Long-term response of the mamane forest to feral herbivore management on Mauna Kea, Hawaii

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Seven exclosure sites located on Mauna Kea, Hawaii and established in the 1960s and 70s were sampled to characterize long-term response of the mamane (*Sophora chrysophylla*) forest to protection from feral sheep grazing, and to assess impacts of non-native plant species and recurrent sheep presence on forest recovery. The forest provides essential habitat for an endangered bird, the palila (*Loxoides bailleui*). Vegetation was sampled inside exclosures during 1972–1976, 1998, and 2009, and also outside exclosures during 2009. Patterns of response varied among exclosures, but overall, mamane trees and native shrubs showed increasing cover between the 1970s and 1998, then a slowed rate of increase in cover or a decline between 1998 and 2009. Cover of native herbaceous vegetation showed variable trends between the 1970s and 1998, and then appeared to decline between 1998 and 2009. Mamane height class distributions inside exclosures indicated that recruitment was initially high but then declined as heights shifted toward larger size classes, and presumably an older age distribution. We found limited evidence of a negative effect of non-native species on forest regrowth, but the effect was not consistent over time or among sites. Recurrent sheep presence outside exclosures negatively affected mamane canopy density and perhaps tree density at all sites, and mamane condition at some sites. Our results indicate that the mamane forest has shown substantial regrowth inside exclosures at some sites, especially those protected the longest. However, these exclosures represent a small portion of the mamane forest. Sheep presence continues to impact mamane recovery outside exclosures, and thus habitat quality for the palila.

Key words: Mamane; forest recovery; herbivore damage; sheep; palila; non-native plants

INTRODUCTION

DOMESTICATED sheep, goats, pigs, and cattle have been introduced to many island ecosystems and subsequently become feral. Feral herbivores often damage native ecosystems, either directly through consumption of native vegetation or indirectly through trampling and erosion (Cruz and Cruz 1987; Van Vuren and Coblentz 1987; Nogueira-Filho *et al*. 2009). Herbivores can be especially damaging on islands because native plants frequently evolved in the absence of herbivores and thus lack the appropriate defenses (Bowen and Van Vuren 1997). The result can be dramatic alteration of vegetation cover and species composition in island ecosystems (Spatz and Mueller-Dombois 1973; Muerk 1982; Allen *et al.* 1984). Herbivores can deplete seedbank reserves and restrict vegetation to inaccessible areas, in some cases driving species to senescence or extinction (Baker and Reeser 1972; Mueller-Dombois 1979; Garcillan *et al*. 2008). Woody species may be especially vulnerable because of their slower growth and longer generation times as compared with herbaceous species. Furthermore, damage to woody species can lead to the decline of native vertebrates that depend on these plants for food or shelter (Leathwick *et al*. 1983; Van Vuren and Coblentz 1987; Kessler 2002).

Managers of many island ecosystems have eradicated non-native herbivores (Campbell and Donlan 2005; Carrion *et al*. 2007; Knowlton *et al.* 2007), and some damaged forests have shown remarkable regeneration after herbivores are excluded (Allen *et al*. 1984; Wehtje 1994; Cabin *et al*. 2000; Morrison 2007). Because eradication is not always practical, management of some populations involves density reduction, either sustained or intermittent; however, this approach maintains the risk of continued damage to palatable plant species (Allen *et al*. 1984; Parkes 1990; Scowcroft and Conrad 1992; Van Vuren 1992). In addition, even when herbivores are eliminated, the trajectory of forest recovery is uncertain. Herbivore preferences for palatable plants can allow other plant species to gain an advantage (Baker and Reeser 1972; Muerk 1982; Allen *et al*. 1984). Non-native plants, especially invasive grasses, may benefit because they are frequently unpalatable, and also can have greater reproductive capacity and/or competitive ability (Scowcroft and Conrad 1992).

The mamane (*Sophora chrysophylla*) forest on the island of Hawaii lies at high elevations on Mauna Kea volcano and has been severely degraded by feral herbivores, especially sheep (Scowcroft 1983; Scowcroft and Giffin 1983; Scowcroft and Sakai 1983). Mamane is an endemic species that is highly preferred by sheep (Scowcroft and Giffin 1983). Furthermore, the forest provides essential habitat for an endangered bird, the palila (*Loxoides bailleui*) (Banko *et al*. 2002). Feral sheep control via density reduction or exclusion resulted in measurable regeneration of native

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PACIFIC CONSERVATION BIOLOGY Vol. **18:** 123–132. Surrey Beatty & Sons, Sydney. 2012.

vegetation in the mamane forest within 15 years (Scowcroft and Giffin 1983; Hess *et al*. 1999). However, forest recovery was variable among localities, which may reflect local differences in grazing history and prevalence of invasive grasses that can suppress establishment of mamane seedlings (Hess *et al*. 1999; Denslow *et al*. 2006). Furthermore, the response of palila to forest recovery has been limited (Hess *et al*. 2001; Banko *et al*. 2009). Palila prefer large mamane trees (van Riper 1980), a size that may require 30 years or more to reach (Scowcroft and Conrad 1988). Few studies, however, have examined long-term community responses to ungulate exclusion on islands (Allen *et al*. 1984; Scowcroft and Giffin 1983; Scowcroft and Conrad 1988; Cabin *et al*. 2000).

In order to assess sheep impacts on the mamane forest, exclosures were established in the 1960s and 1970s on Mauna Kea (Scowcroft and Giffin 1983; Scowcroft and Conrad 1988), providing an opportunity to assess long-term trends in response of the mamane forest after sheep exclusion. Further, unprotected plots adjacent to each exclosure allowed assessment of the effects of intermittent sheep recurrence on forest regrowth. We sampled exclosures at three time intervals since establishment, and also sampled the paired plot of each exclosure at the last time interval. In order to characterize long-term response of the mamane forest and to assess the impacts of non-native plants, we evaluated trends in cover of vegetation and heights of mamane trees over time. In order to assess the impacts of recurrent sheep grazing, we compared characteristics of mamane trees inside and outside exclosures.

METHODS

Study area

The mamane forest occupies a band from 1 800 to 3 000 m in elevation on the island of Hawaii (19° 49' N, 155° 28' W); temperatures range from highs of 20°C to near freezing (van Riper 1980). On eastern windward slopes, median annual rainfall ranges from 70 cm at tree-line to 160 cm at lower elevations. On leeward slopes, precipitation is much lower at all elevations. Soils are unstable due to steep slopes and coarse textures derived from cinders and ash (Hartt and Neal 1940). The coarse structure and low amount of organic matter limit soil capacity to hold water, and create conditions that are harsh for plant growth (Hartt and Neal 1940).

Forest canopy cover ranged from sparse (<5%) to dense (60%) in 1980 (Scott *et al*. 1984), but dense forest was uncommon (Scowcroft and Conrad 1992). Mamane is the dominant tree species in the subalpine zone, and it is co-dominant with naio (*Myoporum sandwicense*) on the southwestern slopes of the volcano (Scott *et al*. 1984). Near tree-line, mature mamane trees average <8 m in height. The trees have polymorphic growth forms, often with more than one stem. The forest supports few shrub species, with the endemic pukiawe (*Leptecophylla tameiameiae*) being the most common. Native herbaceous species include three endemic grasses (*Trisetum glomeratum*, *Deschampsia nubigena*, and *Agrostis sandwicensis*), two sedges, and four ferns (Scowcroft and Giffin 1983; Scowcroft and Conrad 1992). While all the native plants have been damaged by browsing, the most susceptible are mamane and the native grasses (Scowcroft and Conrad 1992).

Sheep grazing history

Feral sheep (*Ovis aires*) became established on Mauna Kea in the 1820s and increased in numbers, reaching 40 000 by the early 1930s (Scowcroft and Conrad 1992). Because of obvious damage, sheep numbers were reduced to about 500 by 1950. Starting in 1955, sheep were managed below 5 000 individuals under sustained yield for public hunting, but damage continued. Mouflon sheep (*O. gmelini musimon*) were introduced in 1962 for hunting purposes (Scowcroft and Conrad 1992). Development of a recovery plan for the palila pursuant to the US Endangered Species Act of 1973, as well as federal court rulings, called for the removal of feral sheep and later mouflon sheep from palila critical habitat (Scowcroft and Conrad 1988; Banko *et al*. 2002). However, sheep were not prevented from re-invading from adjacent areas of Mauna Kea (Scowcroft and Conrad 1992). Further, eradication efforts forced sheep upslope, resulting in greater damage to vegetation near tree-line (Scowcroft and Conrad 1988). By 2008, palila critical habitat appeared free of feral sheep, but hybrid sheep (feral x mouflon) remained and actually may have increased despite intensive control efforts 1999–2008 (Banko *et al*. 2009). In other areas of the mamane forest, all three types of sheep were still present.

Exclosure sites

We sampled a total of seven exclosure sites (Fig. 1). Six of the sites were described by Scowcroft and Giffin (1983) and established in 1963 (Puu Nanaha, Puu Kole, and Kaluamakani) or 1972 (Hale Pohaku, Puu O Kauha and Wailuku). The seventh site, Hill 8987, was established in 1976 as a 0.3 ha exclosure on a southeast-facing, 15-degree slope at an elevation of 2663 m, with soil type being Huikau loamy sand and annual precipitation of 381–635 mm. Exclosures were established near tree line at 2663–2860 m elevation, where browsing pressure was greatest, and their locations were chosen to represent the

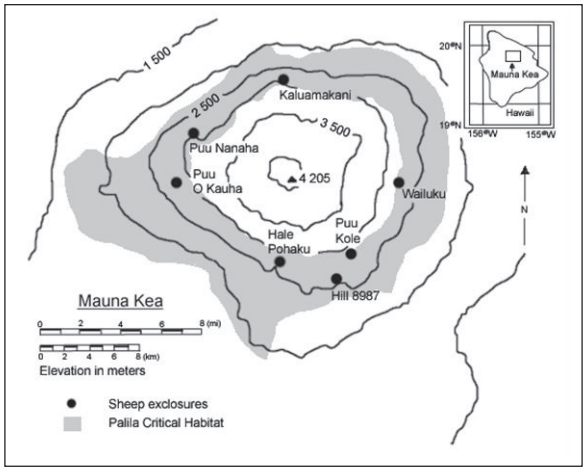

Fig. 1. Location of sheep exclosures within the Mauna Kea Forest Reserve, Island of Hawaii.

diversity of soil and precipitation regimes existing on the mountain (Fig. 1). Exclosures were rectangular, and at each of the seven sites, a paired, unexclosed plot of the same size was established <15 m away at a location selected for similarity of soil type, slope, and exposure. The Wailuku exclosure (0.9 ha), the only exclosure >0.4 ha in size, was subsequently expanded for use as a silversword (*Argyroxiphium sandwicense*) sanctuary; we randomly selected a 0.4 ha region within the original exclosure that did not include silversword plantings.

To evaluate changes in vegetative cover inside each exclosure over time, five of the exclosure sites (Puu Nanaha, Puu Kole, Kaluamakani, Hale Pohaku, and Hill 8987) were sampled during three periods, 1972–1976, October 1998, and April–May 2009. To assess effects of sheep recurrence on forest response, we compared vegetation inside and outside of these five exclosures, as well as two additional exclosures (Puu O Kauha and Wailuku), sampled only during April–May 2009. Sheep presence in outside plots was likely intermittent, and the specific history of sheep presence at each site was unknown.

Vegetation cover sampling

Vegetation cover was sampled at the five long-term exclosure sites, using the line intercept method (Mueller-Dombois and Ellenberg 1974) to estimate percent cover for each species. To assess long-term response of vegetation, we sampled only the inside of exclosures. At the time of initial sampling (1972–1976), five 30 m transects were located systematically inside each exclosure and marked to facilitate relocation. Transects extended parallel to elevational contours at each site, and were spaced approximately 20 m apart (Fig. 2).

Each plant encountered along a transect was recorded by species, and the total length of

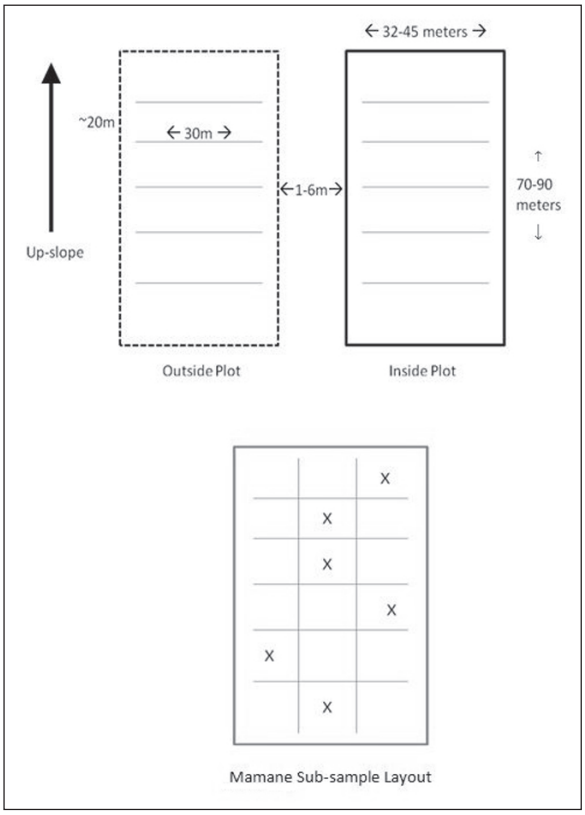

Fig. 2. Schematic showing dimensions of fenced and unfenced sample plots, the location of the line transects that were used to estimate plant cover, and the division of the area into sub-plots that were used to quantify mamane tree attributes.

intercept of each species along the transect was measured to the nearest centimeter. If more than one plant occurred at a given point along the transect, the intercept of the plant with the uppermost cover was recorded. Multiple plant species at a given point were uncommon, and most such instances involved non-native grasses and forbs growing beneath mamane trees, resulting in a slight underestimate of cover of non-native plants.

Mamane sampling

Mamane height was sampled inside the five long-term exclosures in 1998 and again in 2009. In 2009, mamane tree density, canopy density, condition, and reproductive potential were also sampled at all 14 plots (seven inside, seven outside). Each of the plots was divided into six belts, delineated by the five line transects and the edges of the plot (Fig. 2), and the belt in which each tree was encountered was recorded. In 1998 all mamane trees were measured, but by 2009 a total census was not feasible at five of the 14 plots due to high mamane density. Thus, for these five plots we measured a random sub-sample of mamane trees. We divided each belt into thirds, generating a six by three grid. We selected one grid cell at random from each of the six

belts and measured all mamane trees in the six cells (Fig. 2).

Mamane trees were considered to be different individuals if trunks were separated by an arbitrary distance of >0.3 m at the base. Height of each mamane tree was measured to the nearest 0.1m. Tree density (trees/ha) was calculated by dividing the number of trees sampled at each location by the area sampled; for sub-sampled plots, this area was 1/3 the size of the plot. Canopy density (m^2/ha) was determined by measuring the major and minor axes of the canopy of each tree, calculating canopy area of each tree using the formula for an ellipse, summing canopy areas for each location, then dividing by the area of the plot sampled. Condition of each tree was scored on a rank scale, based on a visual estimate of the percentage of canopy branches alive. A ranking of 0 indicated 0–25% live canopy cover, 1 indicated 25–50%, 2 indicated 50–75%, and 3 indicated 75–100%. To assess reproductive vigor we searched each tree for presence of flowers, newly formed seed pods, green seed pods, and dried seed pods, and assigned one point for the presence of each of these structures to create an index of reproductive potential (range, 0–4, with 0 as absence of any structures and 4 as presence of all structures). The average number of reproductive structure types per tree was calculated for each belt, and then values for each belt were averaged to yield one value per location.

Analyses

We characterized vegetation response at the five long-term exclosures by combining species into three life-forms: native trees, native shrubs, and native herbaceous species. To determine if the year of sampling had an effect on percent cover, we performed two-way ANOVAs for each vegetation life form and examined the effects of year, using a logit transformation to satisfy parametric assumptions of the model (Schabenberger and Pierce 2001). To evaluate changes in mamane stand structure over time, we combined tree heights into height-class distributions. To assess the impact of non-native plants, we compared changes in cover between native and non-native plants, and more specifically between mamane trees and non-native grasses. If non-native plants inhibit the establishment and growth of native plants, an increased cover of non-native plants should result in decreased cover of native plants, generating an inverse relationship over time.

We assessed the effect of recurrent sheep presence by testing for differences, inside versus outside exclosures, in mamane tree density, canopy density, height, condition, and reproduction, using data from 2009. We used a

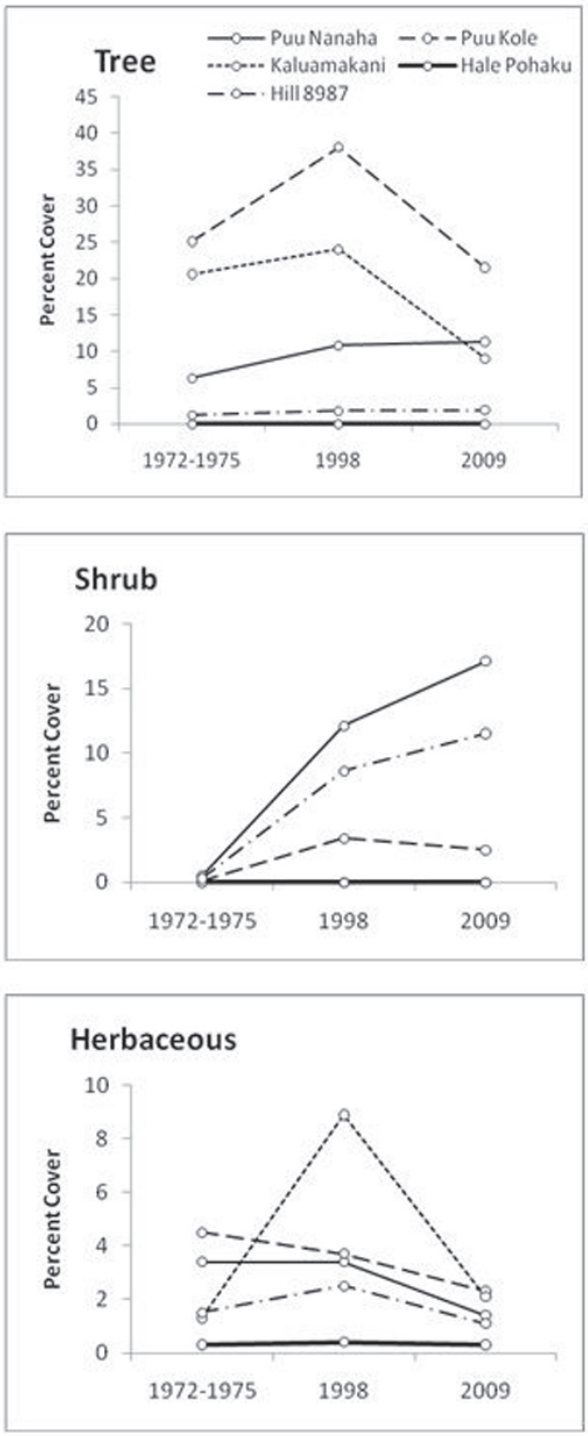

Fig. 3. Changes in percent cover over time for native trees, native shrubs, and native herbaceous vegetation inside of each of five sheep exclosures, Mauna Kea Forest Reserve, Island of Hawaii. Exclosures were established in 1963 (Puu Nanaha, Puu Kole, and Kaluamakani), 1972 (Hale Pohaku), and 1976 (Hill 8987).

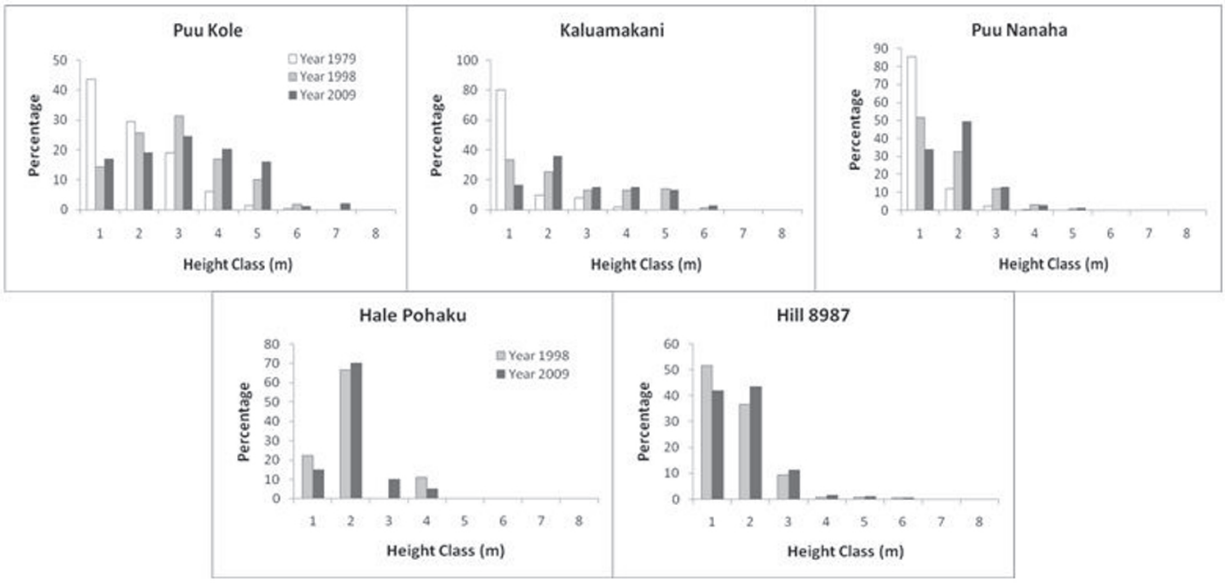

Fig. 4. Changes over time in height class distributions for mamane trees inside of five sheep exclosures, Mauna Kea Forest Reserve, Island of Hawaii. Height class data for 1979 at Puu Kole, Kaluamakani, and Puu Nanaha were adapted from Scowcroft and Giffin (1983) and Scowcroft and Conrad (1988). Exclosures were established in 1963 (Puu Nanaha, Puu Kole, and Kaluamakani), 1972 (Hale Pohaku), and 1976 (Hill 8987).

Wilcoxon signed-rank test among plots for tree density and canopy density because these two variables were calculated for the entire plot, and hence they lacked replication. For height, condition, and reproduction, we performed two-way factorial ANOVAs (Schabenberger and Pierce 2001) for site, inside/outside treatment, and site by inside/outside treatment interaction, with belt treated as a random factor and nested within inside/outside treatment. All statistical analyses were performed using programme JMP, version 5.0.1a.

RESULTS

Native Species Cover

The only native tree recorded along transects was mamane, although naio was present at some sites. Between the 1970s and 1998, percent cover of native trees initially increased at most sites, but between 1998 and 2009 percent cover either increased at a slower rate or decreased (Fig. 3). Native shrub cover, which comprized mostly pukiawe, increased between the 1970s and 1998 at most sites, but between 1998 and 2009 native shrub cover increased at a slower rate or decreased. Cover of native herbaceous vegetation remained sparse at all locations (<10% of total cover at all sampling periods) and consisted primarily of grasses and sedges, with native ferns and forbs <1% of total cover. Native herbaceous vegetation showed a variable response between the 1970s and 1998, with increases in cover at some sites, but decreases in cover at most sites between 1998 and 2009. These trends were supported by the ANOVA. Year effects were not significant for trees ($P = 0.98$) nor herbaceous species ($P = 0.85$), but approached significance for native shrubs ($P = 0.07$), suggesting that shrubs maintained a more consistent trajectory of increased cover over time than did trees or herbaceous species. Changes in cover over time varied considerably among sites for all vegetation life forms, with Hale Pohaku showing very low percent cover of all life forms throughout the study period (Fig. 3).

Mamane Height Distribution

At all sites there was evidence of a shift over time in the distribution of mamane heights toward larger height classes, thus presumably an older age distribution (Fig. 4). At all sites except Hale Pohaku, there was evidence of strong recruitment during earlier time periods, as shown by substantial percentages of trees less than 1 m tall (Fig. 4). Combined with patterns of change in percent cover (Fig. 3), these results suggest that mamane recruitment between the 1970s and 1998 was relatively high at many sites, but was reduced between 1998 and 2009.

Non-native Species

Non-native species recorded along transects were entirely herbaceous, with grasses accounting for 42–100% of non-native cover at each location. In 2009 a previously undetected hybrid grass (native *Trisetum glomeratum* with non-native *Holcus lanatus*) was recorded at Puu O Kauha (21% of herbaceous cover), but was excluded from the analysis since it could not be categorized as either native or non-native. Only two sites, Puu Kole

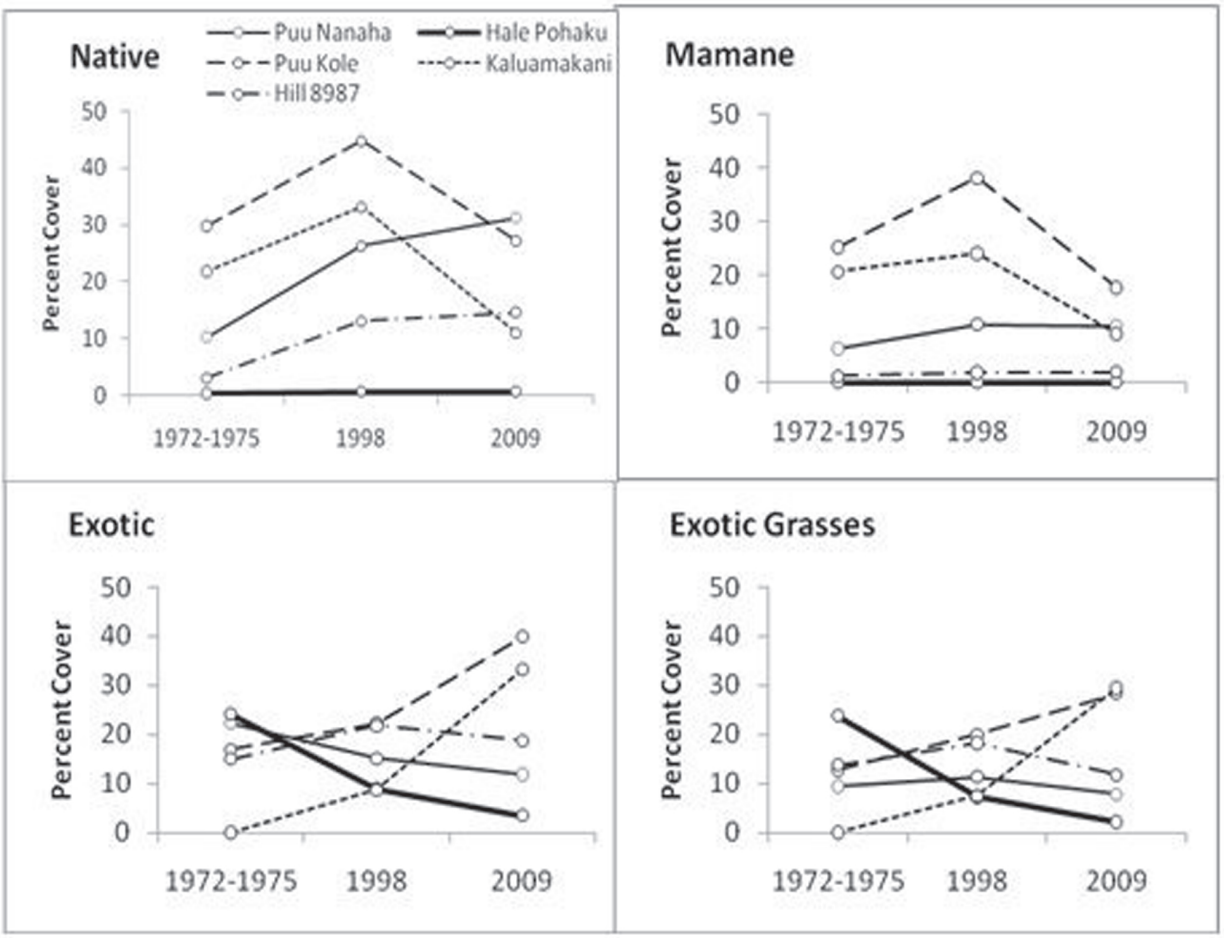

Fig. 5. Changes over time inside of five sheep exclosures for percent cover of native vegetation and non-native vegetation, and mamane trees and non-native grasses, Mauna Kea Forest Reserve, Island of Hawaii. Exclosures were established in 1963 (Puu Nanaha, Puu Kole, and Kaluamakani), 1972 (Hale Pohaku), and 1976 (Hill 8987).

and Kaluamakani, showed evidence of an inverse relationship over time between native and non-native cover, and between mamane and non-native grass cover (Fig. 5). Further, these inverse trends were only apparent between 1998 and 2009.

Effects of Sheep Exclosure

Mamane density ranged from about 500–1 200 stems/ha inside exclosures to about 60–800 stems/ha outside at all sites except for Hale Pohaku, where densities were very low both inside and outside (Fig. 6a). Across sites, the difference in mamane density inside and outside was not statistically significant ($P = 0.15$), but did show a trend toward significance that may have been biologically important.

Mamane canopy density ranged from about 3 000–14 000 m^2/ha inside exclosures to 1 000–6 000 m^2/ha outside at all sites except Hale Pohaku, where canopy densities were again very low both inside and outside (Fig. 6b). The difference in canopy density inside versus outside exclosures was statistically significant ($P = 0.034$).

Mean height of mamane trees ranged about 1.1–2.9 m inside exclosures and 0.8–3.6 m outside (Fig. 6c). The ANOVA model for mamane height was highly significant ($P = 0.002$, Rsq adj = 0.39) and showed no significant main effect of inside/outside treatment ($P = 0.524$), but did show a highly significant effect of site ($P < 0.001$) and a significant site by inside/outside interaction ($P = 0.006$), indicating that the effect of sheep exclusion on mamane height varied by site.

Mean scores for condition of mamane trees ranged about 1.2–2.7 inside exclosures and 0.2–3.0 outside, corresponding to about 30–70% branches alive inside and 5–75% branches alive outside (Fig. 6d). The ANOVA model for mamane condition was highly significant ($P < 0.001$, Rsq Adj = 0.70), and showed no significant main effect of inside/outside treatment, but did show a highly significant main effect of site ($P < 0.001$) and site by inside/outside interaction ($P < 0.001$). The significant interaction indicates that the effect of sheep exclusion on mamane condition varied by site.

Mean scores for mamane reproductive potential ranged about 0.2–1.5 inside exclosures and 0.1–2.3 outside (Fig. 6e). The effect of sheep exclusion on mamane reproductive potential varied by site; the ANOVA model was highly significant ($P < 0.001$, Rsq Adj = 0.19), and indicated that both site and site by inside/outside interaction were highly significant ($P < 0.001$ for each). The effect of sheep exclusion was not found to be significant in the model ($P = 0.99$), indicating that mamane reproductive potential varied in response to site more than in response to sheep exclusion.

DISCUSSION

After 33–46 years of protection from sheep grazing, recovery of native vegetation inside exclosures, as indicated by changes in percent cover over time, has shown variable patterns

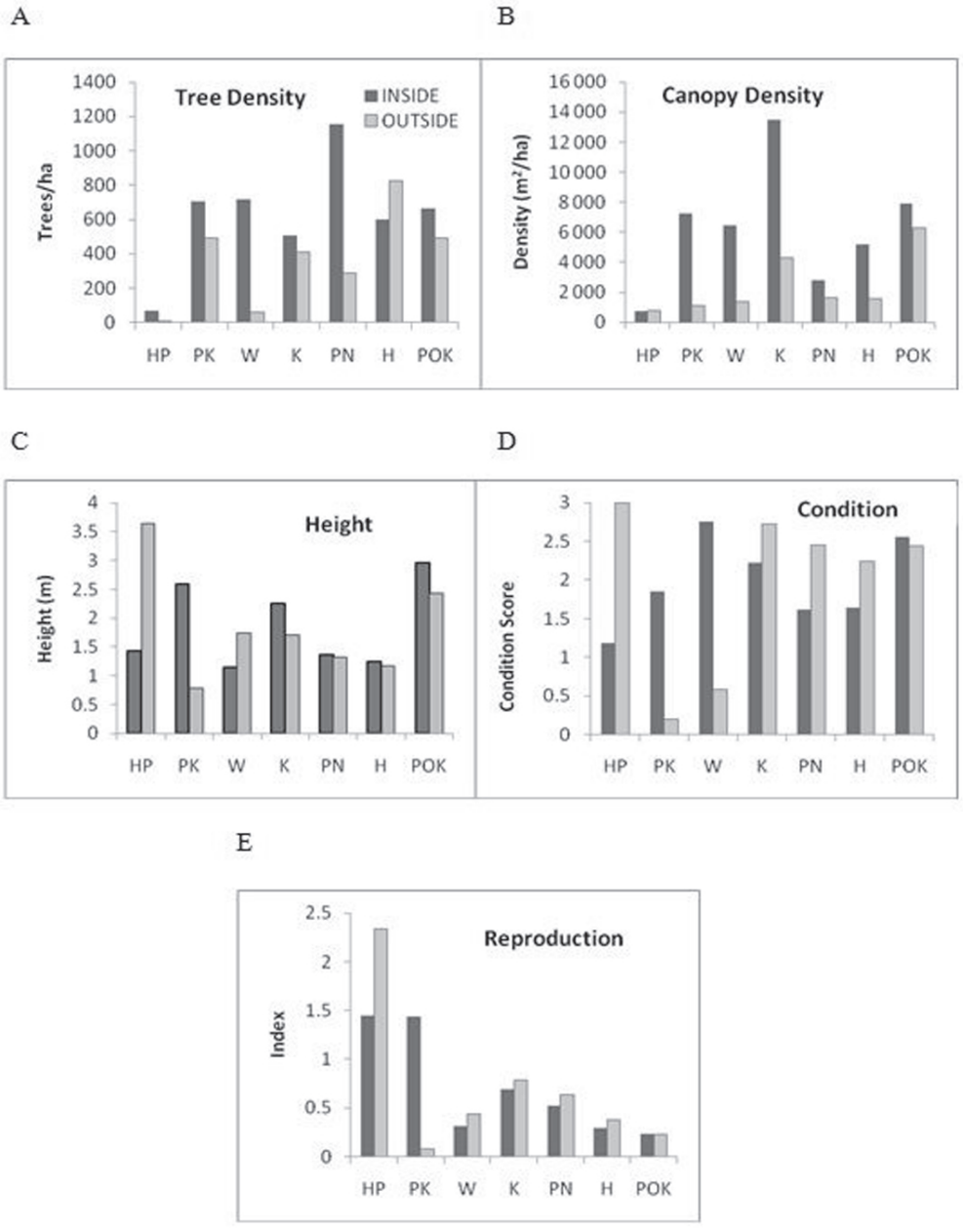

Fig. 6. Comparison of sampled plots inside and outside of sheep exclosures for tree density, canopy density, height, condition, and reproductive potential of mamane trees, Mauna Kea Forest Reserve, Island of Hawaii. Sites and abbreviations, with year of exclosure establishment, are Hale Pohaku (HP, 1972), Puu Kole (PK, 1963), Wailuku (W, 1972), Kaluamakani (K, 1963), Puu Nanaha (PN, 1963), Hill 8987 (H, 1976), and Puu O Kauha (POK, 1972). In 6d), the score for mamane condition ranges from 0 (0–25% of the canopy alive) to 3 (75–100% alive). In 6e), the index of reproductive potential is the average number of reproductive structure types per tree, and ranges from 0 (absence of flowers, dried seed pods, green seed pods, or newly-formed seed pods) to 4 (all four reproductive structure types present).

depending on vegetation life form and location. Part of the variation among locations is due to study design; exclosure locations were selected to represent a diversity of soil, slope exposure, and precipitation regimes (Scowcroft and Giffin 1983). Nonetheless, some general patterns were apparent. Woody species, primarily mamane and pukiawe, showed a general trend of increased cover between the 1970s and 1998, then a slowed rate of increase or a decline between 1998 and 2009. This pattern is mirrored by changes in heights of mamane trees over time, which suggests that mamane recruitment was initially relatively high but subsequently declined. Mamane regrowth at the three oldest sites, Puu Nanaha, Puu Kole, and Kaluamakani, appears to have peaked at about 10–40% cover in 1998. The structure of the mamane forest before sheep introduction is not known, but this degree of canopy coverage may represent the potential for each of these sites under current conditions. Mamane recovery has been minimal at Hill 8987 and Hale Pohaku; in the case of Hale Pohaku, this could be due to cinder soils that are poorly developed and harsh for plant growth (Scowcroft and Giffin 1983). Response of herbaceous vegetation was variable among exclosures from the 1970s to 1998, and then showed a general pattern of a decline in herbaceous cover between 1998 and 2009.

The general pattern of reduced or reversed trajectories of recovery between 1998 and 2009 suggests the influence of a region-wide change. Drought has altered the recovery of plant communities on other islands following removal of herbivores (Klinger *et al*. 1994; Donlan *et al*. 2003; Chapuis *et al*. 2004), and drought may have played a role in our study as well. Annual precipitation at the Halepohaku-111 weather station, located at the southern edge of the study area, averaged 18% less during 1999–2009 (62.2 cm) than during 1963–1998 (75.4 cm). Further, conditions were unusually dry during 2007–2009, when precipitation averaged 39.5 cm, 48% below the 1963–1998 average.

Non-native plants have influenced recovery of native vegetation on other islands (Klinger *et al.* 1994; Donlan *et al.* 2003; Chapuis *et al*. 2004), but their role in our study was unclear. We found evidence of an inverse relationship over time between native and non-native species, but only at two of the sites and only between 1998 and 2009. If non-native species have an effect on recovery of native species, our results suggest it was expressed variably over time, possibly in response to drought. However, perhaps our scale of analysis was too coarse, and effects on native species were real but caused by non-native species whose effects in space and time were obscured by the small percentage of the mountain sampled and the broad classifications (non-native species, non-native grasses) that we used.

Other factors also may have affected the patterns of recovery that we observed, especially the reduced or reversed trajectories between 1998 and 2009. Mamane may have been affected by a root disease caused by the fungus *Armillaria mellea* (Gardner and Trujillo 2001). Sheep may have breached some exclosures and consumed vegetation inside, although to our knowledge the exclosures we sampled were maintained free of sheep. Alternatively, these changes may reflect community dynamics as larger mamane trees outcompete smaller trees and other vegetation for resources, in the relatively harsh conditions of a community located near treeline and in poor soils. These soils may have been degraded even further as a result of long-term overgrazing and trampling by sheep (Scowcroft and Giffin 1983).

Recurrent sheep presence outside exclosures had an overall negative effect on mamane canopy density and perhaps tree density, but not on reproductive potential. For mamane height and condition, the inside versus outside comparison was not significant overall but did vary significantly by site; in particular, two sites, Puu Kole and Wailuku, showed greatly reduced mamane condition outside exclosures (Fig. 6d). Perhaps the principal overall effect of recurrent sheep grazing is seedling mortality that leads to reduced canopy and tree density, but for those trees tall enough to exceed the reach of sheep, reproduction is relatively unaffected. Height and condition seem to be influenced by local variations in site conditions and sheep presence.

Conservation Implications

Results from inside exclosures indicate that the mamane forest will show substantial regeneration if protected from sheep damage. However, the response is variable among localities and over time, perhaps due to the effects of factors such as drought, non-native plants, disease, and soil condition. Moreover, our results may be a conservative estimate of recovery potential. Our sites were located near tree line, which may represent the limits of environmental tolerance for mamane; hence, the potential for recovery from sheep damage may be greater in lower-elevation areas of the forest. Comparisons inside and outside exclosures show that, despite intensive efforts to reduce sheep numbers over several decades, recurrent presence of sheep has a significant negative effect on mamane recovery.

The endangered palila, which feeds almost exclusively on mamane seed pods, prefers mamane forest with taller trees and greater canopy cover (Scott *et al*. 1984, Banko *et al*. 2009), although palila may exist at low densities where mamane trees are relatively short (2–5 m) or scattered (5–20% canopy cover) (Scott *et al.* 1984). Our results indicate that after 33–46 years of protection from sheep grazing, mamane

regeneration at some sites, especially those protected the longest, may approach the point of being able to support palila. However, these protected sites span only a very small portion of the mamane forest, much of which has been exposed to recurrent sheep grazing for several decades. Our results indicate that continued sheep presence has negative effects on mamane canopy density and perhaps tree density, effects that likely diminish habitat quality for palila.

ACKNOWLEDGEMENTS

We thank J. G. Giffin for use of data he collected in 1972–1976; the Selma Herr Endowment Fund for financial support; the Institute of Pacific Islands Forestry (USDA), the Hakalau Forest National Wildlife Refuge, Hans Sin (Hawaii Division of Forestry and Wildlife) and D. Cummings for logistical support; K. Rice and N. Willits for assistance with the manuscript and statistics; H. Main for assistance with fieldwork; and L. Feinstein for comments on the manuscript and assistance with Photoshop.

REFERENCES

Allen, R. B., Payton, I. J. and Knowlton, J. E., 1984. Effects of ungulates on structure and species composition in the Urewera forests as shown by exclosures. *N. Z. J. Ecol.* **7:** 119–130.

Baker, J. K. and Reeser, D. W., 1972. Goat management problems in Hawaii Volcanoes National Park: a history, analysis and management plan. National Park Service National Resources Report 2.

Banko, P. C., Brinck, K. W., Farmer, C. and Hess, S. C., 2009. Palila. Pp. 513–529 *in* Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna ed by T. K. Pratt, C. T. Atkinson, P. C. Banko, J. D. Jacobi and B. L. Woodworth. Yale University Press, New Haven and London.

Banko, P. C., Johnson, L., Lindsey, G. D., Fancy, S. G., Pratt, T. K, Jacobi, J. D. and Banko, W. E., 2002. Palila (*Loxioides bailleui*). Pp. 1–24 *in* The Birds of North America, No. 679 ed by A. Poole and F. Gill. The Birds of North America, Philadelphia, Pennsylvania.

Bowen, L. and Van Vuren, D., 1997. Insular endemic plants lack defenses against herbivores. *Cons. Biol.* **11:** 1249–1254.

Cabin, R. J., Weller, S. G., Lorence, D. H., Flynn, T. W., Sakai, A. K., Sandquist, D. and Hadway, L. J., 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. *Cons. Biol.* **14:** 439–453.

Campbell, K. and Donlan, C. J., 2005. Feral goat eradications on islands. *Cons. Biol.* **19:** 1362–1374.

Carrion, V., Donlan, C. J., Campbell, K., Lavoie, C. and Cruz, F., 2007. Feral donkey (*Equus asinus*) eradications in the Galapagos. *Biodiv. & Cons.* **16:** 437–445.

Chapuis, J.-L., Frenot, Y. and Lebouvier, M., 2004. Recovery of native plant communities after eradication of rabbits from the subantarctic Kerguelen Islands, and influence of climate change. *Biolog. Cons.* **117:** 167–179.

Cruz, J. B. and Cruz, F., 1987. Conservation of the dark-rumped petrel *Pterodroma phaeophygia* in the Galapagos Islands Ecuador. *Biolog. Cons.* **42:** 303–312.

Denslow, J. S., Uowolo, A. L. and Hughes, R. F., 2006. Limitations to seedling establishment in a mesic Hawaiian forest. *Oecologia* **148:** 118–128.

Donlan, C. J., Tershy, B. R. and Croll, D. A., 2003. Islands, non-native herbivores, and invasive plants: their roles in coastal California restoration. *Restoration Ecol.* **11:** 524–530.

Garcillan, P. P., Vega, E. and Lopez-Reyes, E., 2008. Recruitment response of Guadalupe cypress (*Callitropsis guadalupensis*) three years after goat eradication on Guadalupe Island. Pp. 177–183 *in* Proceedings of the Seventh California Islands Symposium ed by C. C. Damiani and D. K. Garcelon. Institute for Widlife Studies, 5–7 February 2008, Arcata, California.

Gardner, D. E. and Trujillo, E. E., 2001. Association of *Armillaria mellea* with mamane decline at Pu'u La'au. *Newsletter Hawaiian Bot. Soc.* **40:** 33–34.

Hartt, C. E. and Neal, M. C., 1940. The plant ecology of Mauna Kea, Hawaii. *Ecol.* **21:** 237–266.

Hess, S. C., Banko, P. C., Brenner, G. J. and Jacobi, J. D., 1999. Factors related to the recovery of subalpine woodland on Mauna Kea, Hawaii. *Biotropica* **31:** 212–219.

Hess, S. C., Banko, P. C., Reynolds, M. H., Brenner, G. J., Laniawe, L. P., and Jacobi, J. D., 2001. Drepanidine movements in relation to food availability in subalpine woodland on Mauna Kea, Hawai'i. *Stud. in Avian Biol.* **22:** 154–163.

Kessler, C.C., 2002. Eradication of feral goats and pigs and consequences for other biota on Sarigan Island, Commonwealth of the Northern Mariana Islands. Pp. 132–140 *in* Turning the Tide: The Eradication of Invasive Species ed by C. R. Veitch and M. N. Clout. IUCN Species Survival Commission Occasional Paper No. 27, IUCN, Gland, Switzerland and Cambridge, UK.

Klinger, R. C., Schuyler, P. T. and Sterner, J. D., 1994. Vegetation response to the removal of feral sheep from Santa Cruz Island. Pp. 341–350 *in* The Fourth California Islands Symposium: Update on the Status of Resources ed by W. L. Halvorson and G. J. Maender. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Knowlton, J. L., Donlan, C. J., Roemer, G. W., Samaniego-Herrera, A., Keitt, B. S., Wood, B., Aguirre-Muñoz, A., Faulkner, K. R. and Tershy, B. R., 2007. Eradication of non-native mammals and the status of insular mammals on the California Channel Islands, USA, and Pacific Baja California Islands, Mexico. *Southwestern Nat.* **52:** 528–540.

Leathwick, J. R., Hay, J. R. and Fitzgerald, A. E., 1983. The influence of browsing by introduced mammals on the decline of North Island kokako. *N. Z. J. Ecol.* **6:** 55–70.

Morrison, S. A., 2007. Reducing risk and enhancing efficiency in non-native vertebrate removal efforts on islands: a 25 year multi-taxa retrospective from Santa Cruz Island, California. Pp. 398–409 *in* Managing Vertebrate Invasive Species: Proceedings of an International Symposium ed by G. W. Witmer, W. C. Pitt and K. A. Fagerstone. USDA Wildlife Services, National Wildlife Research Center, Fort Collins, Colorado.

Mueller-Dombois, D., 1979. Succession following goat removal in Hawaii Volcanoes National Park. Pp. 1149–1154 *in* Proceedings of the First Conference on Scientific Research in National Parks ed by R. M. Linn. USDI National Park Service Transactions and Proceedings Series No. 5.

Mueller-Dombois, D. and Ellenberg, H., 1974. Aims and methods in vegetation ecology. John Wiley and Sons, New York, New York.

Muerk, C. D., 1982. Regeneration of subantarctic plants on Campbell Island following exclusion of sheep. *N. Z. J. Ecol.* **5:** 51–58.

Nogueira-Filho, S. L. G., Nogueira, S. S. C. and Fragoso, J. M. V., 2009. Ecological impacts of feral pigs in the Hawaiian Islands. *Biodiv. Cons.* **18**: 3677–3683.

Parkes, J. P., 1990. Feral goat control in New Zealand. *Biolog. Cons.* **54:** 335–348.

Schabenberger, O. and Pierce, F. J., 2001. Contemporary Statistical Methods for the Plant and Soil Sciences. CRC Press, Boca Raton, Florida.

Scott, J. M., Mountainspring, S., van Riper, C., III, Kepler, C. B., Jacobi, J. D., Burr, T. A. and Giffin, J. G., 1984. Annual variation in the distribution, abundance, and habitat response of the palila *Loxioides bailleui*. *Auk* **101:** 647–664.

Scowcroft, P. G. and Conrad, C. E., 1988. Restoring critical habitat for Hawaii's endangered palila by reducing ungulate populations. *Trans. W. Section Wildl. Soc.* **24:** 72–79.

Scowcroft, P. G. and Conrad, C. E., 1992. Alien and native plant response to release from feral sheep browsing on Mauna Kea. Pp. 625–665 *in* Alien Plant Invasions in Native Ecosystems of Hawaii ed by C. P. Stone, C. W. Smith and J. T. Tunison. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu.

Scowcroft, P. G., 1983. Tree cover changes in mamane (*Sophora chrysophylla*) forests grazed by sheep and cattle. *Pac. Sci.* **37:** 109–119.

Scowcroft, P. G. and Giffin, J. G., 1983. Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. *J. Range Manage.* **36:** 638–645.

Scowcroft, P. G. and Sakai, H. F., 1983. Impact of feral herbivores on mamane forests of Mauna Kea, Hawaii: bark stripping and diameter class structure. *J. Range Manage.* **36:** 495–498.

Spatz, G. and Mueller-Dombois, D., 1973. The influence of feral goats on koa tree reproduction in Hawaii Volcanoes National Park. *Ecol.* **54:** 870–876.

van Riper, C., III, 1980. Observations on the breeding of the palila *Psittirostra bailleui* of Hawaii USA. *Ibis* **122:** 462–475.

Van Vuren, D., 1992. Eradication of feral goats and sheep from island ecosystems. *Proc. Vertebrate Pest Conference* **15:** 377–381.

Van Vuren, D. and Coblentz, B.E., 1987. Some ecological effects of feral sheep on Santa Cruz Island California USA. *Biolog. Cons.* **41:** 253–268.

Wehtje, W., 1994. Response of a bishop pine (*Pinus muricata*) population to removal of feral sheep on Santa Cruz Island, California. Pp. 331–340 *in* The Fourth California Islands Symposium: Update on the Status of Resources ed by W. L. Halvorson and G. J. Maender. Santa Barbara Museum of Natural History, Santa Barbara, California.