Effects of Wild Pigs on Seedling Survival in California Oak Woodlands[1]

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Abstract

Wild pigs were established around coastal Spanish settlements in California in the 1800s and expanded over the last century by hunting introductions, domestic releases, and natural dispersal. The current distribution of wild pigs is closely associated with oak woodlands where foraging and rooting by the species may impinge on many native species. Rooting disturbance by wild pigs may be especially problematic for regeneration of oak woodlands by physical damage to tree seedlings. In 1998 we initiated a long-term study of the ecological effects of wild pigs in California oak woodlands using multiple exclosures paired with nearby control plots that were established in two state parks in the north and central coast region of California, Austin Creek State Recreation Area and Henry Coe State Park. Mesh size and height of exclosure fences were designed to repel wild pigs but allow access by other organisms. We were especially interested in rooting effects on oak seedling number and size. The focus period for the 8-year study ended in May 2005, during which we monitored seedlings in (1) large 50 X 50 m exclosure and control habitat plot pairs centered in oak woodland, and (2) smaller 3 X 3 m exclosure and control canopy plot pairs established beneath the canopies of individual trees producing large crops of acorns in fall 1998 and 1999. In May 2005 the differential for seedling number in exclosure compared to control plots exceeded 400 percent at Austin Creek SRA. An outbreak of tent caterpillars limited seedling production at Henry Coe SP prior to 2003. Nevertheless, mean seedling height was significantly taller for all exclosure plots at both research sites. Rooting was reduced at Henry Coe SP after a control program was initiated in 2002, indicating that such approaches can improve the prospects for regeneration of oak woodlands in California.

Introduction

Pigs (*Sus scrofa*) are a large ungulate native to Eurasia and North Africa, and are now widely distributed as feral animals in many areas including California (Oliver and Brisbin 1993). Wild pigs were first introduced to California during the Spanish colonization period of the late 1700s and early 1800s (Giusti 1993, Sweitzer 1998). By the mid 1800s, scattered populations of wild pigs were established around a number of coastal settlements and Spanish missions. After a 50- to 75-year period of relative stasis, the distribution of feral pigs expanded after the 1950s to encompass many inland areas associated with California's diverse and widespread oak woodland ecosystem. This recent expansion by wild pigs into 49 of California's 58 counties appears related to some combination of natural dispersal by a growing statewide population and continued introductions (Waithman and others 1999). Expanding wild pig populations in California and elsewhere (Mayer and Brisbin 1991) are widely

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

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viewed as a major conservation problem because of ecological damage from their foraging activities, most notably rooting.

Rooting by wild pigs disturbs and overturns surface vegetation and associated belowground plant tissues, thereby exposing the underlying soils to drying, warming, and erosion. By reducing herbaceous cover, rooting may alter competitive relationships among plants to the detriment of disturbance intolerant native species (Spatz and Muller-Dombois 1975, Cushman and others 2004, Kotanen 2004). Rooting also has been shown to alter soil nutrient processes by the combined effects of aeration, mixing of different soil layers, and increased water infiltration that may leach some nutrients (Lacki and Lancia 1986, Cushman and others 2004). Moreover, rooting physically damages or breaks seedlings, thereby limiting tree seedling survival (Bruinderink and Hazebroek 1996, Ickes and others 2003, Sweitzer and Van Vuren 2002).

Previous studies of wild pigs in mainland California have provided information on the population ecology of wild pigs (Barrett 1978, Schauss and others 1990, Sweitzer and others 2000) and the effects of rooting on plant communities (Cushman and others 2004, Kotanen 2004). In 1998, we initiated a large-scale study of the ecological effects of wild pigs in oak woodland ecosystems. Research began in May 1998 and continued through July 2005. The primary objectives of the study were (1) to assess the effects of rooting and foraging by wild pigs on the diversity and abundance of native and nonnative plants and terrestrial vertebrates (small mammals, reptiles and amphibians), and (2) to determine whether wild pig activities limit tree regeneration, thereby threatening important components of California's oak woodland ecosystem. In 1998 and 1999, we established multiple fenced exclosure and control plots at research sites in the central and north coast regions of California to begin to evaluate hypotheses about how rooting and other activities of wild pigs impinge on oak woodland ecosystems. In this paper, we focus on aspects of the study related to objective 2; an experimental investigation of the effects of wild pigs on oak tree regeneration.

Methods

Study Areas

As previously detailed by Sweitzer and Van Vuren (2002), research sites selected for this study were state park areas in the central and north coast regions of California where high-density wild pig populations were found (Sweitzer and others 2000) and free-ranging livestock were absent. Herein we will describe aspects of research conducted at Austin Creek State Recreation Area (Austin Creek SRA; 38°34'6"N, 123°2'7"W) from fall 1988 to summer 2005 and Henry Coe State Park (Henry Coe SP; 38°12'40" S, 121°30'51"W) from summer 1999 to summer 2005. Austin Creek SRA and Henry Coe SP were experimental research sites where we obtained permission to establish fenced exclosures of different sizes; 50 x 50 m habitat plot exclosures and 3 x 3 m oak canopy exclosures. Comparative research also was conducted at two other sites that were very near each other but varied in wild pig density; Sugarloaf Ridge SP (38°27'25"N, 122°31'21"W) and McCormick Sanctuary (38°28'46"N, 122°33'47"W) in Sonoma County. Wild pigs were maintained at very low density at Sugarloaf Ridge SP by long-term pig control, whereas wild pig density was higher at McCormick Sanctuary where there was no organized trapping or shooting of wild pigs. Research at Sugarloaf Ridge SP and McCormick Sanctuary ended in fall 2000, and data relevant to oak regeneration were described by Sweitzer and Van Vuren (2002) as summarized below.

Austin Creek SRA is a 2,430 ha park in western Sonoma County near Guerneville, California. Elevation at the site ranges from 46 m to 458 m over a varied topography of steep canyons, rolling hills, and flat valley bottoms. Woodland habitats include a diverse mix of Oregon oak (*Quercus garryana*), coast live oak (*Q. agrifolia*), black oak (*Q. kelloggi*), bay laurel (*Umbellularia californica*), Douglas fir (*Pseudotsuga menziesii* var *menziesii*), madrone (*Arbutus menziesii*), and coastal redwoods (*Sequoia sempervirens*) with an understory including *Festuca californica*, *Trifolium* sp., and *Cynosurus echinatus*. Grassland habitats are mostly dominated by annual grasses (*Briza maxima*, *Bromus hordeaceous*, *Avena* sp.), some perennial bunchgrasses (*Danthonia californica*), and a wide variety of forbs (*Geranium dissectum*, *Hypochaeris glabra*, *Lotus micranthus*, *Trifolium* sp.). Henry Coe State Park is a large 35,207 ha park located in Santa Clara County east of the cities of Morgan Hill and Gilroy, California. Elevation at the site ranges from 216 m to 1,085 m. Research was focused in the southwestern area of the park where the landscape is dominated by high ridges and deep canyons. Habitats range from open grasslands and open savannah woodlands to dense stands of chapparal/chamise (*Adenostoma fasciculatum*) brush. Grassland habitats include a mix of annual and perennial grasses and forbs (*Avena* sp., *Bromus* sp., *Nassella pulchra*, *Melica californica*, *Trifolium* sp., *Viola* sp.), whereas woodlands are dominated by blue oak (*Q. douglasii*) and gray pine (*Pinus sabiniana*) with occasional coast live oak, valley oak (*Q. lobata*), and bay laurel.

Wild Pigs and Oak Regeneration Potential

The combined effects of intensive foraging on acorns in the fall and widespread rooting during the October to late April wet season may reduce oak tree regeneration in California oak woodlands. Acorn consumption by wild pigs reduces the number of seeds that might otherwise germinate, whereas rooting physically damages or uproots young seedlings. We used four different approaches to assess this hypothesis: (1) comparisons of data on tree seedling sizes along multiple, randomly positioned 4 x 40 m "belt transects" in oak woodland and mixed forest habitats among comparative and experimental research sites varying in wild pig density; (2) monitoring numbers of naturally falling acorns on small plots nested within oak canopy exclosure and control plots beneath multiple high masting oak trees at experimental research sites; (3) comparison of numbers and sizes of tree seedlings in oak canopy exclosure and control plots at experimental research sites; and (4) comparisons of data on tree seedling size and number along belt transects in 50 x 50 m exclosure and control habitat plots in oak woodland and mixed forest areas at experimental research sites.

In a prior paper we reported fewer large oak tree seedlings (≥ 200 mm) along seedling belt transects in oak woodland habitats at research sites with high and very high density wild pigs (Austin Creek SRA and Henry Coe SP, respectively) compared to sites with moderate and very low density wild pigs (McCormick Sanctuary and Sugarloaf Ridge SP, respectively; Sweitzer and Van Vuren 2002). We further described evidence for reduced survival for acorns in control compared to fenced oak canopy plots at Austin Creek SRA and Henry Coe SP (Sweitzer and Van Vuren 2002). To facilitate a more thorough examination of the effects of wild pigs on tree regeneration, we continued monitoring the number and sizes of tree seedlings in habitat and oak canopy control and exclosure plots at Austin Creek SRA and Henry Coe SP from spring 2000 to summer 2005.

Habitat Plot Experiments

Several research activities were focused around 50 X 50 m habitat plot exclosure and nearby control plots in grassland, oak woodland, mixed forest, and meadow habitats. At Austin Creek SRA, we established one 50 x 50 m fence exclosure in each of the four habitat types in summer 1998. Research was initiated at Henry Coe SP in summer 1999 when two 50 x 50 m habitat exclosures each were established in grassland and oak woodland habitats. Fences were designed to allow foraging access by all herbivores except wild pigs, and were constructed in the field by wiring 0.9 m woven wire field fence to 1.9 m fence posts driven into the ground every three meters. Rebar stakes secured fencing to the ground between posts; the low height of the field fence and large mesh openings (10x10 cm) allowed deer and small vertebrates to easily enter. For each exclosure, we staked out a matched 50 x 50 m control plot usually within 500 m of the exclosure. Nested within each 50 x 50 m habitat exclosure and control plot were (1) a 7 x 7 small mammal live trap grid with 8 m spacing between lines, (2) six 4 x 40 m seedling belt transects between and parallel to trap grid lines, (3) a y-shaped pitfall trap array with ten 7.6 liter bucket traps buried to ground level, and (4) several 2 x 2 m vegetation plots near each of the four corners. Details and data on small mammal trapping, pitfall trapping, and vegetation plot analyses will not presented in this paper.

Beginning in May 2000 and every year thereafter until May 2005, we enumerated and measured tree seedlings along each of the six belt transects at all *woodland habitat exclosure and control plots* at Austin Creek SRA and Henry Coe SP; tree seedlings were not present in grassland or meadow habitats.

All seedlings of trees or woody shrubs ≤ 1.5 m (1500 mm) were measured (±2 mm) and identified when possible. We also measured seedlings that originated from the base of dead and living trees, recording these as basal sprouts. Data on tree seedlings along belt transects in woodland habitat exclosure and control plots for Austin Creek SRA and Henry Coe SP were analyzed separately because exclosures were set up one year earlier at Austin Creek SRA. An analysis of variance (ANOVA) model (Zar 1999) was used to compare mean oak seedling size between exclosure and control habitat plots at the end of the monitoring period in spring 2005.

We estimated soil disturbances from wild pigs, rodents (*Thomomys* sp.), and research activities in all oak woodland habitat exclosure and control plots during the study by line-intercept sampling. Six, parallel 50 m line transects were extended across each plot, whereupon we measured the intercept distances (± 1 cm) of all areas of bare soil along each transect.

Oak Canopy Exclosure Experiments

Oak canopy exclosure experiments were originally established beneath the canopies of high masting oak trees in summer 1998 (Austin Creek SRA) and summer 1999 (Austin Creek SRA, Henry Coe SP) to assess the extent to which acorn foraging by wild pigs reduced resource availability for native wildlife. As further detailed by Sweitzer and Van Vuren (2002), multiple high mast producing oak trees were identified at each research site in summers 1998 and 1999, whereupon the corners of two 3 x 3 m plots were delineated beneath appropriately matched areas of the canopies of the trees. Exclosure and control designations were then randomly assigned, whereupon fences were built around the exclosure plots using the same design features as habitat plot exclosures. Research to estimate and compare acorn survival between fenced and non-fenced canopy plots was completed in December 1999, but most of the plots were left in place for assessing tree seedling number and size.

At Austin Creek SRA canopy plot experiments were established beneath a total 16 *Q. kellogi*, two *Lithocarpus densiflorus*, five *Q. agrifolia*, two *Q. lobata*, and one *Q. garryana* in 1998 and 1999 combined. Six canopy plot experiments were removed in summer 1999 prior to establishing canopy plots at ten newly identified high masting oak trees. Among all of these trees, canopy plot exclosures were retained and seedlings monitored at ten *Q. kellogi*, two *L. densiflorus*, five *Q. agrifolia*, and one *Q. garryana* from 2000 to 2005. One additional *Q. kellogi* was monitored from 2000 to 2004 until a large portion of the tree fell over the control canopy plot in 2004. At Henry Coe SP, canopy plot experiments were established beneath six *Q. douglasii*, three *Q. agrifolia*, and six *Q. lobata*. All canopy plots were retained and monitored for seedling number and size from 2000 to 2005.

Data on oak tree seedlings among canopy plots at Austin Creek SRA and Henry Coe SP were analyzed separately because exclosures were established one year earlier at Austin Creek SRA, and the species of individual oaks used for canopy plot experiments varied between sites. Data on the mean number and size of oak seedlings at the end of the monitoring period were evaluated by ANOVA.

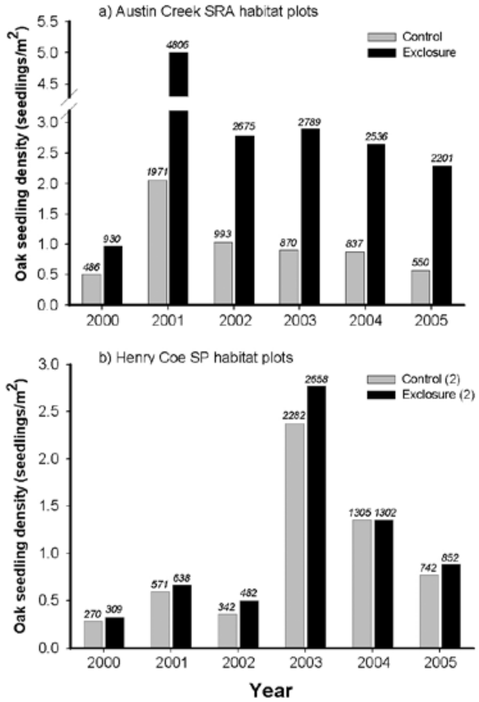
In each year of the study, we estimated the area of each canopy control plot that was disturbed by rooting from scaled-down line drawings (Sweitzer and Van Vuren 2002). Line drawings of rooted areas were prepared for each 3 x 3 m canopy control plot around mid May of each year prior to enumerating and measuring individual tree seedlings. Line drawings were subsequently analyzed using a grid overlay technique to estimate the proportion of each canopy control plot disturbed by rooting.

All means are reported ± 1 standard error (SE).

Results

Habitat Plot Seedlings

At Austin Creek SRA, there were four times as many oak tree seedlings along six belt transects within the oak woodland habitat plot exclosure (n=2201) compared to along six belt transects in the oak woodland habitat control plot (n=550) after seven years of protection from wild pigs (*fig. 1a*). Height of tree seedlings in the oak woodland habitat exclosure plot averaged 83.0 ± 0.88 mm, compared to 74.0 ± 1.8 mm in the oak woodland habitat control plot (α <0.001; *fig. 2a*). In mixed woodland habitat plots at Austin Creek SRA, there were 95 total oak seedlings (mean seedling height 84.4 ± 3.3 mm) along belt transects in the exclosure plot, compared to only eight oak seedlings (mean seedling height 167.9 ± 43.3 mm) along belt transects in the control plot. At Henry Coe SP, there were more total oak seedlings (n=852) along belt transects in exclosure habitat plots compared to control habitat plots (n=742) after six years of protection from rooting. Oak tree seedlings in the exclosure habitat plots were taller (mean = 85.3 ± 1.2) than those in the control habitat plots (mean = 69.3 ± 1.2; α <0.001).



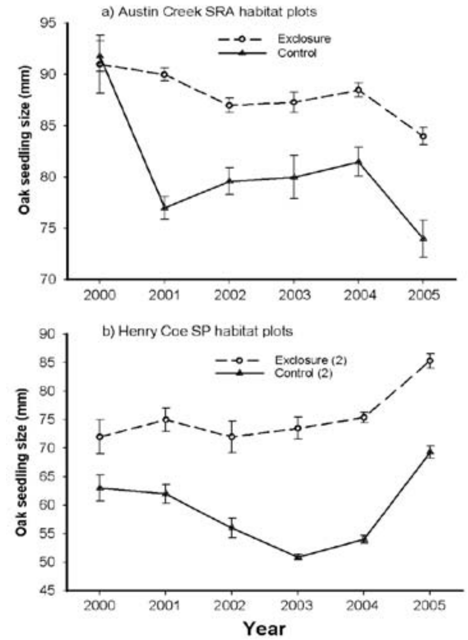


Figure 1—Variation in total number (above bars) and density of oak tree seedlings for the total area searched along six (Austin Creek SRA) or twelve (Henry Coe SP) 4 x 40 m belt transects in oak woodland habitat exclosure and control plots at (a) Austin Creek SRA and (b) Henry Coe SP from spring 2000 to spring 2005.

Figure 2—Variation in mean height (± SE) of oak tree seedlings along 4 x 40 m belt transects in oak woodland habitat exclosure and control plots at (a) Austin Creek SRA and (b) Henry Coe SP from spring 2000 to spring 2005.

Oak woodland control habitat plots at both Austin Creek SRA and Henry Coe SP experienced higher levels of soil disturbances than exclosure habitat plots over the six-year seedling monitoring period (*fig. 3*). Soil disturbances were predominantly from rooting by wild pigs; other sources of bare soil were rodent diggings and researcher activities (pitfall arrays, trails, etc.).

At Austin Creek SRA, there were over five times as many oak tree seedlings in the exclosure canopy plots compared to the control canopy plots at the end of the monitoring period (*fig. 4a*). Oak tree seedlings in the exclosure canopy plots were taller (mean = 123.1 ± 3.2) than those in the control canopy plots (mean = 85.1 ± 6.6; $\alpha < 0.001$; *fig. 5a*). Monitoring results from Henry Coe SP identified around two times as many oak tree seedlings in exclosure compared to control canopy plots (*fig. 4b*). Similar to data from Austin Creek SRA, oak tree seedlings in the exclosure canopy plots were taller (mean = 113.0 ± 2.2mm) than those in the control habitat plots (mean = 80.8 ± 1.8; $\alpha < 0.001$; *fig. 5b*).

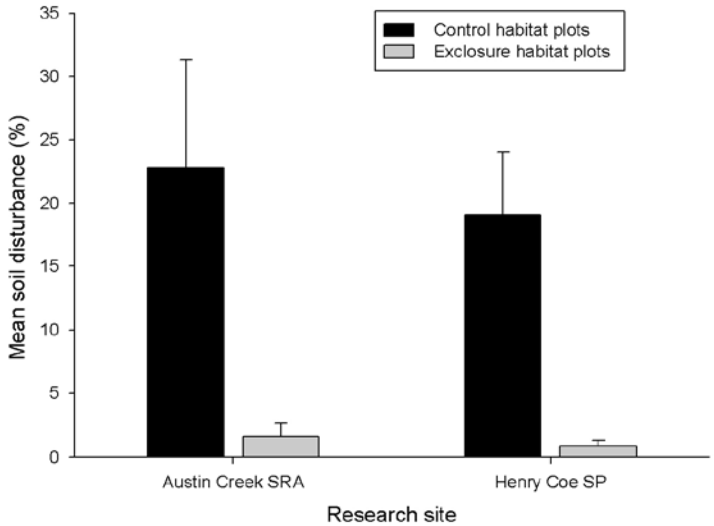


Figure 3—Differences in the estimated mean soil disturbances based on line-intercept sample transects in oak woodland control and exclosure habitat plots at Austin Creek SRA and Henry Coe SP over the tree seedling monitoring period (spring 2000 to spring 2005). Means are with 1 SE.

Over the six-year monitoring period, wild pig rooting disturbance in oak canopy control plots averaged 45.5 percent (± 6.4 percent) for the 18 trees being monitored at Austin Creek SRA, and 22.0 percent (± 6.2 percent) for the 15 trees being monitored at Henry Coe SP.

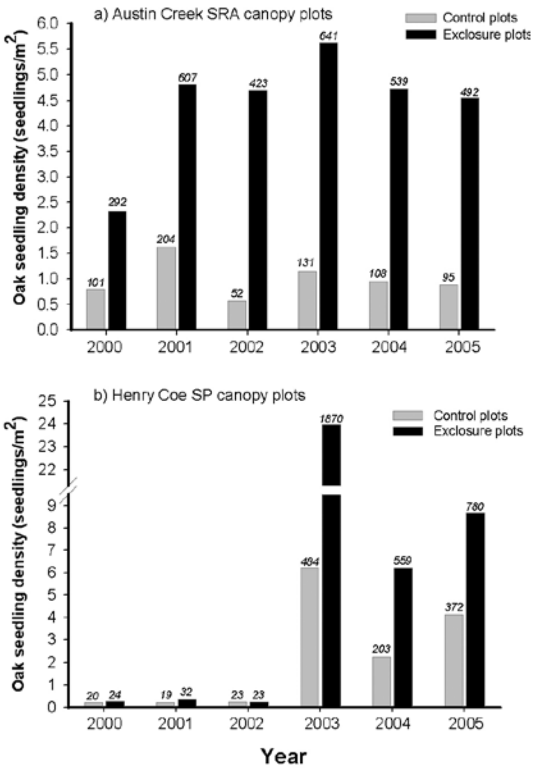


Figure 4—Variation in total number (above bars) and density of oak tree seedlings for the total area searched among multiple 3 x 3 m canopy exclosure and control plots at (a) Austin Creek SRA and (b) Henry Coe SP from spring 2000 to spring 2005.

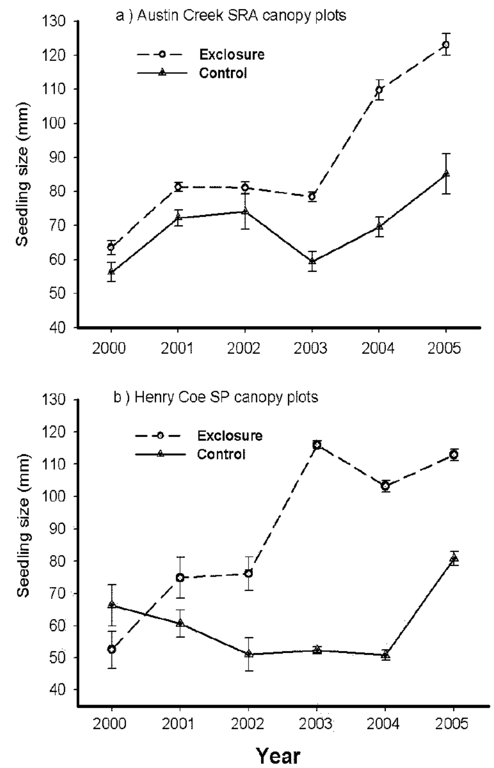


Figure 5—Variation in mean height (± SE) of oak tree seedlings in 3 x 3 m canopy exclosure and control plots at (a) Austin Creek SRA and (b) Henry Coe SP from spring 2000 to spring 2005.

Discussion

We observed and documented a strong and consistent wild pig-related reduction in the number and size of oak tree seedlings in oak woodland habitats at two widely separated research sites in California. With the exception of oak woodland habitat plots at Henry Coe SP, the final differential for numbers of oak seedlings in fenced plots was at least double the number of seedlings in the control plots (*figs. 1, 4)*. The reduction in seedling number in the control plots could be directly attributed to wild pigs, because the plot areas experienced variable but significant levels of rooting over the six-year monitoring period (*fig. 3)*.

One notable difference between the Austin Creek SRA and Henry Coe SP research sites was the relatively low number of oak seedlings for habitat and canopy plots at Henry Coe SP in the first several years of the study. In research years 2000 and 2001, we observed a major population outbreak of tent caterpillars (*Malacosoma californicum*) at Henry Coe SP. The tent caterpillar outbreak at Henry Coe SP was very severe in spring 2000, and resulted in most oak trees being almost completely defoliated in June 2000. By early fall 2000, many oaks at Henry Coe SP had produced a second set of leaves, likely a major nutrient cost to their systems. Although we also observed some tent caterpillars at the Austin Creek SRA site in spring 2000, the insects were nowhere near as abundant as at Henry Coe SP and widespread defoliation did not occur at Austin Creek SRA. The tent caterpillar outbreak at Henry Coe SP had subsided by fall 2001, potentially contributing to oak trees at the site producing a major seed crop in fall 2002 (*figs. 1, 4).* Although we did not directly monitor acorn mast production at either research site during the study, acorn production at Austin Creek SRA appeared more regular than at Henry Coe SP, potentially explaining the overall higher numbers of oak seedlings at Austin Creek SRA.

Although the final number of oak seedlings along belt transects in the mixed forest habitat exclosure (n = 95) far exceeded the number of oak seedlings in the mixed forest habitat control plot (n = 8), mean seedling size was taller in the control plot. Among the eight total seedlings in the habitat control plot were three that exceeded 200 mm, which inflated the mean for the plot that was already based on a small sample size.

Management Implications

Results from the first several years of this study were valuable for demonstrating reduced acorn survival in control areas compared to fenced plots (Sweitzer and Van Vuren 2002). Longer-term monitoring data for research through 2005 leave little doubt that rooting activities of wild pigs also reduces the number and size of oak tree seedlings in California oak woodlands. Research from other areas of North America and worldwide indicate that lethal control may help reduce ecological damage caused by feral pigs (Choquenot and others 1999, Engeman and others 2004).

We detected evidence for a reduction in rooting disturbance in our habitat control plots after managers at Henry Coe SP implemented a wild pig control program in winter 2002. During the first year and a half of the control program, wild pig trapping/shooting was focused in areas away from our research plots. After summer 2003, however, control efforts expanded to the southwestern area of the park, encompassing all of the habitat control and exclosure plots. Diminished rooting in many areas of the state park was readily evident after 2003. In our habitat control plots in grassland and woodland areas in particular, however, the estimated mean rooting was reduced from 19.1 ± 3.6 percent during the four-year research period prior to wild pig control (2000 to 2003) to a mean of 8.8 ± 3.0 percent in the two years after wild pig control (α = 0.07). This wild pig control-related reduction in rooting disturbance likely contributed to the trend for increasing numbers of seedlings observed in our canopy and habitat plot control areas at Henry Coe SP that began in 2003 (*figs. 1, 3*).

In recent years, many state and national parks in California have initiated programs to control wild pigs to protect natural resources. These results are important for suggesting that lethal control efforts directed at wild pigs can improve the prospects for oak seedling survival in California oak woodlands.

Acknowledgments

Renee Pasquinelli, Marla Hastings, Kay Robinson, Tracey Becker, Chaz Pothast, Joanne Karlton, and Barry Breckling of California Department of Parks and Recreation provided research assessment and logistical support at state park research sites. Craig Anderson facilitated research at McCormick Sanctuary. Many technicians assisted with field research, but Juanita Constible, Neil Kadrmas, and Amariah

Anderson provided invaluable multiple-year assistance. Project funding from May 1998 to June 2000 was provided by the California Department of Fish and Game (FG-7113-WM). Funding from fall 2000 to summer 2005 was provided by the Integrated Hardwood Range Management Program.

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