California Fish and Game 100(3):396-403; 2014

Shrub regeneration after removal of feral sheep from Santa Cruz Island, California

Dirk H. Van Vuren*

Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, USA

**Correspondent: dhvanvuren@ucdavis.edu*

I assessed shrub regeneration 29 years after removal of feral sheep (*Ovis aries*) from Santa Cruz Island by measuring shrub density during 1980 and 2013. Collectively, shrubs showed a three- to four-fold increase in density and a near-doubling of species richness. Individually, most species increased, some dramatically so, but a few species showed little change or even decreased. The explanation might be differing strategies for regeneration; most shrubs that did not increase lack a persistent seedbank and germinate best in mesic conditions, under the canopy in a substantial litter layer, and such conditions have been slow to develop. These shrubs should eventually regenerate and could even become dominant, highlighting the importance of a long-term perspective in assessing recovery of insular vegetation from herbivore damage.

Key words: chaparral, exotic herbivore, feral sheep, fire persister, fire recruiter, island recovery, *Ovis aries*, Santa Cruz Island, shrub regeneration, vegetation recovery

---

Domesticated sheep (*Ovis aries*) and goats (*Capra hircus*) were introduced to islands around the world, and many populations subsequently became feral (Rudge 1984). Long-term overgrazing by feral sheep and goats has devastated the vegetation of numerous islands, often resulting in the wholesale alteration of community composition and structure, sometimes to the point of desertification (Coblentz 1978, Van Vuren and Coblentz 1987, Chynoweth et al. 2013). Damage to woody vegetation on islands is particularly important because of its role as habitat for endemic animals, many of which have declined to rarity or even extinction because of habitat degradation by exotic herbivores (Van Vuren and Coblentz 1987, North et al. 1994, Chynoweth et al. 2013). Because of these impacts, feral sheep and goats have been eradicated or excluded on many islands (Schuyler 1993, Campbell and Donlan 2005), and subsequent regrowth of native vegetation is often swift and dramatic (Campbell and Donlan 2005, Chynoweth et al. 2013). However, not all species respond quickly to cessation of overgrazing; for some native trees and shrubs, regeneration can be delayed or, perhaps, even precluded by factors such as depletion of seed banks due

to prolonged overgrazing (Mueller-Dombois 1979), herbivore-caused alteration of soil conditions necessary for seedling germination (Hamann 1993), or competition with exotic grasses (Thaxton et al. 2010).

Santa Cruz Island, California, once supported a large population of domestic sheep. Sheep were introduced in the 1850s, reached numbers of 50,000 or more by the late 1800s, and became feral by the 1920s (Van Vuren and Bakker 2009). Decades of overgrazing by feral sheep had a major impact on shrubs and trees by preventing regeneration, altering growth form, and reducing large contiguous populations of woody plants to isolated clumps (Brumbaugh 1980, Van Vuren and Coblentz 1987, Junak et al. 1995). All sheep were removed from Santa Cruz Island, first on the western 90% of the island during 1981-1989, then on the eastern 10% of the island during 1997-2001, with a total of 47,000 sheep removed (Schuyler 1993; Faulkner and Kessler 2011). Recovery of woody vegetation over much of the island has been obvious, and analysis of aerial photos has revealed a dramatic increase in the cover of coastal sage scrub, island chaparral, and Bishop pine (*Pinus muricata*) communities, with a concomitant decrease in grasslands (Cohen et al. 2009). However, aside from a study of regeneration in the Bishop pine forest shortly after sheep removal (Wehtje 1994), responses by individual shrub species to the cessation of grazing remain unknown. My objective was to assess the response of individual shrub species by comparing densities before and 29 years after removal of feral sheep.

Materials and Methods

Santa Cruz Island (249 km^2) is the largest of the eight Channel Islands located offshore of southern California. A system of interior valleys, including the large Central Valley, is oriented in a generally east-west direction along a geological fault. These valleys are bounded by the Northern Ridge (elevation 750 m) and Southern Ridge (elevation 465 m). Climate is an oceanic, Mediterranean type characterized by hot, dry summers and cool, wet winters. Precipitation averages 50 cm per year, most of which falls as rain from November through April. The island is botanically diverse, with 480 taxa of native plants identified, of which ≥45 are endemic (Junak et al. 1995). Several plant communities have been described (Junak et al. 1995); in 1980, most of the island comprised grassland (46%), island chaparral (31%), oak woodland (7%), and coastal sage scrub (6%) communities in terms of proportion of the island covered (Minnich 1980).

My study was conducted on the south slope of the Northern Ridge, immediately north of the Santa Cruz Island Reserve Field Station of the University of California, in several parallel canyons that drained south into the Central Valley. The 170-ha study area (34º 00' N, 119º 43' W) was characterized by steep, rugged topography, and elevation ranged 75-400 m. Vegetation in 1980 was classified as grassland admixed with woody vegetation (Minnich 1980). Common shrubs were island scrub oak (*Quercus pacifica*), island cherry (*Prunus ilicifolia lyonii*), mountain mahogany (*Cercocarpus betuloides*), island big-pod ceanothus (*Ceanothus megacarpus insularis*), chamise (*Adenostoma fasciculatum*), and lemonade berry (*Rhus integrifolia*). Grassland vegetation was dominated by exotic annual grasses (*Avena* spp., *Bromus* spp., *Festuca* spp., and *Lamarckia aurea*), but scattered individuals of native perennial grasses (*Stipa* spp.) were present.

As part of a study investigating browse preferences by feral sheep (Van Vuren and Coblentz 1987), shrub density was measured in two strip transects, each 5 m wide and 1,000

m long. The exact locations of the transects were determined randomly, but the location of Transect 1 was constrained to a generally east-west direction, and that of Transect 2 to a generally north-south direction, such that the two transects crossed and approximately quadrisected the study area. On 15 April 1980 I walked the center of each transect and counted all shrubs ≥1 m tall that were rooted within 2.5 m of my line of travel; multiple stems that appeared to originate from one base were counted as one shrub. I omitted shrubs rooted outside the transect, whether or not the canopy extended into the transect. Feral sheep were removed from the area during 1984 (P. T. Schuyler, personal communication). On 14 April 2013 I censused shrubs in each transect again, using identical procedures. I calculated density as the number of shrubs per hectare of strip transect, and I classified shrubs that normally grow to ≤2 m tall as short-stature, and those >2 m tall as tall-stature, based on life-history information from Junak et al. (1995).

Results

Results from the two strip transects were generally consistent. During the 29 years after removal of feral sheep, total density of shrubs increased dramatically, from 210-246/ha in 1980 to 666-1148/ha in 2013. Species richness increased as well, from 8 species in each transect in 1980 to 14-15 species in 2013 (Table 1). These data do not include shrub seedlings <1 m tall, which were largely absent in transects in 1980 and too abundant to count in 2013.

Table 1.—Density (plants/ha) of short-stature (≤2 m) and tall-stature (>2 m) shrubs along two strip transects during April 1980, when feral sheep were abundant, and during April 2013, 29 years after feral sheep were removed from Santa Cruz Island, California.

	Transect 1		Transect 2	
	1980	2013	1980	2013
Short-stature shrubs				
Island deerweed (*Acmispon dendroideus*)	0	42	0	178
Coastal sagebrush (*Artemisia californica*)	0	0	0	66
Santa Cruz Island buckwheat (*Eriogonum arborescens*)	0	142	0	144
Northern island hazardia (*Hazardia detonsa*)	0	0	0	12
Monkey flower (*Mimulus* spp.)	0	2	0	8
Tall-stature shrubs				
Chamise (*Adenostoma fasciculatum*)	30	14	34	20
Manzanita (*Arctostaphylos* spp.)	0	6	0	0
Coyote brush (*Baccharis pilularis*)	0	0	0	2
Mule fat (*Baccharis salicifolia*)	0	2	0	0
Island ceanothus (*Ceanothus arboreus*)	0	6	0	0
Island big-pod ceanothus (*Ceanothus megacarpus insularis*)	24	86	36	280
Mountain mahogany (*Cercocarpus betuloides*)	72	240	66	270
Toyon (*Heteromeles arbutifolia*)	2	4	12	14
Island cherry (*Prunus ilicifolia lyonii*)	8	8	12	14
Island scrub oak (*Quercus pacifica*)	62	56	80	64
Island redberry (*Rhamnus pirifolia*)	10	40	2	32
Lemonade berry (*Rhus integrifolia*)	2	16	4	44
Willow (*Salix* spp.)	0	2	0	0

All short-stature shrubs increased in density, especially island deerweed (*Acmispon dendroideus*) and Santa Cruz Island buckwheat (*Eriogonum arborescens*); neither species was identified in transects at all in 1980 but both had become abundant by 2013 (Table 1).

Most tall-stature shrubs showed major increases in density as well, especially island bigpod ceanothus, mountain mahogany, island redberry (*Rhamnus pirifolia*), and lemonade berry, but some shrubs did not. Toyon (*Heteromeles arbutifolia*), island cherry, and island scrub oak were common or even dominant in transects in 1980 but showed no evidence of an appreciable increase in density by 2013. One shrub that was common in 1980, chamise, appeared to have decreased in density by 2013 (Table 1).

Discussion

In 1980 the study area was located within a portion of Santa Cruz Island that was considered to be severely impacted by feral sheep (Van Vuren and Coblentz 1987). In severely impacted areas, which totaled over one-third of island area, sheep density averaged about 2/ha, herbaceous vegetation was mostly or completely consumed, denuded soil appeared dominant, and little or no shrub foliage was present below about 1 m in height (Van Vuren and Coblentz 1987). Within the study area, shrub seedlings were scarce or absent and for those shrubs that produced basal sprouts, sprouts were rapidly consumed by feral sheep (Van Vuren and Coblentz 1987). Because of long-term defoliation by feral sheep, the continued existence of shrubs was thought to be a function of longevity instead of reproduction, suggesting the possibility of an impending die-off as shrubs became increasingly senescent (Van Vuren 1981). A similar dynamic was evident on other islands infested with exotic herbivores (Hamann 1993, Bullock et al. 2002, Stratton 2009).

My results indicate that 29 years after sheep removal, shrubs on Santa Cruz Island have shown remarkable regeneration, with a three- to four-fold increase in total density and a near- doubling of species richness. Further, many of the shrubs that increased are insular endemic taxa (Junak et al. 1995), which are of conservation concern. The physical structure of the community has changed as well, with the proliferation of short-stature shrubs; of the five taxa recorded in 2013, only monkey flower (*Mimulus* spp.) was identified in the area in 1980, and the few individuals encountered along transects fell well below the 1-m height criterion. Monkey flower, which is considered of low palatability to sheep (U.S. Department of Agriculture 1937), remained at low densities in 2013. In contrast, Santa Cruz Island buckwheat (*Eriogonum arborescens*) and coastal sagebrush (*Artemisia californica*), two species considered vulnerable to sheep grazing (Coblentz 1978, Brumbaugh 1980, Minnich 1980), increased from absent to abundant on one or both transects. Buckwheat and sagebrush are important components of the coastal sage scrub community, which was severely depleted on Santa Cruz Island by sheep grazing (Brumbaugh 1980). For both of these shrub species, germination does not appear to be constrained by seed limitation, but seedling establishment is reduced by competition with exotic annual grasses (Yelenik and Levine 2009), as has been demonstrated for native shrubs on the island of Hawaii (Thaxton et al. 2010). Disturbance by feral pigs (*Sus scrofa*), which were common on Santa Cruz Island, created gaps in grassland vegetation that likely facilitated seedling establishment for Santa Cruz Island buckwheat and coastal sagebrush (Yelenik and Levine 2009). Feral pigs were eradicated from the island during 2005-2006 (Ramsey et al. 2009), and the result might be reduced recruitment of Santa Cruz Island buckwheat and coastal sagebrush (Yelenik and Levine 2009).

Island deerweed and northern island hazardia (*Hazardia datonsa*) were two other short-stature shrubs that were absent in transects in 1980 but present or even abundant in

2013; similarly, Wehtje (1994) reported that these two shrubs were absent from a Bishop pine forest on Santa Cruz Island when sheep were present but appeared after sheep were removed. The foliage of palatable shrubs that typically grow to less than 2 m tall would be mostly or entirely within reach of browsing sheep, likely resulting in death via defoliation or trampling. Removal of sheep allowed regeneration of short-stature shrubs from residual seeds or from relict plants surviving in sheep-inaccessible locations.

Most tall-stature shrubs increased in density after sheep removal, some dramatically so. Those shrubs that increased dramatically were recorded in transects in 1980; hence, a local seed source would have been readily available. Four shrubs, however, did not increase or even declined. For three of these shrubs, island scrub oak, toyon, and island cherry, the cause might reflect differing regeneration strategies among shrubs. Most of the shrubs identified on transects are common members of island chaparral, a community that is generally similar in composition to California chaparral on the mainland. California chaparral is a fire-adapted community, but shrubs differ in their adaptations to fire. Many chaparral shrubs, such as *Ceanothus* spp. and *Rhus* spp., are considered "fire-recruiters" and produce relatively small, long-lived, refractory seeds that accumulate in a persistent seed bank, resulting in rapid germination after a disturbance such as fire (Keeley 1991). Germination by seeds of these shrubs is often enhanced or even necessitated by exposure to heat or the chemicals in charred wood (Keeley 1991). There has been no fire in the study area since sheep were removed, and, in fact, the frequency of naturally-occurring fires on Santa Cruz Island in the past appears to be less than that on the mainland (Carroll et al. 1993). However, seeds of at least some shrubs on Santa Cruz Island are less dependent on fire to germinate than are their mainland counterparts, suggesting adaptation to a lower fire frequency (Carroll et al. 1993). Hence, the dramatic response of some shrubs to the removal of sheep probably resulted because of the presence of a large seed bank adapted to germinating in conditions of direct sunlight and minimal soil litter, but in the absence of fire, which characterized the study area at the time sheep were removed. Presumably the seeds of these shrubs were germinating before sheep removal, but all seedlings were killed by consumption or trampling.

In contrast, some chaparral shrubs, including mainland scrub oak (*Quercus dumosa*), hollyleaf cherry (*Prunus ilicifolia*), and toyon, are considered "fire-persisters" that can survive fire and produce relatively large, fleshy, short-lived, non-refractory seeds that do not generate a persistent seedbank (Keeley 1991). Further, seeds of these shrubs are specialized for animal dispersal (Keeley 1991). Hence, seeds produced after sheep were removed would have been vulnerable to consumption by feral pigs; feral pigs prefer acorns and cherries, which are sterilized by passage through the pig's digestive tract (Peart et al. 1994). Perhaps most important, seeds of scrub oak, cherry, and toyon germinate best in mesic conditions, such as those present under the shrub canopy and in association with a substantial litter layer (Keeley 1992). In 1980 the shrub canopy was minimal and the soil surface was bare and eroded, probably providing poor conditions for seed germination. Drought is another possible explanation for a lack of regeneration of fire-persisters, whose seeds are particularly vulnerable to low soil moisture (Keeley 1992). However, the years 1987 through 2011 exhibited average annual rainfall (48 cm) that was near the long-term average (50 cm) and included five different years when rainfall was ≥25% above average.

Chamise is a fire-recruiter species that produces refractory seeds that persist in the seed bank and rarely germinate under the shrub canopy (Keeley 1991, 1992), similar to several other fire-recruiter species that increased dramatically in density after sheep

removal. Nonetheless, density of chamise declined about 50% between 1980 and 2013, and the cause is unclear. Chamise seeds in California chaparral require fire to germinate (Keeley 1992); perhaps chamise seeds on Santa Cruz Island also require fire to germinate, unlike some other island shrubs (Carroll et al. 1993), with the decline caused by a lack of recruitment coupled with a gradual die-off due to senescence.

Twenty-nine years after removal of feral sheep, shrubs on Santa Cruz Island have shown remarkable regeneration, but response has varied among species. Most species have increased in density, including several insular endemic taxa, and for some the increase has been dramatic. A few species, however, have shown little change or even decreased. A similar pattern of regeneration was observed for woody vegetation on Pinta Island, Galapagos, after removal of feral goats; regeneration was rapid for some species but for one species was hindered by the lack of a moderate vegetation cover important for seed germination (Hamann 1993). The future trajectory of shrub regeneration on Santa Cruz Island might be inferred from successional patterns in California chaparral on the mainland. In the absence of fire, species characterized as fire-persisters such as scrub oak, toyon, and hollyleaf cherry begin germinating with the development of a shrub canopy and adequate soil litter; because they can outcompete fire-recruiter species such as *Ceanothus* by overtopping, fire-persisters can come to dominate the community in a successional process that can take 100 years (Keeley 1992). If island chaparral follows this pattern, then in future years island scrub oak, toyon, and island cherry should show increased regeneration, potentially to the point of becoming dominant. Concurrently, the cessation of grazing should increase fuel loads and hence the frequency of wildfires (Carroll et al. 1993), which could alter this trajectory by periodically enhancing recruitment of fire-recruiters, especially chamise. These results highlight the importance of considering a long time frame in assessing the recovery of insular vegetation after removal of exotic herbivores.

Acknowledgments

I thank W. Adler and M. Bray for invaluable assistance in data collection, The Nature Conservancy for financial support, L. Laughrin and the UC Natural Reserve System for logistical assistance, and S. Hess, C. Peters, and L. Souza for helpful comments on the manuscript.

Literature Cited

Brumbaugh, R. W. 1980. Recent geomorphic and vegetal dynamics on Santa Cruz Island, California. Pages 139-158 *in* D. M. Power, editor. The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Bullock, D. J., S. G. North, M. E. Dulloo, and M. Thorsen. 2002. The impact of rabbit and goat eradication on the ecology of Round Island, Mauritius. Pages 53-63 *in* C. R. Veitch and M. N. Clout, editors. Turning the tide: the eradication of invasive species. Occasional Paper Number 27, International Union for Conservation of Nature and Natural Resources Species Survival Commission, Gland, Switzerland.

Campbell, K., and C. J. Donlan. 2005. Feral goat eradications on islands. Conservation Biology 19:1362−1374.

Carroll, M. C., L. L. Laughrin, and A. C. Bromfield. 1993. Fire on the California Islands: does it play a role in chaparral and closed cone pine forests? Pages 73-88 *in* F. G. Hochberg, editor. Third California Islands symposium: recent advances in research in the California Islands. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Chynoweth, M. W., C. M. Litton, C. A. Lepczyk, S. C. Hess, and S. Cordell. 2013. Biology and impacts of Pacific island invasive species. 9. *Capra hircus*, the feral goat (Mammalia: Bovidae). Pacific Science 67:141-156.

Coblentz, B. E. 1978. The effects of feral goats (*Capra hircus* L.) on island ecosystems. Biological Conservation 13:279-286.

Cohen, B., C. Cory, J. Menke, and A. Hepburn. 2009. A spatial database of Santa Cruz Island vegetation. Pages 229-244 *in* C. C. Damiani and D. K. Garcelon, editors. Proceedings of the seventh California Islands symposium. Institute for Wildlife Studies, Arcata, California, USA.

Faulkner, K. R., and C. C. Kessler. 2011. Live capture and removal of feral sheep from eastern Santa Cruz Island, California. Pages 295-299 *in* C. R. Veitch, M. N Clout, and D. R. Towns, editors. Island invasives: eradication and management. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Hamann, O. 1993. On vegetation recovery, goats and giant tortoises on Pinta Island,Galapagos, Ecuador. Biodiversity and Conservation 2:138-151.

Junak, S., T. Ayers, R. Scott, D. Wilken, and D. Young. 1995. A flora of Santa Cruz Island. Santa Barbara Botanic Garden, Santa Barbara, California, USA.

Keeley, J. E. 1991. Seed germination and life history syndromes in the California chaparral. Botanical Review 57:81-116.

Keeley, J. E. 1992. Demographic structure of California chaparral in the long-term absence of fire. Journal of Vegetation Science 3:79-90.

Minnich, R. A. 1980. Vegetation of Santa Cruz and Santa Catalina Islands. Pages 123-137 *in* D. M. Power, editor. The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Mueller-Dombois, D. 1979. Succession following goat removal in Hawaii Volcanoes National Park. Pages 1149-1154 *in* R. M. Linn, editor. Proceedings of the first conference on scientific research in the national parks. U.S. National Park Service Transactions and Proceedings Series, Number 5.

North, S. G., D. J. Bullock, and M. E. Dulloo. 1994. Changes in the vegetation and reptile populations on Round Island, Mauritius, following eradication of rabbits. Biological Conservation 67:21-28.

Peart, D., D. T. Patten, and S. L. Lohr. 1994. Feral pig disturbance and woody species seedling regeneration and abundance beneath coast live oaks (*Quercus agrifolia*) on Santa Cruz Island, California. Pages 313-322 *in* W. L. Halvorson and G. J. Meander, editors. Fourth California Islands symposium: update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Ramsey, D. S. L., J. Parkes, and S. A. Morrison. 2009. Quantifying eradication success: the removal of feral pigs from Santa Cruz Island, California. Conservation Biology 23:449-459.

Rudge, M. R. 1984. The occurrence and status of populations of feral goats and sheep throughout the world. Pages 55-84 *in* P. N. Munton, J. Clutton-Brock, and M. R. Rudge, editors. Feral mammals—problems and potential. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Schuyler, P. 1993. Control of feral sheep (*Ovis aries*) on Santa Cruz Island, California. Pages 443-452 *in* F. G. Hochberg, editor. Third California Islands symposium: recent advances in research in the California Islands. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Stratton, L. 2009. Restoration strategies for overcoming limitations to scrub oak regeneration on Catalina Island. Pages 185-200 *in* C. C. Damiani and D. K. Garcelon, editors. Proceedings of the seventh California Islands symposium. Institute for Wildlife Studies, Arcata, California, USA.

Thaxton, J. M., T. C. Cole, S. Cordell, R. J. Cabin, D. R Sandquist, and C. M. Litton. 2010. Native species regeneration following ungulate exclusion and nonnative grass removal in a remnant Hawaiian dry forest. Pacific Science 64:533-544.

U.S. Department of Agriculture. 1937. Range plant handbook. U.S. Government Printing Office, Washington, DC, USA.

Van Vuren, D. H. 1981. The feral sheep on Santa Cruz Island: status, impacts, and management recommendations. The Nature Conservancy, Arlington, Virginia,USA.

Van Vuren, D. H., and V. J. Bakker. 2009. Rapid morphological change in an insular population of feral sheep. Journal of Zoology 277:221-231.

Van Vuren, D. H., and B. E. Coblentz. 1987. Some ecological effects of feral sheep on Santa Cruz Island, California, USA. Biological Conservation 41:253-268.

Wehtje, W. 1994. Response of a Bishop pine (*Pinus muricata*) population to removal of feral sheep on Santa Cruz Island, California. Pages 331-340 *in* W. L. Halvorson and G. J. Meander, editors. Fourth California Islands symposium: update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Yelenik, S. G., and J. M. Levine. 2009. Processes limiting native shrub recovery in exotic grasslands after non-native herbivore removal. Restoration Ecology 18:418-425.

Received 31 March 2014
Accepted 18 July 2014
Corresponding Editor was V. Bleich