Feral Goats in the Hawaiian Islands: Understanding the Behavioral Ecology of Nonnative Ungulates with GPS and Remote Sensing Technology

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ABSTRACT: Nonnative feral ungulates have both direct and indirect impacts on native ecosystems. Hawai`i is particularly susceptible to biological invasions, as the islands have evolved in extreme geographic isolation. In this paper we explore the ecological impacts of nonnative feral goats (Capra hircus) in the Hawaiian Islands, including both the current state of knowledge and future research directions to address knowledge gaps. Understanding how invasive vertebrates impact island ecosystems is important as it provides an informed context for developing contemporary solutions to pressing management problems. Current knowledge gaps, such as the behavioral ecology of goats and their impacts on specific plant species and communities, limit the effectiveness of ecological restoration and conservation in Hawai`i. Emerging technologies in wildlife tracking and remote sensing will enable a greatly improved understanding of the behavior and ecological impacts of these nonnative animals in what is already a highly degraded ecosystem.

KEY WORDS: Capra hircus, ecological restoration, feral goats, GPS, Hawai`i, movement ecology, nonnative ungulates

INTRODUCTION
The history of introduced vertebrates in the Hawaiian Islands began with the arrival of Polynesians between 300 and 600 A.D. Early introductions included the domestic pig (Sus scrofa), dog and fowl, as well as unintended stowaways such as the Polynesian rat (Rattus exulans), geckos, and skinks (Kirch 1982). Because Hawaiian ecosystems evolved in the absence of such organisms, their introduction, along with colonization by humans, contributed to a largely irreversible transition from a pristine system to the heavily modified biota present in Hawai`i today. Although Polynesians initiated species introductions into native Hawaiian ecosystems, new introductions including large grazing mammals continued with European contact.

Beginning in the late 18th century, Europeans brought a variety of species to the Hawaiian Islands, many of which have subsequently established feral populations. The original purpose of some vertebrate introductions was likely to populate oceanic islands with a food source to access during later voyages (Cambell and Donlans 2005). Other animals became established after arriving as stowaways on ships, or more recently as a result of the purposeful introductions of game animals. Domestic goats (Capra hircus) were introduced to provide food for sailors on long voyages, but they quickly became a self-sufficient feral population (Yocum 1967).

Nonnative feral goats have a tremendous impact on island ecosystems (Coblentz 1978). The Hawaiian Islands are particularly vulnerable to the detrimental impacts of nonnative ungulates, due to their high degree of geographic and evolutionary isolation and large proportion of endemic species. Overall, goats are considered to be “the single most destructive herbivore” introduced to island ecosystems globally (King 1985). Their behavior can directly affect ecosystem processes through grazing and trampling of vegetation. Moreover, feral goats have important indirect effects, including the alteration of plant communities (e.g., via selective feeding and nonnative plant spread) and the destruction of native and endemic wildlife habitat. From an ecological perspective, removal of these animals can have both positive and negative effects (e.g., their overall impact on the spread of invasive species is unclear). Currently, however, most available funding is allocated to eradication and not research. Total eradication is very difficult, if not impossible, in Hawai`i and in many other island settings due to topographically challenging mountain ranges and other physical obstacles. Large populations, extreme and remote terrain, and economic cost can be limiting factors to eradication efforts. Cultural values are also often associated with the animal, such as recreational hunting and provision of a food source, and can affect public support for animal removal. As a result, a better understanding of the history of feral goat introductions and spread, their ecology, and their impacts on native ecosystems should help to provide insight into management techniques designed to minimize their negative impacts and maximize the opportunity for restoring and conserving native ecosystems.
GOAT INTRODUCTIONS AND SUCCESS AS AN INVASIVE SPECIES

Domestic goats were first introduced to the Hawaiian Islands by Captain Cook in 1778 on Ni`ihau, and Captain Vancouver in 1792 on Kaua`i (Marques 1906). Indigenous populations quickly utilized goats as a food source, harvesting both domestic and feral populations. Although estimates of goat populations are unavailable during the 18th century, evidence suggests that feral goats began to spread into remote areas of the islands at this time. Without natural competitors or predators, populations were likely able to grow in a nearly exponential manner. In New Zealand, for example, research has shown that a goat population recovering from an eradication attempt can double in size over only 2 years (Rudge and Smit 1970). Comparatively, the only estimates of population size in Hawai`i for the 19th century exist from records of the export of goat skins to the mainland United States. By 1850, less than 75 years after their introduction, the annual export of goat skins from Hawai`i was 26,519 (Yocum 1967). These large increases in feral goat populations over such a short time period are likely the result of the goat’s unique ability to survive on almost any type of forage, a lack of predators, and the existence of large expanses of unoccupied habitat.

The remarkable adaptability of the goat as a species has enabled feral populations to establish themselves across a wide range of habitats on the main Hawaiian Islands. Today, feral goat populations exist from low to high elevations and in wet to dry habitats in Hawai`i (Stone 1984). As an opportunistic herbivore, the feral goat utilizes an assortment of browse for subsistence, including native and nonnative plants in Hawai`i (Yocum 1967, Morris 1969). Preferred feeding areas appear to be open, dry grasslands, shrublands, or forests (Morris 1969). However, goats can be observed in nearly every habitat in the archipelago. The impacts of goat grazing and browsing is typically detrimental to native Hawaiian flora, as these plants evolved in the absence of large grazing herbivores and therefore lack the chemical and morphological defensive mechanisms to deter herbivory (Kelsy and Locken 1987, Shley and Petroff 1999).

By the mid-20th century, many biologists began to come to a consensus on the negative impacts of feral ungulates on islands (Coblentz 1978). Eradication efforts were successful on Lana`i (1981) in order to provide habitat for more economically lucrative game animals, and on Kaho`olawe (1990) to reduce soil erosion (Scowcroft and Donlans 2005). Today, populations of largely unknown sizes exist on 5 of the 8 main Hawaiian Islands. Ungulates in general have a significant presence in Hawai`i, with associated economic and cultural values. As a result, the continued presence of large herds of nonnative grazing ungulates in Hawai`i’s sensitive and often degraded ecosystems results in the continued risk of extinction for native and endemic species.

IMPACT OF FERAL GOATS ON NATIVE ECOSYSTEMS

As the most remote island ecosystems in the world, Hawai`i’s native species are particularly vulnerable to biological invasions (Wilcove et al. 1998). The Hawaiian Islands are volcanic in origin, and species arrived naturally over time via sea or wind dispersal. During thousands of years of isolation, many plant and animal species evolved without the natural defenses of mainland relatives, and therefore many plants lack defenses against herbivory (Coblentz 1978). Consequently, native plant communities are often unable to recover from the pressures of grazing and trampling, resulting in the replacement by more tolerant and resilient nonnative species (Augustine and McNaughton 1998).

Exclosure studies in Hawai`i have been few, but typically show an immediate response of vegetation to release from grazing pressure. On the Island of Hawai`i, comparisons between heavily browsed and lightly browsed areas demonstrated a lack of recruitment and an older age class structure for the main tree species, mamane (Sophora chrysophylla), in the presence of grazing (Scowcroft and Sakai 1983). Exclosure studies in other dryland Hawaiian forests also demonstrate increased survival rates inside fenced units where goats have been removed (Scowcroft and Hobdy 1987). The endemic koa (Acacia koa hawaiensis) had reduced sucker-growth, an important reproductive strategy, outside of goat exclosures (Spatz and Mueller-Dombois 1973). These studies provide evidence that feral goats are an important introduced disturbance that has drastically altered a landscape of plants that largely lacks defensive mechanisms to deter herbivory.

Few studies have been conducted that analyze the foraging preferences of feral goats in Hawai`i, but goats are known to feed on a variety of plant species, both native and nonnative. Morris (1969) conducted a study of stomach contents of feral goats in two habitats in Hawai`i Volcanoes National Park and found that in areas of high goat density where native vegetation was scarce, nonnative plants comprised 99% of stomach contents. In comparison, in areas of low goat density, where native vegetation was abundant, stomach contents contained 98% native species (Morris 1969). From these observations, it appears that goats help facilitate alteration of plant community composition. Native species are consumed when available, and once plant communities have been converted to nonnative species, goats turn to these less palatable plants that appear to be able to maintain viable populations under grazing pressure.

In addition to direct grazing pressure on native species, a multitude of other factors appear to enable feral goats to alter landscapes in Hawai`i. Specifically, the vulnerability of native plant communities to invasion by nonnative plants is a key component to the success of goats as an agent of landscape change (Wilcove et al. 1998). Nonnative vertebrate herbivores can have positive effects on nonnative plant populations, where native plants are quickly replaced and outcompeted by nonnatives (Oduor et al. 2010). As feral ungulates forage, they disperse both nonnative and native plant seeds via excrement and attachment to the fur (Janzen 1984). Traveling through the landscape, goats trample plants in paths and in wallows where they rest. Nonnative plant species can often rebound quickly from these impacts,
while native plants are frequently unable to reestablish, particularly in areas where nonnative plants have become established (Sheley and Petroff 1999).

Nonnative ungulates in Hawai`i have contributed to habitat loss of endemic wildlife species by altering vegetation structure and composition in many areas. For example, the endangered palila (Loxioides bailleui) is a finch-billed honeycreeper that primarily relies on the native mamane tree as a food source (Jeffrey et al. 1993). Mamane forest habitat has been heavily grazed and degraded by nonnative ungulates, where they prefer accessible foliage, saplings, and bark from mature trees as forage (Scowcroft and Sakai 1983). This behavior limits the growth of native plant communities, results in soil erosion, and promotes the spread of invasive species (Scowcroft and Giffin 1983). To address this issue, a federal court order was issued in 1979 (and again in 1987) to remove grazing animals from palila habitat in order to maintain the only remaining population of this endangered Hawaiian bird on Mauna Kea, Island of Hawai`i (Nelson 1982). Unfortunately, total eradication of ungulates within palila habitat has been unsuccessful, most likely due to ingress from surrounding populations that remain large, and largely unmanaged as well as the lack of fencing.

Feral goats exert a tremendous amount of pressure on ecosystem processes through foraging and movement through vegetation. In heavily modified ecosystems, such as Hawaiian tropical dry forests, ecological impacts are not always straightforward, and long-term studies on the effects of ungulate exclusion indicate that animal removal can promote the spread of invasive, fire-promoting grasses (Cabin et al. 2000). Although ungulate eradication may be an important first step in restoration efforts, it should not be considered a panacea, as nonnative grazing mammals may play an important role in the initial spread and subsequent control of some invasive plants.

Specific ecological impacts of feral goats are often difficult to assess, as their habitat utilization overlaps with other nonnative ungulate species (e.g., feral sheep, Ovis aries, and mouflon sheep, Ovis musimon). In areas with a high density of these ungulates, habitat alteration is clearly visible, from ecological degradation to alteration and replacement of entire ecosystems. Forested areas are often reduced to grasslands, and native plants are frequently replaced by nonnative-dominated communities. Hence, the introduction of large grazing mammals has resulted in long-term modifications of native Hawaiian ecosystems. However, little is known about the effects of individual ungulate species in Hawai`i. Although the overall impact of goats on island ecosystems is considered to be negative (Coblentz 1978), in the context of ecological restoration, feral goats in Hawai`i may help suppress the spread of certain invasive species (Cabin et al. 2000). However, this suppression typically results in detrimental impacts for native plant populations as well. Additional research is clearly needed to further understand the role of feral goats as an agent of landscape change in native Hawaiian ecosystems.

NEW APPROACHES TO ANALYZING ANIMAL BEHAVIOR

Landscape-level studies investigating the impact of feral goats on native Hawaiian ecosystems are conspicuously lacking and are needed to further understand their role as an agent of landscape change. Prior small-scale studies have provided valuable information on nonnative ungulate ecology in Hawai`i, but information at larger scales on behavioral ecology (e.g., foraging patterns, habitat selection, seasonal movement and response to vegetation dynamics) of individual species is conspicuously lacking. Previous studies have determined that nonnative ungulates typically have a negative impact on native Hawaiian ecosystems (Spatz and Mueller-Dombois 1973, Scowcroft and Sakai 1983, Scowcroft and Hobdy 1987), but may also help suppress the spread of some invasive species (Cabin et al. 2000). In order to manage these animals and their impacts holistically, more research and at broader scales is needed. Two factors make additional research on ungulates in Hawai`i a promising avenue: (i) technological advances in animal tracking and remote sensing; and, (ii) the concept of movement ecology, which represents a relatively new analytical framework that places movement as the focal point for investigating ecological interactions.

Technological advances have made it possible to collect high-resolution spatiotemporal movement data for wildlife species (Cagnacci et al. 2010). Contemporary wildlife tracking collars have become lighter weight, have longer battery life, and enable a higher accuracy for location estimates. Location data can be collected using GPS collars at a variety of intervals to catalogue movement at a fine temporal scale. Specific types of movement, or movement phases, can be identified and associated with particular types of activities (Fryxell et al. 2008). For example, foraging movement may appear as many location points close together in many different directions, while predator avoidance may appear as data points separated by long distances in a single direction.

Advances in remote sensing technology have also made habitat analysis possible on a regional scale. Specifically, airborne Light Detection and Ranging (LiDAR) systems can create three-dimensional land cover maps of a study area. LiDAR technology can map at a spatial resolution of 0.1-1.5 meters, enabling a fine scale landscape reconstruction, and can be used to correlate animal movement to composition and structure of vegetation (Asner et al. 2009). At such a high resolution, individual plants can be identified and land cover maps can be used to determine if the foraging behavior of goats is based on a hierarchy of preference. Since LiDAR systems provide data in a third dimension, height, analysis of how structural variability of plant communities across the landscape may affect animal movement is possible. Correlating large herbivore movement and their impacts on vegetation with the structure of the forest (i.e., three-dimensional attributes) can provide new information about the ecological effects of animal populations (Asner et al. 2009).
Temporal dynamics of vegetation can also be detected with remote sensing technology. NASA’s Moderate Resolution Imaging Spectroradiometer (MODIS) sensors produce a composite image of a study area every eight days, enabling analysis of temporal changes in a landscape. Spectral mixture analysis (Adams et al. 1986) can be used to detect and quantify photosynthetic vegetation, non-photosynthetic vegetation, and bare substrate. As pulse precipitation events occur, photosynthetic activity associated with green-up events can be detected with remotely sensed imagery as specific changes in spectral wavelengths (Elmore et al. 2005). MODIS images allow identification of specific areas that are experiencing high plant activity at specific times and, when combined with animal movement data, can be used to determine how feral goats respond to changes in phenology and vegetation activity across the landscape.

Advances in technology allow for detailed investigation of movement patterns and animal behavior. Data from wildlife tracking collars combined with remotely sensed images can be used to describe the utilization distribution of a species (i.e., the intensity of use by an individual or population). The landscape that a species inhabits is inherently heterogeneous, and essential resources are often separated by unsuitable habitat. To describe an organism’s movement between resources, the utilization distribution concept and the emerging paradigm of movement ecology can be used. Movement ecology emphasizes the importance of unifying movement studies in a hypothesis-driven understanding of the role of animal movement in ecological processes (Nathan 2008). The framework promotes an understanding of movement patterns regardless of species or movement method. Instead, the underlying mechanisms driving movement (e.g., resource use, predator avoidance) are analyzed to determine patterns that can be correlated across a variety of scales.

The movement ecology framework is a simplified approach, incorporating four basic components to explain the movement of an organism: internal state, motion capacity, navigation capacity, and external factors (Nathan 2008). This framework allows researchers to explore both patterns of movement and the causal mechanisms. By including current technology in the framework of movement ecology, a comprehensive investigation of the impact of nonnative feral goats on Hawaiian ecosystems will be possible.

FUTURE DIRECTIONS

The overall ecological impact of nonnative feral ungulates in the Hawaiian Islands is clear. Grazing mammals severely degrade and disturb the landscape, which is thought to promote the spread of some nonnative invasive plants. However, management and restoration efforts require consideration of the value of ungulates as a biological control for invasive plants, as results to date have been mixed and appear to be species-specific. Unfortunately, research on individual ungulate species is limited, and the specific impact of feral goats in Hawai`i is largely unknown. A better understanding of the behavioral ecology of these animals would enable more comprehensive management (i.e. conservation and restoration) efforts in Hawai`i, and on other islands throughout the tropics. In particular, a better understanding is needed of which plant species are preferred forage for feral goats, which plant communities are most impacted, and how feral goats move across the landscape in response to vegetation structure and seasonal plant activity. This information can then be used to guide effective management plans not only for nonnative feral animal populations, but also for conserving and restoring populations of native Hawaiian biota.

A detailed analysis of feral goat habitat preference and movement patterns will provide the information needed to determine specific impacts of the animals. In turn, this information can be used to determine best management practices, including the construction of exclosures, locating animals for eradication, or predicting plant community response to ungulate presence or removal. Although feral goats inhabit a broad range of ecosystems in Hawai`i, further investigation into their foraging habits in particular communities should aid land managers in making informed management choices. Currently, management of ungulates in Hawai`i primarily utilizes the construction of exclosure units to protect threatened native species and ecosystems, and animal eradication. However, fenced units are typically small in size, limited by financial constraints and land ownership, and require constant maintenance. In addition, animal eradication is often not feasible, at least on large scales, and feral ungulates typically repopulate areas rapidly where they have been eradicated.

Nonnative ungulates in Hawai`i are a continuing threat to native biota and pose significant challenges for resource managers across the state. In order to make the appropriate choices for the conservation and restoration of critically endangered ecosystems, more information about large grazing mammals is needed. Feral goats are an agent of landscape change, and they contribute heavily to ecosystem degradation in island ecosystems. Understanding habitat and foraging preferences specific to Hawai`i’s unique plant communities will help agencies and landowners make informed, efficient, and practical choices to restore critical island ecosystems.

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