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Abstract

Under the multiple-use paradigm, conflicts may arise when protection of an endangered species must compete with other management objectives. To resolve such a conflict in the Critical Habitat of the endangered Hawaiian honeycreeper, palila (*Loxioides bailleui*), federal courts ordered the eradication of introduced ungulates responsible for damaging the māmane (*Sophora chrysophylla*) forest on which palila depend. During 1980–2011, a total of 18,130 sheep (*Ovis aries* and *O. gmelini musimon*) and 310 goats (*Capra hircus*) were removed from Palila Critical Habitat (PCH) primarily by public hunters (54%) and secondarily by aerial shooting. Nevertheless, our analysis indicates that ungulates have increased over time. Palila numbers have declined sharply since 2003 due to long-term habitat degradation by ungulates and drought. Although culling ungulate populations has allowed some habitat improvement, their complete removal is necessary for palila to recover, especially given the potential for continued drought. Introduced predators are being controlled to reduce palila mortality, māmane and other native trees are being planted to restore some areas, and fencing is being constructed to prevent ungulate immigration. Funds are recently available for more effective eradication efforts, which are urgently needed to eliminate browsing damage in PCH and protect the palila from extinction.

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Introduction

Multiple-use management of natural areas in the Hawaiian Islands often includes sustained-yield public hunting of introduced large game mammals, which presents a fundamental conflict with the conservation of forests, watersheds, and wildlife. The native biotas of oceanic islands are notably vulnerable to the effects of introduced species with which they have not co-evolved (Coblentz, 1978; Bowen and Van Vuren, 1997). Herbivorous mammals, which are among the most consequential of invasive species, were not present in the Hawaiian Islands until their introduction by Western explorers beginning in 1778 (Tomich, 1986). The maintenance of game populations has resulted in the wounding and mortality of mature trees by browsing and bark-stripping, suppressed forest regeneration, and reduced availability of plant hosts to dependent native animals (Scowcroft and Giffin, 1983; Scowcroft and Sakai, 1983; Courchamp et al., 2003).

Western explorers introduced domestic livestock such as cattle (*Bos taurus*), goats (*Capra hircus*), and sheep (*Ovis aries*) throughout the remote Hawaiian Islands to resupply ships on worldwide voyages (Tomich, 1986). Livestock protected by royal order became feral and proliferated with little predation or competition. Sheep were reported at the summit of Mauna Kea, the highest peak in the Pacific Ocean, only 32 years after their introduction in 1793, and by 1822, "immense herds" of wild cattle occupied the area around Mauna Kea (Ellis, 1917). Concern for range conditions prompted ranchers to round up feral cattle by 1830. Territorial foresters also recognized the deforestation caused by feral herbivores in the early 20th century, began fencing a 212-km^2 area of Mauna Kea in 1934, and removed tens of thousands of sheep and other ungulates over the next decade (Bryan, 1937a, 1937b, 1947). Management priorities to enhance game hunting during the mid-20th century, however, allowed sheep populations to rebound and goats to become abundant, although goats had not been present on Mauna Kea before 1925 (Bryan, 1927). To further enhance sport hunting, European mouflon sheep (*O. gmelini musimon*) were released on Mauna Kea during 1962–1966 as pure-bred stock and mouflon x feral sheep hybrids (Tomich, 1986). The condition of Mauna Kea deteriorated until it was considered unsustainable for sheep, native plants, and a once common bird in the endemic honeycreeper subfamily (Drepanidinae), the palila (*Loxioides bailleui*) (Warner, 1960).

Palila inhabited about 1300 km^2 of Hawai'i Island when Westerners arrived, but they were once also distributed in lowland habitats on Kaua'i and O'ahu prior to human occupation (Olson and James, 1982; Burney et al., 2001; James and Olson, 2006). Their range has since been reduced to a core area of about 65 km^2 on Mauna Kea due mainly to browsing damage to the endemic māmane tree (*Sophora chysophylla*), whose seeds are the main food of palila (Fig. 1; Banko et al., 2002a; Banko et al., 2013). While cattle converted low-elevation māmane forest to pasture, goats and sheep degraded high-elevation habitat (Scowcroft, 1983; Scowcroft and Giffin, 1983), restricting the elevation range of māmane forest available to palila (Scott et al., 1984).

The palila was formally listed as an endangered species in 1967 by U.S. Fish and Wildlife Service (USFWS, 1967) and is considered critically endangered internationally (International Union for Conservation of Nature, 2013). Critical Habitat (24,357 ha) was designated in 1977 (USFWS, 1977), and additional habitat was designated in the species' recovery plan (USFWS, 2006; Fig. 1.). Palila Critical Habitat (PCH) includes lands on Mauna Kea between about 2000–3100 m elevation, over 98% of which is managed by the Division of Forestry and Wildlife (DOFAW), of the Hawai'i Department of Land and Natural Resources (HDLNR), as the Mauna Kea Forest Reserve and Ka'ohe Game Management Area (USFWS, 1977). Indicating the severity of the species' conservation status, in 2012 the palila occupied just 27% of PCH (Banko et al., 2013), and the population estimate was 2176 (95% CI = 1749–2640), which was 57% less than the estimate for 1998 (Camp and Banko, 2012).

Juvik and Juvik (1984) summarized the history of human activity on Mauna Kea and analyzed planning and management decisions related to palila, concluding that multiple-use strategies would fail to protect the species and that eradication of sheep and goats was the only viable strategy to ensure long-term survival of the palila. They also reviewed circumstances leading to a federal lawsuit and subsequent court orders to permanently remove introduced feral sheep and goats valued by game hunters from PCH (Appendix). Following the removal by 1982 of "virtually all feral sheep and feral goats" (USFWS, 1986), Juvik et al. (1992) noted improved habitat conditions and others (Scowcroft and Conrad, 1988; Scott et al., 1984) also reported vegetation recovery. Although only "small numbers" of feral sheep remained in PCH, mouflon and feral sheep hybrids continued to occupy the area (USFWS, 1986) because they had been excluded from the original ruling, but in 1987 the court ordered the removal of all *Ovis* spp. (Pratt et al., 1997; Houck, 2004; Appendix).

Decades of study have implicated continued unsustainable browsing by sheep within PCH in degradation of the māmane habitat on which the palila depends (Scowcroft, 1983; Scowcroft and Giffin, 1983; Scowcroft and Conrad, 1988; Reddy et al., 2012). The effects of long-term browsing have recently been compounded by a severe, prolonged drought, which has caused the further deterioration of habitat carrying capacity and a sharp decline of palila abundance (Banko et al., 2013). Although fence construction, habitat restoration, and predator control have recently accelerated, palila may respond slowly to improvements due to their restricted diet, low rate of reproduction, and preference for larger, older māmane trees (van Riper et al., 1978; Scott et al., 1984; Pratt et al., 1997; Banko et al., 2009).

Thirty years after the analysis of Juvik and Juvik (1984), we reconstruct the history of ungulate management from unpublished reports and summarize published and unpublished research to evaluate progress in recovering the palila and restoring its habitat. In the sections that follow, we examine whether sustained game hunting has been an effective tool for improving the carrying capacity of PCH or whether it continues to jeopardize palila recovery by delaying, diluting, and perhaps thwarting conservation efforts. We specifically analyze the history and effectiveness of management to remove ungulates from PCH before 1980 and during 1980–2011, as well as the response of vegetation to ungulate management. We also consider additional threats to palila and the subalpine forest ecosystem from other invasive species and changing environmental conditions. In particular, we evaluate the impacts of prolonged drought on population trends of palila and other sympatric forest bird species during a recent 14-year period. Additionally, we report on efforts to mitigate, manage, and recover habitat for palila and to manage pests and predators. In a synthesis of these topics, we assess the overall compatibility of long-term multiple-use management with the recovery prospects of palila.

History and Evaluation of Ungulate Management

MANAGEMENT BEFORE 1980

The destructiveness of introduced ungulates to native ecosystems led the territorial government to establish the forest reserve system in 1903. Actions to protect water, soil, and forest resourc-

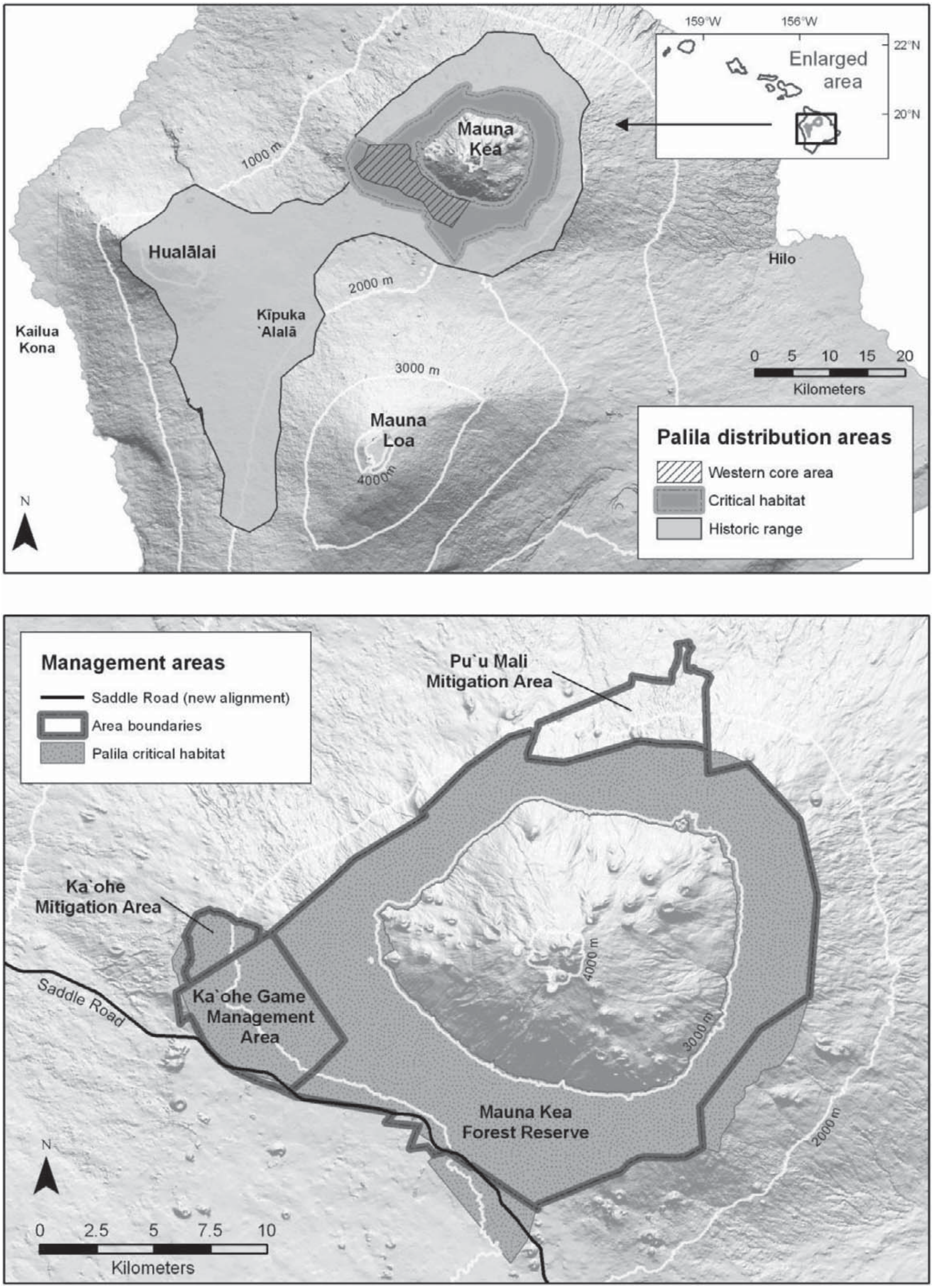

Figure 1. Upper figure shows the historic range of palila on Mauna Kea, Hualālai, and Mauna Loa volcanoes, Hawai'i Island, with the current distribution in Critical Habitat; inset shows the major Hawaiian Islands. Lower figure shows the management jurisdictions on Mauna Kea.

es in the Mauna Kea Forest Reserve were initiated in the 1930s with federal support through the Civilian Conservation Corps and the assistance of cowboys from ranches that would benefit from a reduction in competition for forage with feral livestock (Bryan, 1937a; Warner, 1960). In 20 months, crews constructed 89 km of stock-proof fence around Mauna Kea in 1937 (Bryan, 1937b). From 1921 to 1946, 13 horses (*Equus caballus*), 1447 pigs (*Sus scrofa*), 23 cattle, 797 goats, and 46,765 sheep were removed, most between 1936 and 1946 (Bryan, 1937a, 1947), leading to noticeable habitat recovery (Kramer, 1971).

Roads and trails built to support construction of the forest reserve fence increased access for sport hunting, and during the 1950s management shifted from watershed protection to game management (Kramer, 1971). As a result, the sheep population was allowed to grow through hunting season closures, thereby reversing the initial gains in habitat recovery (Warner, 1960). Attempts to maintain a stable sheep population through the manipulation of hunting seasons and bag limits failed due to opposition from hunters (Kramer, 1971). Habitat damage caused by the increasing population prompted managers to build stock exclosures in 1963 to demonstrate to the public the destructive effects of browsing. Within a few years of construction, recovery of vegetation was marked inside but absent outside the exclosures. Even so, attitudes and management changed little despite visually dramatic differences in vegetation (Kramer, 1971). The introduction of European mouflon sheep further propelled sport hunting as the management goal during the 1960s (Kramer, 1971; Tomich, 1986). Eventually, competition for a limited amount of forage among the growing populations of feral sheep, mouflon, and goats on Mauna Kea became a concern for state game managers. The relatively small population of feral pigs was not thought to compete significantly with the other game animals. To increase habitat carrying capacity for both mouflon and feral sheep, state wildlife biologists recommended eliminating feral goats, the least-favored game species, and closely regulating feral sheep numbers (Giffin, 1976). To protect the palila, however, it would be necessary to "substantially reduce or totally remove all feral sheep," because even relatively small numbers of aggregated sheep heavily damaged the habitat (Giffin, 1976). The original palila recovery plan also recommended the removal of sheep (USFWS, 1978).

MANAGEMENT AFTER 1980

Despite the management recommendations to reduce populations of browsers, litigation was the actual impetus for action to protect PCH (Juvik and Juvik, 1984). Nevertheless, the matter was not simply or quickly resolved and legal battles continue (Appendix). Because the conditions of the original and subsequent court orders still have not been met, the U.S. District Court and plaintiffs continue to evaluate compliance through periodic (usually semiannual) reports prepared by HDLNR and submitted by the Hawai'i attorney general's office (HDLNR 1980–2011: status reports 1–64).

Using information in the HDLNR reports, we analyzed the eradication program during three periods according to the response of managers to changing legal mandates. During the first eight years (Period I: 1980–1987), only feral sheep and goats were targeted for eradication and mouflon sheep and hybrids continued to be managed as game species. During this period, feral sheep and goats were shot from the air only in 1981, but hunting restrictions were eased to encourage greater public participation. During Period II (1988–1998), which began when the court ordered the eradication of mouflon sheep as well as feral sheep, public hunting regulations were further liberalized and staff shot from helicopters in 8 of the 11 years, suspending aerial shooting during 1995–1997. In Period III (1999–2011), helicopter shooting was conducted at least semiannually, as stipulated by court order in 1998 (Appendix).

Period I (1980–1987)

The state's strategy for eradication was to first reduce animal numbers with public hunting before implementing staff hunting to finish the job (HDLNR, 1981: 4th status report). Just eight months before the first court-ordered deadline (31 July 1981) for eradicating feral sheep and goats, the state expressed confidence in this approach and expected no serious problems in complying with the order (HDLNR, 1980: 3rd status report):

> *Although public hunting has been successful as a mechanism of feral sheep and goat removal on Mauna Kea, it is expected that hunter participation and harvest success will decrease as the animal populations lower and the remaining sheep and goats draw back to more remote areas. Therefore, the second phase of the eradication program; i.e., direct action by the staff of the Department in shooting and removing feral sheep and goats, will commence in late January. With the ending of the game bird hunting season on weekends as of January 18, 1981, public hunting for sheep and goats will be shifted back to Saturdays and Sundays. In addition, staff shooting will commence on weekdays beginning January 19, 1980* [sic, 1981]. *The public hunting season will remain open until the eradication is completed or until there is no hunter participation. Staff efforts will continue throughout the period and helicopters will be employed if necessary as the time deadline approaches. The goal will be to eliminate the last sheep and goat by June 30, 1981, a month prior to the deadline set by the court in order to accommodate any last minute difficulties or deal with re-invasions of sheep or goats from outside the forest reserve. No serious problems in complying with the court order are anticipated.*

The State's sport hunting strategy encompassed a variety of hunting techniques, irrespective of their efficacy. To accommodate devotees of archery, handguns, and muzzleloaders, a large area of palila core habitat, Ka'ohe Game Management Area, continued to be reserved for their exclusive use during most—but not all—of the eradication program (HDLNR, 1981: 4th status report). High-powered rifles, the most effective sport hunting tool, were allowed everywhere else. Nevertheless, it was recognized early that if the "hunters-first" strategy was to succeed, hunting regulations would need to be liberalized. During Period I, rifle hunting was allowed over a range of two to seven days per week during open seasons, but seasons were typically open for only three to four months each year until 1987, when they were extended to six months (HDLNR, 1988: 18th status report).

Before 1980, hunting was allowed only by lottery (feral sheep) or permit (mouflon) on weekends during August and September, and bag limits were set (Giffin, 1976, 1981). In September 1979, a special four-day season was opened and 279 hunters participated with a 34% success rate (animals taken per hunter-trip), which was considered slightly above average (HDLNR, 1980: 1st status report). In May 1980, hunting was opened on weekends without a special permit or seasonal bag limit but with a daily bag limit of three goats and one sheep per hunter (HDLNR, 1980: 2nd status report). In 1981, hunting was extended to four and then seven days per week with no daily or seasonal bag limits (HDLNR, 1981: 4th–6th status reports), but the season soon reverted to weekends only "due to the significant lack of public hunting activity (particularly on weekends) … and the necessity to enlist staff shooting in order to continue effective eradication" (HDLNR, 1981: 7th status report). With increased hunting opportunities during June 1980 through October 1982, it was estimated that 1490 sheep were removed during about 4000 hunter-trips, resulting in an overall success rate of 37% (HDLNR, 1983: 9th status report). Our interpretation of the removal information in the status reports (Table 1) indicates that 1347 sheep were eliminated during 1980–1982,

TABLE 1

Numbers of feral goats and sheep (including mouflon and hybrids after 1995) removed from Palila Critical Habitat by public hunters and staff (primarily aerial shooting) during the court-ordered eradication program (1980–2011). Data were derived from unpublished status reports submitted to U.S. District Court, District of Hawai‘i, by Hawai‘i Department of Land and Natural Resources (HDLNR 1980–2012: 1st–64th status reports). Information was extracted from report narratives when possible due to occasional discrepancies or inconsistencies with information in report tables.

	Sheep				Goats		
Year	Public hunting	Aerial/ staff	Total removed	Carcasses salvaged	Public hunting	Aerial/ staff	Total removed
1980	716		716		43		43
1981	611	367	978		69	36	105
1982	20	4[a]	24				
1983	21	1[a]	22				
1984	36		36				
1985	94	47[a]	141				
1986	84	13[a]	97				
1987	915	16[a]	931		25		25
1988	146	1265	1411		1		1
1989	118	48	166				
1990	186	186	372				
1991	93	497	590				
1992	22	130	152				
1993	14	24	38				
1994	50	123	173				
1995	106		106				
1996	142		142				
1997	228		228				
1998	357	196	553				
1999	193	242	435	13			
2000	156	247	403	66			
2001	331	268	599	170			
2002	202	319	521	154			
2003	170	270	440	130			
2004	80	220	300	156			
2005	114	282	396	169			
2006	269	320	589	177			
2007	389	647	1036	234			
2008	863	688	1551	358			
2009	875	920	1795	466			
2010	838	243	1081	126		100	100
2011	1421	687	2108	421		36	36
Total	9860	8270	18,130	2627	138	172	310

[a] No aerial shooting; staff hunting was conducted only on the ground.

yielding a slightly lower success rate of 34%. Nevertheless, these results give an indication, which may be overly optimistic given the long season closures, of the efficacy of public hunting as the primary method for eradicating sheep.

At the time of the July 1981 eradication deadline, aerial surveys detected few remaining feral sheep and goats, but movement in and out of PCH through gaps in the 44-year-old fence and the wariness of the animals made both population estimation and eradication problematic (HDLNR, 1981: 7th status report). Even so, the State concluded that eradication could be achieved with additional hunting by the public and staff and by repairing or constructing fences to stop ingress. In the five years following 1981, no goats and relatively few feral sheep were apparently removed from PCH, despite ongoing public hunting and some fence maintenance (Table 1). The low removal rate during 1982–1986 could be interpreted in various ways, but reports indicate that few animals were being encountered during ground hunts by the public and staff and that few animals were seen during aerial surveys. Alternatively, the low annual harvests could reflect low removal effort, given that public rifle hunting was closed for about 30 months from November 1981 into August 1985 due to "a lack of feral sheep and goats to hunt," and hunting was usually restricted to weekends even during the open season (HDLNR, 1983–1985: 9th–13th status reports). During the same time, hunting by staff was conducted episodically and only on the ground, with only two hunting trips reported during one eight-month period (HDLNR, 1983: 9th status report) and "periodic" hunting at other times, including when other work was being conducted. Archers, on the other hand, were permitted to hunt on a daily basis within Ka'ohe Game Management Area during some of this period (HDLNR, 1983: 10th status report).

Regardless of the factors accounting for the reduced harvest previously, surprisingly large numbers of feral sheep, mouflon sheep, and hybrid sheep were eliminated by hunters in 1987 and by helicopter shooting in 1988 as the second court-imposed eradication deadline, 27 January 1988, approached (Table 1; HDLNR, 1988: 18th status report and supplemental report). Just ahead of the eradication deadline, the season for rifle hunting was increased from three to six months and from weekends only to four days a week (HDLNR, 1988: 18th status report). Limited effort to control hybrids began in 1986 (HDLNR, 1986: 15th status report), but 1987 was the official start of the program to eradicate both mouflon and hybrids (HDLNR, 1988: 18th status report). Until then, mouflon had been managed as a game species.

During Period I, only 448 (15%) of the total 2945 feral sheep eliminated in PCH (Table 1) were removed by staff in helicopters (about 367) or on the ground (about 72 by shooting, 9 by herding). The nine animals that were herded out of PCH were "mouflon/hybrid" sheep and apparently fled through one or more gaps in the then 49-year-old fence (HDLNR, 1986: 15th status report). Staff removed the majority of sheep by helicopter shooting in 1981, the year of the first court-ordered eradication deadline, but they removed none or few in other years. During Period I, staff hunting also accounted for 21% of the 173 feral goats removed.

Period II (1988–1998)

Following the harvest of 915 sheep, including mouflon and hybrids, by public hunters in 1987 and the elimination of 1154 sheep by aerial shooting in 1988, relatively few animals were removed during the remaining 10 years of Period II (Table 1). Staff shot sheep from helicopters in 8 of the 11 years, suspending aerial control during 1995–1997. More than 200 sheep were removed by aerial shooting in only one other year (1991) besides 1988. Even though the hunting season was lengthened considerably and bag limits were abolished, hunters harvested more than 200 sheep only in the two final years of the period.

In 1988, rifle hunting was allowed from three to five days per week, and the season was extended from six to nine months (HDLNR, 1989: 20th status report). In the following year, the open season was expanded to five days a week and hunting was allowed in all months (HDLNR, 1990: 21st [sic] status report). To increase the harvest of animals by the public, staff-assisted hunts were implemented in 1998 whereby participants hunted as they hiked back to their vehicles after being transported by staff to locations near concentrations of sheep. This program was quickly abandoned due to low hunter participation and because only 15 sheep were taken (HDLNR 1998–2000: 37th–40th status reports). Additionally, information about the distribution of animals was made available to hunters by HDLNR staff to increase the efficacy of removal by hunting. In keeping with their efforts to expand hunting opportunities, the State continued to reserve large areas of PCH for low-yield hunting methods, such as archery and pistols. Although still not as effective as high-powered rifles, when muzzleloaders were allowed into the special hunting area in 1997, the harvest rate increased from 9.7% for archers to 78.3% for muzzleloaders (HDLNR, 1998, 1999: 36th and 38th status reports).

Period III (1999–2011)

As stipulated by court order in 1998 (Appendix), the State increased its efforts to remove sheep from PCH by further liberalizing hunting regulations and more frequent aerial efforts. Beginning in 1999, all sheep could be hunted seven days a week, except during a special feral pig hunt in January, March, and April (HDLNR, 1999: 39th status report) and during the game bird hunting season in November–December (HDLNR, 2000: 40th status report). Although a large area continued to be reserved for archers and others not using high-powered rifles, there were no restrictions as to the number, age, or sex of the animals taken. Moreover, helicopter missions were conducted at least semiannually. More than 200 sheep were killed by hunters in 8 of the 13 years, whereas aerial shooting removed at least 200 animals every year (Table 1).

AERIAL SHOOTING PROGRAM

Helicopter shooting and limited ground removal by staff or contractors accounted for 46% of the 18,130 sheep and 55% of the 310 goats removed from PCH (Table 1). The frequency and intensity of helicopter use varied greatly over the 32-year eradication program. Aerial shooting was first used during 30 days in June and July 1981, as the first court-ordered eradication deadline approached. Around the time of the second eradication deadline, 27 January 1988, and in the months that followed, one or two helicopters were deployed daily for 28 helicopter-days (HDLNR, 1988: supplement to 18th status report). Helicopter missions in 1981 and 1988 accounted for 45% of all aerial shooting during the entire eradication program.

From 1989 to 1994, helicopter use totaled only 15 days. Helicopter shooting was suspended in 1995 due to "funding constraints, and more importantly, the lack of a state contract for helicopter rental" (HDLNR, 1996: 32nd status report). Although aerial surveys were resumed in 1996, shooting from helicopters remained suspended until late 1998 (HDLNR, 1996–1999: 33rd–38th status reports). From 1987, when mouflon and hybrid sheep were targeted for eradication, to 1998, when helicopter use resumed after the three-year hiatus, aerial operations accounted for 48% of the 4862 sheep removed. Of the 2485 sheep removed by staff during this period, 2343 were shot from the air, 101 were driven out of PCH, 26 were shot by staff on the ground, and 15 were taken by public hunters in staff-assisted hunts.

Aerial operations during 1999–2011 involved a single helicopter flown from 2–10 days each year and accounted for 48% of the 11,254 sheep removed (Table 1). Of the 136 feral goats eliminated during this 13-year period, 60% were shot from the air and the remainder was removed by staff on the ground.

Aerial shooting was conducted for a total of 134 helicopter-days in 22 of the 32 years of the eradication program (1980–2011). Since 1988, when annual helicopter operations began, and excluding the hiatus of 1995–1997, the aerial shooting effort averaged 5.2 helicopter-days per year, with the length of a helicopter-day varying due to weather conditions and other factors. Although aerial missions have been conducted in all months of the year, most (64%) occurred during August–April, when relatively few palila nest (Banko et al., 2002a).

The wide variation in the number of animals removed annually (Table 1) suggests inconsistency in the aerial removal effort. Several factors may have affected the results of aerial operations, but because the level of effort was not quantified (e.g., animals removed per hours of flight) in State reports, inferences about removal rates should be viewed with caution. For example, radio-tagged sheep were tracked to locate and remove herds more efficiently during 1991–1994, but no mention of radio-tracking appears in later reports.

The practice of salvaging carcasses and distributing them to the public began in 1999 and more than 25% of carcasses were salvaged annually since 2000, reducing the efficacy of aerial shooting. Of the 5111 sheep shot from the air during 2000–2011, 2627 carcasses, or an average of 219 annually (mean = 52%; range = 27%–71%), were hauled by helicopter to access points for the public to claim (Table 1). HDLNR estimated that salvaging carcasses consumed about half of the helicopter flight time (Tummons, 2012), the cost of which was estimated at approximately $800 per hour.

UNGULATE REMOVAL RATES AND STANDING POPULATION

Sheep and goats were counted at least once a year during 1980–1999 (except 1995) to evaluate the efficacy of the eradication program, but population totals were often less than or similar to the number of animals removed during the same time period (HDLNR, 1991: 23rd status report). Although population monitoring was discontinued after 1999, results from the earlier counts suggest that populations were being grossly underestimated (see below for supporting detail). Notwithstanding unreliable survey results and substantial variation in the removal effort by public and staff hunters, it is noteworthy that the numbers of animals removed from PCH increased over time, suggesting that management efforts were being overwhelmed by reproduction and perhaps also to some degree by immigration.

Rates of removal increased over time as the eradication program evolved. During Period I (1980–1987), an average of 56 feral sheep was removed annually by HDLNR staff, mostly by shooting from helicopters. After mouflon and hybrids were targeted (Period II, 1988–1998, excluding 1995–1997), staff removed an average of 309 sheep annually. During Period III (1999–2011), when aerial shooting was conducted at least semiannually, staff removed an average of 412 sheep each year, 33% more than during Period II.

Information in the State reports is insufficient for identifying the responsible factors, but increased helicopter shooting may have accounted for at least some of the increase in removals from Period II to Period III. It is also likely that population growth due to reproduction and immigration contributed to the increase. Nevertheless, immigration of mouflon and hybrids into PCH was possible only because a population had become established on neighboring lands after animals had been driven out through gaps in the fence or had dispersed there unaided. One gap, for example, extended 8 km along the southern boundary of PCH (HDLNR, 1983: 10th status report). Today, in the aftermath of this range expansion, herds of animals are commonly seen inside and outside of PCH along Saddle Road. The problem of immigration was demonstrated in 2009, when feral goats moved into PCH after having been driven out of the adjacent Pōhakuloa Training Area by U.S. Army managers to protect endangered plants (HDLNR, 2010: 61st status report). At least one goat was observed (K. Brinck) as far north as the Puʻu Mali area in 2010, suggesting that the animals dispersed widely. In response to this incursion, ground and aerial shooting by HDLNR staff removed 136 goats from PCH during 2010–2011, more than 20 years after goats were thought to have been eliminated from PCH (HDLNR, 2010–2012: 61st–64th status reports).

The rate of sheep removal by public hunters also increased substantially during Period III of the eradication program. Although hunters claimed an average of 183 sheep annually during Period II (1988–1998, excluding 1995–1997), they removed an average of 454 each year during Period III (1999–2011). State reports do not allow an analysis of trends in hunting effort during these two periods, but longer open seasons in Period III may have contributed to an increase in the annual harvest. Even so, eradication has not been achieved despite the annual removal of hundreds of sheep by the public and hundreds more by aerial shooting, indicating that more effective methods are needed to achieve this goal. Moreover, given an average annual increase of 125 animals removed by public hunting and aerial shooting combined (linear regression: $R^2 = 0.66$, $P < 0.001$, 1999–2011; data not shown), it is likely that the sheep population has been increasing rather than declining since 1999.

Some factors that might affect the rate of sheep removal are changes in the genetic composition and behavioral characteristics of the population. Over the decades, the population has shifted from purely feral animals to hybrids dominated by mouflon characteristics (Hess and Banko, 2011). In 1980, feral sheep were estimated to be six times more abundant than mouflon in PCH (HDLNR, 1980: 2nd status report), but by 2006, feral and mouflon sheep were no longer being differentiated in State reports (HDLNR, 2007: 53rd status report). During 1936–1946, when an average of 4251 feral sheep was removed annually for watershed protection, large herds were rounded up by men afoot or on horseback and killed in holding pens (Bryan, 1947; Kramer, 1971). Despite population fluctuations in the following decades (Tomich, 1986), public hunters also could expect to encounter large herds of sheep whose predictable behavior made them relatively easy targets. In contrast, mouflon sheep were found more often in small bands of 2–10 individuals with herd size rarely exceeding 100 (Giffin, 1981). Thus, as feral sheep numbers were initially reduced and the proportion of mouflon and hybrids increased, the public hunting and aerial shooting strategy that was developed to take advantage of feral sheep aggregation behavior may have become less efficient when applied to mouflon. The apparent increase in the population since 1999 may have resulted partly because methods were not adapted to a population that was becoming progressively dominated by hybrid mouflon. There also might have been effects from animals learning to avoid helicopter activity and from incorporating carcass salvaging into the eradication program.

Although sheep harvest rates have fluctuated annually over the past 60 years, data averaged over approximately 10-year periods indicate that the minimum population has consistently numbered in the thousands, as would seem to be the case even today, as discussed below. The average annual yield of 866 sheep from both public hunting and aerial shooting during 1999–2011 is similar to yields just from public hunting before the eradication program: 735 during 1947–1956, 1201 during 1957–1966, and 852 during 1967–1979 (HDLNR, 1980: 1st status report).

The numbers of sheep removed annually from PCH is indicative of a larger standing population from which these removals have been drawn. The standing population has not been demographically closed to emigration or immigration and it ranges across the boundary of PCH. Although we do not have useful ungulate abundance survey data, we can calculate the minimum size of the standing population from estimates of annual population growth rates of mouflon on Mauna Kea and Mauna Loa. Giffin (1981) reported the annual population growth rate for mouflon on Mauna Kea to be 14.7%–16.9%. Hess et al. (2006) estimated a minimum annual growth rate of 22.1% for unhybridized mouflon at the Kahuku Unit of Hawai‘i Volcanoes National Park on Mauna Loa. Using these estimates, we can determine upper and lower limits for the minimum population of sheep capable of withstanding the levels of removals that have occurred. It is important to understand that to sustain the same level of removal, a standing population with a lower annual growth rate would need to be larger than a population with a higher annual growth rate (Fig. 2). Using a recent peak in removals as an example, a population of 8507 sheep would have been necessary to sustain the 1795 removals in 2009, given an annual population growth rate of 22.1%. A population of 12,210 would have been necessary to sustain the same number of removals if the annual population growth rate had been 14.7%. Therefore, during 2005–2009, when the number of removals increased each year, the population sustaining these removals likely increased as well (Fig. 2). Population levels sustaining the observed numbers of removals could be lower than the levels we project (Fig. 2) if annual growth rates of the Mauna Kea sheep population have increased sharply since the 1980s, as might be expected if, for example, shooting was disproportionately directed at rams, as indicated by Giffin (1981). An additional complication is that increasing immigration rates into PCH from adjacent lands might also be supporting these harvest rates, although there is no data with which to evaluate this supposition. Without regular population surveys, such increases would go undetected, and without a change in the control effort, the population could continue to grow.

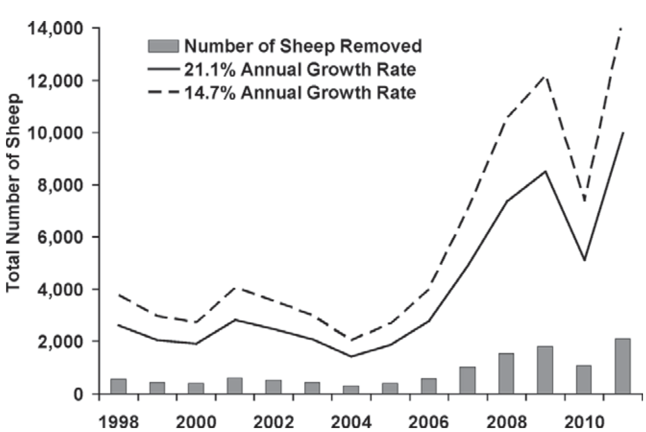

Figure 2. The number of sheep removed annually from Palila Critical Habitat on Mauna Kea and the minimum abundance of sheep necessary to sustain removals at annual population growth rates of 14.7% and 21.1%.

Evidence from vegetation studies, as discussed below, suggest that sheep populations may have rebounded as the carrying capacity of the habitat increased, which would have occurred as māmane and other forage species regenerated following ungulate removals. In fact, managers recommended increasing hunting pressure to reduce the sheep population, which they believed would enhance the habitat carrying capacity for game on Mauna Kea (Kramer, 1971; Giffin, 1976, 1981). Maintaining animal numbers within the sustainable limits of the resources available in the habitat has been a longstanding goal of game managers (Leopold, 1933), but in Hawai‘i, sustaining ungulate populations for game hunting, as generally practiced in North America, is incompatible with native ecosystem protection (Lepczyk et al., 2011).

SUMMARY OF UNGULATE MANAGEMENT

The State's original strategy of using public hunting supplemented with aerial staff shooting to comply with the court orders to eradicate sheep and goats was in effect at least through 2011. Decades after the 1988 eradication deadline, public hunting continues to be the primary method used in PCH to remove all forms of sheep, which are now commonly thought to be mainly hybrids dominated by mouflon characteristics. Not only has the public been the primary agent in the eradication effort, accommodations have been made for a variety of hunting methods, regardless of their effectiveness in culling the sheep population. More sheep were harvested by public hunting than were removed by aerial shooting in most years during 1980–2011. The numbers of sheep eliminated annually by both public hunting and aerial shooting increased over time but especially since 2007. Although population surveys were not conducted to evaluate the effectiveness of the eradication effort, the increasing rate of removals suggests an increase in the population from which they were taken. Increased population growth late in the program would be expected if earlier culling enhanced habitat carrying capacity and efforts to remove animals were not increased. Relaxed hunting regulations and more frequent helicopter shooting since 1999 may also explain some of the increase in the harvest. The sheep population has become dominated by mouflon hybrids, also suggesting that methods adapted for controlling feral sheep are less effective at controlling mouflon. Mouflon and hybrid sheep dispersed and were driven out of PCH, enabling both the spread of these populations to new areas and the immigration of animals back into PCH through gaps in the fence, which was only sporadically maintained since its completion in 1937. For these reasons, the longstanding program to remove ungulates by public hunting with supplementary aerial shooting has fallen far short of achieving eradication.

Response of Vegetation to Ungulate Management

Destruction of the vegetation by feral sheep was widespread and extreme by 1936, when a major program was begun to remove introduced ungulates from the Mauna Kea Forest Reserve (Bryan, 1937a; Hartt and Neal, 1940). The scale of the damage was such that by 1960 the condition of the vegetation and soil was still desperately poor (Warner, 1960), despite the removal of over 61,000 feral sheep in the preceding 25 years. Nevertheless, māmane can regenerate rapidly following the culling of sheep, as was observed early during the HDLNR eradication efforts (HDLNR, 1980: 1st status report) and later, as discussed in the following sections. Evidence presented below suggests that māmane regenerated robustly following the large-scale ungulate removal effort of the 1930s and

1940s, giving rise to many of the medium and large trees observed today (Banko and Farmer, 2014). The effect of the widespread regeneration of māmane observed on Mauna Kea since 1980 may have enhanced habitat-carrying capacity for ungulates, thereby accelerating population rebound.

EXCLOSURE STUDIES NEAR TREE LINE

In an attempt to demonstrate to hunters that sheep were drastically reducing the carrying capacity of the habitat for game populations, HDLNR fenced small plots of habitat to illustrate how native plants would recover if protected from browsing (Kramer, 1971). Three sheep exclosures were built in 1963, three more were added in 1972, and a seventh was added in 1976. The exclosures encircled the mountain near tree line where sheep browsing was most intense and were located near main roads. The initial response of vegetation inside and outside the exclosures led researchers to conclude that sheep were suppressing native forest regeneration and to predict that reducing or eliminating browsing pressure would allow native plants to reproduce and establish despite the inevitable proliferation of introduced plant species (Scowcroft and Giffin, 1983). Subsequent studies confirmed the prediction: as the sheep population was culled, māmane and other native vegetation outside the exclosures began recovering similarly to what had been observed earlier inside the exclosures, although at varying rates due to differences among the study sites (Scowcroft and Conrad, 1988; Scowcroft and Conrad, 1992; Perry and Giffin, 1998).

An evaluation of the long-term response of the vegetation to the sheep control program found that the māmane forest exhibited substantial regrowth inside exclosures at some sites, especially those that had been protected for the longest time (Reddy, 2011; Reddy et al., 2012). The cover of māmane trees and native shrubs increased between the 1970s and 1998, but then the rate of increase slowed or declined between 1998 and 2009, apparently due to drought. Māmane height class distributions inside exclosures indicated that recruitment was initially high before declining as heights shifted toward larger, presumably older size classes. Recurrent sheep browsing outside exclosures negatively affected māmane canopy density and possibly tree density at all sites, as well as māmane condition at some sites. Evidence of a negative effect of non-native species on vegetation recovery was limited and inconsistent over time or among sites, although native species seemed relatively unconstrained by space, given that total plant cover did not exceed 67% and non-native cover did not exceed 40%. Although, the exclosures represented a small portion of the entire māmane forest, Reddy et al. (2012) concluded that browsing was continuing to affect vegetation recovery outside the exclosures.

LANDSCAPE-LEVEL VEGETATION RESPONSE

Results of other studies on the western slope of Mauna Kea in the core habitat of the palila (Fig. 1) also indicated improvements in the regeneration of māmane and other native plants following sheep removals in the 1980s and 1990s (Hess et al., 1999), although recovery was impeded by alien grass cover. In māmane dominated forest, where grass cover was most dense, native plant regeneration was not as prolific as it was in mixed māmane-naio (*Myoporum sandwicense*) forest, where grass cover was less dense. Regeneration of naio, which is the only other abundant native tree in PCH, was comparatively low, suggesting that māmane would eventually dominate in the absence of continued browsing. Presumably naio has become dominant in a major portion of the southwestern slope since the introduction of sheep, which prefer māmane over naio for browsing (Giffin, 1976, 1981). The distribution of māmane saplings (<2 m height) and trees (≥2 m) varied among study sites, indicating uneven recovery due to the intensity of prior browsing and degree of grass cover (Hess et al., 1999).

To investigate forest structure and composition within PCH, intensive vegetation surveys were conducted on 504 plots (40 x 40 m) on the western slope and around Mauna Kea during 1999–2001 (Banko et al., 2009). Palila Report plots Trees (≥2 m height) were widespread, being found in 86% of the plots, but tree cover was sparse, averaging only 19% throughout palila habitat with māmane comprising 7%. Mean māmane density per plot was 13.5 trees. Māmane tree height averaged 3.7 m, and 61% of māmane trees were less than 4 m tall. Growth models (Scowcroft and Conrad, 1988) indicated that māmane trees less than 4 m tall were also less than 25 years old; therefore, nearly two-thirds of all trees had apparently established within the preceding 25 years. Māmane saplings (<2 m height) were found in 91% of plots, but only 38% of plots contained densities equivalent to at least 1 sapling per 100 m^2. Evidence of browsing or bark stripping by sheep was recorded in 219 (43%) plots. Māmane sapling density was relatively high and browse damage was relatively low near roads and where rifle hunting was allowed (Fig. 3). Conversely, sapling density was lower and browse damage was higher away from roads and in Ka‘ohe Game Management Area, where archery hunting was allowed but rifle hunting was prohibited. The reduction in browse damage was most evident within about 700 m of roads in Ka‘ohe Game Management Area, but the effect extended about 2.5 times farther in the adjacent Mauna Kea Forest Reserve, where rifle hunting was permitted (Fig. 4).

Augmenting the results of vegetation surveys in the field, the effect of ungulates on tree cover was tracked over 21 years from aerial photographs taken in 1954, 1965, and 1975 on the western slope of Mauna Kea (Scowcroft, 1983). The greatest loss of tree cover was observed in the area grazed by cattle, indicating their greater destructiveness, but a reduction in cover near tree line was attributed to browsing by sheep. Extending that analysis to the present, satellite images from 1977 and 2011 near tree line on the western slope where hunting pressure along roads has been relatively high show an increase in māmane trees from natural regeneration and demonstration planting projects (Fig. 5).

The dramatic increase in māmane regeneration in areas soon after being protected from browsing is a hallmark of vegetation studies in subalpine Mauna Kea. For example, seedling density was 45 times greater inside than outside the Pu‘u o Kauha sheep exclosure only two months after it had been constructed (Scowcroft and Giffin, 1983). Although rates of regeneration have been variable, due mostly to site differences, māmane can reproduce prolifically even under adverse environmental conditions. During the preceding decade of severe drought, for instance, māmane seedling densities in 2012 were seven times greater in pastures from which cattle and sheep were excluded for six years compared to densities immediately adjacent where sheep were present (Banko et al., 2013). Additionally, seedling survival was higher (Kruskall-Wallis test, $P < 0.07$) over a seven-month period (December 2011 to July 2012) in these same pastures (HDLNR, unpublished data).

Other Threats to Palila Habitat

A variety of factors in addition to ungulates threaten māmane and other native trees and shrubs. Alien grasses and other weeds are pervasive throughout PCH and reduce the availability of resources

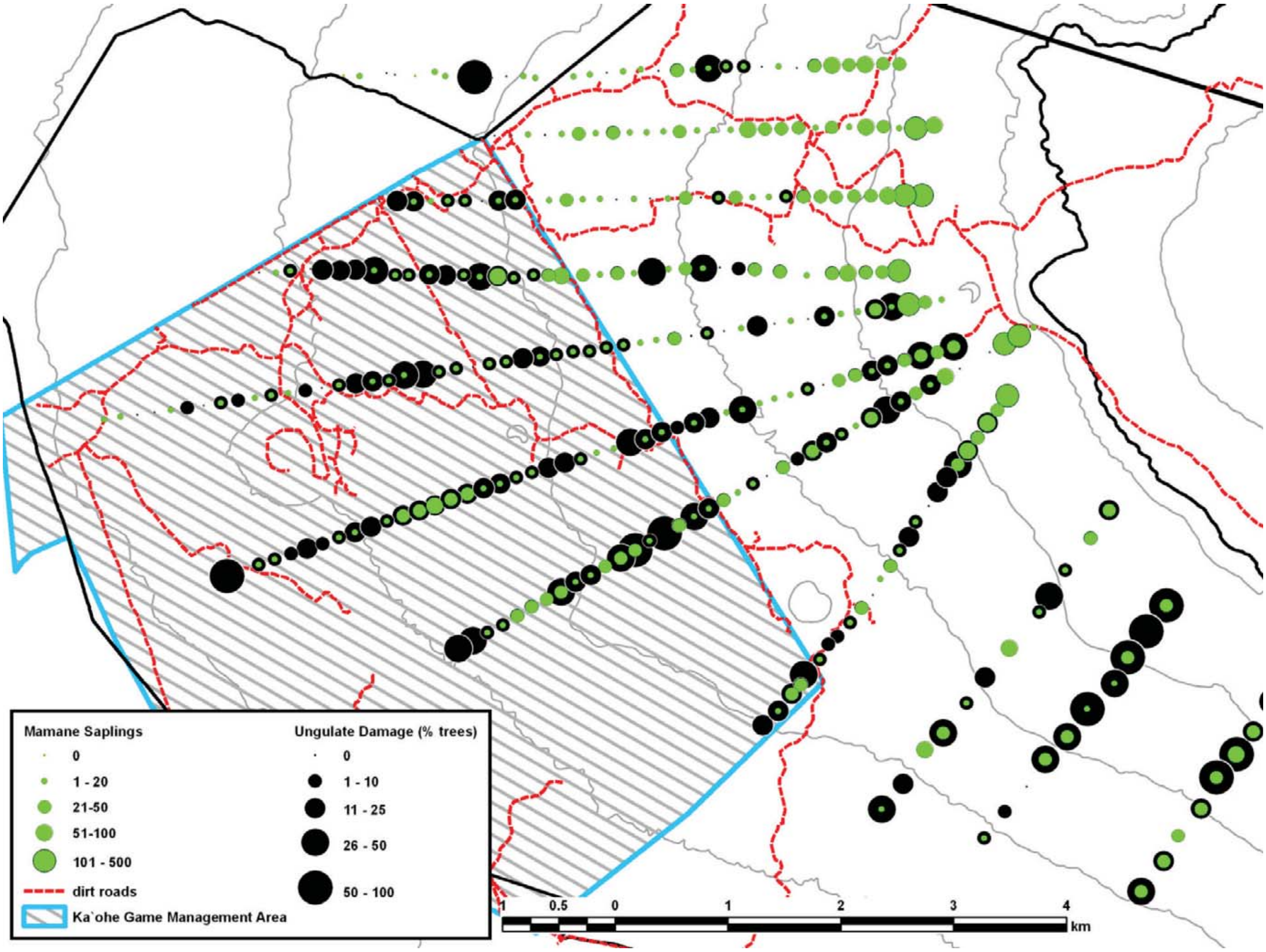

Figure 3. Distribution of māmane saplings and browse damage on vegetation survey plots in a portion of the core palila habitat. Sapling density was high and browse damage was low near roads and where rifle hunting was allowed, reflecting the difficulty of stalking game over rough, steep terrain. Sapling density was low and browse damage was high away from roads and in Ka'ohe Game Management Area, where rifle hunting was not permitted. The heavy black line delineates the core habitat of palila.

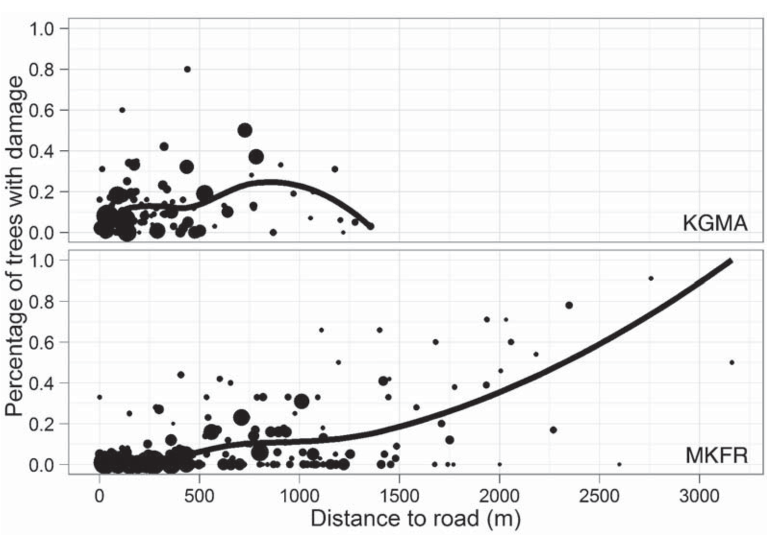

Figure 4. Percentage of trees with ungulate damage on a 40-m × 40-m plot in relation to the distance of the plot to the nearest road in the Ka'ohe Game Management Area (KGMA), where rifle hunting is prohibited, and in an adjacent portion of Mauna Kea Forest Reserve (MKFR), where rifle hunting is permitted. Generally, habitat conditions improved with hunter access (near roads) and where the method of harvesting game was more effective (rifle area). Dot size is proportional to the number of trees taller than 2 m on the plot (minimum = 1, maximum = 61, mean = 14.04). The line is a locally weighted scatterplot smoothing (loess smooth) with a span of 0.75 and degree of 2.

through competition and increased fire risks through the accumulation of fine fuels. About 69% of the 180 species of vascular plants found during the 1999–2001 vegetation surveys were non-native, including 15 highly invasive species (Banko and Farmer, 2014). Alien grasses pose the most serious threats to the ecosystem both in terms of competition (Williams, 1994; Hess et al., 1999) and

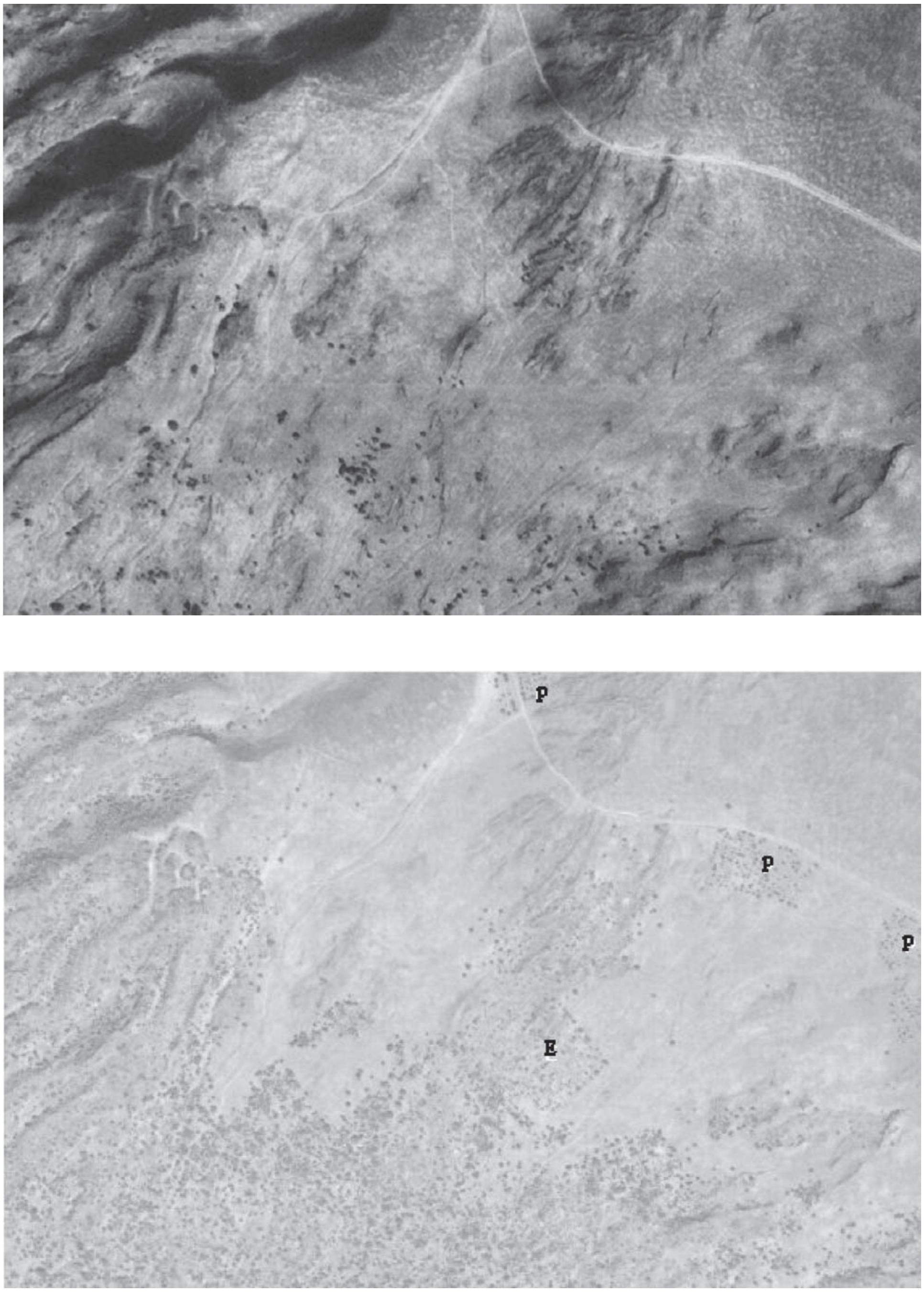

Figure 5. Changes in māmane tree density near tree line on the western slope of Mauna Kea from 1977 (upper image) to 2011 (lower image). Small, unfenced units of planted māmane trees (P) are distributed along the road. A fenced unit of planted māmane trees (E) is shown in the central portion of the lower image.

fire risk (Thaxton and Jacobi, 2009). Efforts have recently been directed toward eliminating scattered patches of the highly flammable fountain grass (*Cenchrus setaceus*), which suppresses native plants and promotes fires in regions of Hawai'i Island below PCH (Cabin et al., 2000).

An alien vine, cape ivy (*Delariea odorata*), can cover māmane and other native trees and shrubs. Although it has spread slowly over the western slope since 1980 (Jacobi and Warshauer, 1992; Banko et al., 2002b), drought may be curtailing its expansion. Cape ivy was significantly ($P < 0.001$) associated with higher tree density, based on the 1999–2001 vegetation surveys, and it has not expanded to non-forested areas. The level of threat posed by an herbaceous species, fireweed (*Senecio madagascariensis*), is unknown, but its explosive spread throughout PCH (see below) demonstrates the vulnerability of this ecosystem to invasion by weeds after long-term disturbance by ungulates. Although it has not yet invaded PCH, gorse (*Ulex europaeus*) occurs in dense stands below PCH on the eastern slope of Mauna Kea and would pose a serious threat to the subalpine habitat if it moved higher.

Fire has occurred in PCH but perhaps less frequently than might be expected, given the abundance of grass and other weedy fuels, the dry climate, and the frequency of human activity. Most fires during the past 30 years were man-caused and started outside of PCH (Thaxton and Jacobi, 2009). Although rapid suppression has kept most fires small, the potential for larger ones is great. In 1977, before the start of the sheep eradication program, a fire that was attributed to accidental human ignition swept across the southwestern slope and burned 198 ha of core palila habitat, as determined from aerial photographic interpretation (Jacobi, 1989). In 2010, a fire apparently started by an arsonist (HDLNR, 2010a) burned 561 ha of PCH (HDLNR, 2010b) near Saddle Road on the southern slope.

The rapid spread of fireweed since its introduction in 1988 has increased fire fuel loading throughout PCH (Thaxton and Jacobi, 2009). In 1999, fireweed was found on only 10% of transect stations (n = 690), but by 2007, it occupied 86% of stations (n = 381) and had spread to tree line (Banko and Farmer, 2014). Although fireweed is toxic to livestock (Motooka et al., 2004; Gardner et al., 2006), ungulates will eat it when little other forage is available, as evidenced by the presence of toxic plant-derived pyrolizidine alkaloids in biopsied sheep livers (B. Schuler and J. Powers, Colorado State University, personal communication). Nevertheless, the abundance of fireweed throughout PCH and surrounding pasturelands indicates that animal consumption probably has a negligible effect on fireweed fuel loading. Therefore, for this introduced plant species, the concept that sheep grazing can reduce fuel loading and associated fire severity is invalid (Thaxton and Jacobi, 2009). Additionally, although the applicability of this concept to other weed species found within PCH has not been evaluated, it has been shown to be invalid for alpine landscapes in Australia (Williams et al., 2006). Thaxton and Jacobi (2009) indicated that managers could reduce landscape-level grass and weed fuel loading by increasing tree cover. Biological control of some weeds may also reduce fuel loading, and the first attempt to slow the spread of fireweed was recently launched (Hawaiʻi Department of Agriculture, 2013).

Pathogens present yet another threat to the forest. An introduced root fungus, *Armillaria mellea*, is pathogenic to māmane and likely contributes to their mortality throughout PCH (Gardner and Trujillo, 2001).The poor condition and mortality of māmane trees outside sheep exclosures may once have been due mainly to browsing damage (Scowcroft and Giffin, 1983), but interactions between browsing, disease, drought, and competition from weeds may be stressing and killing trees in more recent times. Of these threats, management can eliminate browsing to promote native tree recovery, which will reduce weed cover and mitigate the effects of disease and drought, which cannot be managed.

Given the long history of invasive species in Hawaiʻi, it should not be surprising that new alien species are a constant threat. In 2010, the naio thrips (*Klambothrips myopori; Thysanoptera*) was discovered infesting otherwise healthy naio trees on the western slope. The thrips causes severe leaf distortion and can result in the death of leaves, branches, and trees (HDLNR, 2012). Although systematic surveys have not been conducted, thrips have spread to other areas within PCH. No methods for controlling the naio thrips have been identified, but natural enemies from Tasmania could be identified as biological control agents (Anonymous, 2011). Although māmane may eventually become dominant in mixed māmane-naio stands due to higher rates of regeneration (Hess et al., 1999), reducing damage by thrips could benefit palila, which eat naio fruit when māmane resources are scarce (Banko et al., 2002a).

Drought has emerged as a major threat to the health of the subalpine forest on Mauna Kea. Naturally a dry environment with only moderate seasonality (Juvik et al., 1993), a recent and prolonged drought has amplified the level of stress of the already highly disturbed forest. Annual rainfall declined during 2000–2010 and fell below the historical (1940–1977) average in seven of nine

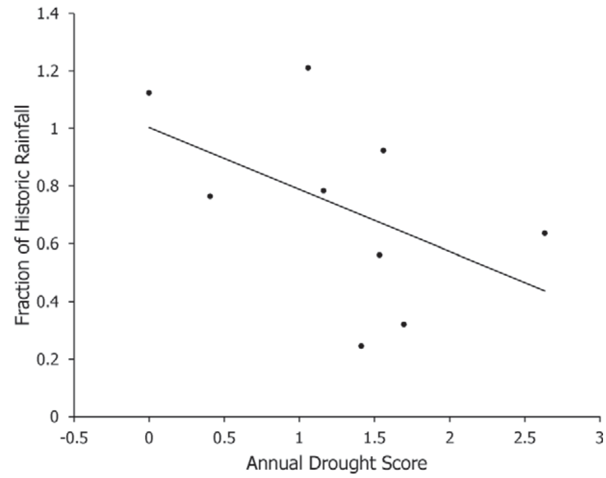

Figure 6. Lower annual rainfall generally corresponded to more severe drought scores, although the relationship was not statistically significant ($y = -0.2151x + 1.0035$, $R^2 = 0.2473$, P = 0.17). Drought severity increases along the x-axis, and values less than or greater than 1 on the y-axis represent years of below or above normal rainfall, respectively. See Banko et al. (2013) for methods used to calculate the fraction of historic rainfall and annual drought score.

years. Over the same period, drought conditions prevailed during 98 (74%) of 132 months, and in 52 of 54 months after June 2006, indicating that drought conditions may be intensifying (Banko et al., 2013). In general, lower annual rainfall corresponded to more severe drought conditions (Fig. 6). The longest break in the drought was 14 months, but other breaks lasted only one to seven months. In response to this drought, māmane cover in sheep exclosures decreased, remained stable, or increased more slowly than before the lower period of rainfall (Reddy et al., 2012).

Annual population estimates of palila were significantly related to drought severity (R^2 = 0.3737; P = 0.047), and drought has been the main proximate factor driving population decline in the palila since 2000 (Fig. 7). Māmane seed production is sharply reduced during drought, explaining the palila's decline (Banko et al., 2013). Even so, the ultimate factor eroding carrying capacity has been long-term browsing by sheep. Browsing reduces the quantity of māmane pods available to palila by thinning the lower branches of trees and suppressing regeneration, thereby decreasing canopy cover and volume across the landscape. Presumably, the reduction of māmane cover by ungulates over many decades (Scowcroft, 1983) was a major factor in the recent extirpation of the ʻakiapōlaʻāu (*Hemignathus munroi*) from subalpine Mauna Kea, and habitat degradation perhaps also contributed to the earlier disappearance of the Hawaiʻi creeper (*Oreomystis mana*) and Hawaiʻi ʻākepa (*Loxops coccineus coccineus*) (Banko et al., 2013), which are both relatively specialized, endangered insectivores that primarily inhabit mesic montane forests (Scott et al., 1986).

The factors influencing the decline of generalist bird species, such as the Hawaiʻi ʻelepaio (*Chasiempis sandwichensis*) and Japanese white-eye (*Zosterops japonicus*) are less clear, although competition for arthropod prey with the much more abundant Hawaiʻi ʻamakihi (*Hemignathus virens virens*) under stressful environmental conditions warrants investigation (Banko et al., 2013).

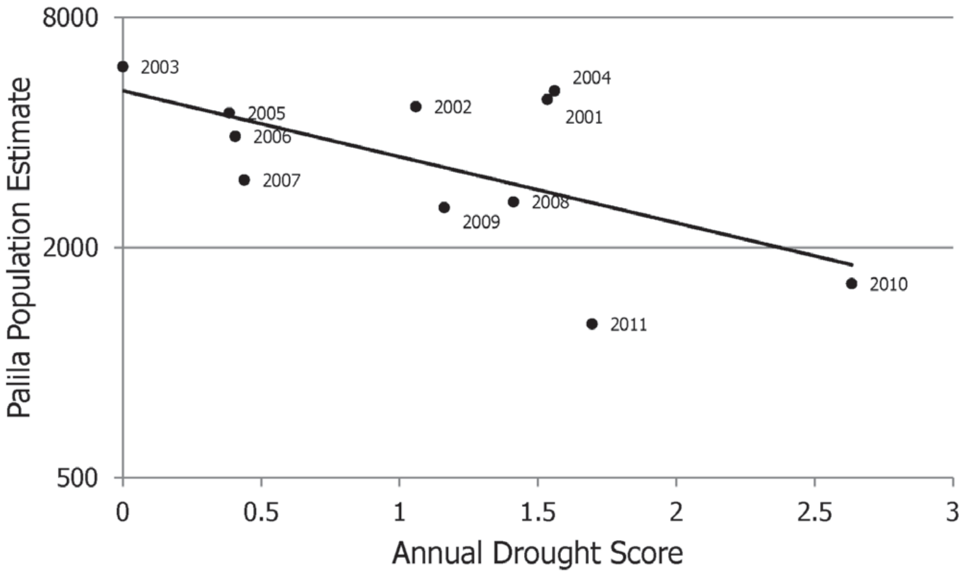

Figure 7. Annual palila population estimates (*y*-axis scaled to natural log) declined with increasing drought severity. The relationship was evaluated using natural log transformed population estimates (regression: $y = 5148.7e^{-0.398x}$, $R^2 = 0.3694$, P = 0.047). Drought values and population estimates are offset from each other by one year so that the population is estimated at the end of an annual cycle of weather (e.g., the palila population that was estimated in Jan 2011 is linked to the weather cycle of Jan–Dec 2010). The population estimate for 2000 is not shown because drought data is not available for 1999. See Banko et al. (2013) for methods used to calculate population estimates and drought scores.

Conservation Research and Management

Research to understand the ecology of the palila and threats to its survival has a long history, yet few protective measures besides court-ordered sheep management were implemented until the proposal to realign Saddle Road through the southern portion of PCH. To partially mitigate the loss of habitat caused by the realignment, cattle grazing leases were terminated on state lands in PCH on the western slope of Mauna Kea (Ka‘ohe) and on lands adjacent to PCH on the northern slope (Pu‘u Mali). The goal was to promote habitat recovery and extend the range of elevation of suitable habitat available to the palila (USFWS, 1998; Federal Highway Administration, 1999; Banko et al., 2009). Additionally, military training lands outside PCH on the northern slope of Mauna Loa (Kīpuka ‘Alalā) were protected from ungulates to allow for habitat recovery and the possible reintroduction of palila. Mitigation funds also were provided to (1) develop techniques for reintroducing palila to the Pu‘u Mali area and for controlling feral cats and other predators, (2) conduct arthropod surveys relevant to understanding palila feeding ecology, (3) investigate aspects of fire ecology and management, and (4) continue other ecological studies of the palila and its habitat. The Saddle Road mitigation program was critical in launching additional recovery efforts by government agencies and private organizations.

PALILA REINTRODUCTION

Reintroducing palila to their former range in the Pu‘u Mali area has been the most ambitious attempt to directly promote recovery. The Pu‘u Mali reintroduction project built upon methods used in an earlier pilot project to reintroduce palila to Pu‘u Kanakaleonui on the eastern slope of Mauna Kea (Fancy et al., 1997), and it involved translocating 188 palila from the western slope to the northern slope during six trials from 1997 through 2006 (Banko et al., 2009). Although many translocated birds eventually returned to the western slope, where habitat conditions were more favorable, a number of birds bred successfully near Pu‘u Mali. In time, at least one first generation offspring produced a fledgling of her own, providing additional evidence that translocation could be used to repopulate former range. The project also demonstrated that some birds traveled repeatedly between the northern and western slopes, potentially providing gene flow between subpopulations. In addition to translocation, 28 captive-reared palila were released near Pu‘u Mali by the San Diego Zoo during 2003–2009. Several of these males bred successfully with females that were translocated or that were apparently raised on the northern slope (Banko et al., 2009). The reintroduced population disappeared five years after the last translocation when severe drought affected the main population on the western slope. These results suggested that a population might be sustainable in the long-term with management to improve habitat quality and perhaps the occasional addition of new birds.

HABITAT RESTORATION

Starting in 1980, HDLNR began planting native shrub and tree species to help speed habitat recovery while removing ungulates. The first species reported was ‘ūlei (*Osteomeles anthyllidifolia*), of which nearly 600 individuals were planted (HDLNR, 1980: 2nd status report). By 1982, small plantations of māmane were established in newly fenced areas near tree line and roads (Fig. 5; HDLNR, 1983: 9th status report). Māmane were planted outside of enclosures from 1985 (HDLNR, 1985: 13th status report) to 1997 (HDLNR, 1997: 35th status report). Survival of these māmane appears high and they have grown sufficiently large that they are used by Hawai‘i ‘amakihi and might be visited by palila, demonstrating the potential for accelerating the expansion of habitat for native birds.

Other native species also were planted in areas of reduced browsing pressure. For example, large numbers of the iconic Mauna Kea silversword (*Argyroxiphium sandwicense sandwicense*) were propagated and more than 15,000 seedlings were planted cooperatively by the non-profit Hawaiian Silversword Alliance, HDLNR, USFWS, and others since about 1995 (USFWS, 2012). Silverswords are highly palatable to sheep, and relatively few survive long outside the five sheep exclosures distributed around Mauna Kea. Moreover, natural recruitment and survival even of protected silversword seedlings have been low, raising doubts about whether populations can become self-sustaining, at least until sheep have been eradicated.

As an outgrowth of the Saddle Road mitigation projects, HDLNR initiated the Mauna Kea Forest Restoration Project (MKFRP), and habitat restoration began on lands withdrawn from cattle grazing leases on the northern and western slopes with support from USFWS, National Fish and Wildlife Foundation, American Bird Conservancy, Natural Resource Conservation Service, the American Reinvestment and Recovery Act, and the Arbor Day Foundation. Puʻu Mali (2080 ha) and Kaʻohe (567 ha) Mitigation Areas were each fenced in 2006 and all hybrid mouflon sheep were removed. Puʻu Mali Restoration Area has been the focus of intensive management efforts with approximately 50,000 native seedlings planted and 62 kg of seed scattered on 91 ha of former grazing land from 2010 to 2012 (MKFRP, unpublished data). Although the main goal has been to restore māmane forest, other native shrub and tree species also have been reestablished. Various trials have been conducted to refine restoration efforts and increase seedling survival; the one-year survival of māmane seedlings that were planted in 2011 was 68%, which was surprisingly high given normally low annual precipitation and drought. Additionally, preliminary results suggest that a cost-effective technique for restoring māmane forest over large areas may be to scatter seeds on land scarified by light bulldozing. One year after scarification and seed scatter in 2011, māmane seedling density was >95 ha^{-1} (MKFRP, unpublished data), which was similar to natural regeneration on high-density vegetation survey plots (Banko et al., 2009).

PREDATOR AND PEST MANAGEMENT

Building on Saddle Road mitigation predator control projects developed by the U.S. Geological Survey, MKFRP began controlling introduced predators on the western and northern slopes in 2009. By 2012, they had removed 168 feral cats, which depredate approximately 11% of palila nests annually (Hess et al., 2004). Feral cats also consume many other bird species; birds were present in the digestive tracts of 69% of the cats sampled from Mauna Kea, whereas only 28% of cat digestive tracts from Hawaiʻi Volcanoes National Park contained birds (Hess et al., 2007). Rats (*Rattus rattus*) occur at very low densities in the dry, subalpine māmane forest of Mauna Kea. Mean capture rates were as high as 0.66/100 corrected trap-nights (CTN; corrected for sprung traps; Amarasekare, 1994) and as low as 0.38/100 CTN (van Riper, 1978) and 0.32/100 CTN (Banko and Farmer, 2014). These subalpine capture rates represent only about 3% of the capture rate found in wetter montane forests, where rats are more significant nest predators (Lindsey et al., 1999). Of five habitat types on Mauna Kea, rats were trapped least often in māmane forest, accounting for only 19% (6 of 31) of total captures (Banko and Farmer, 2014). Rats depredated a low proportion of artificial nests (Amarasekare, 1993), and rats depredated relatively few palila nests (Banko et al., 2002a). Because of higher priority conservation problems, rats are not being controlled in PCH.

Caterpillars and other arthropod prey of forest birds, including palila, are threatened by both native and non-native parasitoid wasps, whose larvae consume their hosts while developing inside them. Overall rates of parasitism of *Cydia plicata* (Tortricidae), the main species of caterpillar eaten by adults and fed to nestling palila (Banko et al., 2009), averaged 40% and involved five wasp species (Brenner et al., 2002; Oboyski et al., 2004). Methods for controlling populations of parasitoids have not been developed. Although control measures for invasive ants and predacious wasps have not been considered a priority, these social insects also pose threats to caterpillars and other arthropods eaten by palila (Banko et al., 2002b), and they disrupt arthropod communities (Cole et al., 1992; Krushelnycky et al., 2005) and pollination systems (Lach, 2008; Hanna et al., 2013). Ant populations have so far been restricted to the lower elevations of PCH, and the abundance of the introduced yellowjacket (*Vespula pensylvanica*) has remained at relatively non-threatening levels (Banko et al., 2002b).

Palila Recovery under Multiple-Use Management

Activities occurring frequently in PCH are game hunting, all-terrain and four-wheel drive vehicle touring, enduro dirt bike racing, ecotourism, cultural gathering and observance, scientific research, and wildlife management. Helicopters also transit the air space over PCH for tourism and military high-elevation flight training. Our analyses suggest that palila recovery has not been the highest priority in this mixed management regime. Instead of an effective program to eradicate sheep, public hunting has been the primary tool, supplemented with limited aerial shooting, and until now there has never been even a cursory assessment of their combined effectiveness. Although the numbers of animals removed annually may provide some useful information, accurately surveying the remaining sheep population would be much more powerful in evaluating progress toward eradication.

With sheep in PCH at harmful levels even after the removal of nearly 18,000 animals over the past 32 years, there is urgency for managers to take stock of results, renew commitments to protect endangered species, and implement new strategies and tactics to achieve the goals that were established by the U.S. District Court for Hawaiʻi (Scott and Conant, 2001; Scott, 2009). Resources to carry out this work are finally at hand. The USFWS funded construction of 29 km of new 2-m-high sheep-proof fence that closed the most problematic corridors of sheep ingress into PCH. Federal funding has also been secured to complete fence construction around nearly all remaining areas of PCH. Moreover, federal funds were provided to Hawaiʻi through a Competitive State Wildlife Grant award to initiate sheep eradication within PCH in 2013 by tracking radio-tagged individuals and eliminating the bands that they have joined (R. Utzurrum, USFWS, personal communication). Applying these federal resources diligently and wisely will be the key to eliminating the top invasive species threat to palila recovery. Also important will be stopping the spread of axis deer (*Axis axis*), which were recently smuggled onto Hawaiʻi Island from Maui in exchange for mouflon sheep (Anonymous, 2011; Dawson, 2011). If they cannot be exterminated, axis deer could become as great a threat to PCH as sheep have been.

Results of other sheep removal programs indicate that eradicating sheep from PCH is an attainable goal. A prime example of what can be accomplished with scarce but carefully allocated resources is the program to protect the Mauna Kea watershed in the 1930s and 1940s (Banko et al., 2009). Also instructive is the National Park Service program in the Kahuku Unit of Hawaiʻi Volcanoes National Park, where the mouflon population and removal rates are monitored (Stephens et al., 2008) so that eradication might be achieved in a matter of years rather than decades.

The conflict between conservation and game hunting is problematic across the Hawaiian Islands. Public opposition to eradication efforts on Mauna Kea was reflected in the Hawaiʻi County ban on aerial shooting (Anonymous, 2012) and vandalism to the replacement fence around PCH, which required repairs on 23 occasions in the initial 16 months of routine inspection and maintenance beginning in October 2011 (R. M. Stephens). Even so, such conflict is not unique to Hawaiʻi. On Santa Cruz Island, off the coast of California, the Nature Conservancy overcame a lawsuit filed by a hunter organization and mounted an effective public outreach campaign to remove over 37,000 feral sheep in 9 years from most of the island (Schuyler, 1993). Over 9200 additional sheep were removed by live capture from the remainder of Santa Cruz Island during 1997–2001 (Faulkner and Kessler, 2011), demonstrating that eradication can be achieved even using inefficient methods when efforts are focused and determined. Public opposition and resentment over sheep management have festered for decades, and thus it may be time to reconsider developing an alternative hunting area outside of PCH that is securely fenced and well managed for sustainable hunting. This idea was proposed over 35 years ago by Giffin (1976) before the U.S. District Court for Hawai‘i issued its orders to eradicate sheep and goats to protect PCH: "The only solution for preventing further injury to the vegetation is to substantially reduce or totally remove all feral sheep from Mauna Kea. The primary difficulty with this plan of action is hunter opposition. Resistance can partially be overcome by providing alternate hunting areas."

Leadership from the hunting and game management communities will be critical for developing a plan for hunting sheep outside PCH, but in the meantime, active restoration of PCH is urgently needed. A template for restoring habitat has been created by the MKFRP, which has been focusing its efforts on Pu‘u Mali and Ka‘ohe, both of which have been freed of browsers. While continuing the essential work of bolstering māmane and other native species in these two highly degraded areas, resources are needed to expand the program to core palila habitat, an area of only 64 km^2, as soon as browsing can be eliminated there. The inclusion of students and volunteers in the restoration work, as is done by MKFRP, will go far in helping the public value native Hawaiian communities and the unique species that depend on them. Furthermore, the Mauna Kea Watershed Alliance was recently created to foster and coordinate management to reduce the threats posed by introduced ungulates, fire, and weeds (http://hawp.org/partnerships/mauna-kea-watershed/).

Although the goal of eradicating sheep has not been achieved, there has been ample evidence that reduced browsing results in improved regeneration of māmane and other native plants. Vegetation plots and satellite imagery revealed that māmane regeneration was greater and browse damage was less near roads, where higher levels of hunting pressure and other human activity would be expected. Habitat conditions were also better close to roads in areas where rifle hunting was allowed compared to areas reserved for archery. Even so, exclosure studies indicated that habitat recovery occurs slowly in this subalpine region; after 48 years without ungulate browsing and grazing, the total plant cover was still only 67% (Reddy et al., 2012). Although the potential extent of canopy cover in the absence of invasive species is unknown, groves of māmane planted decades ago and some natural stands indicate that tree cover can be higher than it is currently. Others also have reported slow responses of ecosystems to reductions in ungulate populations (Tanentzap et al., 2012). Wright et al. (2012) examined 73 pairs of ungulate exclosures and unfenced control plots to evaluate the recovery of woody plant species across New Zealand in response to the culling of ungulate populations. They found that preferred forage species continued to be relatively heavily affected by browsing after culling, presumably because the remaining animals increased their consumption of them as competition was reduced. Results of vegetation studies on Mauna Kea indicate a similar response by māmane, a preferred forage species of sheep, thus reinforcing the point that habitat recovery will accelerate when browsing is entirely eliminated. The regeneration of māmane and other native species during three decades of ungulate culling (Hess et al., 1999; Banko et al., 2009; Banko and Farmer, 2014) may have spurred sheep population growth, which might partially explain the increased rate of sheep removal in recent years. If true, a fixed-effort game management approach will fall short of what is needed to achieve eradication, and accelerated removal rates will be necessary to stay ahead of population growth.

The long-term effects of severe, prolonged drought on the vigor, productivity, and recruitment of māmane and other native species are not fully understood, but we would expect a reduction of tree cover and an increase in grass cover (Lohse et al., 1995; Loope and Giambelluca, 1998). Under this scenario, fire would likely become an even greater threat than it is now. Some federal support for increased fuel breaks and fire suppression capacity has been made available recently, but a robust program of fire prevention and suppression is needed to ensure that palila habitat is not lost, especially when the population is declining and the range is contracting. Reducing fuel loading by increasing tree canopy cover requires that browsers are eliminated, but the strategy would also benefit from planting or otherwise increasing the density of māmane and other trees. Reducing grass and weed cover by mechanical or chemical means would be expensive at the landscape scale, but it could reduce fire risks while accelerating forest restoration in localized areas. Although sheep have been assumed to be useful in reducing fine fuel-loading grasses on Mauna Kea, no supporting data exist. On the contrary, Williams et al. (2006) found no evidence of grazing as a scientifically supported fire reduction technique. Additionally, grazing has been found to stimulate greater long-term biomass of grasses through positive feedbacks in nutrient cycling, increased mineralization, and enhanced light regimes in continental systems with naturally high densities of large herbivores, namely Yellowstone National Park (Wyoming, U.S.A.) and the Serengeti of east Africa (Frank et al., 1998, 2002). One conspecific (*Poa pratensis*) and one congeneric (*Deschampsia caespitosa*) grass from the Yellowstone region also occur on Mauna Kea and widely throughout Hawai‘i, indicating that these processes are not likely to be restricted to continental environments (Frank et al., 2002). In a global meta-analysis of 63 manipulative field studies, including more than 100 non-native plant species, Parker et al. (2006) showed that native herbivores suppressed non-native plants, whereas non-native herbivores facilitated both the abundance and species richness of non-native plants. These findings have major implications for insular ecosystems such as the Hawaiian Islands where there are no existing native herbivores.

Despite high annual variability, surveys indicate that the palila population was relatively stable from 1980 to 1998 (Banko et al., 2009), suggesting that habitat carrying capacity was not declining consistently or markedly prior to the long period of drought recorded since 2000. The increased severity and duration of drought may foreshadow a shift to drier conditions due to climate change (Banko et al., 2013). The palila's alarming population decline and range contraction since 1998 underscores the urgency of increasing habitat carrying capacity. The most obvious methods of improving recovery prospects for the palila are to eliminate browsing damage to the habitat and to accelerate the regrowth of native vegetation through planting, seed scatter, and reducing competition from weeds. Although vegetation recovery may not benefit the palila for decades due to the slow growth of māmane (Scowcroft and Conrad, 1988) and the preference of palila for habitat with high tree cover and large trees (Scott et al., 1984), more food could become available within only a few years as the lower branches of trees regrow in the absence of browsing (Banko et al., 2013). Recovery efforts will necessarily need to focus on the western slope of Mauna Kea, where palila are concentrated, but other areas of former range will need to be restored as the next step in reestablishing additional populations. The vulnerability of the single, small population can ultimately be overcome only by spreading the risk of a local catastrophe by expanding the distribution of the palila on Mauna Kea and at other suitable sites.

Although restoring habitat is critically important to recovering palila, other management options also could help. For example, reducing the rate of predation at nests and on individuals by introduced mammals also provides significant benefits. The effective predator removal program already in place affords significant protection to the small and declining population of birds. Less feasible is management to reduce the threats to key arthropod foods. Methods to control parasitoid wasps have not been developed, and reducing the spread and abundance of ants and yellowjacket wasps is not practical at the landscape scale.

The palila population is rapidly and unambiguously trending toward extinction (Camp and Banko, 2012), but measures to reverse the decline have been slow to develop and their effectiveness has been diluted by conflicting management priorities and unsupportive policies (Ikagawa, 2014). Not implementing effective measures to eliminate sheep has greatly increased the risk of extinction for the palila. We conclude that the long-held admonition against multiple-use management in the critical habitat of a globally endangered species (Juvik and Juvik, 1984) is upheld by compelling and comprehensive evidence from three decades of ecological studies that provide clear direction for those responsible for managing public lands. If the palila joins the long list of other extinct Hawaiian forest birds (Banko and Banko, 2009), it will not be due to a lack of understanding of its threats or uncertainty about the actions needed for its protection.

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APPENDIX

The history of litigation over protecting the palila and its habitat from browsing by introduced ungulates extends over three decades. The landmark events from 1978 to 2009 are highlighted in the following:

- 1978—Palila I. Palila, environmental groups, and an individual sue Hawai‘i DLNR and its chairman for "taking" an endangered species by maintaining populations of feral sheep and goats in Palila Critical Habitat (designated in 1977); U.S. District Court, Hawai‘i, decides for the plaintiffs, thereby introducing persuasive precedent, made binding by the 9th Circuit's subsequent affirmation, that the definition of "take" includes habitat damage (471 F. Supp. 985 [D. Haw. 1979]).
- 1979—U.S. District Court, Hawai‘i, judgment from Palila I orders that State must eradicate feral sheep and goats by 31 July 1981.
- 1981—Palila II. Defendants appeal 1978 decision; U.S. Court of Appeals, 9th Circuit, upholds the District Court decision (639 F.2d 495 [9th Cir. 1981]).
- 1985—Palila III. Plaintiffs amend their original 1978 complaint to include mouflon sheep and hybrids to be eradicated from Palila Critical Habitat. Joined by hunter groups and individuals, defendants argue that the court interpretation of "harm" was inconsistent with a change to the regulation defining "harm" in Section 9 of the ESA and that improvements in the palila population and critical habitat indicated that sheep and palila could coexist; U.S. District Court, Hawai‘i, denies summary judgment for the plaintiffs and orders the case reopened (631 F. Supp. 787 [D. Haw. 1985]).
- 1986—Palila IV. U.S. District Court, Hawai‘i, decides that mouflon sheep in numbers sufficient for sport hunting purposes are harmful to palila (649 F. Supp. 1070 [D. Haw. 1986]).
- 1987—U.S. District Court, Hawai‘i, judgment from Palila IV orders that State must eradicate mouflon sheep and hybrids by 27 January 1988 and reaffirms the order to eradicate feral sheep and goats.
- 1988—Palila V. Defendants and interveners appeal 1986 decision; U.S. Court of Appeals, 9th Circuit, upholds the decision, creating a landmark precedent (852 F.2d 1106 [(9th Cir. 1988]).
- 1998—Defendants and plaintiffs agree to a stipulation, which the U.S. District Court entered as an order, that HDLNR will (1) use its best efforts to minimize migration of ungulates into critical habitat; (2) continue to include public in eradication by reducing or eliminating bag limits and seasonal restrictions and allowing hunting with firearms, guided hunts, and staff hunts; and (3) conduct semiannual aerial hunts in which all ungulates seen will be shot (stipulation between Plaintiffs and Defendants, No. 78-0030, 10 November 1998; *See also* 73 F.Supp.2d 1181, 1185 [D. Haw. 1999]).
- 1999—Palila VI. Hunters, who intervened earlier, move with HDLNR to modify the 1987 order; U.S. District Court, Hawai‘i, denies their motion based on the criteria for modifying a court order not having been met (73 F.Supp.2d 1181 [D. Haw. 1999]).
- 2000—Palila VII. Hunter's organization files appeal of 1999 decision; U.S. Court of Appeals, 9th Circuit, dismisses the appeal because the group lacked standing to appeal without HDLNR (No. 99-17477, 2000 WL 1844302 [9th Cir. 2000]).
- 2009—Plaintiffs file motions to enforce the eradication orders of 1979, 1987, and 1998 by imposing a deadline for HDLNR to construct ungulate-proof fence around the perimeter of PCH; U.S. District Court, Hawai‘i, denies their motion (Orders denying plaintiffs' motions to enforce, No. 78-0030 21 May 2009, ECF No. 311; 25 Nov. 2009, ECF No. 323).