A Tour de Force by Hawaii's Invasive Mammals: Establishment, Takeover, and Ecosystem Restoration through Eradication

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Invited Review

A tour de force by Hawaii's invasive mammals: establishment, takeover, and ecosystem restoration through eradication

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Abstract. Invasive mammals have irreversibly altered ecosystems of Hawai'i and other tropical Pacific islands in numerous cases through novel herbivory, predation, and diseases, thereby causing the disproportionate extinction of flora and fauna that occur nowhere else on Earth. The control and eradication of invasive mammals is the single most expensive management activity necessary for restoring ecological integrity to many natural areas of Hawai'i and other Pacific Islands, and have already advanced the restoration of native biota by removing herbivorous ungulates from >750 km^2. Rodenticides which have been tested and registered for hand and aerial broadcast in Hawai'i have been used to eradicate rats from remote islands to protect nesting seabirds and are now being applied to larger islands to protect forest birds. The exclusion of other invasive mammals is now being undertaken with more sophisticated control techniques and fences. New fence designs are capable of excluding all mammals from areas to protect endangered native birds. Although the eradication of mammals from large areas has resulted in the restoration of some ecosystem processes such as natural forest regeneration, changes in other processes such as fire regimes, nutrient cycling, and invasive plant proliferation remain more difficult to reverse at larger landscape scales.

Key words: control methods, ecological degradation, eradication, Hawai'i, invasive mammals.

The remoteness and extreme isolation of the Pacific islands, both in space and time have contributed to the development of unique and naïve endemic biota which evolved nowhere else on Earth. The most extreme example of isolation is found in the Hawaiian Archipelago, which developed over a 30 million year period and is no closer than 3,200 km from the nearest continent (Ziegler 2002). The founding flora and fauna of Hawai'i had to possess extraordinary dispersal capabilities to cross half of the Pacific Ocean. Consequently, only one species colonized the Hawaiian Islands every ~35,000 years prior to discovery by humans (Loope 1998; Ziegler 2002). Many taxa with lesser dispersal capabilities have never become established naturally.

Examples of animal groups which naturally dispersed to and became established on remote Pacific islands include terrestrial snails, numerous insects, and birds which were primarily migratory species, including many waterfowl and raptors. They then speciated into diverse new arrays of endemic taxa, including >5,200 insects, >750 terrestrial snails, 61 forest passerine birds, >24 flightless birds, and seven raptorial birds, becoming overrepresented in the native fauna relative to groups of organisms that could not disperse; a phenomenon known as biotic disharmony (Ziegler 2002). Terrestrial herbivores consisted of snails, insects, and flightless waterfowl instead of herbivorous mammals. Likewise, predators consisted of raptors instead of carnivorous mammals. Terrestrial mammals were not represented among the native island wildlife except for two bat species (Ziegler 2002). Consequently, island organisms lost defenses to mammalian herbivory and predation (Bowen and Van Vuren 1997).

Other large groups of vertebrates were unable to disperse naturally and become established on the remote islands of the Hawaiian Archipelago; for example, no herptiles or mammals except bats; among birds, no doves or woodpeckers. In the absence of all hoofed mammals (ungulates), most Hawaiian plant taxa lost defenses to mammalian herbivory, such as alkaloids in the "mintless" endemic mints (Lamiaceae), stinging hairs in nettles (Urticaceae), and woody thorns in endemic *Acacia*

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spp. (Fabaceae) (Carlquist 1970). Nonetheless, thorn-like prickles developed in a group of at least ten plant species which evolved within the Hawaiian Islands, probably as a defense against Hawaii's dominant vertebrate herbivores, a diverse group of now extinct flightless geese and goose-like ducks (Olson and James 1982; Givnish et al. 1994; Duncan et al. 2013). Substrates underlying forests were protected by layers of bryophytes, lichens, and ferns, while porous volcanic soils untrammeled by hooves absorbed tremendous rainfall that would have eroded most other substrates.

Most of the organisms with lesser dispersal capabilities which became established later did so only with the assistance of humans. After tens of millions of years of evolutionary isolation from nearly all terrestrial mammals, islands of the central Pacific were quite suddenly besieged by a number of alien rodents, carnivores, and ungulates which proliferated in the absence of large predators (Ziegler 2002). Rapid ecological degradation ensued and whole groups of endemic plants and animals suffered extinctions, including all flightless birds (Olson and James 1982; Steadman 1995), and at least nine percent of all Hawaiian flora (Sakai et al. 2002). Invasive mammals, large and small, have irreversibly altered ecosystems of Hawai‘i and US Administered Islands of the tropical Pacific in numerous cases through novel herbivory, predation, and diseases, thereby causing the disproportionate extinction of flora and fauna that occurred nowhere else on Earth. Although examples in this work primarily focus on the Hawaiian Islands, examples of other US islands of the tropical Pacific primarily administered from Hawai‘i in the biogeographic region of Polynesia are also included. These include: American Samoa, the Line Islands, and Johnston and Wake Atolls. Implications apply to many other oceanic archipelagos such as New Zealand.

A series of devastating herbivore introductions

The rabbit disaster

In the Northwestern Hawaiian Islands, European rabbits (*Oryctolagus cuniculus*) were introduced as a source of food to Lisianski and Laysan islands about 1902, and subsequently discovered on Southeast Island of Pearl and Hermes Atoll in 1916 (King 1973). Rabbits were eradicated from Laysan and Lisianski in 1923 after a failed eradication attempt on Lisianski in 1912–1913 (King 1973). Compounding the effects of house mice (*Mus musculus*) present since 1846, rabbits eliminated most of Lisianski's vegetation by 1914, which then caused starvation of the rabbits (Olson and Ziegler 1995). Nearly simultaneous with their eradication, rabbits caused desertification of Laysan and the extinction of the the Laysan honeycreeper (*Himatione sanguinea freethii*), the Laysan millerbird (*Acrocephalus familiaris familiaris*), and the last observations of Laysan rail (*Porzana palmeri*) on that island (Ely and Clapp 1973). Rabbits were also eradicated on Southeast Island of Pearl and Hermes Atoll in 1928 by shooting (King 1973; Amerson et al. 1974).

Nearer to the larger Hawaiian Islands, rabbits were found on Ford, Mānana, and Molokini islands, but disappeared, perhaps due to starvation (Swenson 1986). An incipient rabbit population was eradicated in Haleakalā National Park (HALE) on Maui in 1990 by shooting, trapping, and snaring (Loope et al. 1992), and another on Kaua‘i was eradicated by trapping in 2003 (C. Martin personal communication). Intensive hunting eradicated rabbits from Lehua Islet near the island of Ni‘ihau in 2005–2006 (B. Keitt and C. Swenson personal communication). Rabbits have been repeatedly released on the larger Hawaiian Islands, but surprisingly, invasive wild populations have generally not become problematic.

Feral goats and sheep

The discovery of the Hawaiian Islands by Europeans, like many other islands of the Pacific, marked the beginning of introductions of many beasts of burden and animals for milk and meat on the hoof. Notably among these were domestic goats (*Capra hircus*) and sheep (*Ovis aries*) on Cook's voyage in 1778–1779 and on Vancouver's voyages in 1793 and 1794 to establish future strategic resupply outposts (Tomich 1986). These livestock proliferated without any predators or competitors and quickly became feral. Sheep were reported at the summit of Mauna Kea, the highest peak in the Pacific, only 32 years after their introduction (Ellis 1917). Goats have been introduced widely throughout the Hawaiian Islands, have repeatedly escaped captivity to become feral, and are able to persist in some of the most arid environments with minimal vegetation (Chynoweth et al. 2013).

Later introductions to the Hawaiian Islands included European mouflon sheep (*Ovis musimon*) from the Mediterranean Islands that have become invasive where they have been introduced to the Canary and Kerguelen archipelagos (Chapuis et al. 1994; Hess et al. 2006; Nogales et al. 2006). Mouflon were first introduced to the Hawaiian island of Lāna‘i in 1954 as a game species (Tomich 1986). Feral domestic sheep were intentionally hybridized with mouflon and released on Mauna Kea from 1962–1966 (Tomich 1986). A third population on Hawai‘i Island's Mauna Loa was founded by only 11 individuals between 1968 and 1974 (Hess et al. 2006). The Mauna Kea and Mauna Loa populations grew and merged by the late twentieth century (Ikagawa 2014). The severe ecological degradation caused by feral goats and sheep was slow to be realized and addressed. The concept of eradicating entire populations of destructive non-native mammals came about as a solution to primarily agricultural or economic problems, but had not been applied to ecological problems until the mid-twentieth century.

The first eradication of goats from an island occurred on the Hawaiian island of Ni‘ihau. Goats had been established in the early 1900s and eradication by contract hunting became warranted by 1911 (Kramer 1971). Lāna‘i was also affected by excessive browsing, and by 1900, large areas were deforested by sheep and goats that had been introduced in the mid-1800s (Hobdy 1993). A rancher began to eradicate goats and sheep from his Lāna‘i property in 1902 and fenced the summit cloud forest to protect the watershed, but feral goats were not eradicated until 1981, and feral sheep were not eradicated until later in the 1980s. Nonetheless, European mouflon and axis deer (*Axis axis*) remain numerous and continue to cause ecological degradation on Lāna‘i (Hess and Jacobi 2011).

One of the most influential assessments on the management of mammals on federal lands in Hawai‘i was the report "Wildlife Management in National Parks" by A. Starker Leopold et al. (1963), who gave national recognition to the overabundance of herbivores throughout the entire US national park system. Managers of national parks in Hawai‘i took action on the recommendation of the Leopold Report, which stated: "*A visitor who climbs a mountain in Hawaii ought to see mamane trees and silverswords, not goats*." Not only did this spur the removal of non-native goats from national parks in Hawai‘i, but also the restoration of ecological integrity to other national parks of the US. Goats had been removed from Hawai‘i Volcanoes National Park (HAVO) on Hawai‘i Island since 1927 but with no lasting effect due to reinvasion from the reservoir of animals in surrounding areas (Baker and Reeser 1972). The re-invasion problem was solved by dividing areas into fenced units of manageable size, a difficult logistical process at the time for large areas and dense tropical forests on volcanic substrates. Managers developed methods necessary to accomplish eradication from the enclosed areas such as the Judas goat technique which uses radio-telemetry to take advantage of gregarious behavior in domestic ungulates (Taylor and Katahira 1988). Until goats were eradicated from the 585 km^2 Galápagos Island of Santiago, Ecuador in 2005, the eradication of goats from 554 km^2 of HAVO during 1968 to 1984 remained the largest area from which goats have been eradicated on any Pacific island (Tomich 1986; Cruz et al. 2009; Chynoweth et al. 2013). After a century and a half of degradation, a previously undescribed endemic plant, ‘āwikiwiki or *Canavalia kauensis* (now *C. hawaiiensis*), was found growing on the dry lowlands of Kukalau‘ula after the removal of goats (St. John 1972).

At Haleakalā national park (HALE) on Maui, eradication of goats from the 137 km^2 ha park began in 1983 and was completed in 1989 using techniques developed in HAVO (Stone and Holt 1990). Goats and sheep were also eradicated from nearby Kaho‘olawe Island in 1990 by ground shooting, helicopter hunting, and the use of Judas animals (Kaho‘olawe Island Conveyance Commission 1993). Goat control in National Parks of Hawai‘i demonstrated not only the technical feasibility of eradicating ungulates from large areas of islands interspersed with privately-owned lands, but also prompted the development of effective techniques used in other locations. The Judas goat technique developed in Hawai‘i has been responsible for the success of many other eradication operations throughout the world (Hess and Jacobi 2011).

Many efforts to eradicate feral goats and sheep have not proceeded as anticipated; challenges to these operations have been sometimes surprising. Feral sheep have repeatedly reached excessive numbers on Mauna Kea, devastating the watershed and semi-arid subalpine woodland environment. Foresters for the Territory of Hawai‘i conducted sheep drives starting in 1934 that eliminated tens of thousands. The Mauna Kea Forest Reserve (MKFR) was fenced in 1935–1937 (Bryan 1937a) and nearly 47,000 sheep were removed in the following 10 years by foresters and Civilian Conservation Corps workers using drives on foot and horseback (Bryan 1937b, 1947). Populations rebounded when sport hunting became a management goal of wildlife biologists after World War II and by 1960, the dire condition of the Mauna Kea forest was decried but not widely known outside of Hawai‘i (Warner 1960). Despite this knowledge, hybrid European mouflon × feral sheep were released from 1962 until 1966 to further improve hunting opportunities (Giffin 1982). Exclosures, aerial photography, and tree size classes all demonstrated the effects of browsing and bark-stripping by sheep and goats and other ungulates on the subalpine vegetation and associated wildlife (Scowcroft 1983; Scowcroft and Giffin 1983; Scowcroft and Sakai 1983). U.S. Federal District court orders of 1979 and 1986 mandated the removal of goats and sheep to protect the endangered Hawaiian finch, palila (*Loxioides bailleui*), that feed and raise their nestlings almost exclusively on the seed pods and other resources from the leguminous māmane (*Sophora chrysophylla*) tree (Hess et al. 2014).

More than 87,000 sheep have been removed from the MKFR over a 75-year period, but sheep have not yet been eradicated (Hess and Banko 2011; Banko et al. 2014). Improved habitat conditions and vegetation recovery was reported following the federal court-mandated removal of "virtually all feral sheep and feral goats" by 1982 from designated Palila Critical Habitat (Scott et al. 1984; U.S. Fish and Wildlife Service 1986; Scowcroft and Conrad 1988; Juvik et al. 1992; Hess et al. 1999). Mouflon and feral sheep hybrids, however, continued to occupy the area (U.S. Fish and Wildlife Service 1986) because they had been excluded from the original court ruling, but in 1987 the court ordered the removal of all *Ovis* spp. (Pratt et al. 1997). The effects of long-term browsing have recently been compounded by a severe, prolonged drought, which has caused the further deterioration of habitat and a sharp decline of palila abundance (Banko et al. 2009, 2013). The fence surrounding Mauna Kea has recently been reconstructed to contemporary standards and sheep removals have accelerated (Hess and Banko 2011). Although the subalpine woodland of Mauna Kea has repeatedly demonstrated the ability to regenerate after feral sheep and goat populations have been reduced, the cumulative degradation to this ecosystem may preclude long-term suitability for dependent native wildlife such as palila.

Feral pigs: ecosystem transformers

Feral pigs (*Sus scrofa*) differ fundamentally from other ungulate species because, in addition to herbivory and trampling, pigs also wallow, dig, and root in soil (Engeman et al. 2006), primarily in wetter forests. They also have a long commensal history on inhabited islands of the Pacific. Polynesians brought the first domestic pigs, known as *pua'a*, which originated from Island Southeast Asia, to the Hawaiian Islands in sailing canoes more than 1,000 years ago (Kirch 1982; Larson et al. 2005). Both skeletal remains and early historic observers indicated that *pua'a* were smaller than contemporary Hawaiian feral pigs, weighing only 27–45 kg and did not stray far from human settlements (Ziegler 2002; Larson et al. 2005). *Pua'a* repeatedly interbred with European wild boars and multiple domestic varieties after their introduction by European explorers beginning in the 1770s. They have since become the most abundant large mammal throughout many Pacific Islands (Tomich 1986).

Pigs are thought to disperse some alien plants (Diong 1982; Aplet et al. 1991; LaRosa 1992), inhibit regeneration of native plants (Cooray and Mueller-Dombois 1981; Diong 1982), selectively browse and destroy native plants (Ralph and Maxwell 1984; Stone 1985; Stone and Loope 1987; Drake and Pratt 2001; Murphy et al. 2013), spread plant pathogens (Kliejunas and Ko 1976), accelerate soil erosion (Stone and Loope 1987), alter soil microarthropod communities (Vtorov 1993), and alter nutrient cycling (Coblentz and Baber 1987; Singer 1981; Vitousek 1986). Feral pigs in Hawai'i also create nutrient-rich wallows and troughs in tree fern (*Cibotium* spp.) trunks which provide breeding habitat for avian disease-carrying mosquitos (Stone and Loope 1987). Some aspects of feral pig ecology in Hawai'i are still poorly studied because of the inaccessible environments they inhabit, and because their effects cannot be disentangled from other sympatric ungulate species.

The National Park Service was among the first to eradicate pigs from large areas of the Hawaiian Islands. Due to the steep terrain of Maui, feral pigs did not begin to invade the remote Kīpahulu Valley until the 1970s (Anderson and Stone 1993). Conventional control methods such as trapping and hunting dogs were precluded because helicopters were needed for access. Snaring was used to eradicate pigs from a 1,400 ha area of Kīpahulu during a 45-month period beginning in 1978. Hunting dogs, shooting and snaring were also used to remove pigs from 7,800 ha of HAVO from 1980–1989 (Katahira et al. 1993) which increased to 16,200 ha by 2007. Hakalau Forest National Wildlife Refuge (HFNWR), a dense, wet montane forest on Hawai'i Island, employed similar methods to remove pigs from a 4,500 ha area in 1988–2004. The long period of time to complete removal was due in part to the large size of one management unit (>2,000 ha), interspersed areas of continued sustain-yield hunting, high densities of pigs, and delayed use of snares (Hess et al. 2007). Feral pigs have now been removed from >750 km^2 in Hawai'i, allowing the gradual recovery of forest ecosystems (Hess and Jacobi 2011). Future control methods which may be highly efficacious but have not yet been applied in Hawai'i may include sodium nitrite toxicants (Shapiro et al. 2015).

Several studies have examined the recovery of plant communities after landscape-scale removal of pigs. Loope et al. (1991) found that the removal of feral pigs from a montane bog on Maui reversed damage to vegetation and subsequent invasion of alien plant species was minimal. Loh and Tunison (1999) found that native understory cover increased 48%, and alien understory vegetation increased 190%, largely in the first two years following pig removal in areas of the 'Ola'a-koa rainforest unit of HAVO. The presence of invasive banana poka vine (*Passiflora tarminiana*), however, was reduced from 81% to 40% within plots. Hess et al. (2010) found strong increases in understory cover of native ferns and slight decreases in cover of bryophytes and exposed soil over a 16-year period concurrent with feral pig removal at HFNWR. In contrast to many other Hawaiian forests, widespread invasion by alien grasses and herbs did not occur after pig removal. Cole et al. (2012) and Cole and Litton (2013) found that stem density and cover of native plants, species richness of groundrooted native woody plants, and abundance of native plants of conservation interest were all significantly higher where feral pigs had been removed from a montane wet forest over 6.5–18.5 years. Abundance of invasive plants such as strawberry guava (*Psidium cattleianum*) increased fivefold at sites where they had established prior to feral pig removal. Results of these studies and others indicated that control of nonnative plants and outplanting of rarer species may be necessary after pig removal.

Indirect effects, novel grazing systems, and ecosystem change

While consumption or trampling results in direct damage and loss of plants, introduced ungulates also indirectly cause soil erosion (Coblentz 1978). After protective ground layers of vegetation have been removed, bare substrates become exposed to physical disturbance from hoof action, precipitation, and wind, all of which may further exacerbate erosion. Hoof action has been implicated in the large-scale ecosystem process of soil compaction, which makes soils hydrophobic (i.e., reduces soil water penetration), causing greater soil runoff. As much as 5 m of soil has been lost on Kaho'olawe Island and an additional 1.9 million tons were lost annually (Kramer 1971; Kaho'olawe Island Conveyance Commission 1993; Loague et al. 1996). Yocom (1967) estimated that approximately 1.9 m of soil was lost as a result of goat activity at Haleakalā Crater on Maui. Damage to near-shore marine environments from silt has been attributed to erosion caused by ungulates as well.

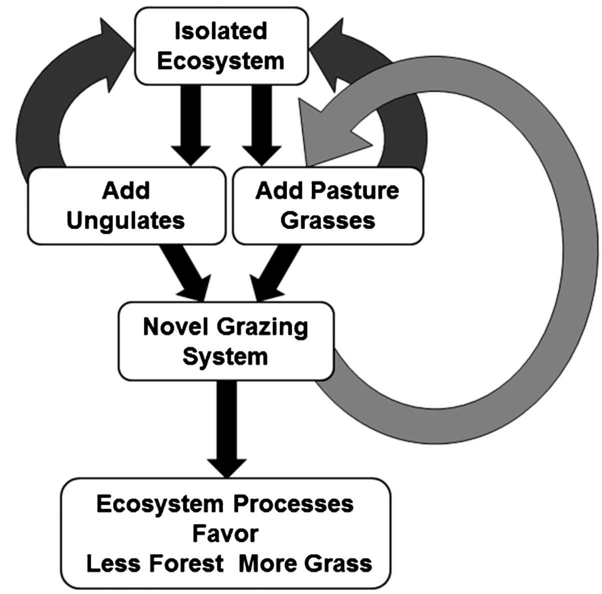

Fig. 1. Diagram of how insular forest ecosystems become novel grazing systems. The introduction of non-native herbivorous ungulates and non-native pasture grasses both have negative feedbacks on isolated ecosystems, favoring novel grazing systems, which have positive feedbacks on pasture grasses favoring less forest and more grasses over time.

Community level interactions among plants and herbivores can aggravate changes in ecosystem processes, leading to positive feedback cycles that reinforce community change (Fig. 1). Herbivory can promote productivity of grasses and accelerate ecosystem processes by enhancing the light regime of grasses and by the resulting deposition of feces (Frank et al. 1998, 2002). The proliferation of alien grasses further contributes to changes in nutrient cycling, hydrology, fire regimes, and gradual conversion from forest to savanna and grassland environments (D'Antonio and Vitousek 1992). Grasses throughout the tropics are instrumental in determining fire frequency and severity, often creating a positive feedback loop known as the 'grass/fire cycle' whereby forest and woodland become gradually replaced by grassland (D'Antonio and Vitousek 1992). The complete restoration of some severely degraded Hawaiian ecosystems may be impossible because transitions from one state to another may cross thresholds that cannot be reversed (Bestelmeyer 2006; Weller et al. 2011). The most severely degraded ecosystems will require intensive management including supplemental control of alien plant species released from herbivory, removal of rodents and other invasive species, and the addition of native species where propagules no longer remain.

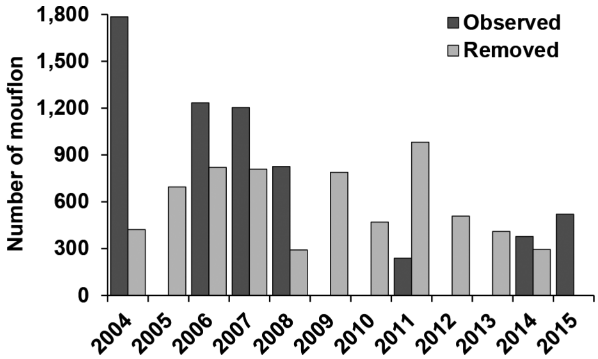

Fig. 2. Total number of European mouflon sheep observed during aerial surveys and the annual number removed at the Kahuku Unit of Hawai‘i Volcanoes National Park, 2004–2015.

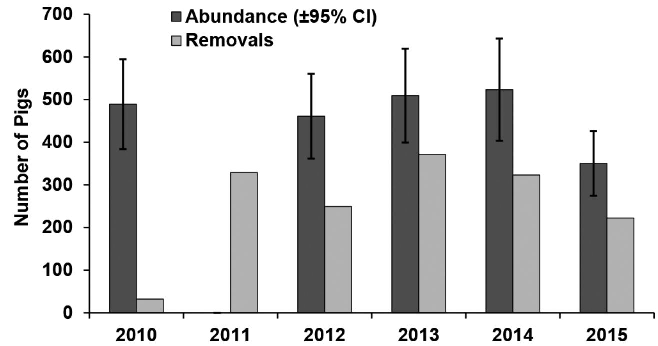

Fig. 3. Estimated total abundance of feral pigs (±95% confidence intervals) and the number of pig removals at Hakalau Forest National Wildlife Refuge, Hawai‘i Island, 2010–2015.

Monitoring the control of invasive ungulates

Control of non-native ungulates is the single most expensive natural resource management activity in many natural areas of Hawai‘i. It is often difficult to detect small numbers of incipient and relictual ungulates in these areas, especially for cryptic species which have never been domesticated. Aerial surveys are the most common method for assessing ungulate populations on a large spatial scale. However, the effectiveness of aerial surveys diminishes after populations have been reduced to low density and animals become more wary of activities associated with control and eradication. Consequently, monitoring on more intensive spatial scales becomes necessary to determine progress towards eradication.

In 2004, after the 468-km^2 Kahuku Ranch was acquired by HAVO, a directed volunteer program was initiated to reduce the abundance of European mouflon and prevent further degradation to native biota (Stephens et al. 2008). Staff hunting, shooting from helicopter, and the use of Forward-Looking Infrared Radar (FLIR) bolstered these efforts into an eradication program. However, aerial surveys demonstrated that volunteer hunters removed a disproportionate number of rams which promoted a strong female-bias and high population growth rates in the remaining population (Stephens et al. 2008). Ground-based surveys, camera trap monitoring, and aerial surveys enhanced with FLIR are now being compared to detect mouflon and other ungulates in a 131 km^2 area at Kahuku. More than 6,600 mouflon were removed from 2004 to 2014, and the number observed during aerial surveys dropped from 1,785 to 378 (Fig. 2). No mouflon were observed in two intensively managed subunits during the last survey, although small numbers have been periodically detected with game cameras and dispatched (USGS, unpublished data). Each monitoring method has strengths, but is limited by effective detection distance, spatial and temporal coverage, as well as intensity of effort. Systematic survey methods coordinated with continuous camera trap monitoring complemented each other when used for detecting small numbers of ungulates. The Kahuku Unit may soon become the largest area from which mouflon have been eradicated.

Because feral pigs are extraordinarily prolific (Hess et al. 2007), reinvasion of from the reservoir of animals in surrounding areas is a perpetual problem, making continuous fence maintenance and population monitoring necessary. HFNWR has intensively managed and monitored feral pig presence and distribution during surveys of all managed areas since 1988. Activity indices for feral pigs, consisting of the presence of relatively recent tracks, digging, browse, or scat were repeatedly recorded at more than 8,000 sample plots (Leopold et al. 2015). A calibrated model based on the number of pigs removed from one management unit and concurrent activity surveys was applied to estimate pig abundance in other management units (Hess et al. 2007). The resulting time series of pig abundance provides managers with a means to evaluate and refine control efforts in an adaptive management framework (Fig. 3). The simultaneous acquisition of rigorous data on ungulate population abundance, plant communities, and ecosystem processes would further advance the scientific basis for the management of natural resources in Hawai‘i.

Ungulate-free areas

There is now substantial evidence that non-native ungulates have degraded native ecosystems throughout

Table 1. Ungulate-free area in the Hawaiian Islands

Island	Ungulate-free (km^2)[a]	Potential Forest Bird Habitat (km^2)[b]	Ungulate-free Forest Bird Habitat (km^2)[b]
Hawai'i	399.2	5,932	151.0
Maui Nui	343.4	545	112.1
Kaho'olawe	115.5	0.0	0.0
Maui	220.8	446	106.0
Moloka'i	7.4	88	6.1
Lāna'i	0.0	11	0.0
Kaua'i	0.7	447	0.4
O'ahu	3.0	783	2.4
Grand Total	746.2	7,707	266.0

[a] Data from The Nature Conservancy of Hawai'i.
[b] Data from Price et al. (2009).

Hawai'i, and that recovery of native plant communities and associated wildlife cannot occur in the continued presence of ungulates (Price et al. 2009). Experimental exclosures and large-scale ungulate removals have demonstrated recovery of native ecosystems (Loope and Scowcroft 1985; Loh and Tunison 1999; Cole et al. 2012; Cole and Litton 2013). Land managers have developed highly effective control methods for large-scale removal of feral ungulates (Taylor and Katahira 1988; Anderson and Stone 1993). Ungulates have been completely excluded or removed from roughly 750 km^2 of important terrestrial ecosystems throughout the Hawaiian Islands to date, primarily on federal lands, but outside of forest bird habitat which contain the greatest biodiversity (Table 1; Hess and Jacobi 2011).

In conjunction with federal landowners, the Nature Conservancy of Hawai'i, the Natural Area Reserve System of the Hawai'i Division of Forestry and Wildlife, East Maui Watershed Partnership and the Three-Mountain Alliance of Hawai'i Island have all adopted and refined techniques for managing ungulates across larger landscapes. Many of these lands adjoin each other, thereby creating buffers and blocks of ungulate-free areas with high conservation value. The removal of ungulates, however, conflicts with sustained-yield hunting programs in that these lands become excluded from public use for the purpose of mammal hunting (Hess and Jacobi 2014). Societal values for hunting necessitate the construction and maintenance of expensive barriers to exclude ungulates from pest-free refuges on larger multi-tenure islands (Hess and Jacobi 2011). Some ungulates, however, pose additional new threats. European mouflon have not yet reached their full distribution on Hawai'i Island in areas that have inadequate fences (Ikagawa 2014). Axis deer populations are growing on Maui where they were introduced in 1959 (Tomich 1986; Hess et al. 2015). Game farms and ranches have also inadvertently (and illegally) released additional ungulate species which had never been previously established.

Illegal introductions of wild ungulates

Despite the overwhelming evidence of the negative effects of non-native ungulates on island ecosystems, illegal introductions of deer between islands have occurred recently. Axis deer are among the wild ungulates introduced to Hawai'i that had never been domesticated. The deer which are native to India, Sri Lanka, and Nepal (Graf and Nichols 1966) were given to King Kamehameha V in 1867 and released on Moloka'i in early 1868 (Kramer 1971). Several deer were moved to Lāna'i in 1920 and then to Maui in 1959 where they have become widespread (Anderson 2003). The introduction of axis deer to Hawai'i Island was debated for many years, but opposed by ranchers and environmentalists (Titcomb 1969; Walker 1969). An investigation by the U.S. Fish and Wildlife Service, however, revealed that a helicopter pilot and rancher from Maui had covertly transported four deer in exchange for about a dozen European mouflon sheep in December 2009 after sightings were reported (Tummons 2011a, b). Because neither species was established in the wild on either of the islands, in June 2012, state lawmakers responded by specifically banning "the intentional possession or interisland transportation or release of wild or feral deer" (Honolulu Star-Advertiser 2012). Two individuals were prosecuted under the Lacey Act for transporting wildlife between islands with the intent to guide hunting for out-of-state residents (Associated Press 2012). While the individual who provided the mouflon was sentenced to community service, the helicopter pilot agreed to provide 500 hours of flight time to locate and eradicate the Hawai‘i Island deer population in restitution (Hess et al. 2015). FLIR has been used intensively to locate and dispatch four individuals to date, but complexity of topography, vegetation, and land ownership prevents the confirmation of eradication of this cryptic species.

Invasive predators

Rodents

Introduced rodents, particularly black rats (*Rattus rattus*), have become superabundant on most of the world's inhabited islands, causing widespread ecological damage and enormous human health problems. Rodents prey on birds at all life history stages and compete for food resources by preying on invertebrates and seeds, often interrupting reproduction in plants (Lindsey et al. 2009). Rodents also carry several diseases that are communicable to humans, domestic mammals, and native wildlife. The bacteriological diseases murine typhus and bubonic plague caused by the organisms *Rickettsia typhi* and *Yersinia pestis* are hosted by many rodent species (Tomich et al. 1984). These diseases have a long history of causing human illness and mortality in Hawai‘i. Although plague has not occurred in the archipelago since 1957 (Tomich et al. 1984), murine typhus outbreaks still occur periodically, with 47 confirmed human cases in a 2002 outbreak (Manea et al. 2001). Leptospirosis, caused by the spirochete *Leptospira interrogans*, is one of the most widespread, sometimes fatal zoonoses worldwide, having an annual incidence of 1.29 per 100,000 people in Hawai‘i (Middleton et al. 2001; Katz et al. 2002). Other diseases associated with rodents, such as cryptosporidiosis, giardiasis, and salmonellosis, pose persistent and serious public health problems (Katz et al. 2002).

Recognizing the severe problems rats cause to nesting seabirds, the U.S. Fish & Wildlife Service (USFWS) and the Samoan Department of Wildlife and Marine Resources eradicated Polynesian rats (*Rattus exulans*) from 6.3 ha Rose Atoll, American Samoa, in 1990 using live- and snap-traps, brodifacoum, a second generation anticoagulant, and bromethalin in bait stations (Morrell et al. 1991; Murphy and Ohashi 1991; Ohashi and Oldenburg 1992). In the Northwestern Hawaiian Islands, Wildlife Services (WS) of the U.S. Department of Agriculture's Animal and Plant Health Inspection Service and the Hawai‘i Department of Land and Natural Resources (DLNR) eradicated Polynesian rats in 1993 from 129 ha Green Island, Kure Atoll, using brodifacoum bait stations (J. Murphy personal communication). In 1994–1996 the U.S. Navy, USFWS and WS eradicated black rats from three islands of Midway Atoll using brodifacoum, live traps, incidental baiting and rat nest removal (J. Gilardi and J. Murphy, personal communication; Witmer et al. 2011). Sand Island of Midway Atoll remains one the largest permanently inhabited islands in the U.S. from which rats have been removed. Growth of the Bonin petrel (*Pterodroma hypoleuca*) population from an estimated 32,000 nesting birds (Seto and Conant 1996) to more than 900,000 provides compelling evidence for the enormous benefits of rat eradication. Native vegetation on Midway also became noticeably more dense and abundant (N. Hoffman personal communication). House mice on Sand Island are now the only small mammal remaining in the Northwestern Hawaiian Islands.

At Palmyra Atoll in the equatorial Line Islands, rats prevented six seabird species from nesting. The first attempt to eradicate black rats from the atoll failed in 2001 due to the complexity of the 275 ha area with 54 islets, and dense vegetation (Wegmann et al. 2011). Notable factors contributing to the failure included bait taken by land crabs (*Cardisonma* and *Coenobita* spp.). A more intensive second attempt was successful by 2013, benefitting coconut palms (*Cocos nucifera*), and *Pisonia grandis* trees (Wegman et al. 2013).

The successes of rat eradication on remote islands have also brought about efforts to restore offshore islets of the main Hawaiian Islands. In 2002, the Offshore Islet Restoration Committee was formed to restore selected islets around the Hawaiian Islands. To date, rat eradications have been successful on Moku‘auia and tiny Mokoli‘i Islet, both near O‘ahu, using traps and diphacinone, a first generation anticoagulant, in bait stations (J. Eijzenga personal communication). Wedge-tailed shearwaters (*Puffinus pacificus*) subsequently began fledging from Mokoli‘i (D. Smith personal communication). A joint project by the USFWS, Hawai‘i DLNR, and WS to eradicate Pacific rats from 7 ha Mokapu Island off Moloka‘i in February 2008 was the first rat eradication using an aerial application of a rodenticide (diphacinone pellets) which was registered by the Environmental Protection Agency (EPA) in 2007 for conservation purposes in the U.S. (P. Dunlevy personal communication). Diphacinone was also broadcast by helicopter for Polynesian rats in January 2009 on 110 ha Lehua Islet, but eradication proved unsuccessful and is now being reconsidered

(VanderWerf et al. 2007; Parkes and Fisher 2011).

Larger areas of multi-tenure islands are now under consideration for the use of registered broadcast rodenticides for rodent control. Rodenticide treatment grids are being established in HAVO where hand and aerial broadcast trials of diphacinone pellets were conducted in support of EPA registration (Spurr et al. 2013). Several native and non-native species will be monitored to examine ecosystem responses. Reinvasion from the reservoir of animals in surrounding areas is inevitable; however, this type of management regime may benefit several species during seasonally important life history stages, such as the nesting period of forest birds, thereby providing an important conservation tool.

Mongoose

The small Indian mongoose (*Herpestes auropunctatus*), a predatory viverrid, was introduced to the Hawaiian Islands from Jamaica in 1883 to reduce rat populations in sugar cane fields on Hawai‘i Island, O‘ahu, Moloka‘i, and Maui (Hays and Conant 2007). Mongooses may have been effective at reducing damage to sugarcane by Norway rats (*R. norvegicus*), but only for a short period of time prior to the arrival of black rats (Atkinson 1977). Mongooses are now regarded only as pests and predators of ground-nesting birds, particularly the Hawaiian goose (*Branta sandvicensis*) and waterbird species (Stone and Loope 1987; Banko 1992). Without adequate prevention, mongooses may yet colonize Kaua‘i and Lāna‘i, the fourth and sixth largest Hawaiian Islands. Large-scale eradications of mongooses would be beneficial to ground-nesting birds but has not yet been achieved except in small enclosed areas.

Feral cats

Domestic cats (*Felis catus*) have been introduced to many of the world's islands where they have frequently become the dominant apex predator in the absence of any other larger predatory mammals. The consequences have been particularly devastating for native wildlife, including the decline, extirpation, and extinction of numerous vertebrate populations, particularly ground-nesting and burrowing landbirds and seabirds, as well as many herptile and small mammals which, in most cases, evolved in the absence of predatory mammals and feline diseases such as toxoplasmosis, caused by the protozoan *Toxoplasma gondii*. In Hawai‘i, *T. gondii* has been known to kill endangered Hawaiian monk seals (*Monachus schauinslandi*) and Hawaiian geese, critically endangered Hawaiian crows (*Corvus hawaiiensis*), and red-footed boobies (*Sula sula*) (Work et al. 2000, 2002, 2015; Honnold et al. 2005). Because surveillance for the pathogen is limited and diagnostic testing is not routinely performed on asymptomatic individuals, the prevalence of toxoplasmosis is still little known among wildlife species other than cats (Danner et al. 2007).

Depredation of endangered bird species in Hawai‘i has been frequently documented and attributed to cats based on the characteristic condition of carcasses (Hess et al. 2007; Lindsey et al. 2009; Judge et al. 2012). Photographic or videographic documentation provides direct evidence that confirms depredation by cats (Judge et al. 2012). However, the most direct and compelling proof of the effects of feral cats on wildlife populations come from comparisons of areas with and without cats (Smith et al. 2002) and examples where cats have been entirely removed from islands. In many cases, several species of extirpated seabirds as well as other wildlife have recovered after the complete removal of cats (Hess and Danner 2013; Hess 2014 and references therein).

In the Central Pacific, five species of seabirds have recolonized the islands of Baker, Howland, Jarvis, and Wake after the removal of feral cats (Rauzon et al. 2011). Worldwide, feral cats have been removed from more than 50 islands, many of which are remote and inaccessible. In cases where follow-up monitoring has been conducted and published, recovery of 22 species of birds on 11 islands has been documented on islands including Ascension, Juan de Nova (Mozambique), Marion, and several islands of Mexico (Hess 2014 and references therein). Where possible, the experimental removal of cats would provide the most conclusive proof of effects on wildlife populations as well as the rationale for removing cats from additional wildlife habitat. Although the use of toxicants may advance the efficacy of new lethal control techniques (Read et al. 2014), opposition from feral cat advocates often limit management practices to live-trapping in Hawai‘i (Hess et al. 2009).

Predator-proof fences

On multi-tenure islands where the eradication of feral cats and other predators may not be possible, predator exclosures provide the best prospects for the recovery of seabirds and other endangered bird species. Four such projects have been undertaken in Hawai‘i. Predator-proof fences have been developed and refined in New Zealand to exclude a wide variety of mammalian predators from vulnerable native bird species. They typically consist of a tall fence mesh fine enough to exclude mice, buried skirt to prevent burrowing, and a curved or floppy top to prevent predators from climbing over (Hess et al. 2009). One of the first predator-proof exclosures in Hawai‘i was a relatively small (~0.7 ha) area in HAVO to protect endangered Hawaiian goose goslings from feral cats, feral pigs, and mongooses (Hess 2011). Ka‘ena Point on O‘ahu became the first site of a predator-proof fence in the Hawaiian Islands to exclude all mammals from mice to dogs (Young et al. 2013). The fence spans 640 meters and encloses an area of approximately 24 ha. Removal of dogs, feral cats, and mongooses has been particularly beneficial to nesting seabirds like wedge-tailed shearwaters, but also to Laysan albatross (*Phoebastria immutabilis*). Dogs frequently ravage shearwater populations by killing nesting adults. Another 3.2 ha predator-proof fence was completed at Kīlauea Point National Wildlife Refuge on Kaua‘i in December of 2015 to protect Hawaiian geese, Laysan albatross, and Newell's shearwater (*Puffinus newelli*). The American Bird Conservancy is currently supporting the construction of a much larger exclosure to protect the largest colony of endangered Hawaiian petrels (*Pterodroma sandwichensis*) on Mauna Loa in HAVO.

Prognosis

Land management agencies have been highly successful by collaborating in scientific research and control of invasive mammals, culminating in the removal of several destructive species across large landscapes and many entire islands, and resulting in demonstrated ecosystem recovery (Hess and Jacobi 2011). The future for management of feral goats and sheep will most likely see the eradication of entire populations from increasingly larger, more complex islands and areas using more sophisticated techniques and tools (Campbell and Donlan 2005; Hess and Jacobi 2011; Chynoweth et al. 2013). In addition to Judas techniques, next-generation tools including remote sensing imagery, real-time telemetry, and thermal imaging devices such as FLIR may greatly improve the efficiency of locating and removing the last remaining animals which require the greatest effort, and aid in post-eradication monitoring. The outcomes of future eradication programs will likely result in overwhelmingly positive ecosystem responses as they have already, but higher-level species interactions, other newly introduced invasive species, and climate change may all present new obstacles to recovery.

Additional multi-species eradications of invasive predators from larger single-tenure islands would benefit numerous species of wildlife. Kaho‘olawe (117 km^2) would not be the largest island in the world from which feral cats have been eradicated, but it would be nonetheless logistically challenging because of unexploded ordnance left after decades of military training, and it would also require coordinated eradication of Polynesian rats and house mice. Aerial broadcast of brodifacoum could be highly effective for eradicating rodents and simultaneously reducing feral cats on Kaho‘olawe, but it presents higher risks to non-target animals than diphacinone, which may be less effective, particularly against feral cats and mice (Parkes et al. 2011). While the best methodological strategy may require careful forethought, there is little question that a pest-free Kaho‘olawe would be important for restoration of native seabirds and potentially other native species of plants and animals, including some that do not occur outside the northwest Hawaiian Islands, such as Laysan Teal (*Anas laysanensis*). The future conservation value of Kaho‘olawe may become increasingly important as feral cat colonies continue to become established on other large islands, threatening the viability of native wildlife (Winter 2003).

Multi-tenure islands where the rights of private landowners prevail are substantially more challenging for invasive mammal management, and the pace of new introductions is increasing. Better prevention strategies, early detection techniques, and control methodology for incipient invasive species would benefit the environment, agriculture, and economy of the entire Hawaiian archipelago. For example, small Indian mongooses, which have infested nearly all of the other Hawaiian Islands, were first discovered and captured on Kaua‘i in 2012, threatening endangered ground-nesting bird populations (Duffy and Capece 2014). Abundant source populations of these and other invasive vertebrates throughout the archipelago present a growing risk for accidental and intentional introductions to cross-contaminate islands. As with axis deer on Hawai‘i Island, detection and control is dependent on the trust and cooperation of landowners, who can deny access at any time. Successful eradication cannot be declared yet in these cases because it is virtually impossible to know if the last individual of a population has been removed from such large, populated islands. Therefore, the best chance for stopping additional invasions includes prevention, early detection, and rapid response before newcomers have a chance to reproduce. Once a small population of invaders starts to reproduce and becomes established, long-term commitment to monitoring and removal in partnership with landowners offers the best opportunity for successful eradication—particularly for cryptic species. Vigorous enforcement, addressing new threats to strengthen importation regulations, and increasing the number of people working in inspection, monitoring, and control would all aid in the prevention of additional introductions. Educational outreach and public awareness about invasive species, biodiversity, and legal and ecological consequences would also help curtail new species introductions. Prioritizing the prevention of new species introductions by natural resource agencies will greatly aid in the protection of endangered species and the prevention of additional species extinctions. The tools, knowledge, and ability to remove many mammal species from ecosystems in Hawai'i and other archipelagos already exist. Remaining obstacles include societal acceptance and limited fiscal resources.

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