MOVEMENT AND RESOURCE SELECTION BY FERAL GOATS

IN A HAWAIIAN MONTANE DRY LANDSCAPE

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Abstract

Where animals range and how they select resources have long been of interest to ecologists and have recently merged together in the field of movement ecology. While movement ecology offers improved understanding of basic ecological questions, it also offers great potential for applied questions. To advance our understanding of movement, I sought to investigate how large herbivores respond to vegetation phenology and to determine if high-resolution remotely sensed data could predict resource selection. To address these objectives 12 feral goats were tracked with GPS satellite collars for one year in the Pōhakuloa Training Area on Hawaiʻi Island. Results suggest that vegetation phenology is a good indicator of feral goat habitat. Feral goats primarily select habitats with low canopy height, high slope and curvature, and high values of photosynthetic and non-photosynthetic vegetation. Ultimately, the results of this study can be used to prioritize conservation activities in native Hawaiian montane dryland ecosystems.

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CHAPTER 1

Introduction

Once established, introduced species can become invasive and subsequently cause animal extinctions (Clavero and García-Berthou 2005), disassemble communities (Sanders et al. 2003) and cause environmental damage reaching up to $120 billion in the United States alone (Pimentel et al. 2005). As such, non-native, invasive species represent a major threat to island ecosystems and contribute significantly to overall human caused global environmental change (Vitousek et al. 1997a). Second only to habitat destruction, invasive species are considered one of the leading causes of biodiversity loss (Vitousek et al. 1997b). The impacts of invasion are often exacerbated in islands ecosystems, where native species have evolved in relative isolation.

Introduced vertebrates present their own suite of challenges for natural resource managers. The history of introduced vertebrates in the Hawaiian Islands began with the arrival of Polynesians between 1219 and 1266 A.D (Wilmshurst et al. 2011). Early vertebrate introductions included the domestic pig (*Sus scrofa*), dog and jungle fowl, and unintended stowaways such as the Polynesian rat (*Rattus exulans*), geckos, and skinks (Kirch 1982). Because Hawaiian ecosystems evolved in the absence of these vertebrates, their introduction began a transition in many areas from pristine systems to the heavily modified biota present today. Although Polynesians initiated novel species introductions to native island ecosystems, new introductions, including large grazing mammals, continued well into the 20th century and still occurs to date (Duffy 2010).

Beginning in the late 18th century, Europeans introduced a variety of domesticated species throughout the Pacific Islands, many of which have subsequently established feral populations (Kirch 1982). The original purpose of some vertebrate introductions was likely to populate oceanic islands with a food source to access during later voyages. Other animals became established after arriving as stowaways on ships or more recently, as a result of the purposeful introductions of game animals (Duffy 2010). Domestic goats (*Capra hircus*) were introduced to provide food for sailors on long voyages, but quickly became a self-sufficient feral population (Coblentz 1978).

Prior small scale studies have provided valuable information on impacts of feral goats in Hawaiʻi (Loope and Scowcroft 1985), but information at larger scales on behavioral ecology (e.g., seasonal movement, resource selection) of the species are lacking, and needed to benefit conservation and restoration of areas with feral goat populations. Previous studies have determined that non-native 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 invasive species (Cabin et al. 2000). In order to manage these animals and their impacts holistically, research at larger scales is needed.

Technological advances have made it possible to collect high-resolution spatiotemporal movement data for terrestrial vertebrate (i.e., wildlife) species (Cagnacci et al. 2010). Radio telemetry has a long history of success in ecological studies, but recently wildlife tracking collars have become more lightweight, have longer battery life, and enable a higher accuracy for location estimates at smaller time intervals. Location data can be collected using GPS collars at a variety of intervals to catalogue movement at various temporal scales. Specific types of movement, or movement phases, can be identified and associated with particular types of activities. 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 (Fryxell et al. 2008).

Advances in remote sensing technology have also made habitat analysis possible on a landscape scale (Hebblewhite and Haydon 2010, Pettorelli et al. 2011). 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. Since LiDAR systems provide data in a third dimension, height, analysis of how structural variability in 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).

Intra-annual temporal dynamics of vegetation (i.e., vegetation phenology) can also be detected with remote sensing technology. NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) sensors produce a composite image of any study area on Earth every eight days, enabling fine scale analysis of vegetation phenology across a landscape. These temporal changes can be triggered by infrequent rainfall events, termed pulse precipitation (Schwinning and Sala 2004). As pulse precipitation events occur, photosynthetic activity associated with 'green-up' 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 animals such as feral goats respond to changes in vegetation phenology across a broad landscape.

These technological advances enable detailed investigation of movement patterns and animal behavior, and allow for novel hypotheses to be tested (Hebblewhite and Haydon 2010). For example, data from wildlife tracking collars, combined with remotely sensed images, could be used to describe the utilization distribution of a species (i.e. the intensity of use by an individual or population). Utilization distributions often vary across space, given that the landscape a species inhabits is inherently heterogeneous and essential resources are often separated by unsuitable habitat.

Feral goats can have a tremendous impact on the island ecosystems they inhabit (Coblentz 1978), yet little information exists on the behavioral ecology of these animals in Hawai'i. Much of the existing data on the movement of non-native ungulates in Hawai'i has been observed anecdotally, and there is a critical need for more quantitative research. In particular, a better understanding of the behavioral ecology of these animals is urgently needed as their behavior is complex and can alter entire landscapes. As feral goats move through their home range, for example, their impact varies depending on the type of movement and their activity level. Since herbivores do not utilize their habitat uniformly, the type of work conducted here is urgently needed to monitor and develop an understanding of their movement ecology. This information, in turn, can provide critical data on habitat preference by feral goats, which can then be used to help prioritize conservation and restoration of this highly degraded ecosystem.

The overall objective of this research is to summarize the biology and impacts of feral goats as an invasive species on Pacific Islands, and based movement data from collared feral goats in Hawai'i determine: (*i*) whether feral goats exhibit seasonal movement patterns, (*ii*) investigate if feral goats respond to intra-seasonal vegetation dynamics on small temporal scales (e.g., changes in plant photosynthetic activity following pulse precipitation events), and (*iii*) determine if feral goats exhibit preference for certain habitats. Research on large herbivore movement suggests that animals respond to vegetation phenology by moving to areas of increased primary productivity and demonstrate clear habitat preference (Hebblewhite et al. 2008, Mueller et al. 2008). Based on research such as this, the followed hypotheses were developed for feral goats in Hawaiian montane dry ecosystems: (*i*) feral goats will respond to intra-seasonal vegetation dynamics on small temporal scales by traveling to areas of recent green-up following pulse precipitation events, and (*ii*) feral goats show preference for plant communities with a high photosynthetic index value.

To address the objectives and hypotheses, three chapters, written as scientific manuscripts, entail the body of the thesis. First, a summary of non-native feral goats on Pacific islands is provided as the second chapter of this thesis. As a review of peer-reviewed literature, this provides a comprehensive summary of the biology and impact of this species, history of introductions, and current management techniques to accomplish conservation goals. This manuscript will be submitted to *Pacific Science* as a contribution to the special series: Biology and Impacts of Pacific Island Invasive Species. Second, home range use and dispersal patterns are quantified based on collared feral goats in the Pōhakuloa Training Area on Hawai'i Island (Chapter 3). Describing space use through home range and dispersal patterns is useful in applied contexts to enable effective management of this invasive species (Kie et al. 2010). This manuscript will be submitted to *Journal of Wildlife Management*. Third, a resource selection function for feral goats is developed to create predicted use maps to guide future conservation and restoration activities specific to the study area. This manuscript will also be submitted to *Journal of Wildlife Management*. Overall, this thesis provides a comprehensive analysis of non-native feral goat movement and habitat use in Hawaiian montane dry forest ecosystems. Resource managers working in the Pōhakuloa Training Area and other similar

ecosystems throughout the state will be able to use this information to effectively manage populations of feral goats and the areas they inhabit.

CHAPTER 2

Biology and impacts of Pacific Island invasive species:

Capra hircus, the feral goat

Abstract

     Domestic goats, *Capra hircus* (Linnaeus 1758), were intentionally introduced to numerous oceanic islands beginning in the sixteenth century. The remarkable ability of *C. hircus* to survive in a variety of conditions has enabled this animal to become feral and impact native ecosystems on islands throughout the world. Direct ecological impacts include consumption and trampling of native plants, leading to plant community modification and transformation of ecosystem structure. While the negative impacts of feral goats are well-known and effective management strategies have been developed to control this invasive species, large populations persist on many islands. This review summarizes the impacts of feral goats on Pacific island ecosystems, and the management strategies available to control this invasive species.

<u>Introduction</u>

Domestic goats (*Capra hircus*) have been introduced to islands worldwide. Descended from the wild goat (*C. aegagrus*) from Central Asia (Zeder and Hesse 2000), the original purpose of insular domestic goat introductions was likely for sailors to populate oceanic islands with a food source to access during later voyages (Campbell and Donlan 2005). Released domesticated goats can quickly develop self-perpetuating feral populations given their ability to survive in a variety of habitats, on a wide variety of forage, and with limited water. Overall, goats are considered to be "the single most destructive herbivore" introduced to island ecosystems globally (King 1985).

Name: *Capra hircus* (Linnaeus 1758)

Synonym: *Capra hircus, Capra hircus aegagrus, Capra aegagrus hircus*

Common names: briar goat, brush goat, feral goat, goat, hill goat, scrub goat, Spanish goat, wood goat

<u>Description and Account of Variation</u>

Goats are even-toed hoofed ungulates of the order Artiodactyla and have been considered to comprise from one to nine species (Shackleton and Shank 1984 and references therein). Feral goats on Pacific islands (Figure 1) are assumed to have been introduced by European sailors as a food source and are, therefore, most likely derived from continental European domestic goat breeds. Feral goats exhibit significant intraspecific variation and are sexually dimorphic. Generally, males are 20% larger and have larger horns than females (Fleming 2004). Both males and females have horns made of living bone surrounded by keratin. Goats typically weigh between 25 kg and 55 kg, stand 1–1.2 m at the shoulder, and are 1–1.5 m long. All males and some females are bearded as adults. Both sexes have 30–32 teeth, with upper and lower teeth in the back to chew cud, and a dental pad in place of upper incisors. Goats sometimes resemble sheep, but can be distinguished by their short, upward pointing tails. Pelage coloration is typically black, but individuals can be white, grey, brown, red, black, or any combination thereof.

<u>Diet</u>

Feral goats are versatile generalist herbivores capable of surviving on grasses, forbs, browse and even marine algae. Coblentz (1977) documented feral goats using almost every plant species present within a study area in California. However, feral goats demonstrate strong dietary preferences. In general ungulates, including feral goats, demonstrate preference and avoidance at least partly based on foliage chemistry (Fortsyth et al. 2002). McCammon-Feldman et al. (1981) suggested that feral goats actively select the highest quality forage. While the most palatable forage is typically sought out and consumed first, poor-quality forage is often used to sustain populations (Coblentz 1977, Green and Newell 1982). Consequently, feral goats can extirpate preferred forage species (Coblentz 1977).

Goats are often regarded as browsers. However, tendency to graze or browse is determined primarily by environmental conditions, such as seasonal and geographic variation of forage. Instead, it may be more appropriate to classify goats as mixed feeding opportunists (Lu 1988). As browsers, goats are known to assume a bipedal stance to reach upper sections of shrubs and trees, and even to climb into trees to access foliage. In the process of browsing, goats often strip bark and girdle trees (Spatz and Mueller-Dombois 1973).

An important trait that enables feral goats to persist in arid island environments is their remarkable ability to survive in the absence of a permanent water source. While domestic goats have a minimum water requirement of 1.0–1.5% body weight per day, selective pressure may enable feral goats to survive in dry ecosystems with even less available water (Dunson 1974). Goats primarily derive preformed water from plant foods in many scenarios (Robbins 2001) but have also been observed drinking salt water (Gould Burke 1988). Limited water requirements have contributed to the success of feral goats as an invasive mammal on numerous Pacific islands.

<u>Environmental Impact and Economic Importance</u>
Detrimental

Non-native feral goats are notorious for their negative impacts on island ecosystems (Coblentz 1978). Remote Pacific island plant species evolved in geographic

isolation from herbivorous mammals, losing many of the secondary chemical (e.g., tannins, turpenes) and morphological (e.g., thorns) defense mechanisms to deter herbivory (Kelsey and Locken 1987, Sheley and Petroff 1999). Consequently, native and endemic plant communities are often unable to recover from persistent herbivory and trampling, resulting in their replacement by more tolerant and resilient non-native species (Augustine and McNaughton 1998). Ungulate exclosures on Pacific islands demonstrate this transformative effect, where native and non-native vegetation typically shows an immediate positive response to release from grazing and browsing pressure. Within fenced units in dryland Hawaiian forests where feral goats have been removed, native species demonstrate increased survival rates (Scowcroft and Hobdy 1987). On Hawaiʻi Island, heavily browsed areas demonstrate a lack of recruitment and an older age class structure for the dominant tree species, māmane (*Sophora chrysophylla*) (Scowcroft and Sakai 1983) and reduced sucker growth on endemic koa (*Acacia koa hawaiiensis*) (Spatz and Mueller-Dombois 1973). Intense browsing and grazing by feral goats can extirpate preferred species and cause the desertification of entire islands. In some cases, such as Santa Fe Island in the Galápagos, feral goats eliminated 100% of seedlings from large trees (Clark and Clark 1981). Importantly, the presence of non-native ungulates can affect competition between native and introduced plants. A comparison of Pacific islands with and without introduced ungulates indicates that some island plant species can more effectively resist non-native plant invasions in the absence of non-native ungulates (Merlin and Juvik 1992).

Foraging preferences of feral goats on Pacific islands vary greatly, depending largely on the composition of available plant species. While feral goats are observed feeding on both native and non-native species, native Pacific island plants are often consumed first, as they lack defenses against herbivory and are, therefore, often more palatable. In Hawaiʻi Volcanoes National Park, Morris (1969) observed that stomach contents of feral goats depended largely on density of animals present in an area. In areas with low feral goat density, where native vegetation was abundant, stomachs contained 98% native species. In contrast, non-native plants comprised 99% of stomach contents in areas of high feral goat density where native vegetation was scarce. While native species

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are often preferentially consumed when available, non-native plants support feral goat populations where native species do not occur.

In addition to direct effects from browsing, grazing and trampling, feral goats have important indirect effects, including alteration of plant communities through modification of plant structure, destruction of habitat leading to declining native wildlife populations, and alteration of nutrient cycles (Gabay et al. 2011; Zhang et al. 2009). These indirect effects can lead to ecosystem state changes that alter the function of an ecosystem. Notably, browsing and grazing can promote a cycle of pyrogenic plant invasion and proliferation of fine fuels leading to increased fire frequency and severity (Cabin et al. 2000), thereby facilitating the conversion of tropical dry forests to invasive grasslands (D'Antonio and Vitousek 1992).

Native island plant communities are particularly vulnerable to invasion by non-native plants (Wilcove et al. 1998), which quickly occupy the available space created after feral goats remove native vegetation. The impacts of non-native herbivores differ between native and exotic plant communities. Non-native herbivores are known to facilitate both the abundance and species richness of non-native plants, whereas native herbivores often suppress non-native plants (Parker et al. 2006, Oduor et al. 2009). These impacts include dispersal of both non-native and native plant seeds via excrement and attachment to fur (Janzen 1984), and trampling of plants on paths, wallows, and in resting beds. Non-native plant species can often quickly replace native plants as a direct or indirect result of non-native ungulates by overwhelming seed banks and manifesting pioneer traits (Sheley and Petroff 1999). These effects can be enhanced or reduced with extreme weather events such as drought or enhanced precipitation.

Following intense grazing and trampling of feral goats on islands, erosion can occur (Coblentz 1978). Feral goats can remove 6 kg/d of dry matter compared to 3.8 kg/d for sheep and 2.9 kg/d for cattle (Thornes 1985 and references therein). Once vegetation is removed, erosion can occur rapidly with precipitation, wind and further disturbance via feral goat movement. Yocom (1967) speculated that approximately 1.9 m of topsoil disappeared as a result of feral goat activity on Haleakala Crater on the island of Maui. As such, overgrazing by feral goats can contribute to massive erosion and subsequent

runoff that can damage near-shore marine ecosystems, as in the case of Kahoʻolawe Island, Hawaiʻi (Loague et al. 1996).

Feral goats have been associated with the decline of native fauna because of habitat modification as well as direct competition with native herbivores. Examples include the Hawaiian goose (*Branta sandvicensis*) on Maui (Yocom 1967), as well as declines in populations of yellow-footed rock-wallabies (*Petrogale xanthopus*), brush-tailed rock-wallabies (*Petrogale penicillata*), mallee fowl (*Leipoa ocellata*), the thick-billed grasswren (*Amytornis textilis*) in Australia (Biodiversity Group 1998), and native jackrabbits (*Lepus insularis*) and woodrats (*Neotoma lepida*) on Isla Espíritu Santo, Mexico (León-de la Luz and Domínguez-Cadena 2006). In Hawaiʻi, the endangered palila (*Loxioides bailleui*), an endemic finch-billed honeycreeper, relies primarily on the native māmane tree (*Sophora chrysophylla*) as a food source (Banko et al. 2009). Non-native ungulates have heavily browsed and degraded māmane forest habitat where they prefer accessible foliage, saplings, and bark of mature trees as forage (Scowcroft and Sakai 1983).

In addition to ecological impacts, feral goats pose several potential health problems for domestic livestock populations (Heath et al. 1987). Feral goats may introduce novel pathogens or act as a reservoir for existing diseases and parasites (Hein and Cargill 1981). For example, in New Zealand feral goats have been found to carry 22 nematode, two cestode, two trematode, four arthropod, and three protozoan parasites (Parkes et al. 1996). Disease and parasite transmission to domestic populations could occur either in pasture areas or if feral populations are gathered and driven to slaughter. Zoonotic diseases such as tuberculosis, brucellosis and rabies are potentially transferable to humans (Smith 1994). Feral goats also compete with domestic livestock for forage and contribute to overall degradation of rangelands (Thompson et al. 2002).

Beneficial

Economically, the goat may be more valuable to the world's agricultural system than any other animal species (Dunbar 1984). Domestic goats are one of the primary livestock species in the developing world used for both dairy and meat, but domestic goat dairy products also provide for special dietary needs in developed regions. Feral goats

represent a major source of meat and skins. In the past, feral goat populations were harvested from Pacific islands for the goat skin trade (Yocom 1967), but Australia has become a leader in the industry more recently. In Australia, feral goats continue to be harvested for both commercial enterprise and conservation objectives (Forsyth et al. 2003, Ramsay 1994).

In addition to limited commercial value on islands, feral goats also have recreational, subsistence, and cultural value for some Pacific Islanders. Feral goats are harvested as a source of meat and provide a small number of employment opportunities through hunting outfitters. There are divergent societal views regarding the value of feral goats, with some individuals and groups regarding these animals as a sustained-yield hunting resource and others regarding them as an undesirable pest (Hess and Jacobi 2011, Kessler 2011). To address these issues related to conservation and ecological restoration, decision analysis can be used to incorporate social values and stakeholder preferences into management strategies (Maguire 2004).

Ecologically, although often considered negative, long-term impacts of feral goats on Pacific islands are not always straightforward (Cabin et al. 2000). In highly modified ecosystems, such as heavily-invaded tropical dry forests, removal of generalist herbivory by feral goats has been shown to facilitate the short-term proliferation of an invasive plants (Kellner et al. 2011). Long-term studies on the effects of ungulate exclusion indicate that animal removal can also release invasive pyrogenic grasses from top-down control (Cabin et al. 2000). However, when invasive grasses are controlled after ungulate removal, an increase in natural regeneration of native plants has been observed (Thaxton et al. 2010). Importantly, non-native ungulates are a known critical barrier to native species conservation and restoration efforts, and the ecological benefits of feral goat populations on Pacific islands are very few.

Although direct benefits are not often seen from feral goat presence, it is possible that native species could benefit from feral goat presence by moving nutrients from inaccessible areas through fertilization via feces (Gould and Swingland 1980). However, it can also be assumed that exotic plant species disproportionately benefit from this same process, and often respond much faster (Funk and Vitousek 2007, Ostertag et al. 2009). In some cases, an initial rapid spread of introduced species has occurred following non-

native ungulate eradication (Kessler and Ave 1997, Kellner et al. 2011), but some invasions have also stabilized over longer periods of time, benefitting native biota (Kessler 2011). Limited examples also exist where native fauna may experience benefits. Desender et al. (1999) observed an increase in the diversity of xerophilic terrestrial invertebrates in the Galápagos as a result of feral goat grazing due to a temporary increase in habitat heterogeneity.

Both domestic and feral goats have often been used for biological control of weeds, improvement to ranges (Sakanoue et al. 1995, Goehring et al. 2010), and even to control brush in fuel breaks (Green and Newell 1982). Domestic goat breeds, such as Angora or Nubian, can provide mohair and milk respectively while simultaneously improving rangelands or controlling weeds. While feral goats can be used for the same purposes, small scale prescribed or targeted grazing and browsing by domestic animals typically yields better results (Green and Newell 1982).

Geographic Distribution in the Pacific Region

The geographic distribution of the feral goat in the Pacific Region includes essentially all islands that have suitable habitat (Table 1). Domestic Goats have been deliberately introduced to most islands, and these introductions have failed only on atolls (e.g., Kiribati and Tuvalu; see Hussain 1987). Feral goats have been eradicated to maintain watershed function and protect native species on numerous islands (e.g., Lānaʻi in Hawaiʻi, Santiago in the Galápagos; Keitt et al. 2011).

Habitat

The remarkable adaptability of goats as a species has enabled feral populations to establish themselves across a wide range of habitats throughout the Pacific. Goats demonstrate a wide range of physiological capabilities which allow them to survive in a variety of temperatures, altitudes, and habitats (Shackleton and Shank 1984). Few factors limit their distribution, such as deep snow, tundra and desert habitats. However, feral goats generally appear to prefer xeric grasslands and high topographic variability (Shackleton and Shank 1984).

On Pacific islands, feral goat populations exist from low to high elevations and in xeric to mesic habitats (Stone 1985). As opportunistic herbivores, feral goats use an assortment of forage for subsistence, including native and non-native plants (Yocom 1967, Baker and Reeser 1972). Preferred feeding areas appear to be open, dry grasslands, shrublands, or forests (Morris 1969 cited in Baker & Reeser 1972). However, feral goats can be observed in nearly every tropical insular habitat. The majority of native plant communities on islands are heavily invaded, and subsequently impacted by feral goat populations in some manner.

History of Introductions

Domestic goats have arguably been intentionally introduced to more islands worldwide than any other mammal with the possible exception of domestic cats (Duffy and Capece 2012). Goats have been introduced to all continents (except Antarctica) and can inhabit a range of climates and conditions. Their unique ability to survive on a wide variety of forage and limited water supply made them ideal candidates for food supplies on remote and arid islands. In addition to intentional introductions, domesticated goats have also repeatedly escaped captivity to establish feral populations.

The earliest known introduction to an oceanic island was St. Helena in 1513 (Dunbar 1984). In the Pacific region, the Juan Fernández Islands may have had the first known introduction in the sixteenth century (Wester 1991). Most famous for feral goat introductions was Captain Cook, who is responsible for releasing domestic goats in New Zealand, Hawai'i, and many smaller islands in the South Pacific during the late eighteenth century (Tomich 1986). In other locations, domestic goats were imported to control brush or for the agricultural industry, only to escape captivity and establish feral populations. Domestic goat introductions are not well documented as it was common practice to carry these animals aboard ships and release them as a future food source. Shipwrecks could also have released domestic goats onto oceanic islands (Dunbar 1984).

Only on small oceanic atolls with very limited resources have feral goat populations failed to become established. In some cases, feral goat populations have crashed due to over browsing and desertification. However, this evidence should be considered circumstantial because feral goats may often be the only animal present

during the final stages of land cover change (Dunbar 1984). Interestingly, isolation on islands has caused some feral goat populations to experience substantial genetic drift. In some cases, such as San Clemente Island, California, domestic breeds that are derived from feral populations are of conservation interest.

<u>Physiology and behavior</u>

Feral goats are well adapted to survive in a wide variety of conditions, exhibiting a suite of behaviors that are remarkably similar to conspecific domesticates. Feral goats are social animals that prefer traveling in herds (i.e., tribe or trip), with a modal group size of 2–4 animals (O'Brien 1988). Large herds of up to 100 individuals are not uncommon. In Hawai'i feral goats have been observed to occur in groups of up to 200, at least temporarily (MWC pers observation). Three types of herds usually exist: (*i*) all males (bachelor herds); (*ii*) mixed sex and age groups; and, (*iii*) females and young. Frequent fission and fusion occur throughout the day as feral goats travel through their home range in search of forage. Average home range size differs significantly between males and females, and also between geographic areas and resource availability (O'Brien 1984a). Estimates range from 0.4–5.3 km^2 on Aldabra Island (Gould Burke 1988) to 139.2–587.7 km^2 in Australia (King 1992). Although some social characteristics vary between populations, others are more common. Group size, group composition, home range variations, sexual segregation, and use of permanent night camps are all common characteristics among populations (O'Brien 1988).

Goats have excellent eyesight with a panoramic field view of 320°–340°. Their unique rectangular pupil, common to other ungulates, enable increased peripheral depth perception (Abbott 1907). Furthermore, tests on male goats indicate capacity for color vision (Buchenauer and Fritsch 1980). Feral goats also possess an acute sense of hearing, able to direct their ears towards a source of sound. Likewise, their sense of smell is well-developed, which is often used to evaluate potential food items. Feral goats make several distinct vocalizations (bleating) related to offspring, danger, and agonistic behavior. Mothers and offspring are able to locate each other based on these auditory cues (Ruiz-Miranda et al. 1993).

Physiologically, goats have a mean body temperature of 38.6–39.7 °C, resting heart rate of 70–90 beats per minute, respiration rate of 12–20 breaths per minute and a life span of 10–12 years (Nowak and Paradiso 1983). As ruminants, goats have a four-chambered stomach consisting of rumen, reticulum, omasum, and the abomasums. As goats consume grasses and forbs (grazing) as well as weeds shrubs and trees (browsing), the muscular and microbial action of the rumen physically and chemically breaks down nutrients at 1–1.5 ruminal movements per minute (North 2004).

Reproduction

Breeding systems of feral goats are highly variable, ranging from year-round breeding in Hawaiʻi (Ohashi and Schemnitz 1987) and New Zealand (Rudge 1969) to seasonally polyestrous breeding cycles in more temperate latitudes (Turner 1936, Asdell 1964). Reproductive cycles vary greatly, as females have the ability to come into estrus year-round (Phillips et al. 1943). Coblentz (1980) observed quadri-modal birth pulses on Santa Catalina Island, of which the proximate cause was unknown. Males appear to be able to bring females into estrous, but number of ruts throughout the year may ultimately depend on environmental conditions.

Feral goats typically reach sexual maturity at six months of age (Ohashi and Schemnitz 1987), with young females typically entering breeding stage immediately, while young males are often outcompeted by older, more experienced males. Operational and actual sex ratios are normally female biased (O'Brien 1988, Keegan et al. 1994). During the rut, a buck will release an oily substance with a strong scent to attract females. This type of scent-urination is a form of communication for both males and females (Coblentz 1976) during flehmen (open mouth, curled back lip) behavior involved in olfactory perception of this and other compounds (O'Brien 1982). As in many social ungulates, males compete for females in estrus. However there is some evidence that females have substantial control over which male with whom they choose to breed (Margiasso et al. 2010). Males demonstrate two principle mating techniques: tending, where a dominant male defends estrus females, or coursing, where males of all ages attempt to disturb a tending pair (Saunders et al. 2005).

Gestation period is approximately 150 days (Yocom 1967) with twinning being common (Rudge 1969). Where environmental conditions are favorable, females may give birth twice a year (Ohashi and Schemnitz 1987). In New Zealand, average live weight for female kids is 4.6 ± 0.7 kg and average live weight for male kids is 5.7 ± 1.1 kg (Kirton 1977). Following parturition, females either leave or stay with kids for a brief lying-out phase (O'Brien 1984b), often in a protected shaded location (O'Brien 1983) followed by a crèche (i.e., nursery group) formation in some herds (O'Brien 1988). Females accompanied by kids often separate themselves from other adults in order to reduce competition for resources (Calhim et al. 2006a). Offspring begin to feed themselves after two to three weeks but remain close to their mother until approximately six months when they either remain with the family group or join another herd.

Population Dynamics

Reproductive abilities of feral goats enable rapid population growth, particularly in island ecosystems where competition and predation are typically minimal. Watts and Conley (1984) state that "the combination of an early initial breeding stage, short gestation, postpartum estrus, high breeding rate, and twinning allow feral goat populations to achieve annual growth rates of 10–35%." Hence, population doubling times can be as low as 2.3 to 7.3 years (Watts and Conley 1984). This rapid growth rate needs to be considered in management of these animals, as Rudge and Smith (1970) predict that a population reduced by 80% could potentially recover to 90% of the original level in four years.

Feral goat densities on Pacific islands depend on a variety of factors, including environmental conditions and level of animal control. In harsh atoll conditions, densities can be low as 5–8 goats/km^2 (Burke 1987). In favorable conditions, such as Macauley Island, New Zealand, densities have reportedly reached as high as 400 goats/km² (Nowak and Paradiso 1983). Feral goat populations can expand rapidly under favorable environmental conditions, making these animals formidably invasive on Pacific islands.

Isolated island populations of feral goats are quite variable in many aspects, which may be related to small initial introductions from which these populations were derived. Gould (1979) observed variation in color, body size, reproductive rate,

population size, water balance, and behavior between two isolated populations separated by water on Aldabra Island. Variations in genetics and behavior may be a combination of a founder effect and the variable environmental conditions that feral goats inhabit. However, over the past centuries, additional introductions may have reduced this founder effect.

Management

By the mid-twentieth century, many biologists came to a consensus on the negative impacts of feral ungulates on islands (Coblentz 1978) and began developing techniques to remove feral goat populations from them (Daly 1989). Strategies to control feral goats include: taking no action; eradication; annual control in perpetuity; or occasional control in perpetuity (Parkes 1990). In many areas, such as Haleakalā National Park in Hawai'i, intense feral goat control programs occurred sporadically since the early twentieth century, with active hunting numbering 10,000 person-days over four decades (Kjargaard 1984). Due to their large physical size and gregarious behavior, feral goats are an ideal candidate for successful eradications on small to mid-sized islands. Worldwide, >95% of 165 eradication attempts on islands have been successful (Keitt et al. 2011), and feral goats have been removed from more than 1,360 km^2 in the central Pacific region alone. The largest land area from which feral goats have been eradicated on any Pacific island was from the 585 km^2 Galápagos Island of Santiago, Ecuador, in 2005 (Cruz et al. 2009). However, a highly technical eradication from 554 km^2 of Hawai'i Volcanoes National Park on Hawai'i Island was accomplished in 1984, requiring perimeter fences to exclude adjacent populations (Hess and Jacobi 2011).

Trapping, hunting, poisoning, biocontrol or any combination thereof can be used to eradicate populations of invasive mammals (Veitch and Clout 2002). All techniques have been used on feral goats, however the most common method is hunting. Tools to aid in hunting efforts include dogs, aerial hunting from helicopters, exploiting the social behavior of feral goats, and utilizing local hunters. If the ultimate goal is eradication, public hunting by recreational and subsistence hunters can be ineffective, as hunters often select for trophy-quality males and can shift the sex ratio, leading to increase in per capita population growth (Stephens et al. 2008). Although helicopter activity does not appear to

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cause long-term behavioral changes, short-term effects occur frequently (Tracey and Fleming 2007). Feral goats with previous exposure to aerial hunting via helicopter are twice as likely to exhibit evasive activity (Bayne et al. 2000).

Toxicants have been briefly explored as an option for population control. Limitations exist due to effects on non-target species and the ability to distribute across the range of an entire feral goat population. Aerially distributed baits are not considered effective because feral goats do not often eat from the ground (Forsyth and Parkes 1995). Although the sodium fluoroacetate (1080) is not a registered toxicant for feral goat control in New Zealand, Veltman and Parkes (2002) suggested that it may be useful for high-density feral goat populations in areas that are inaccessible to ground or aerial hunting.

Biological control of feral goats is unlikely, as both pathogens and predators are not target-specific, posing significant risks to livestock populations. Feral goats have no natural predators on Pacific islands. Feral goat populations may experience minimal predation from feral dogs (*Canis lupus familiaris*) and golden eagles (*Aquila chrysaetos*). One example exists of successful biological control using dingoes (*Canis lupus dingo*) on Townshend Island (Allen and Lee 1995). However, large predators are not suitable for most areas, as they pose serious potential risks to livestock, native fauna, and humans.

Judas goats are one of the most effective tools to aid in eradication efforts. Judas animals are individual feral goats, typically female, equipped with a telemetry collar used to locate remnant herds (Taylor and Katahira 1988). Finding collared individuals will lead to another herd because feral goats are highly social animals. As each herd is eliminated, collared animals are spared to find additional herds. On San Clemente Island in California, Judas goats were used to locate other individuals in their maximum search range within three days of eradication of the rest of the herd (Keegan et al. 1994). All animals can be removed using this method (Rainbolt and Coblentz 1999).

Judas goats can also have their reproductive systems manipulated to increase efficacy. Methods to sterilize feral goats, including tubal occlusion and epididymectomy can be accomplished in the field (Campbell et al. 2005). Female Judas goats can be further modified to become Mata Hari goats, by inducing either prolonged duration or increased frequency of estrus (Campbell 2007, Campbell et al. 2007). Numerous males

may be repeatedly attracted by implanting hormones in females to heighten estrous periods.

Removal of all animals is necessary for successful eradication; a small number of failed eradication attempts have resulted from the recovery of few remaining animals because of high reproductive rates (Parkes 1984). Use of multiple techniques and technology such as Global Positioning Systems (GPS), Geographic Information Systems (GIS), Remote Sensing, and Forward Looking Infrared Radar are helpful for successful eradication of feral goats on islands. Immigration and recolonization may occur if barriers are not adequate to exclude nearby feral goats. In New Zealand, a population recovered 30–40% of the original size in 10 months due to immigration (Brennan et al. 1993).

On many larger islands, feral goat populations have been excluded from distinct management areas, particularly management areas with high densities of native species and/or native species populations of conservation concern. Fences have been built around sensitive ecosystems to exclude feral goats from the area, which is technically difficult, but more feasible than island-wide eradication from multi-tenure islands (Campbell and Donlan 2005). Fence construction can be a costly management technique requiring continual monitoring, maintenenance, and cyclical replacement to prevent ingress, however, it is an important first step towards native species restoration at a broad landscape scale. Given the costs of controlling populations in perpetuity, it is more cost-effective in the long-term to eradicate all animals from an entire island, regardless of island size.

Fencing and eradication of ungulates from ecologically sensitive areas have been important steps in conservation and restoration, however, most disturbed sites require continual monitoring and specific alien plant management strategies after ungulates have been eliminated. Invasions of non-native plant species have occurred in areas where animals have been removed (Kessler 2002, Kellner et al. 2011), but some invasive species have stabilized over time (Kessler 2012). In a study of 50 ungulate exclosures throughout Hawaiʻi, native biota held their own or increased following removal of ungulate damage in most situations, however, the chance of recovery became reduced as the extent of degradation increased (Loope and Scowcroft 1985). Damage by non-native

ungulates was a prerequisite for large-scale invasion of alien plant species. Displacement by alien grasses appeared to be the most significant factor inhibiting reproduction of native species in areas other than rain forest. Comparative studies suggest that some plant communities recover better than others after ungulate disturbance is curtailed (Stone 1985). Remote, lightly disturbed rain forest, coastal strand, ʻōhiʻa (*Metrosideros polymorpha*), and native subalpine bunchgrass and shrub are among the least affected by long-term disturbance by feral goats and other ungulates in Hawaiʻi.

Prognosis

Capra hircus populations are present on islands throughout the Pacific and remain a significant threat to native flora and fauna, as well as a critical barrier to conservation and ecological restoration. Most important, it should be recognized that feral goats have a substantial impact on ecosystem structure, and need to be controlled or eliminated to accomplish most, if not all, conservation goals that include restoration of native plant communities. The coupled features of being a generalist and the ability to thrive in arid environments make feral goats a formidable invasive species on Pacific islands. Although the techniques and technology for eradication have been developed and proven effective, resource constraints and conflicting societal values limit the success of their management, making eradication on many larger multi-tenure islands challenging (Campbell and Donlan 2005). Ungulate removal is often considered an essential first step in conservation and restoration of native ecosystems on most Pacific islands. The construction of barrier fences and eradication of feral goats by ground and aerial hunting, coupled with the use of telemetry and other technologies, have been the primary tools that have proven successful on islands throughout the world.

Given the recent gains in knowledge, technological advances, and logistical experience in non-native mammal eradication, biological limitations to feral goat control no longer exist. In addition, research overwhelmingly supports the removal of these animals to achieve conservation and restoration goals in native island ecosystems. These ecosystems represent significant holdings of global biodiversity and are currently experiencing a disproportionately high number of extinctions (Keitt et al. 2011). As more resources are allocated to conservation and restoration of island ecosystems, feral goat

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eradications will continue on islands of all sizes, including enclosed areas on multi-tenure islands. Larger and more technical projects will incorporate next generation tools (e.g., advancements in GPS, GIS, and remote sensing) to execute effective feral goat removal plans. However, it is important to recognize that management of native island ecosystems will not typically end with feral goat eradication, but rather will entail a long-term commitment to control of other non-native invasive species, along with active management of native species of conservation concern (Cole et al. in press).

While feral goats undoubtedly have had a negative impact on native island ecosystems, their long history on Pacific islands and their impact on ecosystem structure and function should not be overlooked. As Cabin et al. (2000) suggest, feral ungulates may play an important role in non-native species control in limited circumstances, notably in highly degraded ecosystems that already have large non-native plant populations. On many Pacific islands novel ecosystems have emerged that have no natural analog and are increasingly managed as a mix of native and non-native species (hybrid ecosystems). Removal of feral goats from these novel and hybrid ecosystems is a critical first step, but management activities that include monitoring and control of other invasive species are essential to maintain biodiversity and ecosystem structure. Monitoring ecosystem structure and function before, during, and after feral goat management will help land managers understand the role of feral goats in shaping emerging island ecosystems and will guide a management approach to better conserve native species on Pacific islands.

Table 2.1. Presence of feral goats on select Pacific Islands

Pacific Islands	Present	Absent	Notes
American Samoa		x	
Australia	x		
Bonin Islands		x	Eradicated in 1972**
Cocos Islands	x		
Cook Islands	x		
Easter Island		x	Domestic goats present
Fiji	x		
French Polynesia	x		
Galápagos Islands	x		
Guam	x		
Hawaiian Islands	x		
Indonesia	x		
Japan	x		
Juan Fernandez	x		
Kiribati		x	Introduced, but failed*
Marshall Islands		x	Introduced, but failed*
Micronesia	x		
Nauru		x	
New Caledonia	x		
New Zealand	x		
Niue	x		
Norfolk Island		x	Eradicated in 1856**
Northern Mariana Islands	x		
Palau		x	Domestic goats present
Papua New Guinea	x		
Philippines	x		
Pitcairn Island	x		
Solomon Islands		x	Domestic goats present
Taiwan	x		
Tokelau Island		x	Introduced but failed*
Tonga	x		
Tuvalu		x	Introduced but failed*
Vanuatu	x		
Wake Island		x	
Wallis and Futuna		x	Domestic goats present

*(Alik et al. 2010) **(Campbell and Donlan 2005)

Figure 2.1. Feral goats, *Capra hircus*, on Hawaiʻi Island. Photo by Mark Chynoweth.

CHAPTER 3

Dispersal and home range use of non-native feral goats
in a Hawaiian montane dry landscape

Abstract

Recent advances in wildlife telemetry and remote sensing technology have allowed for studies of broad scale movements of ungulates in relation to phenological shifts in vegetation. These temporal patterns in primary productivity can be used to predict herbivore abundance and distribution to aid in conservation management. In Hawaiian dry landscapes, dispersal and home range use by non-native feral goats (*Capra hircus*) are largely unknown, yet this information is important to help guide the conservation and restoration of some of Hawai'i's most critically endangered ecosystems. The objective of this study was to quantify home ranges, dispersal movements, and correlations between animal movement and vegetation phenology. I hypothesized that feral goats will respond to pulses in vegetation activity on small temporal scales by traveling to areas of recent green-up following pulse precipitation events. To address this hypothesis, 11 individuals in 10 separate herds were captured and fitted with GPS collars which collected location data every two hours for one year. Annual home range size varied between males and females ($P < 0.025$), with mean 95% adaptive kernel home ranges for males and females of 40.0 km^2 (SE = 7.9, $n = 6$) and 13.3 km^2 (SE = 4.7 km, $n = 5$), respectively. Movement patterns of 50% of males and 40% of females suggested conditional dispersal via movement between non-overlapping home ranges throughout the year. Dispersing individuals traveled a mean distance of 9.4 km (SE = 1.3 km, $n = 5$) between primary and secondary home ranges. The mean Normalized Difference Vegetation Index (NDVI) was calculated using NASA's Moderate-Resolution Imaging Spectrometer (MODIS) sensor for all home ranges. A shift in NDVI values corresponded with movement between primary and secondary ranges of feral goats, suggesting that vegetation phenology as captured by NDVI is a good indicator of feral goat habitat and movement patterns in Hawai'i. The results of this research indicate that feral goats respond to resource pulses in vegetation by traveling to areas of recent green-up.

Introduction

        Studies of animal movement include a broad range of methods to understand how an organism interacts with the surrounding environment (Holyoak et al. 2008). Movements can range from fine scale observations of animal behavior to broad scale migrations across landscapes. Understanding these movement patterns can help to manage species and address conservation issues at a variety of scales. Recent literature aims to unify movement studies into the emerging paradigm of movement ecology (Nathan 2008). The focus of movement ecology is to introduce a general framework to analyze organism movement, built on four basic components: internal state; motion capacity; navigation capacity; and, external factors (Nathan et al. 2008). This 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 scales.

        Characterizing the four components of movement ecology is challenging in many systems (Nathan et al. 2008). How the movement is performed, or motion capacity, can be determined by classifying animal movement into phases or modes (Fryxell et al. 2008). Internal state and navigation capacity are notably more difficult to define without measuring additional variables with biosensors (Mandel et al. 2008). Key external factors governing movement of large mammals can be identified using geographic information systems (GIS) and remote sensing datasets to quantify habitat structure/composition and vegetation dynamics (Hebblewhite and Haydon 2010, Pettorelli et al. 2011). To understand how external factors influence movement, observed locations of individuals or populations can be used to estimate home ranges and broader movement patterns such as migration and dispersal.

        The most common definition of an animal's home range is the measure of the area used by an animal during its normal activities, excluding occasional exploratory movements outside the area (Burt 1943). These two dimensional home range estimates include a boundary around areas expected to be used by animals during normal activities. While home range is an important biological concept, it can be very difficult to define statistically and has evolved over time to incorporate estimations of space use by animals

(Kie et al. 2010). With location data, standard techniques such as kernel smoothing can be used to generate a utilization distribution to estimate intensity of space use (Worton 1989). Intensity of space use varies within a home range and is assumed to be based on landscape characteristics and distribution of resources (Borger et al. 2008).

Movement also includes long distance travel such as dispersal and migration. Migration refers to movement from a defined home range and includes the animal returning to a primary range (Stenseth and Lidicker 1992). Definitions of dispersal vary widely in scientific literature (Holyoak et al. 2008), but for the purposes of this study, dispersal is considered as the movement of a species away from an existing population to a new spatial unit (Stenseth and Lidicker 1992). These broad scale movement patterns are particularly important in evolutionary processes such as habitat fragmentation and biological invasions (Nathan 2008).

While ultimate causes for dispersal such as kin interactions and inbreeding avoidance can be a selective advantage, proximate causes for dispersal exist related to resource availability and inter-patch movement (Bowler and Benton 2005). In some systems, phenological events (i.e. vegetation green-up) represent a resource pulse, or a high intensity, infrequent event of increased resource availability for herbivores (Yang et al. 2010). These variations in vegetation resources are often the result of precipitation events occurring as 'pulses' in arid ecosystems (Ostfeld and Keesing 2000, Svoray and Karnieli 2011). A common hypothesis is that these phenological shifts in vegetation responding to seasonal weather patterns and pulse precipitation events drive migration of large ungulates (Boone et al. 2006a, Hebblewhite et al. 2008). Only recently, the combination of remotely sensed and animal movement data has allowed ecologists to test this hypothesis.

Ungulates inhabiting grasslands have shown a strong response to temporal changes in aboveground net primary productivity (Frank et al. 1998). Net primary productivity is often quantified using a variety of vegetation indices generated from global remote sensing datasets. In particular, the Normalized Difference Vegetation Index (NDVI) has shown a strong correlation with phenological characteristics (Cihlar et al. 1991a). Recently, NDVI has been recognized as a valuable tool in coupling net primary productivity to behavioral ecology of animals (Pettorelli et al. 2011), and has been used

to analyze ungulate movement patterns in multiple ecosystems (Boone et al. 2006b, Pettorelli et al. 2007, Mueller et al. 2008, Beck et al. 2008).

To date, the difficulty and expense of monitoring large mammals over long periods have prevented managers from acquiring empirical data documenting fine scale movement of animals across broad landscapes. The use of Global Positioning System (GPS) wildlife collars has allowed the collection of high resolution spatiotemporal data, providing a detailed examination of home range use by large mammals (Cagnacci et al. 2010). By combining these high resolution GPS data with remotely sensed imagery, home range, dispersal and migration events can be examined at broad scales, and hypotheses related to resource availability can be tested (Hebblewhite and Haydon 2010). Specifically, broad scale movement patterns in response to phenological shifts characterized with NDVI data can be investigated across ungulate home ranges (Leimgruber et al. 2001, Ito et al. 2006, Mueller et al. 2008)

The main objectives of this study were to estimate home range size and group dynamics of non-native feral goats, determine whether they exhibit dispersal movement, and determine if pulses in vegetation resources relate to movement. Previous work on large herbivore movement suggests that several species respond to vegetation phenology by moving to areas of increased primary productivity (Leimgruber et al. 2001, Ito et al. 2006, Pettorelli et al. 2011). Based on previous research, I hypothesized that feral goats will respond to resource pulses in vegetation on small temporal scales by traveling to areas of recent green-up, while seasonal movements and dispersal events would be driven by selection for high quality forage.

Non-native feral goats (*Capra hircus*) have a tremendous impact on island ecosystems where they have invaded and represent a significant threat to conservation of native ecosystems (Coblentz 1978). Introduced to Hawai'i in the late eighteenth century, feral goats have altered native ecosystems across the Pacific islands, with a particularly deleterious impact in Hawaiian montane dry ecosystems. While ungulate exclosure studies have thoroughly documented the effect of ungulates on native Hawaiian ecosystems (Loope and Scowcroft 1985, Cabin et al. 2000), understanding home range, space use, and dispersal patterns with the aid of next generation tools (e.g., GPS and

remote sensing) will help prioritize conservation and restoration efforts in montane dry ecosystems.

Materials and Methods

Study Area

To address my objectives and test my hypothesis, I carried out a feral goat collaring study between July 2010 and July 2011 in the Pōhakuloa Training Area (PTA) on Hawai'i Island (19°45′36″N 155°33′13″W; Figure 3.1). PTA is a 438 km^2 military installation lying in the saddle of three volcanoes, Mauna Kea (4205 m), Mauna Loa (4169 m), and Hualalai (2521 m), which covers both the Koppen temperate climate zones Cfb (maritime temperate climates: continuously wet warm temperate) and Csb (dry-summer subtropical: summer-dry warm temperate). High climatic variability exists in PTA, with temperatures ranging from 10 to 22 °C during at least 4 months of the year. Seventy percent of the annual rainfall (561.2 mm) typically occurs between November and March, and the driest summer month has less than 30 mm of rainfall in the Csb climate (Weise et al. 2000). PTA is comprised of a complex mosaic of vegetation communities that have resulted from spatial variability in substrate type and age, and subsequent soil development. Sections of Hawai'i's last remaining tropical montane dry forest are present in the area, including the following major plant communities: *Metrosideros* treeland, *Dodonea* shrubland, and *Myoporum-Sophora* shrubland, as well as *Eragrostis* and *Pennisetum* grasslands (Figure 3.2). Although feral goats occur across five of the eight main Hawaiian Islands in virtually every habitat type, a particularly high density of these animals exist in the dry montane ecosystems of PTA. No quantitative data exist on feral goat abundance at PTA, but a 2009 animal drive forced 1800 feral goats out of a newly fenced management unit of 21.3 km² (Kellner et al. 2011), which equates to a density of 1.9 animals ha^{-1}.

Feral Goat Capture

On July 2nd, 2010, 12 adult (>18 months old; Watts and Conley, 1984) feral goats were captured by net gun using an MD 500D helicopter as a shooting platform in the northern portion of PTA (Figure 3.3). Capture locations were recorded using a handheld

GPS (Garmin International Inc., Olathe, Kansas). Potential capture locations were limited due to extensive ungulate exclosures and a large off-limits impact area with active artillery training (Figure 3.3). To achieve a representative sample, individuals were selected based on spatial location (i.e., individuals from 12 distinct herds or groups to maximize collar efficiency), as well as sex and age classes. Twelve distinct herds could not be located on the day of the operation, so some capture locations were closer together than anticipated. Six adult males and six adult females from 11 herds were captured to obtain a representative sample.

Upon capture, each animal was blindfolded and hobbled while measurements were taken for tooth eruption and body condition. Observing tooth eruption of permanent incisors and canines provided age estimates for individuals (Holst and Denney 1980). The dental formula of goats is:

$$I = \frac{0}{3}; C = \frac{0}{3}; P = \frac{4}{4}; M = \frac{3}{3} \qquad \text{[Eq. 1]}$$

where I = incisors, C = canines, P = premolars, and M = molars, and the numerator represents the upper mandible and the denominator the lower. Although each age class relates to a range of ages, the recognition of juveniles, sub-adults, and adults can easily be accomplished with this method (Holst and Denney 1980).

Animals were assigned a Body Condition Score (BCS) based on an established meat goat index (Luginbuhl et al. 2002; Appendix A). Assessing body condition (i.e. fleshiness of the goat) included physically handling the spinous process, rib cage, and loin eye to determine general health of the animal. Gums and eyes were also examined to assess whether animals were anemic. Animals were constantly monitored for signs of stress during handling. All animals were healthy adults (Table 3.1). Capture and handling methods were approved by the University of Hawai'i at Mānoa Institutional Animal Care and Use Committee (Protocol #10-868).

Feral Goat Monitoring

GPS Argos wildlife collars (model GPS7000SA, accuracy ± 10 m, Lotek Wireless, Newmarket, Ontario Canada) weighing approximately 450 grams (< 2% body weight) were attached to the animals after aging and health assessment. Collars were equipped with two separate transmitters: (*i*) a VHF transmitter for real time collar

locations, and (*ii*) an Argos transmitter for remote data download via satellite. Collars were programmed to log a GPS location and ambient temperature every two hours (120 second maximum time with no reattempt on failed fixes) for one year, and download location data via the Argos network once every five days. Logging fixes every two hours allows for the maximum amount of data (shortest interval) to be collected over the desired one year period of the study.

Animals were relocated using the VHF transmitter throughout the summer of 2010 to confirm that individuals were in separate herds and to ensure that collars were not impeding movement. Throughout the summer, ten animals were located multiple times. The other two individuals were regularly in the restricted impact zone of PTA, making visual observations impossible. Whenever possible, group size, herd composition, and behavior were recorded. These data were used to summarize general behavioral information on feral goats in Hawaiian montane dry ecosystems. Each collar was also equipped with a mortality sensor that provided an alert via the Argos satellite network if an animal remained motionless for >12 hours.

Data were collected from collars in two ways. Collars stored all data onboard for downloading upon final retrieval when a pre-programmed mechanism caused collars to drop off animals after 365 days. In addition, due to the high risk of losing equipment in the study area, data were downloaded remotely from individual collars every five days via the Argos network. Collars can be lost for many reasons including equipment failure, theft from hunters, or death in a secluded location with no VHF coverage (e.g., cave or lava tube). In the unique case of PTA, there are also large areas of restricted access where retrieving the collar is impossible due to unexploded ordinance.

Animal locations were input into a GIS using ArcInfo/ArcMap 9.3.1/10.0 (Environmental System Research Institute Inc., Redlands, CA, USA). Only location fixes with a three dimensional fix and low Positional Dilution of Position (PDOP) value (96.1% of collected points) were included in datasets for analysis (Lewis et al. 2007). Argos location data were also collected from collars during remote data downloads, but due to inaccuracy and infrequency of data collection, Argos locations were discarded from analysis (Costa et al. 2010). A total of 31,108 GPS fixes from were collected from July 2010 to July 2011. Nine collars lasted the full study period, while two collars

experienced collar failure for unknown reasons, and two mortality events occurred (Figure 3.4). After the initial mortality event one collar was redeployed; in total 13 adult feral goats we captured over the course of this study (6 male, 7 female). Collars with over 250 days of data were used in seasonal movement analysis (n = 11).

Feral Goat Home Range and Interaction Analyses

Utilization distribution, home range area and core-use area estimates were calculated using adaptive-kernel density estimators (Worton 1989) with the Home Range Tools (HRT) Analysis Extension in ArcMap 9.3 (Rodgers and Carr 1998). Home range estimates were generated with an ad hoc smoothing parameter ($h_{ad\ hoc}$) using the smallest increment of the reference bandwidth (h_{ref}) that provided a contiguous 95% kernel home range (i.e. $h = 0.5 \times h_{ref}, 0.6 \times h_{ref},... h_{ref} - R$. Long, pers. comm.). The number of points used to generate annual and seasonal utilization distributions ranged from 381 to 3,033, providing robust estimate of kernel density (Seaman et al. 1999). Home range estimates provide a 95% utilization distribution (UD), 95% home range, and a 50% core-use area for each feral goat at a 5×5 m resolution.

Daily home ranges were also calculated to determine if any differences existed between movements of males and females on a smaller temporal scale. Adaptive-kernel density estimators could not be used since daily sample sizes were not large enough (Seaman et al. 1999), therefore 100% Minimum Convex Polygons (MCP) were generated around the outermost locations for individuals at a daily level. MCPs are particularly sensitive to sample size, but provide a crude estimate of animal home range (Harris et al. 1990).

Interactions between collared individuals were estimated using two methods. First, congruence of 95% fixed kernel UDs was measured for overlapping individuals by using the Utilization Distribution Overlapping Index (UDOI) developed by Fieberg and Kochanny (2005):

$$\text{UDOI} = A_{i,goat} \iint_{-\infty-\infty}^{\infty\infty} \widehat{UD}_1(x, y) \times \widehat{UD}_2(x, y)\, dx\, dy \qquad \text{[Eq. 2]}$$

where $A_{i,goat}$ is the area (m^2) of overlap between the two individuals, and $\widehat{UD}_1$ and $\widehat{UD}_2$ are the estimated utilization distributions for the two feral goats. Index values range from 0.0 (no overlap) to 2.0 (complete overlap). UDOI values <1 indicate less congruence in

UD than would be expected from overlapping distributions, whereas values >1 indicate greater congruence in overlapping UD than would be expected. UDOI values were calculated in R (R Devlopment Core Team, 2011) using the *adehabitat* extension (Calenge 2006).

Second, association between individuals was estimated based on distance between each individual location, since association or segregation between individuals may occur at a finer scale than UDOI can detect. Influences within home ranges, such as social or habitat factors, may cause segregation. To address this, the software package ASSOC1 (Weber et al. 2001) was used to investigate the spatiotemporal association of individual collared animals at the 24 hour temporal scale. ASSOC1 uses association matrices to determine the amount of time each individual feral goat was located within a user-defined spatial threshold of every other individual. Given that each individual represents a sampling unit, this analysis assured that pseudo-replication (Hurlbert 1984) was avoided in further analyses, and allowed examination of social associations between collared individuals (Harris et al. 2007). Spatial and temporal parameters were determined based on field observations of herd dynamics and repeated runs of the model. A spatial threshold of 400 m and temporal threshold of 75%, meaning individuals had to be within 400 m for 75% of the location estimates, captured the major group interactions.

Feral Goat Dispersal Analysis

Dispersal was defined as a movement from an existing home range to a new, non-overlapping home range in a different location (Brinkman et al. 2005). To identify dispersal movements, each animal's movement patterns were examined for unidirectional movements over a long distance (> diameter of home range) and short period of time (<2 days). The harmonic mean of animal locations was used to determine the geographic center of non-overlapping home ranges (Dixon and Chapman 1980). Non-overlapping ranges were termed primary and secondary ranges to distinguish between the two areas used by feral goats, but these terms are not meant to suggest any difference in importance between ranges. Linear distances between activity centers of non-overlapping home ranges were measured in GIS (Brinkman et al. 2005).

Phenological Monitoring

        I used NDVI to quantify temporal changes in vegetation phenology and link this to dispersal events of feral goats. NDVI has been shown to respond to several different environmental variables, including precipitation events (Cihlar et al. 1991b, Davenport and Nicholson 1993). In Hawaiian dry ecosystems, 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). To obtain NDVI values, data were calculated from the Moderate Resolution Imaging Spectrometer sensor (MODIS, Raytheon Co., Waltham, MA USA). MODIS sensors are part of NASA's Earth Observing System (EOS) program to observe spatial and temporal variations in vegetation with a coordinated set of polar orbiting satellites. Daily global images are used to estimate vegetation indices (e.g., NDVI) to provides a measure of vegetation greenness based on the ratio between near-infrared and visible reflectance:

$$NDVI = \frac{\rho NIR - \rho red}{\rho NIR + \rho red} \qquad\qquad\qquad [\text{Eq. 3}]$$

where ρNIR is the near-infrared band and ρred is the red band (Huete et al. 2002). NDVI values range from -1.0 to +1.0, with negative values indicating surfaces with little or no vegetation (i.e. barren ground, water, rock) and positive values indicating increasing amount of green vegetation.

        For calculation of NDVI, I used 16-day composite MODIS Vegetation Index NDVI data sets (MOD13Q1 product) with 250 m pixel resolution. Data were acquired through NASA's EOS Data and Information System (http://reverb.echo.nasa.gov/reverb/; tile number: H03V07). Using 24 images, a time series was created from 26 June 2010 to 26 June 2011. MODIS data were reprojected using the MODIS Reprojection Tool (NASA Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota). Downloaded images were only available in the Sinusoidal Universal Transverse Mercator projection Zone 5 on the North American Datum projection. I used the MODIS Reprojection Tool to project the data into the Universal Transverse Mercator projection Zone 5 on the North American Datum 1983.

        Reprojected images were then imported into ArcMap 10.0 to calculate mean NDVI of each range for each time interval. Following the methods of Leimgruber et al.

(2000) and Ito et al. (2006), mean NDVI values of annual ranges were subtracted from every time interval to obtain an index of relative quality of different ranges within annual ranges. A Wilcoxon signed rank test was used to examine the differences in relative NDVI values between primary and secondary ranges (Leimgruber et al. 2001).

Statistical Analysis

Individual mean values were used for home range comparisons between sexes and between primary and secondary ranges of dispersing individuals. All means are reported with associated standard errors. For home range comparisons, dispersal periods, and dispersal distances, a two-way Welch's *t-test* was used to account for small sample sizes and heterogeneous variances. Two-tailed significance values were reported as the hypotheses were two-sided, and significance was assessed at $\alpha = 0.05$. To compare NDVI rank values of repeated measures of primary and secondary ranges, a Wilcoxon signed-rank was used to test differences in mean ranks. Two-tailed significance values were reported as the hypotheses were two-sided, and significance was assessed at $\alpha=0.05$. All statistical analysis were conducted in R: A language and environment for statistical computing 2.13.2 (R Development Core Team, 2011).

Results

Feral Goat Home Ranges and Interaction Analyses

Home ranges ranged from 3.4 to 27.7 km^2 for both sexes of feral goats (Table 3.2). Male mean annual home range was 40.0 ± 7.9 km^2 (range $5.9 - 60.0$ km^2) vs. 13.3 ± 4.7 (range $3.4 - 27.7$ km^2) for females. Simlarly, mean annual 50% core use area for males was 8.0 ± 1.9 (range $1.1 - 15.1$ km^2) compared to 2.9 ± 1.1 (range $0.8 - 7.8$ km^2) for females. The 95% annual home ranges were significantly larger for males than females (t $= 2.65$ df $= 8.67$, $P = 0.027$), but the annual 50% core use areas were similar between genders (t $= 2.13$, df $= 8.687$, $P = 0.063$). Likewise, mean male (0.6 ± 0.02 km^2) and female daily home ranges (0.6 ± 0.02 km^2) were similar (t $= 0.92$, df $= 722$, $P = 0.36$; Figure 3.5) over diel scales.

Herd composition varied and was often difficult to determine in the field due to similarities between male and female sub adults. Three types of herds were typically

observed: (*i*) female groups, composed of adult and/or sub adult females plus kids of either sex, (*ii*) male groups, composed of adult and/or sub adult males, and (*iii*) mixed groups, consisting of kids, sub adult males and sub adult females. The average group size was 11.8 ± 17.2 (range 1 − 196) with small groups more common than large groups (Figure 3.6). Notably, both juveniles (kids) and pregnant nannies were observed during every field visit.

The UDOI index of UD overlap indicated that most feral goats showed less overlap than would be expected from overlapping distributions at the 95% and 50% contour levels (Figure 3.7). Mean UDOI values of 95% UDs for males and females were 0.17 ± 0.06 and 0.33 ± 0.05, respectively. For 50% UDs, mean UDOI values for males and females were 0.009 ± 0.005 and 0.023 ± 0.005, respectively. On average, males showed less overlap than females. Daily mean social association was 5.9 ± 0.5% during the day and 12.7 ± 0.1% at night (Figure 3.8). Collared animals had higher levels of association during nocturnal times compared to diurnal times, suggesting fission of herds during the day and fusion of herds to bed down at night.

Feral Goat Dispersal Analysis

Among all feral goats, five out of 11 individuals had 7 dispersal movements (one individual dispersed 3 separate times). The remaining six individuals demonstrated limited variation in home range size and no dispersal events. Of the five individuals that demonstrated seasonal movement, mean dispersal distance was 7.71 km (SE = 0.63). While movements to secondary home ranges usually took place over a one day period, departure date varied throughout the year (Table 3.3). There was no difference (t = 0.02, df = 9.82, *P* = 0.99) between primary ($\overline{X}$ = 11.69, SE = 2.01) and secondary ($\overline{X}$=11.64, SE = 2.31) home range sizes.

Mean NDVI values in primary and secondary home ranges showed similar trends over the one year period. Both primary and secondary ranges showed an increase in NDVI during the second half of the study associated with increases in frequency and intensity of precipitation events (Figure 3.9). However, a greater increase in NDVI occurred in secondary home ranges of all dispersing individuals. Wilcoxon signed-rank test indicated significant increases in NDVI values between primary and secondary

ranges. Four out of five individuals dispersed to a secondary range that had significantly higher NDVI values compared to their primary ranges (Table 3.4).

Discussion

Annual home ranges demonstrated extensive two-dimensional overlap, but analysis of utilization distribution overlap and herd association suggests that feral goats exhibit herd fission during diurnal periods and herd fusion during nocturnal periods. Five out of 11 individuals demonstrated dispersal behavior, and six individuals were non-dispersing. Based on NDVI values of primary and secondary home ranges of dispersing individuals calculated with kernel density estimators, results partially support the hypothesis that feral goats travel to areas of recent vegetation green-up following pulse precipitation events.

Feral Goat Home Range and Interaction Analyses

Feral goat home ranges in PTA ranged from 3.44 – 60.04 km^2, which is similar to home ranges of feral goats on other tropical islands (0.4 – 587.7 km^2; Gould Burke 1988, King 1992). In comparison to these other studies, home ranges in this study encompassed an average amount of space, but 50% core use areas were substantially smaller (0.78 – 15.05 km^2) than annual ranges. This difference suggests that feral goats are demonstrating nonrandom space use, returning to multiple core use areas within annual ranges. Based on collar data and field observations, core areas are bedding grounds used on a nightly basis, which often include areas of high topographic variability with high lookout points, a valuable resource for bedding areas (Coblentz 1978).

Annual home range estimates were highly variable between individuals and sex (Table 3.1). For individuals demonstrating dispersal movements, mean annual estimates included primary and secondary ranges, which may have overestimated home range size. The differences between male and female home ranges relating to activity budgets here is common in many ungulate species (Michelena et al. 2004). This difference between sexes could be attributed to sexual segregation of herds, which was observed throughout the study period. Sexual segregation does not appear to be a function of habitat preference. Instead, four principal hypotheses potentially explain segregation in feral goats:

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predation, forage quality, social preferences, and activity patterning (Calhim et al. 2006b). Predation is likely to occur to some unknown extent due to feral dogs and interacts simultaneously with the three remaining hypotheses, making it difficult to determine exact proximate causes.

Feral goats are highly social animals and their gregarious behavior certainly affects range size and movement across the landscape (O'Brien 1988). Herd size and composition observations suggest that feral goat herds in PTA have similar structure to feral goat populations on other islands (O'Brien 1984a, Shi et al. 2005). Two-dimensional home range overlap suggests that animals are sharing large portions of their home range. However, based on the UDOI index, animals occupying overlapping home ranges have multiple core areas throughout the range that are used at different times during the year. Sexual segregation of ungulates is common, and it is important to note that juvenile feral goats were observed during every field visit, evidence of a year round breeding cycle observed in other island systems (Coblentz 1980).

The UDOI index compares the volumetric overlap of kernel home range estimates, but does not compare proximity of each location estimate. Using the ASSOC1 software package (Weber et al. 2001), I compared the proximity of each collar fix to every other collar fix at each time interval. Concordant with other studies on herd dynamics of feral goats (Yocom 1967, Gould Burke 1988, Shi et al. 2005), results here suggest that collared individuals are near other collared individuals more frequently during nocturnal hours and less frequently during diurnal hours.

Feral Goat Dispersal Analysis

Both males and females dispersed, with each dispersal movement being unidirectional. With the exception of two individuals, feral goats dispersed at different times throughout the year. Each movement was a shift from the eastern section (primary range) to northwestern section (secondary range) of PTA, and each dispersal movement followed the hypothesis that feral goats will respond to intra-seasonal vegetation dynamics on small temporal scales by traveling to areas of recent vegetation green-up.

Dispersal movements by feral goats in this study were not classified as animal migration, although migration is sometimes defined as movement from one spatial unit to

another (Baker 1978), it is more appropriate to classify migration as including the animal returning to a primary range (Stenseth and Lidicker 1992). Four of the five dispersing animals exhibited one single movement from primary to secondary ranges, suggesting dispersal but not migration. One individual (M5) did make three dispersal movements throughout the year, moving to a secondary home range, back to the individual's same primary range, and returning to the same secondary range later in the study period. However, because of the time frame of this study, the collars' lifespan was not able to capture annual movement patterns in which other individuals may have displayed this behavior.

Six animals (three females and three males) exhibited no dispersal movement. However, four of those six animals resided year-round in or near the secondary range of dispersing animals. The primary range of these animals experienced the same NDVI patterns exhibited by secondary ranges of dispersing animals. This suggests that available resources increased in the primary range of feral goats, making dispersal movements unnecessary. NDVI values were examined throughout the study area for green-up events, and few areas experienced a deviation of 100% from the mean NDVI values. The secondary home ranges of dispersing animals, and the primary ranges of 66% of non-dispersing animals were the only large areas that experienced substantial green-up events in the study area during collar deployment. During the 12 months of this study, the weather stations within the primary study area received record low levels of precipitation (218.4 mm) compared to the mean annual precipitation (561.2 mm; Giambelluca et al. 2011). This decrease in annual precipitation clearly influenced the infrequency of green-up events throughout this study.

Results of this study suggest that dispersal movements by non-native feral goats in Hawaii are spatially and temporally complex. Five individuals demonstrated some type of conditional dispersal, while six individuals remained in their primary range throughout the year. Other factors that were not measured in this study (e.g., herd dynamics, social structure) have been observed to influence the conditional dispersal movements of non-native feral goats in other study areas (O'Brien 1984a). As shown by UDOI values and Association matrices (Figures 3.6 and 3.8), several collared individuals interacted on a semi-regular basis, demonstrating the fission-fusion pattern of herd dynamics evident in

other studies (Calhim et al. 2006b). Reproductive cycles, agnostic behavior, and density dependence are also examples of other factors not included in this study that may impact feral goat home ranges and movement (O'Brien 1984a, 1988). Collectively, these same factors may have influenced the lack of dispersal in the six individuals that remained stationary throughout the year.

As an active military training area, PTA encompasses a suite of challenges to incorporate into movement data analysis. Field work in intended areas was often impossible due to training activities and large, off-limit areas with unexploded ordinance. Several factors also may have limited the movement of the animals themselves. Feral goats may have avoided areas of human disturbance including structures for training exercises, a gravel pit mine and a high-traffic road when humans were present. In addition, large ungulate exclosures prevented the movement of animals in certain areas. These factors were all incorporated into spatial analyses by excluding areas such as fence units from home range estimates. Training activities are not public information and, therefore, could not be assessed as a factor influencing animal movement.

Based on this research, strong evidence exists that feral goats disperse to areas of high NDVI values following pulse precipitation events. Movement patterns of collared feral goats in PTA do not suggest migration, rather, more a nomadic behavior. Further research over a longer time period (>1 year) would be beneficial to investigate whether the dispersal patterns observed in this study are the result of ultimate or proximate causation. Results presented here contribute to a growing field of research in ecology that combines GPS telemetry data with remotely sensed phenological data to test hypotheses of resource availability based on net primary productivity, as well as the impact of resource pulses on ungulate movement.

Management Implications

Despite their identification as a critical barrier to conservation and restoration of island ecosystems, little work has been done in Hawai'i to quantify feral goat movement. Feral goat space use has been examined on other islands (Coblentz 1977, O'Brien 1984a), but no home range studies have been conducted in montane dry landscapes on Hawai'i Island. Knowledge of home range and dispersal patterns of feral goats will

enable managers to make informed decisions concerning their management in Hawaiian montane dry landscapes. Management of natural resources in PTA is actively occurring and includes fencing of ecologically sensitive areas, removal of ungulates, and restoration of native species (Kellner et al. 2011). A comprehensive understanding of the movement ecology of these animals in this area will help prioritize conservation and restoration activities in native Hawaiian montane dry landscapes both in PTA and across the islands.

Feral goats impact native ecosystems directly through the grazing, browsing, and trampling of vegetation, as well as indirectly through the modification of plant community structure, impacts on native wildlife, and promotion of non-native plant species (Cabin et al. 2000, Thaxton et al. 2010). Consequently, the spread of invasive grasses has converted native montane dry landscapes into exotic grasslands and created an ongoing grass-fire cycle (D'Antonio and Vitousek 1992). This research suggests that feral goats respond to pulses in resource availability, which offers evidence that indirect effects of these animals are complex, and they act as an agent of landscape change in island ecosystems.

Table 3.1. A summary of individual collared feral goats. Table includes physical condition upon capture (Body Index), Sex, Age, and the ultimate fate of the collar (Fate).

Collar ID	Alias	Sex	Age	Body Index	Fate
2901	F1	F	1-2	2-5	found deceased after 299 days, collar retrieved
2902	F2	F	1-2	2-4	collar successfully retrieved
2903	F3	F	1-2	2-5	battery died after 310 days, collar lost
2907	F4	F	3-4	2-4	collar successfully retrieved
2908A	F5	F	3-4	2-3	found deceased after 48 days, collar retrieved and redeployed
2908B	F6	F	1-2	4-6	battery died after 127 days, collar lost
2909	F7	F	3-4	3-5	collar successfully retrieved
2900	M1	M	1-2	2-5	collar successfully retrieved
2910	M2	M	3-4	2-5	collar successfully retrieved
2911	M3	M	4-5	5-7	collar lost (Impact Area)
2912	M4	M	4-5	4-8	collar successfully retrieved
2913	M5	M	3-4	4-6	collar successfully retrieved
2914	M6	M	2-4	4-6	collar successfully retrieved

Table 3.2. Adaptive-kernel density estimates with *href* for the smoothing parameter of home range and core-use area of 13 feral goats in PTA, 2010-2011. Mean (±SE) of each variable for sex is also provided.

GoatID	Number of points	95% Area (km^2)	50% Core-use Area (km^2)
F1	2554	27.7	6.4
F2	2519	7.0	1.3
F3	2512	34.7	7.8
F4	2990	7.1	1.3
F5	381	3.4	0.8
F6	636	7.7	1.7
F7	2513	5.8	0.9
M1	2870	43.3	7.5
M2	2568	60.0	15.1
M3	2622	53.8	9.8
M4	3033	5.9	1.1
M5	2985	44.9	8.5
M6	2925	31.9	6.2

Table 3.3. Distances between primary and secondary home ranges and departure dates for dispersal movements.

Goat	Distance (km) between ranges	Departure date
F1	5.86	10/31/2010
F3	6.61	1/31/2011
M1	8.50	02/28/2011
M2	9.20	03/02/2011
M5*	8.38	08/20/2010; 10/18/2010; 03/04/2011

*M5 made three separate dispersal movements; distance is averaged between three events.

Table 3.4. Two-tailed probabilities for differences in relative NDVI values between primary and secondary ranges of each feral goat and higher HDVI ranges.

Goat ID	Z	V	*p*	Higher NDVI range
F1	-0.14	17	0.945	n.s.
F3	-2.7011	1	0.004	Secondary
M1	-2.5205	0	0.008	Secondary
M2	-2.2404	2	0.023	Secondary
M5	-2.4006	6	0.014	Secondary
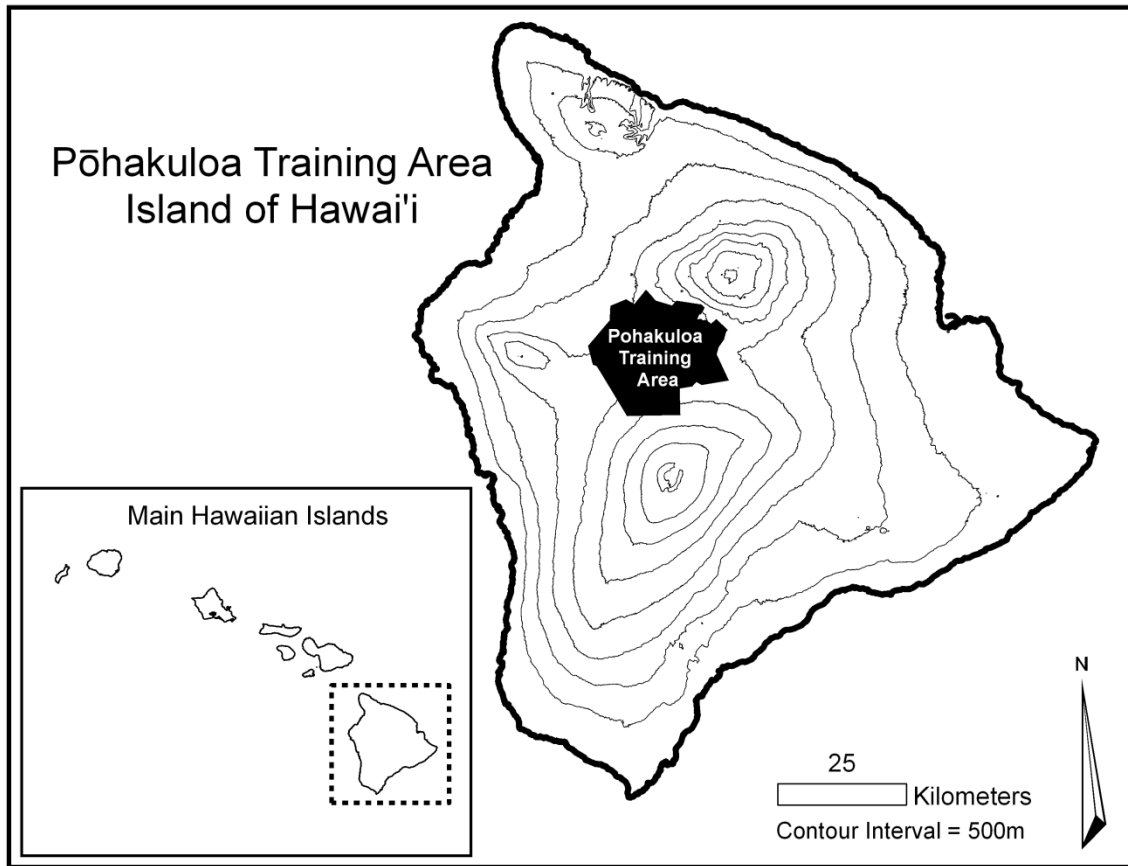
Figure 3.1. Location of study area, the Pōhakuloa Training Area on Hawai'i Island.
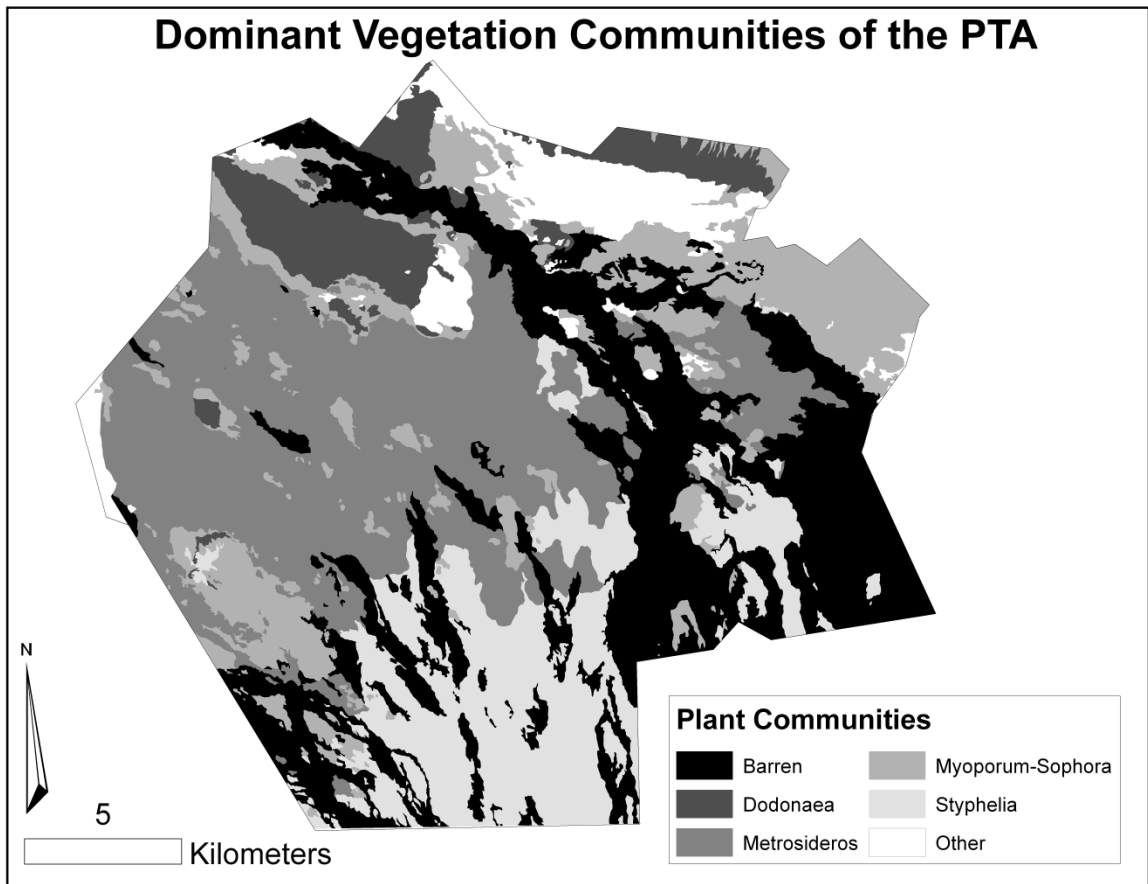
Figure 3.2. Dominant vegetation types of the Pōhakuloa Training Area on Hawaiʻi Island. The 'other' class includes *Chamaesyce* treeland, *Chenopodium* shrubland, disturbed areas, *Pennisetum* grassland and *Erograstis* grassland.
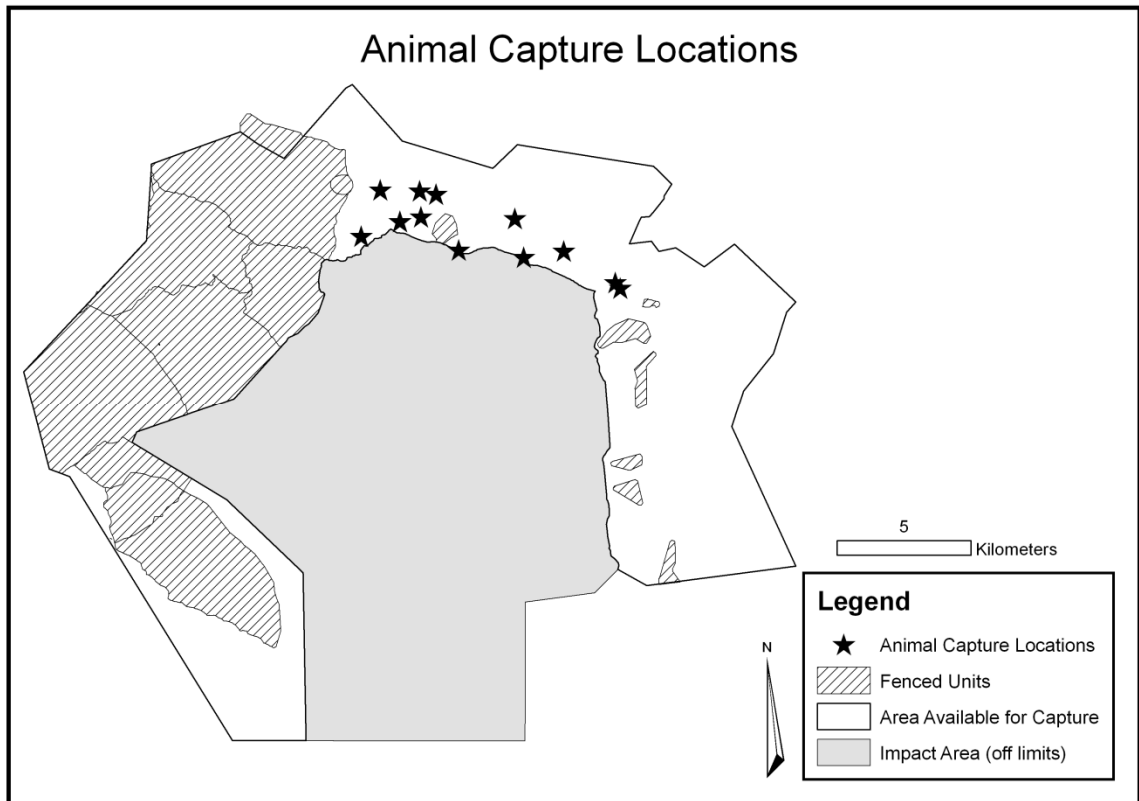
Figure 3.3. Potential capture locations (white area) and actual capture locations (black stars) for feral goats in the Pōhakuloa Training Area.
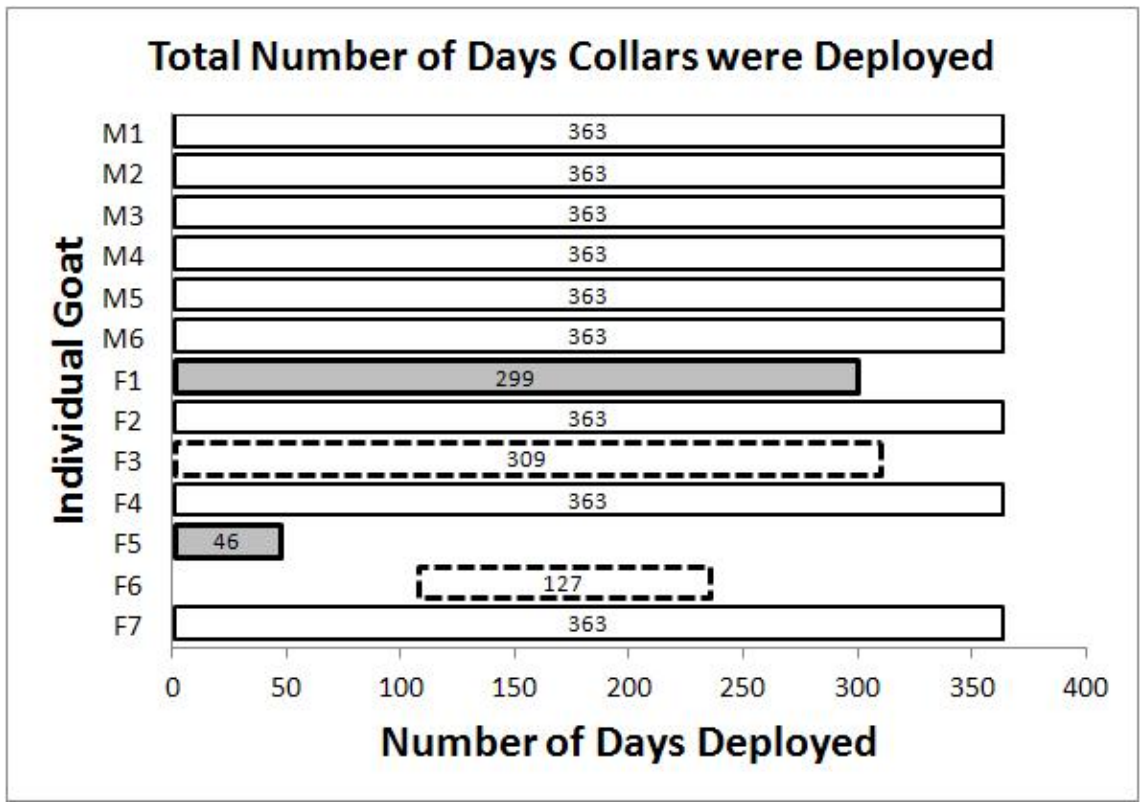
Figure 3.4. Number of days collars were deployed on each individual. White boxes indicate collars that lasted the full study period (July 2010-July2011), dashed boxes indicate battery failure which led to lost collar, and gray boxes indicate mortality events.
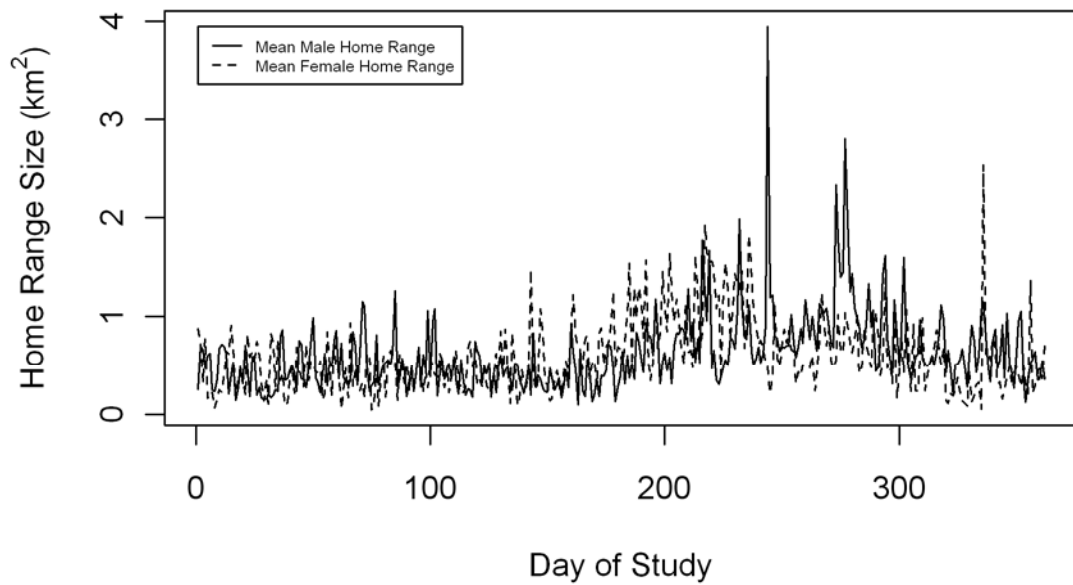
Figure 3.5. Daily mean minimum convex polygon home ranges of male (solid line) and female (dashed line) feral goats in the Pōhakuloa Training Area over the entire study period (July 2010 – July 2011).
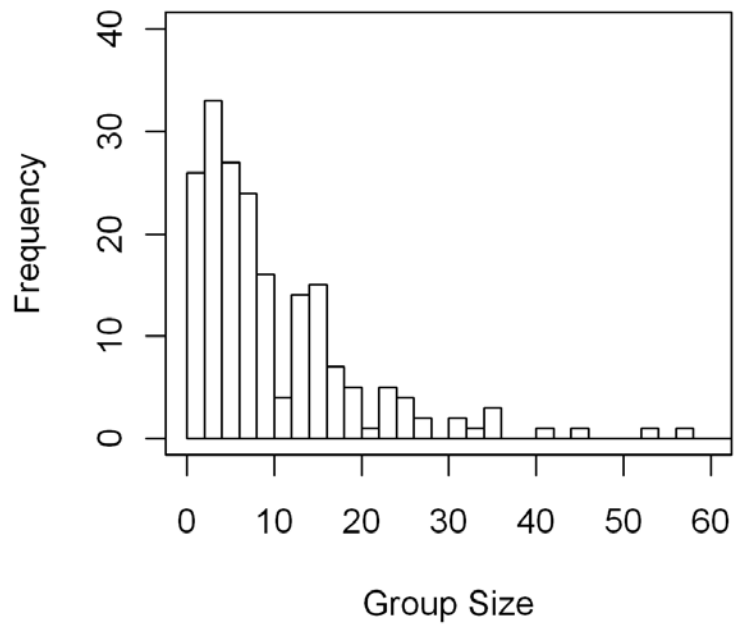
Figure 3.6. Frequency of feral goat group size observed during field visits in the
Pōhakuloa Training Area. Group size ranged from 1 – 196 individuals. Two outliers have
been removed from the histogram: 191 and 96.
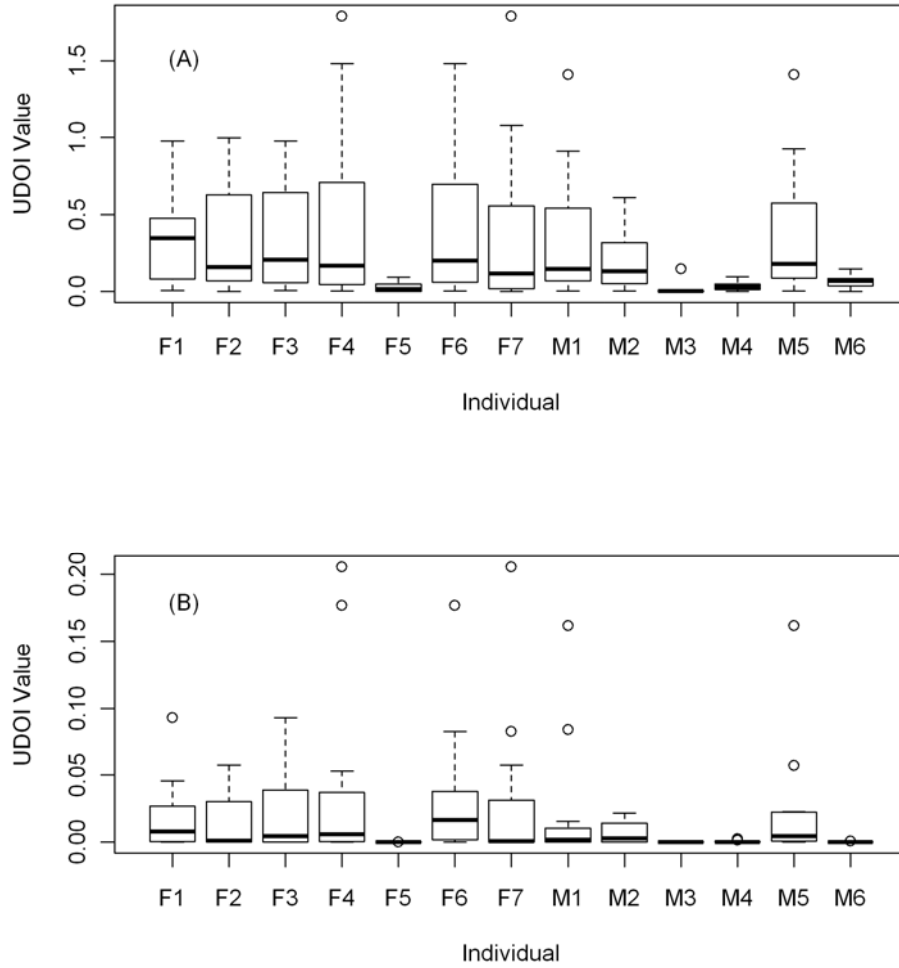
Figure 3.7. The utilization distribution overlap index (UDOI) between annual home ranges of each collared feral goat. Individual home range overlap is compared to all other goats in the study. Overlap index values are presented for 95% UDs (graph A) and 50% UDs (graph B).
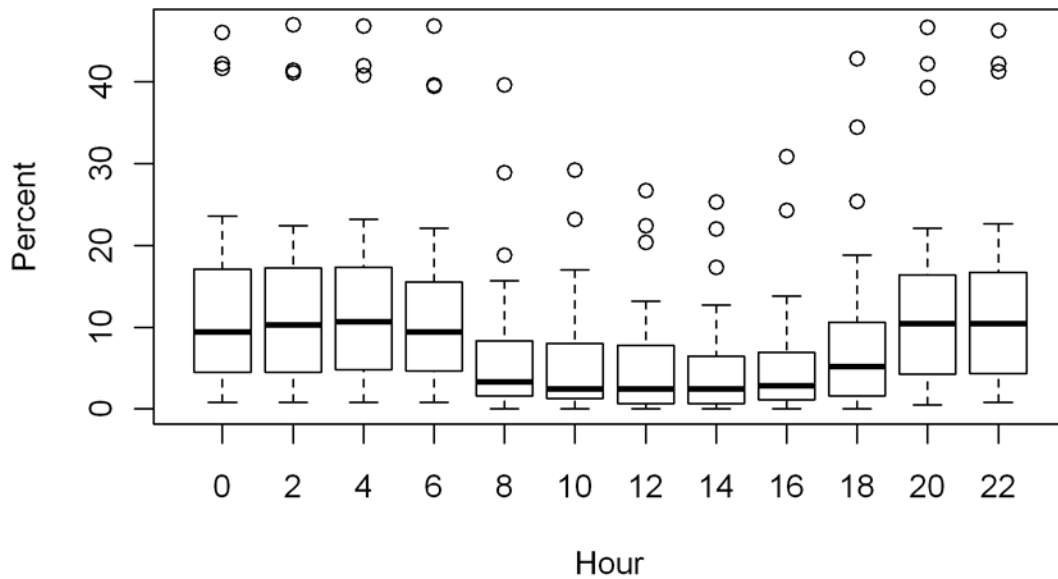
Figure 3.8. Mean daily association between all individual feral goats for each hour based on each location estimate. Spatial threshold: 400 m, temporal threshold: 75%. Percent refers to percent of total fixes that were within 400m 75% of the total time.
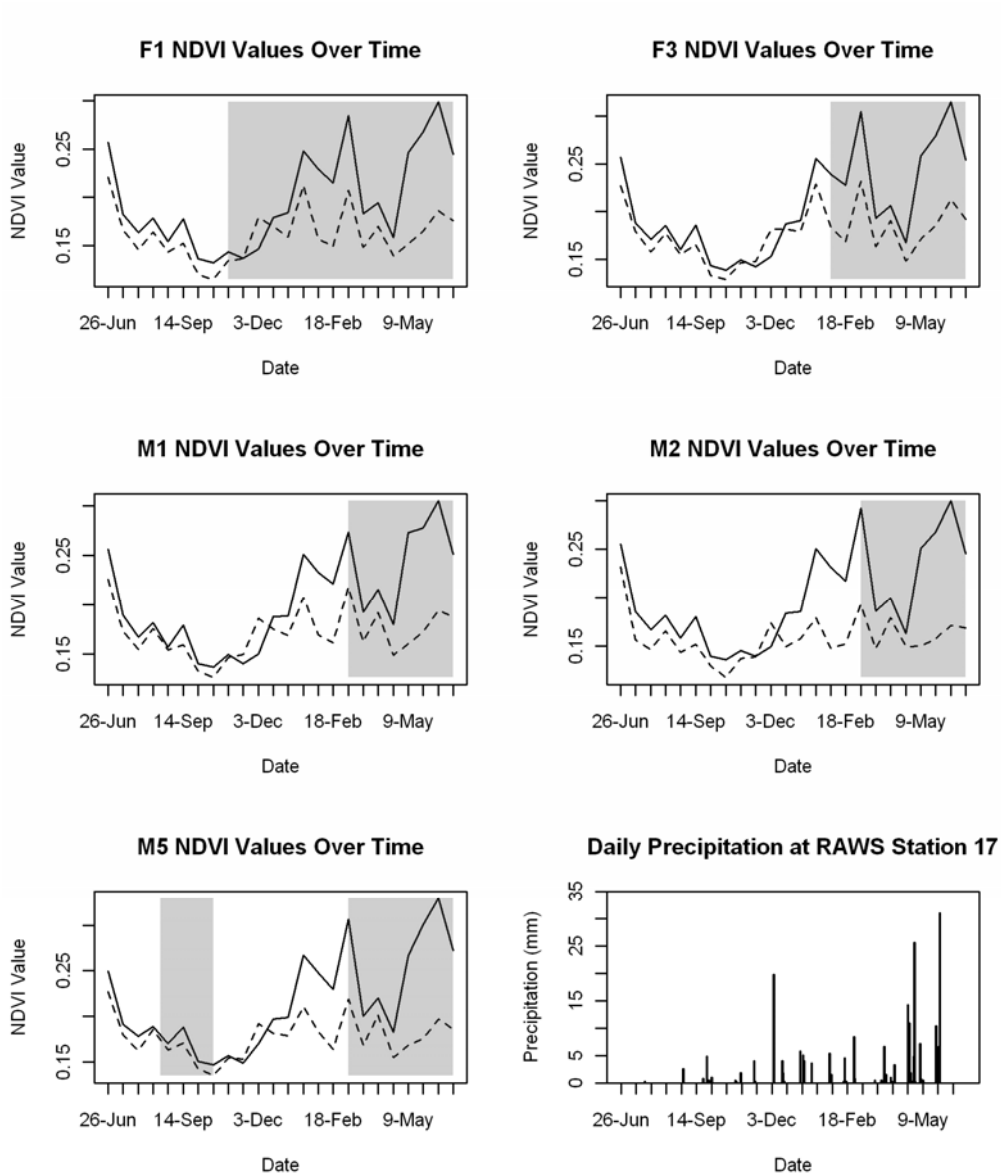
Figure 3.9. Annual changes in mean Normalized Difference Vegetation Index (NDVI) in 95% utilization distributions of Primary Range (dotted line) and Secondary Range (solid line) for all individuals demonstrating dispersal behavior. White regions of the graph represent time when individuals are located in Primary Ranges and shaded regions represent time when individuals are located in Secondary Ranges.

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CHAPTER 4

Resource selection by feral goats in a Hawaiian montane dry landscape

Abstract

Non-native feral goats (*Capra hircus*) are generalist herbivores that impact native ecosystems on islands throughout the world. In Hawaiʻi, feral goats are considered a critical barrier to restoration and conservation activities, but little is known about their distribution or habitat preferences. From July 2010 to July 2011, I monitored the movement of 11 adult feral goats ($\geq$18 months old) with GPS collars that collected location data every two hours in Pōhakuloa Training Area (PTA) on Hawaiʻi Island. A resource selection function (RSF) habitat model was created for nocturnal and diurnal hours for each individual animal, and model coefficients were averaged to create a population level model of feral goat habitat selection in the overall study area. Logistic regression was used to compare habitat variables at used locations (collar location estimates) to a random sample of available habitat generated within each animals 99% kernel utilization distribution. The RSF values were transformed to a relative probability of habitat and coefficient estimates were used to generate a fine scale map depicting relative probability of diurnal and nocturnal habitat use by feral goats. During diurnal hours, feral goats in PTA select habitats with lower canopy height, higher slope and curvature, and higher values of both photosynthetic and non-photosynthetic vegetation than randomly available habitats. During nocturnal hours, habitat use by feral goats includes areas with lower canopy height, higher slope and curvature, and higher values of photosynthetic vegetation and lower values of non-photosynthetic vegetation than randomly available habitats. A predictive map was created that identifies potential areas of high habitat use by feral goats in PTA, which provides a valuable tool for managing feral goat populations and prioritizing conservation and restoration activities in one of the most critically endangered ecosystems in Hawaiʻi.

<u>Introduction</u>

Studies of resource selection aid in understanding what resources are required by wildlife, and can subsequently help guide conservation and management decisions (Manly et al. 2002). While more fundamental home range estimates such as kernel density estimators based on collar location data are still very useful in applied conservation management to describe space use by animals (Kie et al. 2010), resource selection studies can evaluate the significance, direction and magnitude of relationships between animal movement and resources to predict future patterns of space use by animals (Johnson et al. 2006). A Resource Selection Function (RSF) is a common approach to improve understanding of how animals use surrounding habitats. A form of habitat selection study, RSFs can compare resource use by an animal (through direct or indirect observation) to resource availability in an attempt to show how animals select for certain habitat variables (Manly et al. 2002).

A variety of statistical techniques can be used to interpret data on resource selection for wildlife species, and more techniques are constantly being developed. Manly et al. (2002) proposed the RSF as a unified theory for ecologists to analyze data. By measuring attributes of resource units, an RSF can predict probability of animal occurrence based on resource availability. The most common technique for RSFs has been logistic regression to compare used vs. available or used vs. unused resource units as a binary response variable (Johnson et al. 2000, Anderson et al. 2005, Long et al. 2009). In telemetry studies, animal relocations can be used as the sampling unit for used resources. Available or unused habitat is much harder to sample, and has been criticized for having arbitrary definitions (Aebischer et al. 1993). A common method to sample available resources across broad landscapes is to generate random points within a specified range and determine habitat characteristics with a geographic information system (GIS) (Manly et al. 2002).

Resources included in an RSF should identify any component of an animal's environment that can be selected or avoided in an effort to maximize fitness (Manly et al. 2002). Habitat type, food resources, and human disturbance are all examples of potential resources that animals may want to select or avoid. Traditionally, resources have been identified though direct measurement or observation. However, with the advent of GIS

and remote sensing technology, high resolution resource data have increasingly become available to use as predictors of resource use by animals. Emerging technologies in active remote sensing include Light Detection and Ranging (LiDAR), whose primary use is to measure properties of scattered light to find the range of a distant target and Airborne Visible and InfraRed Imaging Spectrometer (AVIRIS), which measures hyperspectral radiance. In terrestrial environments, LiDAR can determine structural properties of forests (Lefsky et al. 1999) and hyperspectral data from the AVIRIS can measure fractional cover (*f*) of photosynthetic and non-photosynthetic vegetation (PV and NPV), and bare substrate (B) (Asner and Heidebrecht 2002, Asner et al. 2005). Collected at high resolution (1.5 m), integration of LiDAR and AVIRIS data in RSFs has potential to increase the ability to characterize habitat and improve resource selection studies (Hyde et al. 2005, Garcia-Feced et al. 2011) .

While LiDAR and AVIRIS data has the ability to greatly improve RSFs, it has been little used in this regard. Given the potential for these technologies, the goal of this study was to integrate these data with other habitat information to evaluate feral goat resource selection across home ranges in Pōhakuloa Training Area (PTA) on Hawaiʻi Island. According to Johnson (1980), selection for resources can occur at several spatial scales: geographic range of a species (first-order); home range selection within geographic range (second-order); within home range (third order); and selection of particular food items by an individual (fourth-order). Resource variables for this study were selected based on a review of previous research on ungulate movement and available data. The variables described below were included with the assumption that they would have an impact on feral goat resource selection within individual home ranges (third-order selection; Johnson, 1980). Potential predictor variables included: plant community, canopy height, slope, curvature, and proportion of photosynthetic vegetation vs. non-photosynthetic vegetation vs. bare ground.

Abiotic resource variables included slope and curvature due to their known influence on feral goats and other ungulates in habitat selection (Poole and Heard 2003, Sawyer et al. 2007). Biotic resources included potential food resources such as canopy height and proportion of photosynthetic vegetation vs. non-photosynthetic vegetation. Canopy height indicates a potential browse resource, while photosynthetic and non-

photosynthetic vegetation represent either grazing or browsing resources for feral goats. In addition, large mammalian herbivores have been observed to significantly alter three-dimensional forest structure in other ecosystems (Asner et al. 2009). Finally, vector-based plant community provided by the Center for Environmental Management of Military Lands at Colorado State University was included to investigate whether feral goats exhibit resource selection based on preferential forage species.

The objective of this research was to integrate high resolution remotely sensed data into an RSF to evaluate the significance, direction and magnitude of relationships between animal movement and resources to predict future patterns of space use by animals. I hypothesized that LiDAR and AVIRIS data would be a significant predictor of resource use by feral goats, and allow for predicted resource use to be projected at a high resolution across a broad landscape. High resolution LiDAR data has not been previously incorporated in RSF models for large ungulates, offering a unique potential to test the ability of an emerging technology.

Most resource selection research has focused on species of conservation interest, such as threatened and endangered species, and game mammals in order to maximize protection of important habitat or increase population sizes (Boyce and Mcdonald 1999). However, resource selection by invasive species can also be used to help prioritize conservation and restoration activities in highly degraded ecosystems. In Hawaiian montane dry forests, feral goats are a significant threat to conservation and restoration of native ecosystems (see Chapter 2). Constructing a resource selection function for feral goats in Hawaiian dry forest ecosystems will allow for managers to focus efforts on restoring areas with a high potential to return to native states, and avoid highly degraded areas that may not be cost effective for ecological restoration.

Materials and Methods

Study Area

To address my objective, I carried out a feral goat collaring study between July 2010 and July 2011 in the Pōhakuloa Training Area (PTA) on Hawaiʻi Island (19°45′36″N 155°33′13″W; Figure 4.1). PTA is a 438 km^2 military installation lying in the saddle of three volcanoes, Mauna Kea (4205 m), Mauna Loa (4169 m), and Hualalai

(2521 m), which covers both the Koppen temperate climate zones Cfb (maritime temperate climates: continuously wet warm temperate) and Csb (dry-summer subtropical: summer-dry warm temperate). High climatic variability exists in PTA, with temperatures ranging from 10 to 22 °C during at least 4 months of the year. Seventy percent of the annual rainfall (561.2 mm) typically occurs between November and March, and the driest summer month has less than 30 mm of rainfall in the Csb climate (Weise et al. 2000). PTA is comprised of a complex mosaic of vegetation communities that have resulted from spatial variability in substrate type and age, and subsequent soil development. Sections of Hawai'i's last remaining tropical montane dry forest and native grasslands are present in the area, including the following major plant communities: *Metrosideros* treeland, *Dodonea* shrubland, *Myoporum-Sophora* shrubland, and *Eragrostis* and *Pennisetum* grasslands (Figure 4.2). Although feral goats occur across five of the eight main Hawaiian Islands in virtually every habitat type, a particularly high density of these animals exist in the dry montane ecosystems of PTA. No quantitative data exist on feral goat abundance at PTA, but a 2009 animal drive forced 1800 feral goats out of a newly fenced management unit of 21.3 km² (Kellner et al. 2011), which equates to a density of 1.9 animals ha^{-1}.

Feral Goat Capture

On July 2nd, 2010, 12 adult (>18 months old; Watts and Conley, 1984) feral goats were captured by net gun using an MD 500D helicopter as a shooting platform in the northern portion of PTA (Figure 4.3). Capture locations were recorded using a handheld GPS (Garmin International Inc., Olathe, Kansas). Potential capture locations were limited due to extensive ungulate exclosures and a large off-limits impact area with active artillery training (Figure 4.3). To achieve a representative sample, individuals were selected based on spatial location (i.e. individuals from 12 distinct herds or groups to maximize collar efficiency), as well as sex and age classes. Twelve distinct herds could not be located on the day of the operation, so some capture locations were closer than anticipated. Six adult males and six adult females from 11 herds were captured to obtain a representative sample.

Feral Goat Monitoring

GPS Argos wildlife collars (model GPS7000SA, Lotek Wireless, Newmarket, Ontario Canada) weighing approximately 450 grams (< 2% body weight) were attached to the animals after aging and health assessment. Collars were equipped with three separate transmitters: (*i*) VHF transmitter for real time collar locations, and (*ii*) an Argos transmitter for remote data download via satellite. Collars were programmed to log a GPS location and ambient temperature every two hours (120 second maximum time with no reattempt on failed fixes) for one year, and download location data via the Argos network once every five days. Logging fixes every two hours allows for the maximum amount of data (shortest interval) to be collected over the desired one year period of the study.

Animal locations were input into a Geographic Information System (GIS) using ArcInfo/ArcMap 9.3.1/10.0 (Environmental System Research Institute Inc., Redlands, CA, USA). Only location fixes with a three dimensional fix and low Positional Dilution of Position (PDOP) value (96.1% of all collected points) were included in analyses (Lewis et al. 2007). Argos location data were also collected from collars during remote data downloads, but due to inaccuracy and infrequency of data collection, Argos locations were discarded from analysis (Costa et al. 2010).

To create a spatial extent for third order selection analysis, utilization distributions were calculated using adaptive-kernel density estimators (Worton 1989) with the Home Range Tools (HRT) Analysis Extension in ArcMap 9.3 (Rodgers and Carr 1998). The 99% boundary for each animal was generated with an ad hoc smoothing parameter ($h_{ad\ hoc}$) using the smallest increment of the reference bandwidth (h_{ref}) that provided a contiguous 99% kernel home range (i.e. $h = 0.5 \times h_{ref}$, $0.6 \times h_{ref}$,... h_{ref} – R. Long, pers. comm.). These boundaries were used to generate random points to represent available habitat characteristics for each individual.

Habitat Variables

Developing an RSF requires selecting appropriate habitat variables that represent available resource units to an animal. The following habitat variables were selected for development of an RSF based on a review of previous research on ungulate movement and the goal of investigating the effectiveness of LiDAR data in RSF development: plant

community, canopy height, slope, curvature, fPV, fNPV and fB. Each of these variables potentially influences feral goat behavior.

Categorical plant community vector data were provided by the Center for Environmental Management of Military Lands at Colorado State University. The original data were classified into 24 community classes based on vegetation type. Several classes were designated as mixed communities (e.g., *Myoporum-Dodonaea*) of which I reclassified to reflect dominant vegetation type, resulting in 11 final habitat classifications. These 11 habitat classes were converted into 5 × 5 m cell raster data to match resolution of remotely sensed data. Principal community types included: Barren Lava, Disturbed (human activity), *Metrosideros* treeland, *Dodonea* shrubland, *Myoporum-Sophora* shrubland, *Eragrostis* grasslands, *Pennisetum* grasslands, *Styphelia* shrubland, *Chamaesyce* treeland and *Chenopodium* shrubland (Figure 4.2).

Continuous resource variables were processed based on data provided by the Carnegie Airborne Observatory (CAO). The CAO produces high resolution surface cover mapping using laser detection and ranging (LiDAR; Lefsky et al., 1999). In contrast to ground based monitoring of ecological variables, remote sensing allows for a broad scale assessment of environmental factors that may influence resource use of wildlife populations. On January 7, 2008, the CAO was flown with an airborne LiDAR system to create three-dimensional land cover maps of PTA at a spatial resolution of 0.1-1.5 meters, enabling a fine scale reconstruction of this large landscape (Asner et al. 2007). Airborne visible and infrared imaging spectrometer (AVIRIS) data were joined with LiDAR data (i.e. CAO beta system). Data were collected within a several day period, offering a snapshot in time of vegetation state. Reflectance values were used to estimate fractional cover f(PV, f NPV, and fB (Asner and Heidebrecht 2002, Asner et al. 2005). At such high resolution, small variations in land cover type, canopy and terrain were detectable and, thus, included in the RSF.

A Digital Elevation Model (DEM) was derived from elevation data provided by the CAO beta system from which slope and curvature values were generated. Curvature was generated using ArcGIS 10.0's DEM Surface Tools (Jenness 2012) to quantify landscape ruggedness, or topographic variability. Canopy height was also obtained from data provided by the CAO using ENVI version 4.7 (Exelis Visual Information Solutions,

Boulder, Colorado). The f PV, f NPV and f B were also included as habitat variables in the RSF. A high proportion of cells contained majority f B (81.5%) and f NPV (11.9%), with f PV (7.7%) distributed primarily in the northern section of PTA. Non-photosynthetic vegetation represents senescent, dormant, or woody structures of plants (including trunks and stems).

I generated correlation matrices in Program R 2.13.2 (R Development Core Team 2011) to test for collinearity among the selected RSF variables prior to model development. Only covariates below the correlation coefficient threshold of $|r| < 0.6$ were used as candidates for RSF models (Hosmer and Lemeshow 2000). One variable, fB, was correlated with fNPV ($|r| > 0.6$) and was subsequently removed from model development. fNPV was retained it was assumed to be more ecologically relevant than bare ground as a potential food source.Finally, if a variable did not occur within the 99% utilization distribution of an individual feral goat, it was not included in the candidate models.

Nocturnal versus Diurnal Models

Feral goat location data were divided into two separate datasets based on nocturnal (N) vs. diurnal (D) space use for two reasons. First, by dividing data into two subsets based on displacement distances, it is possible to identify differences between resource use during bedding hours and foraging hours. Second, feral goats are known to have substantially higher impacts in bedding areas due to site fidelity and total amount of time spent in lying out areas (O'Brien 1983). To distinguish between periods of high and low movement activity, displacement distances were calculated between each collar fix using the Home Range Tools (HRT) Analysis Extension in ArcMap 9.3 (Rodgers and Carr 1998). A two-tailed Welch's *t-test* ($\alpha=0.05$) was used based on unequal variances to compare displacement distances between nocturnal (20:00 – 06:00 hrs) and diurnal hours (08:00 – 18:00 hrs).

Model Development

I used the Resource Selection Function approach with a use-availability design (Manly et al. 2002) to examine the relationship between resource use and habitat variables (Keating and Cherry 2004). Interpreting resource use by animals with a use-

availability design is complex and has been criticized as biased based on experimental design (Johnson et al. 2006, Beyer et al. 2010a). Specifically, two of the main problems with classic logistic regression are independence of sampling units and unbalanced samples. Experimental design in telemetry studies limits the ability to control these problems, but several solutions are available. To address this issue, separate models were created for each individual and coefficients were averaged to create a population-level model (Manly et al. 2002, Long et al. 2009).

I developed seven models *a priori* from additive combinations of the six explanatory variables (Table 4.1). The seven models were selected because they addressed the hypothesis that high resolution LiDAR and AVIRIS data would be a good predictor of feral goat resource use. Both nocturnal and diurnal RSFs for each individual feral goat were based on a use-availability design (Manly et al. 2002). A 99% Utilization Distribution (UD) boundary was generated for each individual to act as a spatial boundary for each animal. Animal locations within the boundary were considered used, and an equal number of random points were generated within the 99% UD to represent available resources. Used locations were excluded from generation of available locations. By generating available points within each individual's home range, and developing models for individual feral goats, RSFs corresponded with third-order habitat selection (Johnson 1980). All points were assigned habitat variables from a 1.5×1.5 m pixel basis from a database created of all habitat variables.

Logistic regression models were fit to each individual feral goat in SAS (PROC LOGISTIC; SAS Institute 2002). A RSF is generated using the coefficients and significant variables from a logistic regression formula (Manly et al. 2002, eq 5.11):

$$\omega(x_i) = \exp\left\{\beta_1 x_{i1} + \cdots + \beta_p x_{ip}\right\} \qquad \text{[Eq. 1]}$$

where $\beta_{1\ldots p}$ are significant regression coefficients and $x_{1\ldots p}$ are significant variables selected during model creation. Akaike's Information Criterion (ΔAIC; Manly et al. 2002) was used to identify the best model for individual feral goats from the set of candidate models. Models were ranked using ΔAIC and relative likelihood was determined using Akaike weights (Burnham and Anderson 2002). To select the best population level model, model ranks were summed to select the lowest overall rank, indicating the most effective population-level model.

Assuming each animal is independent, and to give each animal equal weight, individual animal coefficients were averaged to create the population-level RSF (Marzluff et al. 2004, Sawyer et al. 2006, Long et al. 2009). The resulting RSF values were used to predict relative probability of selection in the study area. Because these values are based on the use-availability design, where sampling probabilities are not known (Manly et al. 2002), the values generated by the logistic regression were transformed to scale predicted values (ω) between 0 and 1 to estimate the probability that the ith unit is used as follows:

$$\widehat{\omega} = \frac{\omega(x)}{1+\omega(x)} \hspace{3cm} \text{[Eq. 2]}$$

where probability of resource selection increases as ($\widehat{\omega}$) approaches 1 (Manly et al. 2002).

The accepted RSF model was input in ArcGIS 10.0 to generate an RSF value for each 1.5 m resolution cell in a subset of the study area. Given that the study area is comprised of several million cells (1.25×10^8), the entire area was divided into subsets for processing as ArcGIS was unable to process a single coverage at this resolution. The RSF probabilities were classified into four quantiles to represent areas of low, medium-low, medium-high, and high, which represent categories of increasing habitat selection (Johnson et al. 2006).

Statistical Analyses

All covariates were screened for collinearity using the Pearson's correlation coefficient threshold of $|r| > 0.6$ for covariate removal (Hosmer and Lemeshow 2000). To analyze variables in individual models, the Wald Chi-Square test statistic was used to assess the probability that individual predictor's regression coefficient is zero with other predictors in the model ($\alpha = 0.05$). In addition, 95% Wald confidence limits were examined to determine if the confidence intervals included 1, indicating a failure to reject the null hypothesis that a regression coefficient is zero. *A priori* models were assessed using AIC values, ΔAIC, and Akaike weights to identify the best model for individual feral goats from the set of candidate models.

Habitat Variables

High-resolution LiDAR and AVIRIS data were significant predictors of individual feral goat resource use in most models. Plant community variables were not found to be significant predictors of individual feral goat habitat use in most models. Models that included plant community consistently had higher AIC values, low significance of predictor variables, and overall were ranked either 6 or 7 (Tables 4.2 and 4.3).

Nocturnal versus Diurnal Models

Locations for nocturnal and diurnal RSFs were based on observations that feral goats move significantly longer distances during diurnal hours (Figure 4.4; $t = -95.36$ df $= 30558.11$, $P < 0.0005$). Few differences existed between diurnal and nocturnal models. All 5 variables were significant in both models, and had the same relative ranks (Table 4.5). Only *f*NPV differed in sign between models (positive in diurnal, indicating selection for high *f*NPV areas, and negative in nocturnal, indicating avoidance of high *f*NPV area). With the exception of *f*NPV, coefficient values were higher for each variable in nocturnal than diurnal models.

Model Development

Based on summed AIC ranks, model 7 had the most support for both nocturnal and diurnal feral goat resource use in Hawaiian montane dry landscapes (Table 4.2 and 4.3). All 5 resource variables (i.e. canopy height, slope, curvature, *f*PV, and *f*NPV) were statistically significant (Pr > ChiSq < 0.05) in the individual RSFs. Models that incorporated high resolution LiDAR and AVIRIS data explained more variation in resource use than models incorporating only plant community type. In the population-level diurnal model (Table 4.4), coefficients for canopy were negative, indicating selection for areas with a lower canopy, while coefficients slope, curvature, *f*PV and *f*NPV were positive, indicating selection for areas with higher values of these variables (Table 4.5). In the population-level nocturnal model (Table 4.4), coefficients for canopy and *f*NPV were negative, indicating selection for areas with a lower canopy and *f*NPV,

while coefficients slope, curvature, and *f*PV were positive, indicating selection for areas with higher values of these variables (Table 4.5). Relative rankings of variables based on coefficients were, from 1-5: canopy, curvature, slope *f*NPV, *f*PV, and were the same ranking for both population-level models.

Using a GIS, these two RSF models for diurnal and nocturnal resource use were projected onto a spatial subset of PTA, and classified into areas of low, medium-low, medium-high, and high, which represent categories of increasing habitat selection (Johnson et al. 2006). A high degree of overlap existed between diurnal and nocturnal resource use. However, consistent with model results, high probability areas of feral goat space use during nocturnal periods were confined to fewer areas than diurnal periods (Figure 4.4).

Discussion

Results support the hypothesis that LiDAR and AVIRIS data would be a significant predictor of resource use by feral goats. High resolution remotely sensed data proved to be a better predictor of feral goat habitat use in PTA compared to models incorporating vector-based plant community data. Models that incorporated plant community type performed poorly for all individuals, suggesting that plant community had less influence on feral goat space use than abiotic characteristics and general patterns in vegetation (i.e. canopy height, *f*PV and *f*NPV). Based on RSF coefficients estimated with the selected model, probability of feral goat resource use can be projected at a broad scale, enabling identification of areas highly impacted by goat activity.

Habitat Variables

Studies in resource selection are an important management tool for animals in areas of conservation interest. However, one caveat of RSFs is that predictions of high probability does not suggest optimal habitat (Manly et al. 2002). The RSF for feral goats in PTA provides an estimate of probability of feral goat habitat use based on known locations. Given that feral goats are generalist herbivores and are highly adaptable to a variety of habitats, no one variable is likely to be able to explain their abundance. Instead, a variety of characteristics is most likely correlated with habitat use.

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During both diurnal and nocturnal times, this research indicates that feral goats in PTA selected habitat based on terrain and general vegetation patterns, but not on specific plant communities. Feral goats exhibited increased habitat use in areas of higher slope and greater topographic complexity. On a broad scale, PTA has limited topographic relief, but small scale, highly topographically variable areas are sporadically dispersed throughout the landscape and easily identified with LiDAR data. Model results and field observations are consistent with other studies that have found feral goats to prefer areas of high topographic variability (Poole and Heard 2003), as well as other large grazing ungulates (Sappington et al. 2007, Long et al. 2008) and large predators (Kertson and Marzluff 2010).

Plant community type was likely a poor predictor of feral goat presence for several reasons. First, feral goats are generalist herbivores and can survive on a wide variety of forage (Coblentz 1977). While preferred forage species may be actively sought out, feral goats can survive and persist on most plant species (Yocom 1967). In this study, the home ranges of several collared feral goats were dominated by one or a few plant communities, and lacked plant communities that were dominant in other individuals' home ranges. Second, abiotic habitat characteristics, such as topography, most likely have a stronger influence on habitat selection than plant community type, as they offer important resources for protection against weather, potential heat source at night, and protection from predators. Predation of feral goats in Hawaiʻi is largely unknown, but feral dogs exist in many areas and may influence feral goat movement. Predator avoidance may be an ultimate causation of resource selection, as selection for high, steep slopes as lookouts are observed in many populations of feral goats (Poole and Heard 2003, Enright and Williams 2010). Third, selection for habitat based on fPV vs. fNPV, rather than specific plant community types, may reflect this animal's success as a generalist herbivore. Feral goats consume photosynthetic vegetation, but also routinely strip bark from trees and browse non-photosynthetic vegetation as a food source (Scowcroft and Sakai 1983). However, coefficients for both PV and NPV variables were ranked below slope, curvature and canopy, suggesting these predictors are less influential for habitat selection.

Nocturnal versus Diurnal Models

Feral goats also appear to demonstrate stronger selection during nocturnal hours compared to diurnal hours. Feral goats are diurnal, traveling throughout their range in search of forage and social interactions during daylight hours. Nocturnally, individuals demonstrate site fidelity to bedding areas, preferring areas that are steep sloped and topographically variable (O'Brien 1984a). Based on field observations these areas are often devoid of vegetation, which may be due to impact of repeated use by feral goats. The slightly higher coefficients for nocturnal RSFs reflect a stronger selection for steeper areas with lower vegetation height at night.

Model Development

Some key assumptions of resource selection studies include: (*i*) random sample of animals is representative of the population; (*ii*) sampling units are independent; (*iii*) sampled animal's selection is independent of other sampled animals; and, (*iv*) resource units are known and do not change during the course of the study period. While mild violations of these assumptions may have occurred in this study, they were unavoidable. For example, given the gregarious nature or feral goats, sampling units (individuals) cannot be considered independent at all times throughout the study (see Chapter 3). In addition, annual changes in fPV and fNPV values may not be accurately represented since data were collected by the CAO over just a several day period.

Use of logistic regression to produce a RSF is a common method to evaluate and predict resource selection of wildlife species (Johnson et al. 2000, Anderson et al. 2005). In recent years, using logistic regression has been criticized as a technique for developing RSFs (Keating and Cherry 2004, Johnson et al. 2006). New techniques to predict resource use are constantly being developed, such as Resource Utilization Functions (RUFs) that use utilization distributions of animals as a response variable (Marzluff et al. 2004). However, a comparison of this approach to RSFs suggests that RUFs represent advances in resource selection theory, but predict resource use less accurately than traditional RSFs (Long et al. 2009). In addition, while logistic regression is a simple approach to generating RSFs, the technical expertise and computational power necessary to implement new methods of resource selection suggests that these approaches will

continue to be valuable to home-range studies (Fieberg et al. 2010). Modern mechanistic modeling approaches may be more accurate, but often require custom written computer code and substantial statistical expertise (Beyer et al. 2010).

Given the ecology of feral goats, it may be inherently difficult to fit an RSF to location data. Feral goats are a habitat generalist, and are observed to inhabit PTA ubiquitously, regardless of habitat type. Quantifying habitat selection is challenging for generalist species, which utilize a wide range of habitats and resources. Ultimately, the results of this model suggest that a generalist herbivore demonstrates limited resource selection, particularly during diurnal periods. During nocturnal periods, site fidelity to bedding grounds that share common characteristics and the tendency for individuals to congregate may lead to more rigorous model performance.

This study contributes to the knowledge of feral goat habitat use in montane dry landscapes in Hawai'i where they are commonly found in large numbers. The RSF habitat model produced here could be used by conservation managers in several ways. First, understanding resource selection by feral goats allows generation of predictive maps of habitat use, which can be used to identify areas that may be degraded by feral goat activity and are, subsequently, poor choices for native plant restoration in the absence of fencing. Second, predictive maps can be used to identify prospective areas for maximizing the efficacy of feral goat control. That is, areas of high predicted use could be selected for efficient control through hunting efforts. Alternatively, areas of low predicted use could be targeted for potential exclosure and control sites to utilize low impact areas for priority restoration sites.

Table 4.1. Seven *a priori* RSF models. Plant community is a categorical variable. All other predictors are LiDAR and AVIRIS derived continuous variables. The response variable in each model is binary (used/available).

Model #	Predictor Variables
1	plant community
2	plant community + slope + curvature
3	plant community + canopy + NPV + PV
4	plant community + slope + curvature + canopy + NPV + PV
5	slope + curve
6	slope + curve + canopy
7	slope + curve + canopy + NPV + PV

Table 4.2. Nocturnal RSF model ranks for individual feral goats based on AIC values (1 = lowest AIC, 7 = highest AIC). Model ranks were summed across individuals to designate the best population level model (potential range: 9 – 63).

Model	Animal									Sum
	M2	M3	M4	M5	M6	F2	F3	F4	F7	
1	7	6	6	7	7	7	7	7	7	61
2	5	5	4	4	4	3	4	4	4	37
3	6	7	7	6	6	6	6	6	6	56
4	4	4	3	3	3	4	3	3	3	30
5	3	3	5	5	5	5	5	5	5	41
6	1	2	2	2	2	2	2	2	1	16
7	2	1	1	1	1	1	1	1	2	11

Table 4.3. Diurnal RSF model ranks for individual feral goats based on AIC values (1 = lowest AIC, 7 = highest AIC). Model ranks were summed across individuals to designate the best population level model (potential range: 9 – 63).

Model	Animal									Sum
	M2	M3	M4	M5	M6	F2	F3	F4	F7	
1	7	7	6	7	6	6	7	7	7	60
2	3	4	4	4	4	4	5	4	4	36
3	6	6	7	6	7	7	6	6	6	57
4	4	3	2	3	4	3	3	3	3	28
5	5	5	5	5	5	5	4	5	5	44
6	2	2	3	2	2	1	2	2	2	18
7	1	1	1	1	1	2	1	1	1	10

Table 4.4. Population-level RSF model coefficients for diurnal (D) and nocturnal (N) time periods.

	Model
D	$\hat{\omega}$ = exp{-0.43(Canopy) + 0.06(Slope) + 0.17 (Curvature) + 0.0002 (PV) - 0.0030(NPV)}
N	$\hat{\omega}$ = exp{-0.13(Canopy) + 0.03(Slope) + 0.09 (Curvature) + 0.002 (PV) + 0.0026(NPV)}

Table 4.5. Estimated mean coefficients and SE for the population-level diurnal and nocturnal resource selection function (RSF) habitat model for feral goats in the Pōhakuloa Training Area on Hawaiʻi Island.

	Diurnal RSF			Nocturnal RSF		
Variable	β	SE	Rank [a]	β	SE	Rank [a]
Continuous						
Canopy	-0.1332	0.0537	1	-0.4260	0.0967	1
Curvature	0.0936	0.0201	2	0.1659	0.0250	2
Slope	0.0273	0.0049	3	0.0557	0.0056	3
fNPV	0.0026	0.0003	4	-0.0025	0.0005	4
fPV	0.0021	0.0002	5	0.0002	0.0003	5

[a] Ranking based on absolute value of coefficient. (β).
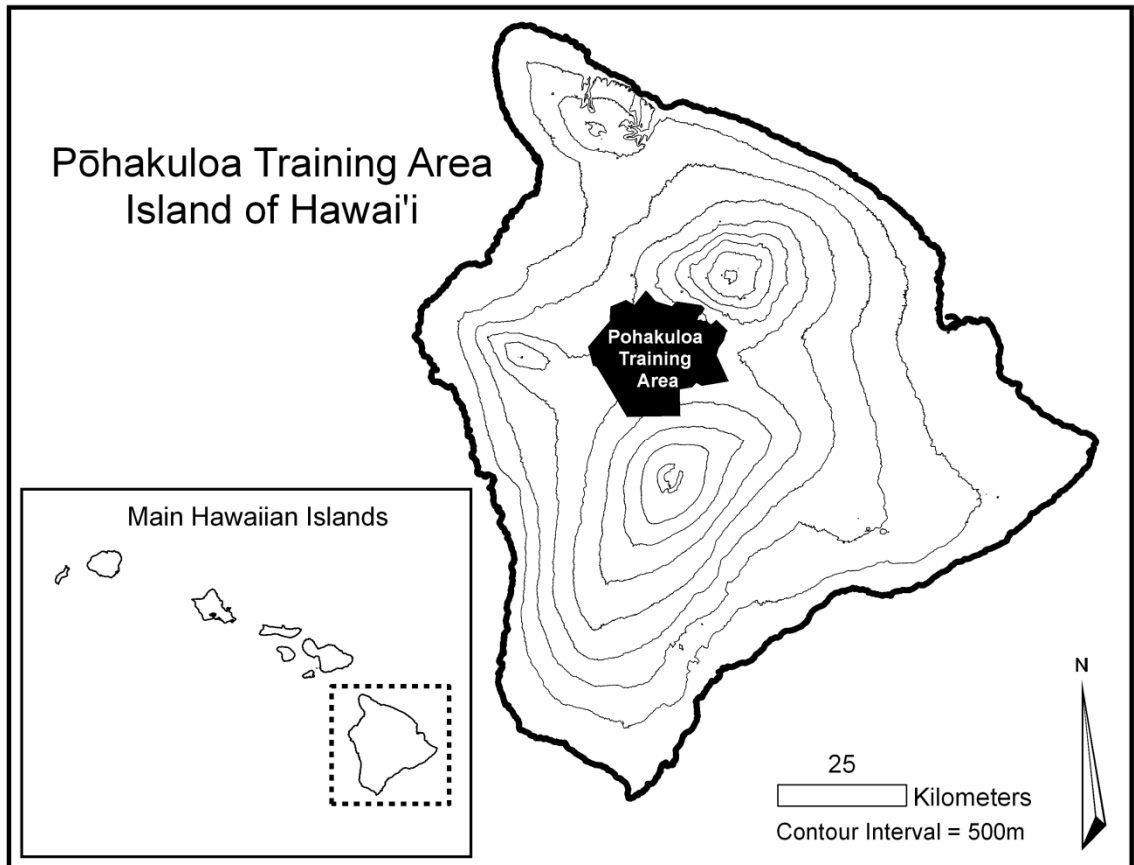
Figure 4.1. Location of study area in the Pōhakuloa Training Area on Hawaiʻi Island.
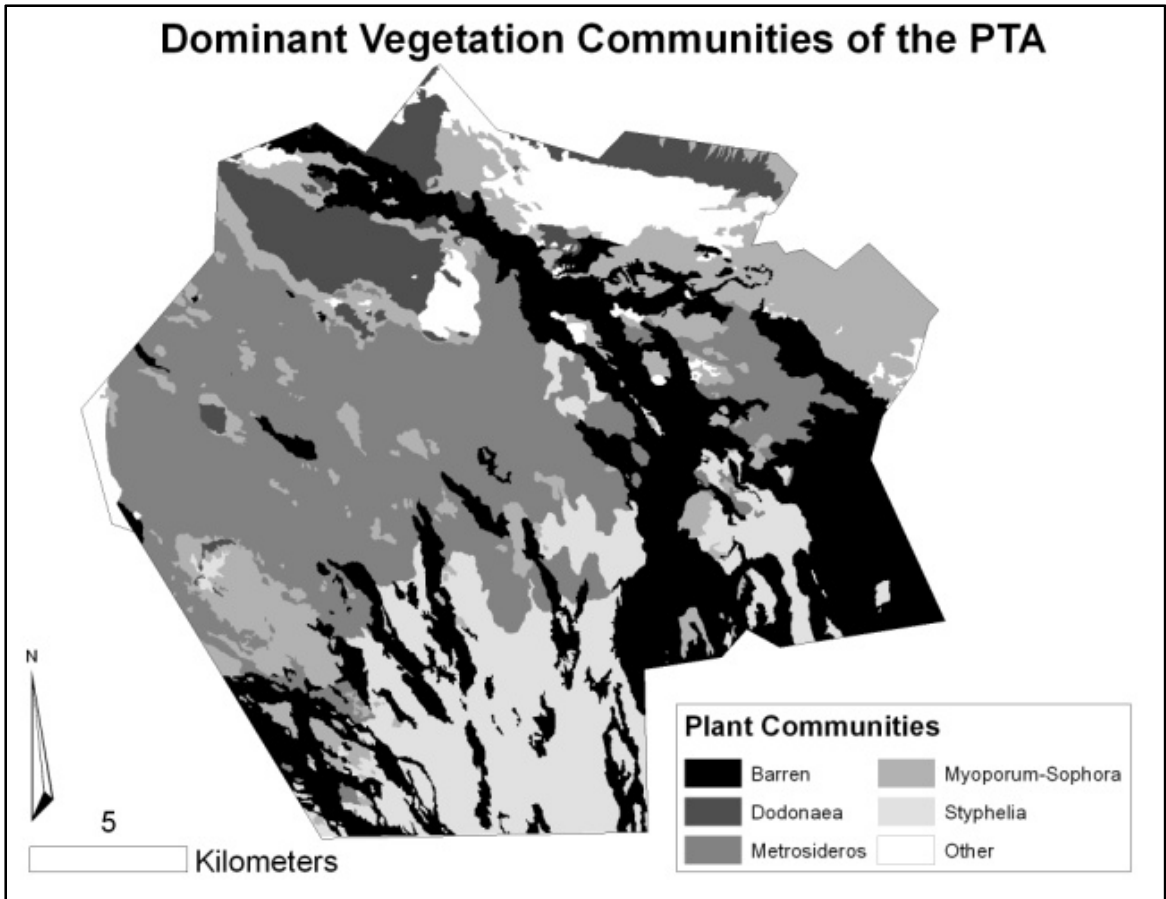
Figure 4.2. Dominant vegetation types of the Pōhakuloa Training Area on Hawai'i Island. The 'other' class includes *Chamaesyce* treeland, *Chenopodium* shrubland, disturbed areas, *Pennisetum* grassland and *Erograstis* grassland.
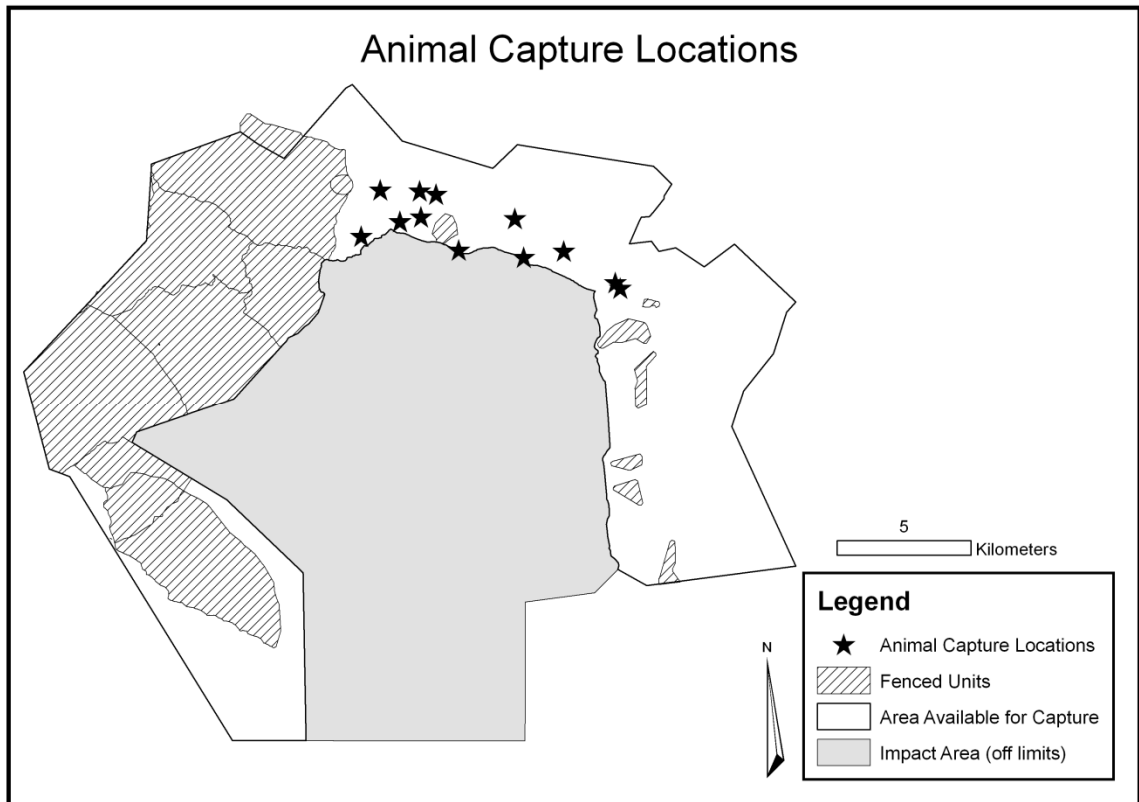
Figure 4.3. Potential capture locations (white area) and actual capture locations (black stars) for feral goats in the Pōhakuloa Training Area.
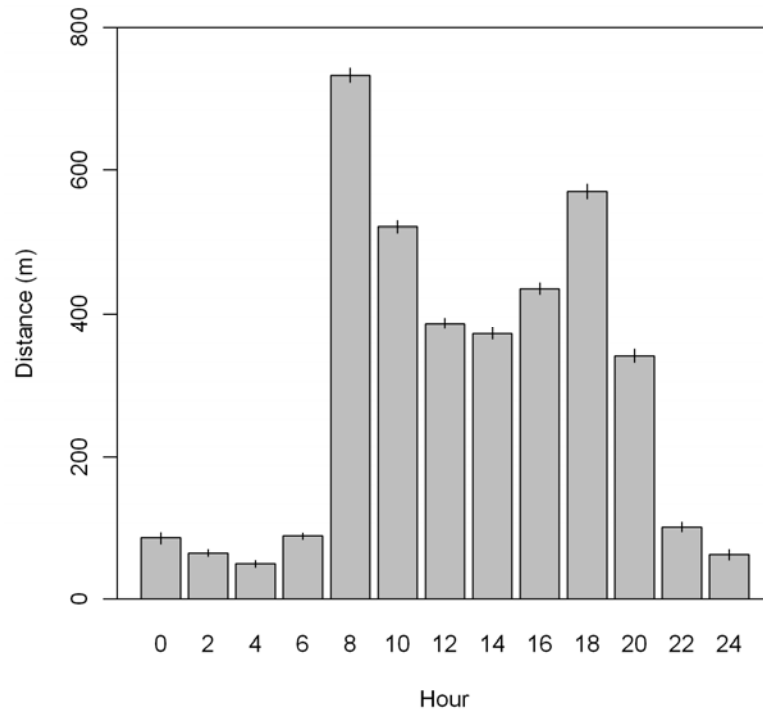
Figure 4.4. Mean displacement distances (± SE) between two hour interval collar fixes of all individuals. Displacement distances were pooled by hour over the entire study period and displayed by two hour interval for a 24 hour period.
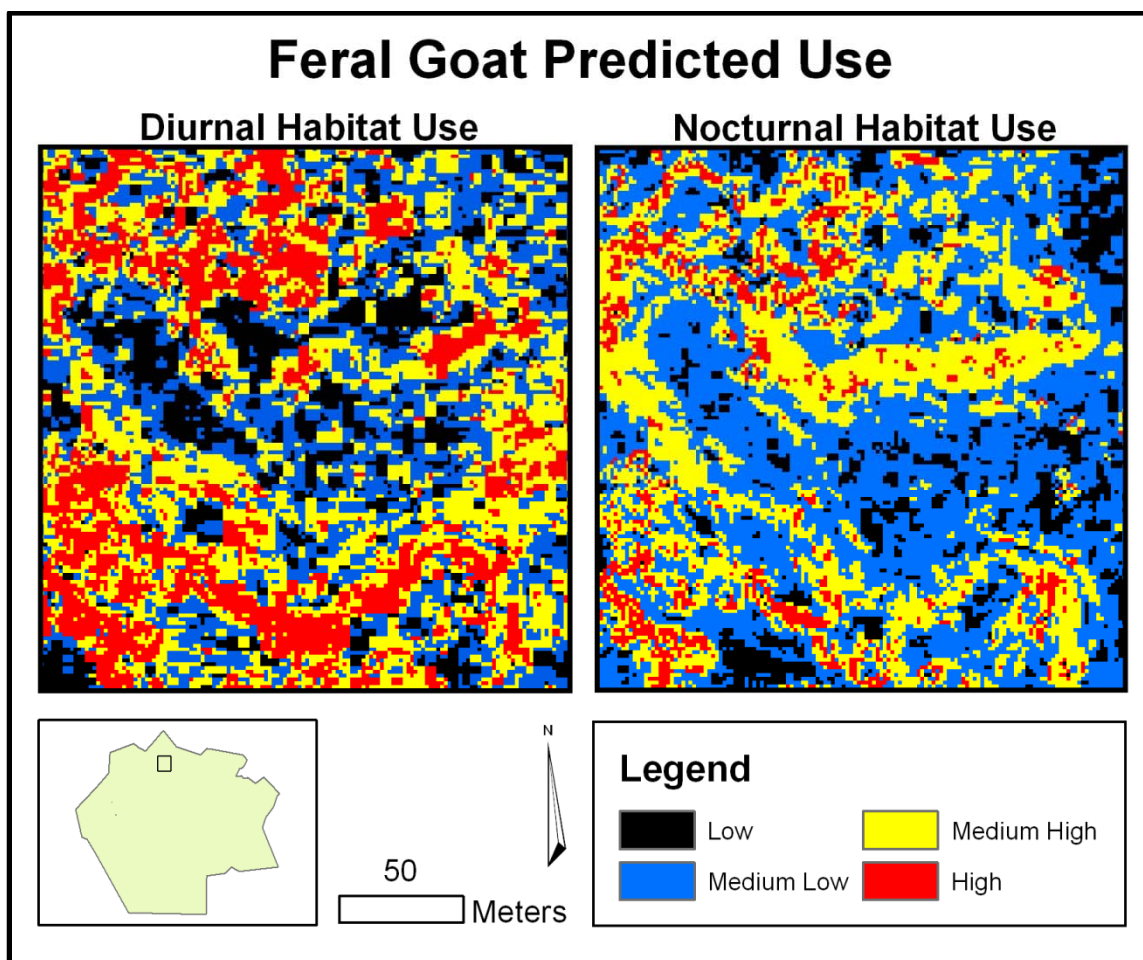
Figure 4.5. Relative probability of diurnal and nocturnal habitat use by feral goats in a spatial subset of the Pōhakuloa Training Area at a 1.5 m pixel resolution. Red, yellow, blue and black color indicates high, medium-high, medium-low, and low probability of use respectively.

CHAPTER 5
CONCLUSION

The Hawaiian archipelago represents a unique island ecosystem as one of the most isolated landmasses on Earth. A volcanic oceanic island archipelago, the evolution of flora and fauna on these islands are defined by extreme isolation, following island biogeographic theory, resulting in high levels of endemism and adaptive radiation (Paulay 1994). Evolving separately from entire genera of plants and animals, Hawaiian biota are particularly vulnerable to species invasions, posing an ongoing threat of extinction.

Introduced species in Hawaiʻi began with human settlement by the Polynesians between 1219–1266 A.D. who brought an assortment of non-native plants and animals (Kirch 1982). Introductions continued with the colonization of the islands by Europeans in the late 18th century causing an inundation of non-native species introductions leading to further alteration of native ecosystems. While all introduced species potentially threaten native ecosystems, non-native mammals were a novel introduction to the Hawaiian Islands. As an isolated oceanic island, the only terrestrial mammalian inhabitants prior to human contact were one or two endemic bats (Eldredge and Miller 1995). The impacts of mammals vary greatly by species, from predation of native avifauna to degradation of entire watersheds. Large grazing ungulates, such as feral goats, can push ecosystems into alternative states and require multifaceted approaches to restore native species (Weller et al. 2011).

Management of these animals is particularly important in Hawaiian dry forests as over 90% of original tropical dry forests in Hawaiʻi has been lost (Bruegmann 1996). Agricultural activities, invasive species and fire all play important roles in transforming dry forest ecosystems. Importantly, fire has become a regular disturbance in Hawaiian ecosystems (Hughes et al. 1991). Ungulates are known to alter fire regimes though grazing and browsing (Hobbs 1996), and in Hawaiian dry forests non-native ungulates can facilitate biological invasion and a promote a grass-fire cycle (Cabin et al. 2000). The spread of invasive grasses plays a primary role in converting native dry forest into exotic grasslands through an ongoing grass-fire cycle (D'Antonio and Vitousek 1992).

In a comprehensive literature review of feral goats on Pacific Islands (Chapter 2), I summarized the impacts of feral goats on islands ecosystems and current control techniques available to address management goals. This resource can be referred to by scientists and managers looking for a single resource for general information about this invasive species. The overall ecological impact of non-native feral ungulates in the Hawaiian Islands is clear. Non-native herbivores severely degrade and disturb the landscape, aid in the spread of invasive plants, and alter the structure and function of entire ecosystems. However, management and restoration efforts require consideration be given to specific ungulate species, as results to date have been mixed and may be species-specific (Cabin et al. 2000, Kellner et al. 2011). Removing ungulates from native ecosystems is a critical first step in ecological restoration, but it is not a panacea, and continued management is necessary if conservation goals are to be met (Weller et al. 2011).

In the analysis of home range and dispersal patterns based on collared animals (Chapter 3), I estimated home range sizes and analyzed dispersal patterns of feral goats in the Pōhakuloa Training Area on Hawai'i Island. Home ranges often occupy the same area, but individuals utilize different core areas and spent little time together during diurnal hours. Individuals congregate during nocturnal hours at bedding grounds, and disperse into smaller groups during the day in search of forage. While overall home ranges are relatively small, as a generalist herbivore feral goats can survive consuming almost any plant species present in the study area, requiring limited daily movement throughout their home range. Home range size should be included in control strategies for feral goats; if fence construction does not occur alongside management of feral goats, home range size and overlap analysis suggests that animals will quickly immigrate into areas where eradication has occurred (Holt and Pickles 1996).

I was also able to establish that individuals demonstrating dispersal behavior appear to move into secondary ranges with a higher difference in NDVI value compared to the mean NDVI value across annual ranges. Not all individuals demonstrated dispersal behavior, suggesting that other factors such as herd dynamics and social structure may influence intra-annual dispersal events. NDVI values appear to be a good overall indicator of feral goat habitat, suggesting that animals respond to resource pulses that

occur within their annual home range. Given the large populations, wide distributions, and high mobility of feral goats present in Hawaiian dry forests, animals may be able to successfully consume all vegetation that is actively experiencing a green-up event. This intra-annual movement indicates that resource pulses may influence the movement of feral goats, but given the lack of seasonality in the study area and limited duration of the study period, migration patterns could not be assessed. Restoration efforts that artificially generate green-up events (e.g., irrigation of native species, creation of green fire breaks) could also influence animal movement. Attracting feral goats to areas of conservation interest would be counterproductive to the goals of restoration activities.

The development of a resource selection function (Chapter 4) revealed high resolution LiDAR and AVIRIS data can be an effective predictor of feral goat habitat use. Coarse resolution plant community data proved to not be a significant predictor of habitat use. Model results suggest that feral goats select for areas of higher slope, greater topographic variability, and higher non-photosynthetic and photosynthetic cover. As a generalist herbivore, feral goats can survive in every habitat type in Hawaiian dry montane ecosystems. Therefore, selecting for areas based on more general vegetation patterns (i.e., vegetation vs. no vegetation) and abiotic factors such as areas of high topographic variability that offer protection from weather may be more likely explanations for resource use than selecting for particular plant communities.

RSFs are also able to provide an estimate of relative probability of occurrence of feral goats across a broad landscape. Predictive maps generated by the RSF are potentially of high value to conservation scientists working in PTA and other montane dry forests throughout Hawai'i. Maps generated for PTA provide high probability areas of feral goat occurrence, suggesting areas that may be highly degraded due to direct and indirect impacts of feral goats. Conversely, areas could also be located that have not been severely impacted by feral goats, and therefore may be potential sites for ecological restoration.

Conservation and restoration of native ecosystems in areas impacted by feral goats is a challenging task for natural resource managers. Ungulates have been present in Hawai'i for over two centuries, and their impacts modify both the structure and function of ecosystems, and occur on a broad landscape scale. When considering entire

landscapes, in some cases restoration may not be feasible due to resource constraints, but as a large and social mammal, successful control techniques exist to effectively manage feral goat populations. If broad scale control is not possible, decisions can be made at smaller scales to prioritize conservation and restoration activities to more efficiently reach management goals. Previous research informs managers that feral goat removal is a first step towards successful restoration, and additional efforts must be made to control invasive species that may subsequently experience higher rates of success in the absence of feral goats. In addition to contributing to knowledge of the general ecology of feral goats on Pacific Islands, the research presented in this thesis will aid in identification of high priority areas for conservation and ecological restoration of native Hawaiian montane dry forest ecosystems.

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Table A.1. Body Condition Score descriptions. Adapted from (Luginbuhl et al. 2002).

Body Condition Score (BCS)	General Condition	Animal Characteristics
BCS 1	Extremely thin	Extremely thin and weak, near death
BCS 2	Extremely thin	Extremely thin but not weak
BCS 3	Very thin	All ribs visible. Spinous processes prominent and very sharp. No fat cover felt with some muscle wasting
BCS 4	Slightly thin	Most ribs visible. Spinous processes sharp. Individual processes can be easily felt. Slight fat cover can be felt over the eye muscle
BCS 5	Moderate	Spinous processes felt but are smooth. Some fat cover felt over eye muscle
BCS 6	Good	Smooth look with ribs not very visible. Spinous processes smooth and round. Individual processes very smooth, felt with considerable pressure. Significant fat cover felt over eye muscle
BCS 7	Fat	Ribs not visible, spinous process felt under firm pressure. Considerable fat felt over eye muscle
BCS 8	Obese	Animal is very fat with spinous processes difficult to feel. Ribs can not be felt. Animal has blocky obese appearance
BCS 9	Extremely obese	Similar to an eight but more exaggerated. Animal has deep patchy fat over entire body
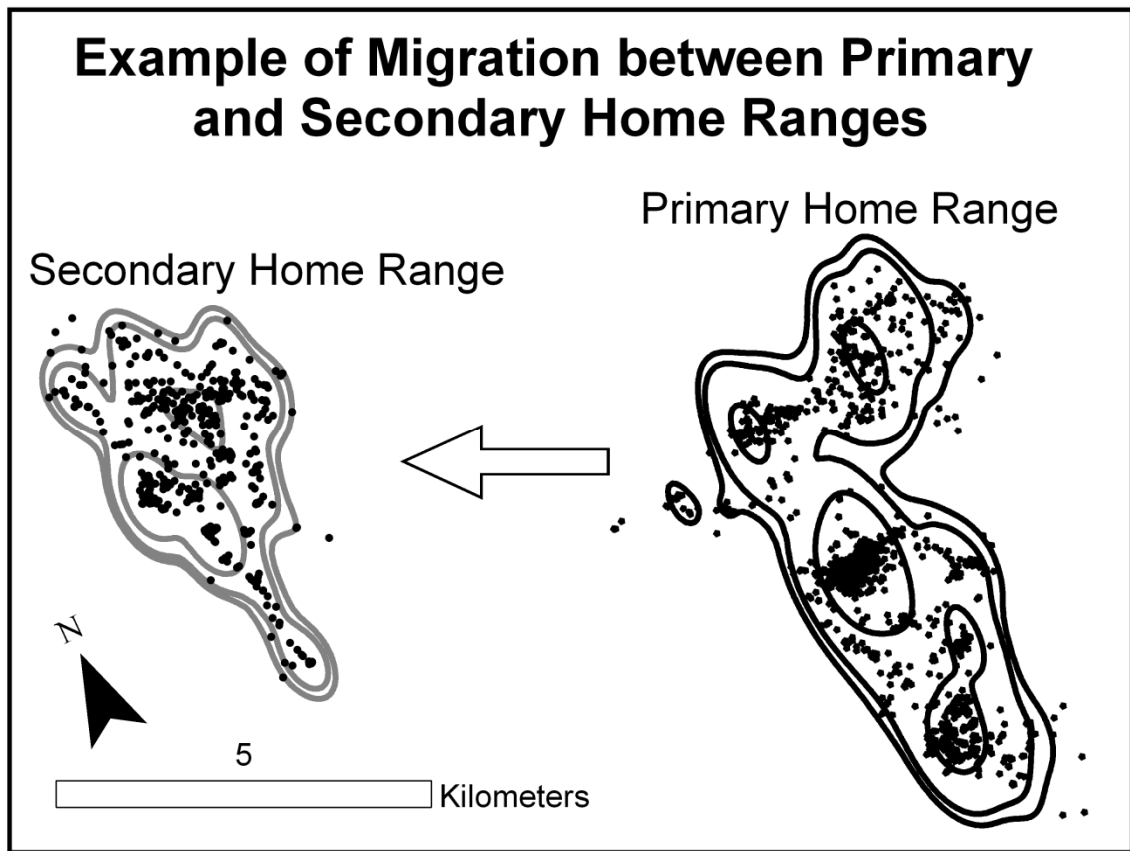
Figure B.1. An example of goat locations (solid circles) and primary (solid polygon) and secondary (gray polygon) for M2 from July 2010 to July 2011.

APPENDIX C

Table C.1. F2 nocturnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i), where N is the sample size.

Model	N	-2LL	AIC	ΔAIC	w_i
7	1338	1065.161	1095.161	0	0.000878
6	1338	1092.159	1116.159	20.998	2.42E-08
2	1338	1135.225	1161.225	66.064	3.96E-18
4	1338	1174.765	1194.765	99.604	2.06E-25
5	1338	1263.783	1278.047	182.886	1.7E-43
3	1338	1349.483	1363.875	268.714	3.92E-62
1	1338	1583.869	1595.869	500.708	1.6E-112

Table C.2. F3 nocturnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i)

Model	N	-2LL	AIC	ΔAIC	w_i
7	1364	1249.326	1279.326	0	0.000972
6	1364	1263.978	1287.978	8.652	1.29E-05
4	1364	1394.096	1420.096	140.77	2.63E-34
2	1364	1401.658	1425.265	145.939	1.98E-35
5	1364	1408.356	1429.354	150.028	2.57E-36
3	1364	1412.317	1432.317	152.991	5.84E-37
1	1364	1697.556	1709.556	430.23	3.67E-97

Table C.3. F4 nocturnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	2035	1515.172	1545.172	0	0.000518
6	2035	1544.712	1568.712	23.54	4E-09
4	2035	1729.95	1755.95	210.778	8.8E-50
2	2035	1771.797	1791.797	246.625	1.45E-57
5	2035	1835.254	1860.325	315.153	1.9E-72
3	2035	1956.248	1976.325	431.153	1.23E-97
1	2035	2237.305	2249.305	704.133	6.5E-157

Table C.4. F7 nocturnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
6	1739	1169.001	1199.001	0	0.000791
7	1739	1177.285	1201.285	2.284	0.000252
4	1739	1296.092	1322.092	123.091	1.48E-30
2	1739	1313.933	1333.933	134.932	3.96E-33
5	1739	1345.238	1373.658	174.657	9.37E-42
3	1739	1384.658	1412.235	213.234	3.93E-50
1	1739	1803.572	1815.572	616.571	1E-137

Table C.5. M2 nocturnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
6	1568	1754.042	1784.042	0	0.001885
7	1568	1760.187	1784.187	0.145	0.001753
5	1568	1779.256	1802.647	18.605	1.72E-07
4	1568	1818.235	1846.256	62.214	5.83E-17
2	1568	1911.501	1923.501	139.459	9.82E-34
3	1568	1905.581	1931.581	147.539	1.73E-35
1	1568	1926.522	1946.522	162.48	9.85E-39

Table C.6. M3 nocturnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	1754	1896.041	1926.041	0	0.001235
6	1754	1908.382	1932.382	6.341	5.18E-05
5	1754	1939.354	1968.256	42.215	8.41E-13
4	1754	1963.548	1996.235	70.194	7.07E-19
2	1754	2033.318	2045.318	119.277	1.55E-29
1	1754	2156.706	2182.706	256.665	2.28E-59
3	1754	2221.232	2241.232	315.191	4.45E-72

Table C.7. M4 nocturnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	2098	2204.055	2234.055	0	0.000661
6	2098	2238.138	2262.138	28.083	5.28E-10
4	2098	2357.514	2383.514	149.459	2.32E-36
2	2098	2394.603	2414.603	180.548	4.12E-43
5	2098	2408.286	2435.235	201.18	1.36E-47
1	2098	2689.256	2708.325	474.27	6.8E-107
3	2098	2700.578	2712.578	478.523	8.1E-108

Table C.8. M5 nocturnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	2042	1973.629	2003.629	0	0.000816
6	2042	1985.873	2009.873	6.244	3.59E-05
4	2042	2085.254	2113.354	109.725	1.22E-27
2	2042	2142.986	2175.325	171.696	4.25E-41
5	2042	2218.095	2244.095	240.466	4.95E-56
3	2042	2240.245	2260.245	256.616	1.54E-59
1	2042	2433.035	2445.035	441.406	1.2E-99

Table C.9. M6 nocturnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	1918	2147.538	2177.538	0	0.000895
6	1918	2290.734	2224.026	46.488	7.19E-14
4	1918	2296.839	2322.839	145.301	2.51E-35
2	1918	2321.271	2341.271	163.733	2.5E-39
5	1918	2363.547	2387.256	209.718	2.58E-49
1	1918	2432.874	2451.356	273.818	3.11E-63
3	1918	2444.192	2456.192	278.654	2.77E-64

Table C.10. F2 diurnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
6	3699	3147.861	3171.861	0	0.000332
7	3699	3143.324	3173.324	1.463	0.00016
4	3699	3222.545	3248.545	76.684	7.39E-21
2	3699	3254.765	3274.015	102.154	2.18E-26
5	3699	3289.627	3312.834	140.973	8.1E-35
1	3699	4442.658	4458.657	1286.796	1.2E-283
3	3699	4567.874	4579.874	1408.013	0

Table C.11. F3 diurnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	3659	3359.226	3389.226	0	0.000479
6	3659	3395.727	3419.727	30.501	1.14E-10
4	3659	3459.838	3485.838	96.612	5.03E-25
5	3659	3507.206	3527.206	137.98	5.23E-34
3	3659	3625.547	3654.257	265.031	1.35E-61
2	3659	3738.518	3765.279	376.053	1.05E-85
1	3659	4558.263	4570.263	1181.037	1.7E-260

Table C.12. F4 diurnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	3944	3477.719	3507.719	0	0.000498
6	3944	3534.24	3558.24	50.521	5.32E-15
4	3944	3627.324	3653.324	145.605	1.2E-35
2	3944	3637.335	3657.335	149.616	1.61E-36
5	3944	3642.549	3669.475	161.756	3.73E-39
3	3944	3667.486	3687.891	180.172	3.74E-43
1	3944	4818.006	4830.006	1322.287	3.7E-291

Table C.13. F7 diurnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	3286	2328.467	2358.467	0	0.000564
6	3286	2348.876	2372.876	14.409	4.19E-07
4	3286	2413.88	2439.88	81.413	1.18E-21
2	3286	2424.576	2444.576	86.109	1.13E-22
5	3286	2465.429	2489.548	131.081	1.94E-32
3	3286	2479.548	2502.986	144.519	2.34E-35
1	3286	3661.376	3673.376	1314.909	1.7E-289

Table C.14. M2 diurnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	3568	4150.429	4180.429	0	0.000893
6	3568	4211.41	4235.41	54.981	1.03E-15
2	3568	4255.247	4281.247	100.818	1.14E-25
4	3568	4363.851	4383.851	203.422	6E-48
3	3568	4372.568	4395.245	214.816	2.02E-50
5	3568	4373.568	4398.586	218.157	3.79E-51
1	3568	4495.583	4507.583	327.154	8.14E-75

Table C.15. M3 diurnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	3490	4162.243	4192.243	0	0.001208
6	3490	4176.715	4200.715	8.472	1.75E-05
4	3490	420.457	4229.568	37.325	9.49E-12
2	3490	4269.412	4286.675	94.432	3.77E-24
5	3490	4293.833	4319.833	127.59	2.38E-31
3	3490	4352.725	4372.725	180.482	7.78E-43
1	3490	4559.757	4571.757	379.514	4.7E-86

Table C.16. M4 diurnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	3968	3541.379	3571.379	0	0.000325
4	3968	3604.597	3628.597	57.218	1.22E-16
6	3968	3637.307	3663.307	91.928	3.55E-24
2	3968	3762.019	3782.019	210.64	5.92E-50
5	3968	3839.761	3865.564	294.185	4.27E-68
1	3968	4743.579	4767.457	1196.078	6.1E-264
3	3968	4784.957	4796.957	1225.578	2.4E-270

Table C.17. M5 diurnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	3933	3977.704	4009.704	0	0.000705
6	3933	4004.731	4030.731	21.027	1.91E-08
4	3933	4115.193	4143.193	133.489	7.26E-33
2	3933	4145.853	4167.853	158.149	3.21E-38
5	3933	4147.265	4175.691	165.987	6.37E-40
3	3933	4154.297	4186.658	176.954	2.65E-42
1	3933	4761.33	4773.33	763.626	1.1E-169

Table C.18. M6 diurnal model ranked with Akaike's Information Criteria, the difference from top AIC model (ΔAIC), and model weights (w_i).

Model	N	-2LL	AIC	ΔAIC	w_i
7	1918	2147.538	2177.538	0	0.000895
6	1918	2290.734	2224.026	46.488	7.19E-14
4	1918	2296.839	2322.839	145.301	2.51E-35
2	1918	2321.271	2341.271	163.733	2.5E-39
5	1918	2363.547	2387.256	209.718	2.58E-49
1	1918	2432.874	2451.356	273.818	3.11E-63
3	1918	2444.192	2456.192	278.654	2.77E-64