population exhibited a compensatory rate of increase as a result of eradication efforts.

Keywords: Capra hircus; eradication; feral; goat; goats; Judas; radio-telemetry; San Clemente Island.

Introduction

The U.S. Navy instituted an intensive feral goat eradication program on San Clemente Island, California, in 1972. Despite the removal of more than 28,000 goats between 1972 and 1989, feral goats persisted and continued to damage native flora and fauna (J. K. Larson 1993, pers. comm.). Eradication planning and implementation did not include data collection of population characteristics or goat ecology. Consequently, no data, other than numbers removed and costs of control efforts, were available. Traditional eradication methods were not effective on San Clemente Island, and goat population responses to these methods are unknown. To better understand feral goat responses to population reductions, an intensive sustained control effort was implemented using the Judas

322

Hunting can be a form of compensatory mortality if breeding stock and their subsequent reproductive rates are unaffected (Peek 1986). For San Clemente Island goats, the intent was for hunting mortality to be additive, that is, causing mortality in excess of the populations' ability to compensate through increased natality or survivorship, and thereby reducing feral goat population densities. Feral goats have a relatively high reproductive

potential for an ungulate; gestation is 150 dy and goats reach sexual maturity at 6 mo of age (Yocum 1967). Multiple births are common (Rudge 1969; Baker and Reeser 1972; Parkes 1984) and females may give birth twice a year (Rudge 1969; Ohashi and Schemnitz 1987). These reproductive traits allow feral goats to respond to population reductions with increased natality (Coblentz 1982; Parkes 1984). Parkes (1984) documented an increase in goat productivity after population reduction on Raoul Island, New Zealand. Furthermore, Rudge and Smit (1970), using a fixed value for rate of increase, predicted that a goat population reduced by 80% could rebound to 90% of the original level in only 4 yr. Feral goats have a considerable capacity to increase in number and respond to control efforts in a compensatory manner. Unless control programs are financially insured in perpetuity, protection of a natural community from the negative effects of goats requires complete eradication of feral populations. Furthermore, considering long term effects, eradication is probably less expensive and more ecologically efficient than perpetual control.

goat technique (Taylor and Katahira 1988). This procedure allowed remnant feral goats to be located and eliminated on San Clemente Island.

The Judas goat technique helped eliminate 263 feral goats on San Clemente Island between June 1989 and April 1991 (Keegan et al. 1994). Two-hundred and nineteen carcasses were examined to determine if natality,

survivorship, and condition of San Clemente Island goats varied with decreases in population size. However, because no baseline data was available, inferences were made by comparing San Clemente Island goats with goats from other oceanic islands. For these comparisons, we assumed reproductive and condition parameters of San Clemente Island goats, prior to the inception of control programs, were similar to feral goat populations on other islands in Aldabra, Australia, British Columbia, Hawaii, New Zealand, and on neighboring Santa Catalina Island, California.

Study Area

San Clemente Island is located approximately 100 km west-northwest of San Diego, California, and is the southernmost of the 8 Channel Islands. The island is 34 km long, from 1.6 to 6.5 km wide and is approximately 148 km² in area.

The climate on San Clemente Island is semi-arid maritime with mean summer and winter temperatures of 18° and 12° C, respectively (Kasaty 1978). Average annual precipitation is 16 cm (Kasaty 1978), but 1989 to 1991 were the third to fifth consecutive years of drought. Precipitation was < 8 cm/yr and resulted primarily from morning fog; thus, plant productivity on San Clemente Island was low throughout the study.

Most of San Clemente Island is densely vegetated with several species of cacti (Opuntia spp., Bergerocactus spp.) and exotic annual grasses. Island oak (Quercus tomentella), Catalina Island ironwood (Lyonothamnus floribundus), and Island cherry (Prunus lyonii) occasionally occur in canyon bottoms.

Methods

The study was conducted from June 1989 until April 1991. Twelve female goats (8 in June 1989 and 4 in April 1990) were captured by net-gun on Santa Catalina Island, California, transported by helicopter to San Clemente Island, and fitted with radio-collars. These Judas goats were then released into canyons known to contain feral goats and were located as often as naval operations allowed, sometimes daily. We identified all individual goats they encountered by variations in age, coat color or pattern, horn shape or size, and association with other group members (i.e., juvenile with its mother).

An initial evaluation of the Judas goat technique was conducted from 15 to 18 September 1989; 28 goats associated with 3 Judas goats in 3 canyons were shot. After an additional 5 mo of data collection, an intense eradication effort began in February 1990. Ground shooting was conducted throughout the study, and was combined with periodic aerial gunning after April 1990.

The Judas goat technique helped eliminate 263 feral goats on San Clemente Island by April 1991. Age, sex, condition, and reproductive data were recorded ($\underline{n} = 219$) to determine whether the recently reduced San Clemente Island feral goat population exhibited a compensatory increase in recruitment and/or improved condition.

Sex was determined for 262 of the 263 goats killed. and necropsies were performed on 219 (83.3%); the other 44 were killed at locations where they could not be reached safely. The chi-squared goodness-of-fit statistic (Devore and Peck 1986) was used to determine if adult and fetal sex ratios varied from 1:1. Age was estimated to the nearest month by tooth eruption and wear (Silver 1970). Five age classes were established: birth to 0.5 yr, > 0.5 yr to 1 yr, > 1 yr to 2 yr, > 2 yr to 3 yr, and > 3 yr.

Physiological condition was quantified with a subjective kidney fat index (KFI) in which 1 = no fat around kidneys (poor condition), 2 = a thin layer of fat partially covering the kidneys (fair condition), 3 = a thin layer of fat surrounding the kidneys (good condition), and 4 = kidneys surrounded by a thick layer of fat (excellent condition). Mean and standard deviations were derived for comparative purposes.

For all female goats, teat condition (dry, lactating, or secreting colostrum gravidarum), and reproductive status (non-gravid or gravid uterus) were recorded. Colostrum gravidarum is secreted from the teats of pregnant goats before parturition (Hafez 1980). Number and sex of fetuses in pregnant goats were recorded and crown-rumplengths were measured to estimate fetal ages (Parkes 1984). Fetal and kid conception dates were determined (assuming a 150-dy gestation period) and combined. Natural mortalities in the feral goat population on San Clemente Island were noted as they occurred.

From these data, we derived sex ratio, age structure, condition, reproductive status, production and recruitment, multiple births rates (twins and triplets), and intrinsic rate of increase.

Results

Sex and Age Structure

The overall male:female sex ratio of 1:1.5 (Table 1) was significantly different from 1:1 (P = 0.001, n = 262). There were more females (n = 156, 59.5%) than male goats (n = 106, 40.5%) in the San Clemente Island feral goat population despite a male biased fetal sex ratio. The fetal sex ratio was 1:0.77 (n = 62) and was significantly different from expected (P = 0.01). However, the sex ratio varied from 1:2.33 for single fetuses (n = 10) to 1:0.09 in the 4 sets of triplets (n = 12).

One-hundred and sixty-one goats inhabited San

Table 1. Age and sex of feral goats killed on San Clemente Island, California, June 1989–April 1991.

Age (yr)	n	%	Male	Female	Sex ratio (male:female)
00.5	82	32.9	40	42	1:1.1
> 0.5–1	42	16.9	11	31	1:2.8
> 1-2	16	6.4	4	12	1:3.0
> 23	40	16.1	10	30	1:2.0
> 3	69	27.7	35	34	1:1.0
Total	249	100.0	100	149	1:1.5

Table 2. Subjective kidney fat indices of goats > 0.5 yr old killed on San Clemente Island, California, between June 1989 and April 1991.

		Kidney fat index						
	n	1	2	3	4	x	SD	
Males	91	8	14	19	50	3.2	1.0	
Females								
Pregnant	32	0	2	12	18	3.5	0.6	
Lactating	41	0	8	11	22	3.3	0.8	
Both	15	1	2	5	7	3.2	0.9	
Non-reproductive	40	5	2	7	26	3.9	0.7	
Total	219	14	28	54	123	3.3	0.9	
Percentage	100	6	13	25	56	_		

Clemente Island the day this study was initiated. During the next 16 mo, 105 births were recorded. Approximately 50% of the goats killed on San Clemente Island were < 1yr old (Table 1).

Condition

Mean KFI was 3.3 (SD = 0.9) for 219 goats (Table 2). Kids and lactating females were under the highest physiological stress (Oftedal 1985), but mean KFI for these 2 groups exceeded 3.2, which may be attributed to low population density.

324

Survival

Only 3 natural mortalities were recorded from June 1989 to April 1991 on San Clemente Island. A Judas goat apparently fell off a cliff, and 2 newborn goats were killed by a billy attempting to mate with their mother moments after their birth. The remaining mortalities were limited to those goats shot during the study. Excluding hunting mortalities, survival rate for all age classes combined during the period of this study was 98%.

Table 3. Reproductive condition of female feral goats > 0.5 yr old on San Clemente Island, California, June 1989–April 1991.

Age (yr)	n	Pregnant	Lactating	Both ^a	Non-Reproductive	
June 1989_May 1990						
0.5-1.0	21	6	3	3	9	
> 1.0-2.0	9	7	0	2	0	
> 2.0-3.0	24	6	15	2	1	
> 3	25	4	15	5	1	
Iune 1000 April 1991						
0.5.1.0	10	1	1	0	8	
5.5-1.0	3	1	2	0	0	
> 2.0-2.0	4	1	2	0	1	
> 3	9	2	3	3	1	
Total	105	28	41	15	21	

^a Goats that were both pregnant and lactating, in addition to those in the pregnant or lactating classification.

Reproductive Condition

Reproductive condition for 105 of 107 females > 0.5yr of age was recorded on San Clemente Island. More than 80% (n = 84) of these females were pregnant, lactating, or both pregnant and lactating (Table 3). Pregnant or lactating females comprised 26.7% (n = 28) and 39% (n = 41) of the female goat population, respectively, whereas 14.3% (n = 15) were both pregnant and lactating. Of the 21 non-reproductive goats, 81% (n = 17) were < 12 mo old; only 4 non-reproductive females were > 12 mo old.

Production and Recruitment

Observation of in utero fetuses indicated that 10 single kids, 20 twins, and 4 triplets were conceived between June 1989 and April 1991 (Fig. 1). During the same period, females gave birth to 20 single kids, 26 twins, and 4 triplets (Fig. 2). Conception dates for kids born during the study were combined with fetus conception dates (Fig. 3). Feral goats on San Clemente Island bred year-round, but peaks occurred between September and December during 1989 and August and September during 1990. As the number of feral goats on San Clemente Island decreased, the percentage of pregnant females increased to 100%.



Figure 1. Number of pregnant female goats (n = 34) with 1, 2, or 3 embryos at death on San Clemente Island, California, June 1989-April 1991.

Rate of Increase

There were at least 146 kids born to 84 adult female goats on San Clemente Island from June 1989 to May 1990; 84 were female kids. Productivity averaged 1.7 kid/female/yr or 1 female kid/female/yr. Using a birth rate





Figure 2. Number of female goats (n = 50) that gave birth to singles, twins, and triplets on San Clemente Island, California, June 1989-April 1991.



Figure 3. Conception dates for female goats that were pregnant or gave birth to kids and percentages of adult female feral goats that were pregnant or gave birth to kids on San Clemente Island, California, April 1989-April 1991.

(b) of 1 female kid/female/year and annual survival rate of 98%, death (d) = 0.02, the intrinsic rate of increase (r) is b - d = 0.96.

Discussion

There are no baseline data for the 28,000 goats removed from San Clemente Island prior to initiation of the Judas goat project in June 1989. Therefore, we can only compare compensatory response and physiological condition of feral goats on San Clemente Island to data from other studies of feral goat populations on oceanic islands.

About 50% of the goats killed on San Clemente Island were < 1 yr old, but the lack of baseline data prevented examination of potential changes in the age structure. In contrast, goats < 1 vr old comprised < 33% of hunted populations on 3 oceanic islands in New Zealand and Aldabra (Williams and Rudge 1969; Coblentz and Van Vuren 1988). However, Coblentz (1982) found a noticeably greater proportion of juveniles in a more intensely hunted feral goat population than in a less intensely hunted population (Mt. Orizaba and Coffee Pot Canyon, respectively) on Santa Catalina Island.

Most goats on San Clemente Island were in excellent condition, which was probably attributable to increased resource availability brought on by low population density. Body mass, a measure of condition, of feral goats varied inversely with population density on Raoul Island, New Zealand, (Rudge and Clark 1978) and Santa Catalina Island, California (Coblentz 1982). Caughley (1970) found a similar relationship in female Himalayan thar (Hemitragus jemlahicus). Coblentz and Van Vuren (1988) found that male goats had the lowest mean condition (based on KFI), whereas pregnant females were in the best condition in 3 low density populations in Aldabra. Generally, feral goats on San Clemente Island were in good or excellent condition. Based on KFI, the average condition of females that were both pregnant and lactating equaled that of male goats (x = 3.2) on San Clemente Island, and were the lowest 2 categories. Non-reproductive females had the highest mean KFI (x = 3.9), but pregnant or lactating females also had means above 3.3.

Feral goats display a variety of breeding systems ranging from year-round breeding in British Columbia (Geist 1960), North Island, New Zealand (Rudge 1969),

Sex and Age Structure

There were significantly more female than male goats on San Clemente Island, but because the survival rate was approximately 98%, juvenile male mortality, a common explanation for female biased sex ratios (Williams and Rudge 1969; Caughley 1970; Coblentz 1982), could not have contributed much to this difference. Eradication efforts may have selectively culled more males because of morphological and behavioral differences. Because of their larger body size (Coblentz and Van Vuren 1988), horns (Williams and Rudge 1969), and beards, males were easier to see than females and, therefore, more likely to draw the attention of shooters. Sometimes males were exposed to shooters longer than females because they were slower to react to disturbances on San Clemente Island.

Condition

Reproductive Condition

and Hawaii (Ohashi and Schemnitz 1987), to quadrimodal birth pulses on Santa Catalina Island (Coblentz 1980). Feral goats on San Clemente Island bred yearround, but peaks occurred between September and December during 1989 and August and September during 1990. This breeding cycle coincides with birth peaks in domestic goats from temperate latitudes (Asdell 1964). Domestic goats are seasonally polyestrous and the main breeding season occurs during the autumn and winter months (Turner 1936), but females may come into estrous year-round (Phillips et. al. 1943). Rudge (1969) stated that although feral goats were capable of producing kids twice each year, they usually do not fulfill this potential.

More than 16% of females in 2 age classes (n = 43and 62 for < 2 yr and > 2 yr, respectively) were simultaneously pregnant and lactating. This frequency was slightly lower than the 20-30% identified in 3 other insular feral goat populations (Williams and Rudge 1969; Coblentz 1974, Parkes 1984). Based on the number of females that were both pregnant and lactating, it is suspected that several San Clemente Island females would have had a birth interval of 180 dy, similar to that noted by Ohashi and Schemnitz (1987) in Hawaii, if they were not killed.

Production and Recruitment

Fourteen female goats on San Clemente Island were either pregnant or had given birth by the time they were 12 mo old (8 singles, 6 twins). However, reproduction by goats < 12 months old was commonly reported in feral goat populations (Geist 1960; Yocum 1967; Rudge 1969; Rudge and Clark 1978). Multiple births were also common (Rudge 1969; Baker and Reeser 1972; Parkes 1984). On San Clemente Island, we recorded 4 sets of triplets in utero, and 4 other females produced triplets. This relatively high occurrence of triplets was unusual because triplets were only recorded 5 times in the literature (Parkes 1984; Burke 1988). Furthermore, the condition of a Judas goat from Santa Catalina Island improved enough for her to produce 1 of the sets of triplets merely 4 mo after release on San Clemente Island. Production of triplets on San Clemente Island was extraordinary in light of the fact that single births were far more common than twins on Santa Catalina Island (Coblentz 1982), and triplets were never recorded.

Twinning rates for fetuses in utero (51%) and kids (52%) on San Clemente Island fell within or above the range for other feral goat populations (50% in Hawaii, (Yocum 1967); 52% in utero and 25% of births in New Zealand, (Rudge 1969); 30.5% in another New Zealand population, (Williams and Rudge 1969); 26.1% to 80% on Santa Catalina Island (Coblentz 1982); and 21.4%, 22.2%, and 60%, for 3 islands in Aldabra (Coblentz and Main 1988). The combination of twinning rate and triplet rate (in utero = 9.8% and kids born = 8%) during the study on San Clemente Island brought the overall multiple birth rate to approximately 60%.

Ohashi and Schemnitz (1987) concluded that the ability of females to kid twice in the same year depended on physiological condition. Approximately 7% (n = 4) of female feral goats > 12 mo old, all of which where in excellent condition, gave birth twice in a single year on San Clemente Island. Another female had 3 sets of kids within 11 mo. She gave birth to 2 female kids and 5 mo later, she had 2 more kids. Six mo later, she had 2 more kids; at which time the first kids were 11 mo old. One month later, each of the first 2 kids gave birth to twins. Essentially, 10 goats were produced from 1 adult female goat in 1 yr. The last 2 sets of twins from the original female were killed within 2 wk of birth, which likely induced a post-partum estrus (Watts and Conley 1984) in their mother. This individual was an exceptionally prolific goat, and most female goats on San Clemente Island did not produce kids twice a year; however, success of eradication efforts prevented determination of long-term reproductive capacity.

Rate of Increase

Hunted populations of goats often have high reproductive rates. Parkes (1984) documented an increase in productivity of goats after population reduction. As the feral goat population decreased on San Clemente Island, the percentage of pregnant females increased to 100%. Rudge and Smit (1970) derived a recruitment rate of 1.7 kids/female/yr for a hunted population in New Zealand that was similar to that on San Clemente Island. Lower recruitment was reported by Coblentz (1982) on Santa Catalina Island, California, (0.75 births/females/yr) and Yocum (1967) in Hawaii (100-164 kids/100 females). Rudge and Smit (1970) determined a minimum estimate of r = 0.375 and predicted that a New Zealand feral goat population reduced by 80% would increase to 90% of the former level in 4 yr. The intrinsic rate of increase for goats on San Clemente Island (r = 0.96) was twice that found in New Zealand. At this rate, assuming a survival rate of 98%, a population of 100 goats on San Clemente Island would double in < 8 mo and reach approximately 680 goats in 2 yr. In comparison to goats in New Zealand (Rudge and Smit 1970), if the San Clemente Island goat population was reduced by 80%, it could increase to 930% of the original population in 4 yr.

The combination of (1) high twinning and triplet rates, (2) early reproductive maturation, (3) postpartum estrus that allowed production of offspring twice a year, and (4) low kid and juvenile mortality rates allowed near maximum population growth rate for San Clemente Island goats.

Because of their high reproductive potential, goats are capable of achieving rapid population increases even after the most effective control efforts (Rudge and Smit

1970; Baker and Reeser 1972; Watts and Conley 1984). When feral goats are culled, remaining goats experience reduced competition for existing resources. Incomplete eradication only culls static populations, stimulates breeding, and may result in short-term population increases (Rudge and Clark 1978).

In addition, as a goat population decreases, the amount of vegetative cover increases, making remaining goats more difficult to locate for 2 disparate reasons: (1) they are simply more difficult to locate visually; and (2) they move less frequently and for shorter distances because of increased forage availability. Parkes (1990) advocates quick eradication after participating in a long hunting campaign in New Zealand that allowed time for the forest understory to regenerate, thereby restricting access and visibility. In addition, with increased food availability, goat breeding rates doubled from 0.96 kids/female/year in 1972 (Rudge and Clark 1978) to 1.70 kids/female/yr in the 1980s (Parkes 1984).

Based on comparisons with goat populations elsewhere, goat reproductive performance on San Clemente Island was probably density dependent; increased natality, recruitment, and individual condition, and decreased natural mortality resulted from decreased density. These findings support those of Coblentz (1982) on Santa Catalina Island, California, and are further evidence that animal populations reduced below equilibrium densities generate a positive rate of increase through densitydependent changes in age-specific rates of fecundity and mortality (Caughley and Birch 1971; Caughley 1985; Choquenot 1990).

Management Implications

As remnant feral goat populations are reduced, reproduction increases, thereby counteracting control efforts. Consequently, we strongly advocate complete eradication of feral goats over periodic control. Eradication is less expensive than indefinite periodic control because considerable hunter effort is required to constrain a population that is being induced to increase reproduction. Managers should become increasingly relentless rather than sporadic in eradication efforts as a population of goats dwindles and individuals become more difficult to locate.

Acknowledgements. We thank J. Larson, Natural Resource Office, NAS North Island, US Navy, for funding and logistical support, and more importantly, the insight to begin the arduous task of eradication 20 yr ago. We are grateful to USDA Animal Damage Control personnel, especially J. Turman and R. Phillips, and M. Cain's Skydance Helicopters, Inc. for ground and aerial shooting assistance. We thank D. Edge and S. Olson-Edge for providing critical review of the manuscript.

Literature Cited

- Asdell, S. A. 1964. Patterns of mammalian reproduction. Cornell University Press, Ithaca, New York.
- Baker, J. K., and D. W. Reeser. 1972. Goat management problems, Hawaii Volcanoes National Park. United States Department of Interior, National Park Service Research Report 2. 63 pp.
- Burke, M. G. 1988. The feral goats of Aldabra: ecology and population dynamics. National Geography Research 4(2):272-279.
- Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalyan Thar in New Zealand. Ecology 51:53-72.
- Caughley, G. 1985. Harvesting of wildlife: past, present, and future. In: Game harvest management (edited by S. L. Beasom and S. F. Roberson), Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, pp. 3 - 14.
- Caughley, G. and L. C. Birch. 1971. Rate of increase. Journal of Wildlife Management 35:658-663.
- Coblentz, B. E. 1974. Ecology, behavior, and range relationships of the feral goat. Ph.D. Thesis University of Michigan, Ann Arbor. 259 pp.
- Coblentz, B. E. 1980. A unique ungulate breeding pattern. Journal Wildlife Management 44:929-933.
- Coblentz, B. E. 1982. Reproduction of feral goats on Santa Catalina Island, California. Bulletin of Southern California Academy of Science 81(3):128-137.
- Coblentz, B. E., and M. B. Main. 1988. Biology and control of feral goats on Aldabra Atoll, Republic of the Seychelles. Unpublished data for Seychelles Islands Foundation, Victoria, Mahe, Republic of the Seychelles. 19 pp.
- Coblentz, B. E., and D. Van Vuren. 1988. Comparative demography of two adjacent, reproductively isolated feral goat populations on Aldabra Atoll. Unpublished data for Seychelles Islands Foundation, Victoria, Mahe, Republic of the Seychelles. 22 pp.
- Choquenot, D. 1990. Rate of increase for populations of feral donkeys in Northern Australia. Journal of Mammalogy 71:151-155.
- Devore, J. L., and R. L. Peek. 1986. Statistics, the exploration and analysis of data. West Publishing Company, St. Paul, Minnesota. 699 pp.
- Geist, V. 1960, Feral goats in British Columbia. Murrelet 41:34-40.
- Hafez, E. S. E. 1980. Reproduction in farm animals. Bulliere Tindall, London. 627 pp.
- Kasaty, P. 1978. 1978 conservation award report, March 28, 1978. Naval Ocean Systems Center Technical Document 150. Natural Resource Program Office, Naval Ocean Systems Center, San Diego, California 77 pp.

- Keegan, D. R., B. E. Coblentz, and C. S. Winchell. In press, 1994. Feral goat eradication on San Clemente Island, California. Wildlife Society Bulletin.
- Oftedal, O. T. 1985. Pregnancy and lactation. In: Bioenergetics of wild herbivores (edited by R. J. Hudson and R. G. White), CRC Press, Boca Raton, Florida, pp. 215-238.
- Ohashi, T. J., and S. D. Schemnitz. 1987. Birth pattern of feral goats on Haleakala. Journal of Hawaii Audubon Society. Elapaio 47(10):99-102.
- Parkes, J. P. 1984. Feral goats on Raoul Island. I. Effect of control methods on their density, distribution, and productivity. New Zealand Journal of Ecology 7:85-93.
- Parkes, J. P. 1990. Feral goat control in New Zealand. Biological Conservation 54:335–348.
- Peek, J. M. 1986. A review of wildlife management. Prentice-Hall, Englewood Cliffs, New Jersey 486
- Phillips, R. W., V. L. Simmons, and R. G. Schott. 1943. Observation on the normal estrous cycle and breeding season in goats and possibilities of modification of breeding with gonadotrophic hormones. American Journal of Veterinarian Research 4:360-367.
- Rudge, M. R. 1969. Reproduction of feral goats Capra hircus L. near Wellington, New Zealand. New Zealand Journal of Science 12:817-827.
- Rudge, M. R., and J. M. Clark. 1978. The feral goats of Raoul Island, and some effects of hunting on their body size and population density. New Zealand

Journal of Zoology 5:581-589.

- Rudge, M. R., and T. J. Smit. 1970. Expected rate of increase of hunted populations of feral goats (Capra hircus L.) in New Zealand. New Zealand Journal of Science 13:256-259.
- Silver, I. A. 1970. The aging of domestic animals. In: Science in Archaeology (edited by D. Brothwell and E. Higgs), Thames and Hudson Publishing, Bristol, England, pp. 283-302.
- Taylor, D., and L. Katahira. 1988. Radio telemetry as an aid in eradicating remnant feral goats. Wildlife Society Bulletin 16:297–299.
- Turner, C. W. 1936. Seasonal variation in the birth rate of the milking goat in the United States. Journal of Dairy Science 19:619-622.
- Watts, T., and W. Conley. 1984. Reproductive potential and theoretical rates of increase for feral goat populations. Journal Wildlife Management 48:814-822.
- Williams, G. R., and M. R. Rudge. 1969. A population study of feral goats (Capra hircus L.), from Macauley Island, New Zealand. Proceedings of New Zealand Ecological Society 16:17-28.
- Yocum, C. F. 1967. Ecology of feral goats in Haleakala National Parks, Maui, Hawaii. American Midland Naturalist 77:418-451.

The Fourth California Islands Symposium: Update on the Status of Resources Edited by W. L. Halvorson and G. J. Maender. 1994. Santa Barbara Museum of Natural History, Santa Barbara, CA

Response of a Bishop Pine (Pinus muricata) Population to Removal of Feral Sheep on Santa Cruz Island, California

Walter Wehtje

Western Foundation of Vertebrate Zoology, 439 Calle San Pablo, Camarillo, CA 93012-8506 Tel. (805) 388-9944; Fax (805) 388-8663

Abstract. A Bishop pine (Pinus muricata) population was sampled on the northern shore of Santa Cruz Island 4 yr after the removal of feral sheep (Ovis aires) from the area. I measured foliar cover of woody perennials, and recorded new establishment of woody perennials. I compared my results to those obtained by a previous study in 1977–1978 and an aerial photograph from 1985, when sheep were still present in the area. More woody perennial species were recorded in 1990 than in 1978. Newly established woody perennials were abundant in 1990. whereas few if any were recorded in 1978. The age structure of the pines changed from senescent to having successful seedling germination and survival. Bishop pine more than doubled in extent between 1985 and 1990. Reestablishment of native woody perennials in this area, including Bishop pine, coincided with the removal of feral sheep.

Keywords: Santa Cruz Island; feral sheep (Ovis aires), Bishop pine (Pinus muricata)

Introduction

Domestic sheep (Ovis aires) have been present on Santa Cruz Island for close to 150 yr (Brumbaugh 1983). Their detrimental effect upon the native vegetation of the island has been noted for almost as long (Rothrock 1876). Despite this, active sheep ranching took place until the late 1930s (Stanton and Daily 1989), and feral sheep were not eliminated from much of the island until the mid 1980s (Schuyler 1993). The purpose of this study was to measure the effect that the removal of feral sheep had upon a Bishop pine (Pinus muricata) population on the northern shore of Santa Cruz Island.

Study Area

Santa Cruz Island, the largest of the California Channel Islands at approximately 250 sq km, lies at 34°N,

119° 45' W, approximately 40 km south of the city of Santa Barbara (Fig. 1). It is 39 km long, and ranges in width from 3 to 11 km. The island is aligned along an east-west axis, and is bisected by a central valley created by the Santa Cruz Island fault. This valley separates the northern and southern mountain ranges. The northern side of the island is more rugged, with a maximum elevation of approximately 750 m. The southern range is lower, with a maximum elevation of 465 m. Santa Cruz Island is geologically complex, being composed of plutonic, volcanic, metamorphic, and sedimentary parent material (Weaver et al. 1969).

The island has a Mediterranean climate, marked by warm dry summers, and cool rainy winters (Brumbaugh 1983). Rainfall measured at the main ranch in the central valley averaged 506 mm per year between 1904 and 1990 (Main Ranch, unpubl. data). Most precipitation falls between October and March. Mean temperatures for the central valley range from 12° C in the winter to 21° C in summer (Brumbaugh 1983). Roughly 90% of the island is owned by The Nature Conservancy (TNC), while the eastern 10% of the island is controlled by the Gherini family.

There are 3 primary populations of Bishop pine on Santa Cruz Island (Fig. 2): (1) the western population, located on the north-facing slopes of Cañada Christy and Cañada de los Sauces; (2) the northern population with most of the trees found between Pelican Bay and Twin Harbors; and (3) the eastern population, which consists of scattered groves above China Harbor on the eastern isthmus of the island.

The study area is located between Pelican Bay and Twin harbors, amidst the greatest concentration of Bishop pines within the northern population. This is the only area where the pines approach sea level. The site is approximately 160 ha in size, and ranges in elevation from sea level to 230 m. The area is primarily open, with scattered groves of mature pine. Other common woody perennials are coast live oak (Quercus agrifolia), scrub oak (Q. aff. dumosa), manzanita (Arctostaphylos sp.), summer holly (Comarostaphylis diversifolia), toyon (Heteromeles