Palila (*Loxioides bailleui*), a member of the endemic Hawaiian honeycreeper family, first gained official recognition as an endangered species in 1966 (USDI 1966). The bird was listed because: (1) it no longer occupied a significant portion of its historical range, (2) its present habitat was being adversely modified by feral sheep (*Ovis aries*) browsing, and (3) the total population at that time was estimated to be in the low hundreds (Berger et al. 1977).

Despite the palila’s endangered status, conservation and restoration efforts failed to materialize until after enactment of the Endangered Species Act of 1973. Under its auspices, the palila recovery team was organized. The recovery team delineated critical habitat (U.S. Government Printing Office 1977) and developed a plan for restoring the bird to nonendangered status on State-owned lands flanking Mauna Kea (Berger et al. 1977). The plan was approved by the U.S. Fish and Wildlife Service in 1978.

Foremost among the action items listed in the plan was the “eradication” of feral sheep, feral-mouflon sheep hybrids (*Ovis aries* x *musimon*), and feral goats (*Capra hircus*) from the palila’s critical habitat. The majority of recovery team members believed that restoration of palila to nonendangered status depended mainly on stopping the ecosystem degradation caused by feral sheep and goats. This key action item was accomplished in 1981 (Juvik and Juvik 1984).

The original plan reserved judgement on the need for eradication of mouflon sheep (*Ovis musimon*) pending completion of ecological studies by State wildlife biologists. Those studies were completed (Giffin 1982) and, on the basis of their findings, the revised recovery plan called for the eradication of mouflon sheep (USDI, in press). The State of Hawaii essentially completed this action item between 4 July 1987 and 18 February 1988. During this period, hunters and resource managers killed 809 mouflon. They also shot 1,161 feral and hybrid sheep and 25 feral goats that had become reestablished in the palila’s critical habitat.

The large number of feral and hybrid sheep taken during eradication of mouflon emphasizes the impossibility of total and permanent eradication of ungulates. Even if every ungulate in the palila’s critical habitat were removed, reinvasion over, under, around and through fences would occur. The best that can be hoped for is population control through intensive annual or biennial hunts. In this paper the term eradication means reduction of the population to as low a level as is physically possible to achieve.

Three questions arise now that the palila’s habitat has been under reduced pressure from feral sheep and goats for over six years. Has the forest responded to the reduction in grazing and browsing pressure? Will the elimination of mouflon elicit a forest response similar to that observed after removal of feral sheep? Has the forest response been paralleled by a palila response? In the remainder of this paper we attempt to answer these questions.

### THE STUDY AREAS

Feral sheep were once distributed throughout the woodland ecosystem. However, by the time the palila was declared endangered, game management activities had reduced the sheep population and forced most of the survivors to concentrate in the uppermost fringes of the woodland between 2,400 m elevation and tree line (about 2,900 m elevation). Restricted to a relatively narrow band around the mountain, the sheep overgrazed the forest (Fig. 1). The original recovery plan recognized that...
Fig. 1. Feral sheep concentrations and animal damage to the mamane woodland were greatest on Mauna Kea in the tree-line zone (between about 2,400 and 2,900 m elevation). Habitat degradation caused by natural attrition of mature mamane trees and the complete suppression of mamane regeneration by sheep seriously threatened the palila's existence.

greatest damage was occurring in this tree-line zone (Berger et al. 1977). Consequently, research was concentrated there.

The vegetation type of the tree-line zone is open mamane (Sophora chrysophylla) woodland and trees average less than 8 m in height. Naio (Myoporum sandwicense), a major component of the subalpine ecosystem at lower elevation on the south flank of Mauna Kea, is absent in the tree-line zone except for scattered individuals on the south flank. Other tree species are scarce. Woody native understory species include Styphelia douglasii, Vaccinium sp., Geranium cuneatum, and Rallardia arborea. Herbaceous vegetation consists predominantly of introduced species including Anthoxanthum odoratum, Bromus rigidus, Danthonia pilosa, and Holcus lanatus. Native grasses are Agrostis sandwicensis, Deschampsia australis, and Trisetum glomeratum.

The climate of the tree-line zone is cool and dry. Temperatures range from nighttime lows near freezing to daytime highs above 20 C (van Riper 1980b, Scowcroft 1981). Median annual rainfall ranges from about 700 mm on eastern slopes to 400 mm on western slopes in the rainshadow of Mauna Kea (State of Hawaii 1982).

Generally, the edaphic conditions of tree-line portions of the palila’s critical habitat are harsh for plant growth (Hartt and Neal 1940). The soils are poorly developed, and in some cases plants are growing in undifferentiated parent material (cinders and volcanic ash). Coarse structure and little organic matter result in low water-holding capacity. Steep slopes result in unstable soils.

PRE-ERADICATION VEGETATION RESPONSES

Two sets of exclosures were studied during the 1970’s in the tree-line zone (Fig. 2). The older exclosures were built in 1963 by the Hawaii Division of Fish and Game and the U.S. Soil Conservation Service. Their purpose was to visually demonstrate the effect of sheep browsing and grazing on vegetation. The newer exclosures were built in 1972 by the Hawaii Division of Fish and Game and the U.S. Forest Service. Their purpose was to quantitatively determine vegetation response to protection at other sites around the mountain. The sites were selected to represent a diversity of soil, water, and animal
damage regimes. Mouflon, feral, and feral/mouflon hybrid sheep occupied the areas around the Puu Kole exclosure (1963) and the Wailuku exclosure (1972). Only feral sheep occupied woodlands around the other exclosures.

The 1963 exclosures demonstrated that habitat improvement would occur in some areas following removal of ungulates. Twelve years after these exclosures were built, herbaceous plant cover was denser and vegetation generally taller inside than outside the exclosures (Scowcroft and Giffin 1983). More important from the standpoint of specific habitat requirements for palila, mamane regeneration established in large numbers inside the exclosures, while none established outside. For example, at Kaluamakani, the harshest and remotest of the three exclosure sites, over 760 mamane had established inside the exclosure, but none had established outside (Scowcroft and Giffin 1983). Flowers and pods were observed on many young mamane.

Additional evidence that habitat improvement would occur after control of ungulates came from the 1972 exclosures. Not surprisingly, mamane and other vegetation recovered rapidly in some areas (Scowcroft and Giffin 1983). For example, two months after the Puu O Kauha exclosure was built on the southwest flank of the mountain, 45 mamane seedlings were tallied inside compared to only 1 seedling outside. Likewise, basal area cover of vegetation inside the Puu O Kauha exclosure...
METHODS

On the basis of the preceding exclosure research, we predicted that control of feral sheep would allow tree-line vegetation to recover, especially mamane. In 1986, about five years after control was imposed, we reexamined the Puu O Kauha exclosure, the tree-line vegetation to either side of it, and the lower elevation woodland near Puu Laau to evaluate our prediction. Also in 1986, we reexamined vegetation inside the Wailuku exclosure, which was located in the center of the mouflon range on the east side of the Mauna Kea. Recovery inside Wailuku provided a glimpse of the broader recovery expected after eradication of mouflon sheep.

Abundance and height class distributions of mamane were determined with 100 percent inventories. Plot transects were used to sample the woodlands surrounding Puu O Kauha and that at lower elevation near Puu Laau. Methodology is more fully described in Scowcroft and Conrad (in review).

RESULTS

The following discussion centers on mamane because of its importance to the survival of palila. Responses of introduced and native herbaceous and woody species other than mamane are described in Scowcroft and Conrad (in review).

Recovery from Feral Sheep at Puu O Kauha

**Abundance of Regeneration and Stand Structure.**—Recovery of mamane was under way outside the Puu O Kauha exclosure. In 1977, when feral sheep still roamed the area, the outside control plot contained three live mamane seedlings. These seedlings were new emergents that averaged 0.06 m in height. Their life expectancy was less than one year. In 1986, five years after feral sheep were eliminated, the control plot contained 116 mamane that averaged 0.9 m in height. Based on the 1986 height class distribution (Fig. 3), we believe this population developed mainly after feral sheep were controlled.

During the five years after sheep eradication, mamane seed regeneration became established in the woodland surrounding Puu O Kauha at 2,750 m elevation. The height class distribution (Fig. 3) for the area indicated a youthful population and strong recovery.

Seed regeneration was also evident in 1986 in the mamane woodland at 2,350 m elevation. But compared to the Puu O Kauha exclosure and surrounding woodlands near tree line, the lower woodland had little seed regeneration (184 mamane/ha), although it had been relatively sheep free for 20 to 30 years. The height class distribution for regeneration in this area (Fig. 3) indicated that rate of recruitment was low or mortality was high or both. It is possible that dense, introduced herbaceous species inhibited mamane regeneration (Scowcroft and Conrad, in review).

Recovery was not limited to seed regeneration. Mamane also regenerated from root sprouts. After 14 years of protection, there were the equivalent of 34 sprout clusters/ha inside the exclosure. Each cluster averaged 2.5 m in height and about 4 m in crown diameter. Although sprout clusters were one-fifth as numerous as seedlings, the projected crown areas of both types of regeneration were equal at 410 m²/ha. Sprouts were confined to areas directly beneath live older trees.

Five years after sheep eradication, there were 23 sprout clusters/ha in the control plot just outside the exclosure. Each cluster averaged 1.8 m in height and 3 m in crown diameter. The sprout population for surrounding woodland areas was almost identical to the control plot population (22 sprout clusters/ha with an average cluster height of 1.8 m). Although many of these clusters probably existed before sheep eradication, they were prevented from growing until browsing stopped.

Sprout regeneration was also encountered in woodlands at 2,350 m elevation near the Puu Laau cabin. There were about 50 sprout clusters/ha and each cluster averaged 2.2 m in height.

**Variability of Seedling Recruitment.**—Mamane recovery in and around Puu O Kauha provided evidence of spatial and temporal variability of recovery. The height class distribution inside Puu O Kauha was markedly different from the distributions inside each of the older exclosures even though all were about 15 years old.
Regenerate spontaneously. Function of abundance of mamane seed and weather. Sites without living or skeletal remains of mamane will probably not regenerate spontaneously.

Spatial variability was also evident in the woodland surrounding Puu O Kauha. Mamane seed regeneration was not uniformly distributed. Rather, data from five plots laid out to the north and five plots laid out to the south of the exclosure showed that density of seed regeneration ranged from 32 seedlings/ha to 1,590 seedlings/ha. The first plot to the north and first plot to the south contained two-thirds of the seedlings tallied. We attributed the spatial variability to differences in parent tree density and, hence, differences in the quantity of buried seeds.

Temporal variability in recovery should be expected also. Inside Puu O Kauha, mamane continued to reproduce after the 1977 measurement. Sixty individuals of seed origin were tallied in 1986 compared to 41 individuals in 1977. About 25 of the 41 mamane present in 1977 were still alive in 1986. Thus, net recruitment in the nine years after 1977 was 35 mamane.

The 1986 height class distribution of young mamane inside Puu O Kauha (Fig. 2) indicated the existence of two populations. One population was composed of mamane recruited after 1977. These trees were generally less than 2 meters tall. The other population was composed of older regeneration recruited soon after the exclosure was built. These older trees were more than 2 m in height and the tallest measured 3.6 m. Flowers and pods were being sparsely produced by some of the larger mamane regeneration.

The existence of two populations of young mamane inside Puu O Kauha indicated that seedling recruitment can be episodic (Fig. 4). The older population was recruited soon after the exclosure was built. Survival was high, but additional recruitment was low until some time after the 1977 measurement (Scowcroft and Giffin 1983). Then, a second flush produced the younger population.

We believe the second flush occurred recently, perhaps about 1983. The height class distribution for the younger population (Fig. 4) is consistent with a flush about that time. However, the same distribution would have resulted if seedling recruitment after 1977 had been steady and survival was low.

Growth Rates.—Height of seed regeneration inside Puu O Kauha appeared to increase linearly with age during the first 14 years of recovery (Fig. 5a). However, when an exponential growth model (Fig. 5b) was fitted to age-height data and predicted mean heights were plotted along with the actual mean heights (Fig. 5a), it was clear that our data lay on the nearly linear portion of an exponential height growth curve. If the exponential model is valid, height growth will decline rapidly after 25 years of age. At that age, mamane should be over 4 m in height or 67 percent of maximum height. Full height should be reached at 100 to 140 years of age.

Mamane crown cover is an important habitat correlate for palila (Scott et al. 1984). A logarithmic model was used to describe the relationship between tree height and crown diameter (Fig. 6). Using the height model in conjunction with the crown diameter model, we estimated that 25 year old seed regeneration on the west side of Mauna Kea should have a crown diameter of about 4 m. At 100 to 140 years of age, trees should have crown diameters in excess of 7 m.

Recovery from Mouflon Sheep at Wailuku

In this section we use recovery of mamane inside the Wailuku exclosure as an indicator of the broader recovery that should occur on the east side of Mauna Kea now that mouflon have been partially eradicated.

Abundance of Regeneration and Stand Structure.—Recruitment of mamane seedlings continued inside the Wailuku exclosure from 1977 to 1986. There were the equivalent of 69 seedlings/ha in 1977 and 136 seedlings/ha in 1986. Seed regeneration in 1986 averaged 0.8 m in height and 0.7 m in crown diameter.

Sprout regeneration of mamane was observed inside Wailuku. We counted the equivalent of 37 sprout clusters/ha. Those averaged 1.2 m in height and 1.3 m in crown diameter. Even though seedlings outnumbered sprouts by a ratio of about 4:1, sprouts comprised almost
one-half of the crown cover created by natural regeneration. So after 14 years of protection, sprouts form a significant component of the recovering stand.

**Variability of Seedling Recruitment.**—Like Puu O Kauha, the height class distribution inside Wailuku was markedly different from those inside the three older exclosures even though all had been protected about the same length of time when the data were collected. The three older exclosures each contained over 600 individuals/ha that were 1 m or less in height at 16 years of age, while Wailuku contained fewer than 100 such individuals/ha at 14 years of age (Fig. 2). These differences again emphasize that recovery will not be uniform around the mountain.

The height class distribution for seed regeneration indicated that the population was sustaining itself (Fig. 2). This distribution was consistent with a low, but steady rate of seedling recruitment coupled with a low to moderate rate of survival (Scowcroft and Giffin 1983).

There was no evidence of episodic recruitment at Wailuku.

**Growth Rates.**—Growth of mamane regeneration was slower at Wailuku than at Puu O Kauha and the older exclosure sites. The tallest mamane of seed origin at Wailuku was 2.6 m while the tallest at each of the other sites was 3.6 m at Puu O Kauha, 3.8 m at Kaluamakani and Puu Kole, and 3.1 m at Puu Nanaha.

Like seed regeneration at Puu O Kauha, young mamane at Wailuku showed a linear rate of height growth (Fig. 5a). But the data fit an exponential growth model equally well and this model made more biological sense than the linear model (Fig. 5b). As at Puu O Kauha, the Wailuku height growth data fit a linear model only because the data fell on the nearly linear portion of the exponential growth curve.

The growth model emphasizes the slower rate of growth at Wailuku. The Wailuku model predicts rapid growth through 50 years of age, whereas the Puu O Kauha model predicts rapid growth only through 25 years of age. If the model is valid, full height should not be achieved at Wailuku until trees are over 150 years of age.

**Response of Palila to Mamane Recovery**

The palila population has been monitored by the Hawaii Division of Forestry and Wildlife and U.S. Fish and Wildlife Service since 1980. Their data indicated that the palila population during the non-breeding season was greatest in 1981, the year that feral sheep eradication was completed (Fig. 7). The population decreased for the next five years and in 1985 it reached its lowest level since the original census of 1975 when the population during the non-breeding season was estimated at 1,595 birds (van Riper et al. 1978). The population expanded in 1986, 1987, and 1988, but it is not known if this expansion will continue.
We suspect that the improvement in habitat brought about by the eradication of feral sheep has not advanced far enough to benefit palila. However, no one to our knowledge expected a favorable response so soon.

LONG TERM IMPLICATIONS

Throughout this paper we have emphasized mamane and for good reason. The tree supplies the palila with its staple food, mamane pods. Van Riper (1980a) found that timing and success of palila breeding were correlated with peak production of mamane pods. Scott et al. (1984) reported that low availability of mamane pods appears to be a key factor limiting growth of the palila population.

The recovery now underway over large portions of the tree-line zone will eventually mean a larger food supply for palila. We have observed sparse pod production on 14 and 16 year old mamane. By extension, we expect the developing stands of mamane to come into pod production about the year 2000. But because production will be below its potential, the increased food supply may not benefit palila until well into the 21st century.

The minimum size of mamane used by palila may be a factor controlling the birds response to habitat improvement. Large mamane trees are preferred for nesting and feeding (van Riper 1980a). Palila are found in greatest densities in pure mamane woodland composed of relatively tall trees, a high proportion of mamane crown cover, and a native understory (Scott et al. 1984). Small trees with pods may not benefit palila if the birds avoid them.

Our data indicated that it may take more than 30 years for mamane regeneration to reach large size (e.g., 5 m in height and 4 m in crown diameter). Assuming that 80 percent of the seed regeneration outside Puu O Kauha survives (a residual stand of 350 trees/ha), then mamane crown cover would be about 45 percent, a marked increase over the current level of 17 percent (Scowcroft 1983). Thus, we do not foresee the increase in individual tree size and crown cover measurably benefiting palila until the early part of the 21st century.

The recovery now underway should increase the food production capacity of the forest, but as noted above, this effect is still years away. Until then, large annual fluctuations in the size of the palila population, such as those in Fig. 8, will probably continue as a function of weather and food stocks (Scott et al. 1984). Even after recovering areas come into full pod production, palila will remain susceptible to weather-induced, mountain-wide reductions in food production.

Recovery of mamane in the low elevation woodlands near Puu Laau has not been as vigorous as in the tree-line zone. Yet the highest density of palila is centered around the 2,300 m elevational contour near Puu Laau (Scott et al. 1984). Benefits of recovery near Puu Laau will therefore accrue slowly and may not be detectable due to the large and overriding contribution of mature trees, which dominate the area. Provided that no catastrophe befalls the woodland around Puu Laau, such as wildfire, we expect the high-density cell to expand upslope with time rather than downhill or laterally. This expansion will be due to a growing capacity of upslope woodlands to supply palila with food and other habitat requirements.

Recovery of mamane and associated native vegetation is well under way in the tree line zones where feral sheep once did the greatest damage. But as shown in an earlier section, recovery will not be uniform. For this reason, managers may wish to plant mamane and other native species to impose a measure of uniformity and to hasten recovery. The Hawaii Division of Forestry and Wildlife has already done some successful reforestation work in the tree-line zone, even planting mamane in areas devoid of living or skeletal remains of mamane. We believe such effort will benefit palila in the long run.

Now that mouflon have been controlled, our data indicate that mamane and other native species will also reestablish in tree line areas on the eastern flank of Mauna Kea. There too managers may wish to hasten recovery by planting native species.

Our studies indicate that recovering woodlands on the west side of the mountain will not benefit palila...
until well into the 21st century. Until then, the largest concentration of palila (that centered around 2,300 m elevation near Puu Laau) will remain dependent on the woodland’s existing food production capacity. But dense, highly-flammable understory vegetation, mainly naturalized grasses, put the woodland at risk. If a wildfire occurred in this area, it would probably destroy most mamane, the major source of palila food. The result for palila could be disastrous. Thus, it is imperative that fire prevention plans recognize this threat and that suppression actions be swift if needed.

The future holds the answer to restoration of palila to non-endangered status. We are, as one wildlife biologist stated recently, “cautiously optimistic that the birds may positively respond to the removal of ungulates from palila habitat” (Sparling 1987).

LITERATURE CITED


