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A Tour de Force by Hawai‘i’s Invasive Mammals: Establishment, Takeover, and Ecosystem Restoration through Eradication

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ABSTRACT: Invasive mammals, large and small, have irreversibly altered Hawai‘i’s ecosystems in numerous cases through unnatural herbivory, predation, and the transmission of zoonotic 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 has already advanced the restoration of native biota. Science applications supporting management efforts have been shaped by longstanding collaborative federal research programs over the past four decades. Consequently, feral goats have been removed from >1,358 km², and feral pigs have been removed from >723 km² of lands in Hawai‘i, bringing about the gradual recovery of forest ecosystems. The exclusion of other non-native ungulates and invasive mammals is now being undertaken with more sophisticated control techniques and fences. New fence designs are now capable of excluding feral cats from large areas to protect endangered native waterfowl and nesting seabirds. Rodenticides that have been tested and registered for hand and aerial broadcast in Hawai‘i have been used to eradicate rats from small offshore islands to protect nesting seabirds and are now being applied to montane environment of larger islands to protect forest birds. Forward-looking infrared radar is also being applied to locate cryptic wild ungulates that were more recently introduced to some islands. All invasive mammals have been eradicated from some smaller islands, resulting in the restoration of some ecosystem processes such as natural forest regeneration, but changes in other processes such as fire regimes and nutrient cycling remain more difficult to reverse at larger landscape scales. It may soon be possible to manage areas on larger islands to be free of invasive mammals at least during seasonally important periods for native species, but at the same time, new mammal introductions continue to occur.

KEY WORDS: control methods, ecological degradation, ecosystem recovery, eradication, Hawai‘i, island conservation, invasive mammals

INTRODUCTION

The 165-million-km² watery world of the Pacific Ocean contains numerous small islands in the tropical latitudes, many of which are administered by, or in cooperation with, the United States. These include the Hawaiian Archipelago with 137 islands that are part of the State of Hawai‘i; the Mariana Archipelago with 15 islands administered by the U.S. Territory of Guam and the Commonwealth of the Northern Marianas Islands; the Samoan Archipelago with 16 islands administered by American Samoa and the Independent State of Samoa; the Line Islands with 13 islands administered by the United States and the Republic of Kiribati; and Johnston and Wake Atolls, administered entirely by the United States. These are some of the most isolated islands on the planet, thus the remoteness of the Pacific islands contributes to the difficulty in managing or even visiting many islands on a regular basis.

The remoteness and extreme isolation in the Pacific islands, both in space and time, have also contributed to the development of unique flora and fauna that 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 biota of the Hawaiian Archipelago had to possess extraordinary dispersal capabilities to cross half of the Pacific Ocean. Only one species colonized the Hawaiian Islands every ~35,000 years prior to discovery by humans, and many groups of organisms with lesser dispersal capabilities have never become naturally established (Loope 1998, Ziegler 2002). Extreme isolation precluded the establishment of entire groups of organisms that have been highly successful throughout the rest of the world. For example among terrestrial birds, there are no woodpeckers and doves; no terrestrial herptiles dispersed to these remote islands; and terrestrial mammals were limited to two bat species. Predators were restricted to raptorial birds, and herbivores were represented by snails, insects, and flightless waterfowl that consisted of about 11 species of large ducks and geese (Olson and James 1982). None of the vertebrate herbivores of Hawai‘i possessed hooves or teeth, but some had serrated bills, and there is evidence that several plants developed secondary defenses, primarily thorns, against herbivory by Hawaiian waterfowl (Givnish et al. 1994). The arrival of terrestrial mammals came only with the assistance of humans, which forever altered the ecosystems of these islands, first from Polynesian settlers, and then from European explorers (Tomich 1986). The Polynesian or Pacific rat (Rattus exulans) and domestic swine (Sus scrofa) were among the first terrestrial mammals to be introduced to the Hawaiian Islands, nearly 1,000 years ago (Kirch 1982).

HORDES OF INTRODUCED HERBIVORES

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: 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 re-supply outposts (Tomich 1986). These livestock proliferated without any predators or competitors and quickly became feral. Goats have been introduced widely to islands throughout the world, have repeatedly escaped captivity, and are able to persist in some of the most arid environments with minimal vegetation (Chynoweth et al. 2013). The severe ecological degradation caused by feral goats 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 it had not been applied to ecological problems until the 20th century. The first mammal to be eradicated from any island in the central Pacific was the feral goat from the island of Ni’ihau in 1911 (Kramer 1971). It was also clear that goats were damaging forests and watersheds on other Hawaiian islands. The eradication of goats from the island of Lāna‘i began in 1902 but wasn’t finished until 1981 (Hobdy 1993).

One of the most influential assessments on the management of goats in Hawai‘i was by Starker Leopold in 1963, who reported to Congress that wildlife in U.S. national parks included a notable overabundance of herbivores throughout the park system (Leopold et al. 1963). Not only did this spur the removal goats from national parks in Hawai‘i, but it resulted in the restoration of ecological integrity of other parks such as Yellowstone. The largest area in Hawai‘i from which feral goats were eradicated was Hawai‘i Volcanoes National Park (HAVO), which was the largest area from which goats were eradicated on any island in the world until it was surpassed by the Galápagos island of Santiago in 2005 (Cruz et al. 2009). Goats had been removed from HAVO since 1927 but with no lasting effect, due to reinvasion from the reservoir of animals in surrounding areas (Baker and Reeser 1972). The reinvasion 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 such as the Judas goat technique necessary to accomplish eradication from the enclosed areas by using radio-telemetry to take advantage of gregarious behavior in domestic ungulates, and it is now widely used throughout the world (Taylor and Katahira 1988, Cruz et al. 2009). Feral goats have been eradicated from 1,358 km² on seven islands of the central Pacific (Hess and Jacobi 2011).

Vancouver strategically liberated livestock throughout the Hawaiian archipelago and meticulously documented these introductions, including four sheep at Kawaihae in 1793 and four others at Kealakekua in 1794 (Tomich 1986). Vancouver was able to convince King Kamehameha I, who had recently unified his authority over Hawai‘i Island, to enforce a 10-year kapu, which forbade the killing of livestock. Sheep were later reported near the summit of Mauna Kea, the highest peak in the Pacific, only 32 years after their introduction (Ellis 1917). Sheep were destructive to forests and watersheds, prompting territorial foresters to construct fences in 1935-1937 and create the Mauna Kea Forest Reserve (Bryan 1937). More than 47,000 sheep were removed in 10 years, which allowed the māmāne (Sophora chrysophylla) forest to regenerate and protect the watershed. Sheep populations were allowed to rebound when sport hunting was promoted after World War II and the forest of Mauna Kea was found to be in dire condition by 1960 (Warner 1960). Nonetheless, feral sheep were intentionally hybridized with European mouflon and released on Mauna Kea from 1962 to 1966 (Tomich 1986).

Federal court rulings ordered the removal of goats and sheep from Mauna Kea in 1979 and 1986 to protect critical habitat for the federally endangered palila (Loxioides bailleui), an endemic Hawaiian forest bird (Hess and Banko 2011). Reductions in ungulate populations in the 1980s resulted in uneven forest recovery by 1990s (Hess et al. 1999). Goats had been eradicated by 1988, but sheep persisted and rebounded in numbers. More than 87,000 sheep have been removed in the past 75 years (Banko et al. 2014). More recent court rulings have revitalized the effort to reconstruct the fence around Mauna Kea Forest Reserve; however, the decline of Palila has been compounded by drought, bringing the long-term persistence of Palila into question (Banko et al. 2013). There are only two islands where sheep have been eradicated: Lāna‘i and Kaho‘olawe, comprising 478 km² (Hess and Jacobi 2011). However, there are large areas of Hawai‘i Island where eradication is being attempted. Efforts on Mauna Kea have had limited success, but there are areas of the Kaukku Unit of HAVO that are nearly sheep-free now.

**WILD UNGULATES**

Other ungulates which have never been domesticated were also introduced to Hawai‘i beginning in 1868 including deer, sheep, and pronghorn (Antilocapra americana) (Hess 2008). Pronghorn were one of the few unsuccessful introductions. Axis deer (Axis axis) were in introduced to Moloka‘i in 1868, Lāna‘i in 1920, and to Maui in 1959 (Tomich 1986). Axis deer have never been domesticated, their range is still expanding, and there is the potential for more releases on other islands, such as the illegal introduction to Hawai‘i Island in 2009 that was confirmed by game cameras in 2011 (Hess et al. 2015).

European mouflon sheep (Ovis orientalis), the world’s smallest wild sheep, is another wild ungulate to become widely established in the Hawaiian Islands. Mouflon originate from Mediterranean islands of Sardinia, Corsica, and Cyprus. They were introduced to Hawai‘i in 1954 (Tomich 1986). A directed volunteer program was implemented in 2004 to curtail further degradation of the environment from mouflon at the Kaukku Unit of HAVO, a 468-km² area. The program removed >2,440 mouflon between May of 2004 and September of 2008, taking an average total >28 mouflon per field day. There was, however, a major disparity in the proportion of females removed and the proportion at large, especially in 2006-2007, resulting in a selective removal of rams from the population (Stephens et al. 2008). This may possibly lead
to a shift in the population toward a higher proportion of females and thus greater reproductive potential, although there is not yet a significantly higher proportion of females in the population compared to when the program started (Judge et al. 2016). Aerial surveys with Forward-Looking Infrared Radar (FLIR), ground-based sign surveys, and trail cameras are currently being used in multi-scale population monitoring to determine when management units at Kahuku become mouflon-free (Judge et al. 2016).

FERAL PIGS

Feral pigs differ fundamentally from other ungulate species because in addition to herbivory and trampling, pigs also wallow, dig, and root in soil, primarily in mesic and wet forests. Archaeological evidence documented signs of domestic pigs, which originated from Island Southeast Asia (Larson et al. 2005), at permanent Polynesian settlements on the islands of O’ahu (Pearson et al. 1971), Moloka‘i (Kirch 1982), and Kaua‘i (Burney et al. 2001). Despite the fact that domestic swine have become one of the most widely distributed large feral mammals on most islands throughout the Pacific, there is no evidence that pigs strayed far from commensal situations in Hawai‘i until the admixture of European strains (Maly 1998, Ziegler 2002, Larson et al. 2005). The scientific literature on feral pigs in Hawai‘i contains 36 peer-reviewed publications: 31 studies addressed direct detrimental effects of pigs on native vegetation; 13 studies addressed indirect effects or ecosystem processes; and seven studies addressed both direct and indirect effects of pigs (Leopold and Hess 2016). Managers of natural areas in Hawai‘i have fenced and removed pigs from about 7 pigs (Leopold and Hess 2016). Managers of natural areas established prior to pig removal (Leopold and Hess 2016). Proliferated, particularly where they had become species often recovered, some invasive plant species also landscape-scale removal of pigs; while dominant native entire watersheds (Hess and Jacobi 2011). Several studies addressed indirect effects or ecosystem processes; and detrimental effects of pigs on native vegetation; 13 studies have been addressed or otherwise extirpated from much of the most frequently eradicated species in the Central 2

UNGULATE-FREE AREAS

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 km² of important terrestrial ecosystems throughout the Hawaiian Islands to date, primarily on federal lands, but outside of habitats that contain the greatest biodiversity (Hess and Jacobi 2011). The effects of ungulates on native vegetation and ecosystems have been addressed in 58 original studies and mostly showed strong short-term regeneration of dominant native trees and understory ferns after ungulate removal, but other altered processes such as fire regimes and nutrient cycling remain more difficult to reverse at larger landscape scales (Leopold and Hess 2016). The removal of ungulates, however, also 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).

RABBITS

One of the earliest and most disastrous episodes involving the introduction of invasive wildlife to fragile insular ecosystems occurred in the Northwestern Hawaiian Islands, where European rabbits (Oryctolagus cuniculus) were introduced, as a source of food, to the small islands of Lisianski and Layson about 1902, and subsequently discovered on Southeast Island of Pearl and Hermes Atoll in 1916 (King 1973), resulting in the extinction of several endemic bird species (Ely and Clapp 1973). Attempted eradications from Layson and Lisianski beginning in 1912 were unsuccessful until rabbits eliminated most of Lisianski’s vegetation by 1914, which eventually resulted in their own starvation (Olson and Ziegler 1995). Nearly simultaneous with their eradication in 1923, rabbits caused desertification of Layson and the extinction of the Layson honeycreeper (Himatione sanguinea freethii), the Layson millerbird (Acrocephalus familiaris familiaris), and the last observations of Layson rail (Porzana palmeri) on that island (Ely and Clapp 1973). Rabbits have been repeatedly released on the larger Hawaiian Islands but, surprisingly, invasive wild populations have generally not become problematic. The fate of rabbits on some islands is not clearly known, having disappeared on several islands, probably by drought-induced starvation. Rabbits are one of the most frequently eradicated species in the Central Pacific, having been removed or otherwise extirpated from 9.5 km² on nine islands (Hess and Jacobi 2011).

RODENTS

The Polynesian rat, originating from Southeast Asia, accompanied early Polynesian voyagers to virtually every island in the Pacific (Kirch 1982, Matisoo-Smith and Robins 2004). Because of its introduction to Hawaii‘i perhaps nearly 1,000 years ago, its major influences on the Hawaiian native biota are assumed to have occurred long
before Europeans arrived (Blackburn et al. 2004). The devastating effects of the third-most-widely-distributed rat on Earth have only recently come to light and may have included the catastrophic disappearance of native lowland forests of Hawai‘i in as little as 50 years (Athens 2009). House mice (Mus musculus) were brought unintentionally to the Hawaiian Islands by 1816 and reached the summit of Mauna Kea by 1825 (Tomich 1986). Norway rats (Rattus norvegicus) were noted by 1835. Black rats (R. rattus) were a later arrival not documented until 1899, apparently after the construction of shipping wharfs (Atkinson 1977).

Introduced rodents, particularly black rats, have become superabundant on most of the world’s inhabited islands, causing widespread ecological damage and enormous human health problems (Lindsey et al. 2009). Rodents carry several zoonotic diseases that are communicable to humans, domestic mammals, and native wildlife, including bacteriological diseases such as murine typhus and bubonic plague, which have a long history of causing human illness and mortality in Hawai‘i (Tomich et al. 1984, Sasaki et al. 2003). Leptospirosis is also a widespread and sometimes fatal zoonotic disease in Hawai‘i (Katz et al. 2002). Other diseases associated with rodents, such as cryptosporidiosis, giardiasis, and salmonellosis, pose persistent and serious public health problems (Sasaki and Ikeda 2000, Katz et al. 2002). Rodents also 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).

Hawai‘i has been a leader in registration of diphacinone, a first-generation anticoagulant, as a broadcast rodenticide. Diphacinone has fewer non-target and secondary effects than some second-generation anticoagulants. Bait boxes with diphacinone were first registered for use in natural areas in Hawai‘i in 1997, and at least 13 agencies have been involved in several aerial rodenticide operations conducted under experimental conditions in support of registration for hand and aerial broadcast, which was approved by the Environmental Protection Agency and the Hawai‘i Department of Agriculture in 2007 (Hess et al. 2009). Aerial broadcast of diphacinone was used to eradicate Polynesian rats from Mokapu Islet, near the island of Moloka‘i, in 2008: the first rat eradication using aerial application of diphacinone pellets. Polynesian rats have now been eradicated from 6.2 km² on five islands, and black rats have been eradicated from 12.9 km² on six islands (Hess and Jacobi 2011). These actions have already benefitted several species of seabirds as well as native plants. Larger areas of multi-tenure islands are now under consideration for the use of registered broadcast rodenticides for rodent control.

**Mongoose**

The small Indian mongoose (Herpestes auropunctatus) was deliberately introduced to the Hawaiian Islands from Jamaica in 1883 by sugar planters to reduce rat populations in cane fields on Hawai‘i Island, O‘ahu, Moloka‘i, and Maui, probably before the establishment of black rats (Atkinson 1977, Hays and Conant 2007). Mongooses are now regarded as pests and predators of ground-nesting birds, particularly the Hawaiian goose (Branta sandvicensis) and waterbird species (Stone and Loope 1987, Banko 1992). Large-scale eradication of mongooses would be beneficial to ground-nesting birds but has not yet been achieved except in small enclosed areas. Without adequate prevention, mongooses may yet colonize Kaua‘i and Lāna‘i, the fourth and sixth largest Hawaiian Islands. A road-kill mongoose was discovered on Kaua‘i in 1976, and more recent trapping efforts captured three individuals in May and July 2012, and October 2016.

**Cats**

One of the most important predators on native wildlife throughout the Pacific islands was also introduced by European explorers. The domestic cat (Felis catus) has been present in Hawai‘i since the early days of European contact, soon after which feral populations became established, although the spread of this species in the wild was not well documented (Tomich 1986). Cats were reported to be abundant predators of native birds in forests of Lāna‘i and O‘ahu by the late 1800s (Rothschild 1893, Perkins 1903). Depredation of endangered bird species in Hawai‘i has been frequently documented and attributed to cats (Hess et al. 2007a, Lindsey et al. 2009), and recent photographic and videographic documentation confirms direct evidence (Judge et al. 2012). However, the most compelling proof of the effects of feral cats on wildlife populations comes from 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 2012, 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 from a total area of 15.2 km² (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).

**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. One of the first predator exclosures in Hawai‘i was a relatively small (~0.7-ha) area in HAVO to protect Hawaiian goose goslings from feral cats, feral pigs, and mongooses. The American Bird Conservancy is currently supporting the construction of a much larger exclosure to protect the largest Hawaiian Petrel (Pterodroma sandwichensis) colony on Mauna Loa in HAVO. Ka‘ena Point on O‘ahu became the first site in the Hawaiian Islands to get a predator-proof fence to exclude all mammals from mice to dogs (Young et al. 2013). The fence spans 640 m and encloses an area of approximately 24 ha. Removal of dogs, feral cats, and mongooses is particularly beneficial to nesting seabirds like wedge-tailed shearwaters (Puffinus pacificus), but also...
to Laysan albatross (*Phoebastria immutabilis*). Another 3.2 ha predator-proof fence was completed at Kilauea Point National Wildlife Refuge in December of 2015 to protect Hawaiian goose, Laysan albatross, and Newell’s shearwater (*Puffinus newelli*).

**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). 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. The value of larger uninhabited islands for wildlife, such as Kaho'olawe, becomes greater as some low-lying islands face rising sea levels from climate change, human population density continues to increase on inhabited islands, and as feral cat colonies continue to become established on other large islands, threatening the viability of native wildlife (Winter 2003). However, feral cats, Polynesian rats, and mice currently occur on Kaho'olawe. Eradication of these invasive mammals may prove challenging because of unexploded ordnance remaining on the island from military training. Nonetheless, 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*).

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**LITERATURE CITED**


