

**WILD UNGULATE IMPACTS ON RANGLANDS AND ACROSS MANAGED
LANDSCAPES IN THE HAWAIIAN ISLANDS**

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF
HAWAII AT MĀNOA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL MANAGEMENT
May 2025

By
Lauren S. Katayama

Thesis Committee:
Melissa R. Price, Chairperson
Kirsten Oleson
Karen Steensma
Clay Trauernicht

Keywords: agriculture, forage, invasive species, feral pigs, *Sus scrofa*, axis deer, feral goats,
mouflon sheep

Acknowledgements

I would like to express my deepest gratitude to the following people and organizations who made this research possible. Thank you to Dr. Melissa R. Price for your expert guidance, mentorship, and support in both my undergraduate and graduate school journey, I would not be where I am today without you. Thank you to Derek R. Risch for the countless hours of discussion and advice from the beginning to end of this research, including the design and analysis. Thank you to my committee member Prof. Karen Steensma for setting up the foundations for this project, including building bridges between conservation and agriculture. Thank you to committee member Dr. Clay Trauernicht for your expertise in modeling and shaping my analysis. Thank you to committee member Dr. Kirsten Oleson for your insight and supporting my research.

This research would not have been possible without the funding of the U.S. Department of Agriculture (USDA) Western Sustainable Agriculture Research (WSARE), thank you for your support. Thank you to the project advisors Kristin Mack Almasin, Carolyn L.W. Auwelo, Kyle Caires, Maika‘ike English, Greg Friel, Jordan Jokiel, Lani Cran Petrie, Stephanie A. Shwiff, Jason Omick, and Mark Thorne who have all set the groundwork and contributed greatly to my research. A special thanks to Maika‘ike and Noriko English, Brissa Christophersen, Kūākea Yasak, Lani Cran Petrie, Bill Petrie, and Alex Petrie for hosting and taking care of my assistants and I. Thank you to Mark Thorne and Kyle Caires for helping with setting up the facilities for my research and for processing forage samples. A special thanks to the four ranches and all the ranch partners for collaborating with us and allowing us to collect data!

I am grateful to everyone in the Hawai‘i Wildlife Ecology lab for helping me throughout my academic career. I am especially grateful to my research assistants who have made the

collection of this data possible. Thank you to Wade Naguwa, Koa Grabar, and Hudson Shaw for traveling with me and spending long exhausting but fun days away from home! I would also like to thank Robert Tada and Kaylee Lopes for their hard work in the field collecting data.

A special thank you goes to my mom, dad, and sister, I truly would not be able to be successful without all your constant encouragement, patience, and laughter when I needed it. Thank you to my friends for your support and especially to Dawson for caring for me in some of the most stressful moments in my life.

Abstract

Invasive wild ungulates pose significant ecological and economic challenges worldwide, particularly in island ecosystems where the absence of large predators exacerbates their impacts. Across the Hawaiian Islands, wild ungulates such as axis deer (*Axis axis*), mouflon sheep (*Ovis musimon*), feral goats (*Capra hircus*), and wild pigs (*Sus scrofa*) contribute to overgrazing, habitat degradation, and impacts to agricultural production. While their effects on native ecosystems are well-documented, less is known about their influence on forage availability in ranchlands and how their distribution aligns with land management designations. This thesis examined the relationship between wild ungulate abundance, forage availability, and land-use classifications across the Hawaiian Islands. We investigated how wild ungulate presence affects forage loss and plant community composition using game cameras, exclusion cages, and vegetation surveys. Results indicate that while elevation is the primary driver of forage availability, wild ungulate detections were associated with reduced vegetation biomass at many sites, consistent with rancher concerns regarding overgrazing by wild ungulates. We analyzed predicted wild ungulate abundance across Sensitive Conservation Areas, Priority Hunting Areas, and Other Areas. Findings suggested that on the islands of Hawai‘i and Maui, wild pigs and mouflon sheep are more abundant in conservation lands, while axis deer are more prevalent in agricultural and private lands, highlighting key areas for management intervention. These findings provide insights into the ecological impacts of wild ungulates on ranchlands and conservation areas, emphasizing the need for targeted, landscape-scale management strategies for invasive wild ungulates that achieve biodiversity conservation and sustainable agriculture goals.

Table of Contents

Acknowledgements	i
Abstract	iii
Table of Contents	iv
List of Tables	v
List of Figures	vi
Chapter 1: Introduction	1
Chapter 2	3
Abstract	3
Introduction	4
Methods	7
Results	14
Discussion	22
Chapter 3	28
Abstract	28
Introduction	29
Methods	32
Results	36
Discussion	41
Chapter 4: Conclusion	47
Literature Cited	54
Appendix: Detailed Data Tables	49

List of Tables

Table 2.1. Detections of wild ungulates on the island of Hawai‘i and Maui. On the island of Hawai‘i, detections include wild pigs, feral goats, mouflon sheep, and feral sheep, while on Maui, detections include wild pigs, feral goats, and axis deer. For each wild ungulate species, the table presents the number of sites where they were detected, the total number of photos, the number of episodes (defined as a sequence of photos captured within a one-minute time span), and the maximum group size observed in a single photo.....	15
Table 2.2. Summary of linear mixed-effects model results for the effect of elevation (m) and rainfall (mm) on forage production (kg/ha) without exposure to wild ungulates (samples from inside exclusion cage) with random intercept for site. The top model was elevation (AICc = 1885.79 weight = 0.53), with other models showing less support ($\Delta\text{AICc} \geq 1.91$).....	16
Table 2.3. Summary of linear mixed-effects model results for the effect of elevation (m), rainfall (mm), and wild ungulate abundance ($\text{RAI}_{\text{grazing}}$) on forage production (kg/ha) with and without the exposure to wild ungulates (all samples from inside and outside exclusion cages) with random intercept for site. The top model was elevation (AICc = 3688.11, weight = 0.36) with the second model adding $\text{RAI}_{\text{grazing}}$ ($\Delta\text{AICc} = 0.51$, weight = 0.28) showing additional support as a predictor of forage production.	16
Table 2.4. Generalized linear model result of all possible combinations of $\text{RAI}_{\text{grazing}}$ (wild grazing ungulates detected: axis deer, mouflon sheep, feral goats) with predictor variables grass, forb, shrub, bare ground percent cover, and rainfall.....	20
Table 2.5. Summary of fixed effects from the linear mixed-effects model assessing predicted forage production (kg/ha) across wild ungulate species. The model includes “site” as a random effect. The reference category is forage samples collected inside exclusion cages with no wild ungulate exposure (“none”). Estimates represent the difference in predicted forage production relative to this baseline.....	21
Table 3.1. Land area designated by Sensitive Conservation Areas, Priority Hunting Areas, and All Other Areas regarding wild ungulates on the islands of Hawai‘i, Kaua‘i, Maui, and ‘Oahu.....	39

List of Figures

Figure 2.1. Wild ungulate species across the Hawaiian Islands and timeline of historical introductions from Shwiff et al. 2024. All wild ungulates are introduced and have become invasive in Hawai‘i with no natural predators besides humans (Duffy & Lepczyk, 2021).....6

Figure 2.2. Study locations on the islands of Hawai‘i (left) and Maui (right). Areas are generalized by *moku* (historic Hawaiian land division roughly correlating to watersheds) from the Hawai‘i Statewide GIS Program layer “Moku” for the privacy of the ranches.....8

Figure 2.3. Example of a game camera (6) and grazing exclusion cage (3) arrangement at one site. Game cameras are set 50 meters apart on two imaginary transect lines while the grazing exclusion cages are set up on the outside and inside of the camera array.....10

Figure 2.4. The top left graph shows the top model for forage production from samples inside the exclusion cage plotted against elevation (Estimate = 0.44, $t = 2.08$, $p = 0.05$). The bottom left is the top model for all forage samples, where elevation is the sole fixed predictor of forage production (Estimate = 0.49, $t = 2.59$, $p = 0.01$). The bottom right graph displays the second-best model for all forage samples, illustrating forage production as a function of the relative abundance of wild grazing ungulates (RAI_{grazing}) (Estimate = -15.96, $t = -1.27$, $p = 0.21$).....17

Figure 2.5. Linear regression of average forage loss (kg/ha) (inside exclusion cage – outside exclusion cage) as a function of total wild ungulate relative abundance index (RAI), which includes wild pigs, feral goats, axis deer, and mouflon sheep across all sites on Hawai‘i Island and Maui (Intercept = 212.43, SE = 183.92; Slope = 17.79, SE = 15.49, $t = 1.15$, $R^2 = 0.04$), but a slight positive trend is observed.....18

Figure 2.6. Linear regressions of the average forage loss (kg/ha) (inside exclusion cage – outside exclusion cage) and the relative abundance index (RAI) of wild ungulates an estimation of the number of wild ungulates detected. The two top panels show the relationship for all detected wild ungulates, including wild pigs, feral goats, and mouflon sheep on the island of Hawai‘i (Intercept = 234.57, SE = 248.08; Slope = -50.44, SE = 30.47, $t = -1.66$, $R^2 = 0.17$) and wild pigs, feral goats, and axis deer on Maui (Intercept = 446.18, SE = 235.34; Slope = 25.41, SE = 16.77, $t = 1.52$, $R^2 = 0.17$). The bottom panels display species-specific relationships, with mouflon sheep on the island of Hawai‘i (Intercept = 352.35, SE = 376.84; Slope = -61.86, SE = 39.94, $t = -1.55$, $R^2 = 0.11$) and axis deer on Maui (Intercept = 451.57, SE = 231.78; Slope = 25.72, SE = 16.64, $t = 1.55$, $R^2 = 0.11$).....19

Figure 2.7. Predicted forage production (kg/ha) across wild ungulate species categories based on a linear mixed-effects model with "Site" as a random effect. Forage production was lowest in areas dominated by axis deer and feral goats when compared to forage production without exposure to wild ungulates (“none”) and highest in areas dominated by wild pigs and mouflon sheep. Error bars represent ± 1 standard error of the predicted means.....22

Figure 3.1. Maps of the island of Hawai‘i, Kaua‘i, Maui, and ‘Oahu. Maps on the left-hand side show designated categories of parcels, Sensitive Conservation Areas (blue), Priority Hunting Areas (yellow), and All Other Areas (dark grey) where wild ungulate management goals are variable or unknown. Tax map key (TMK) parcel boundaries are hidden for visual simplicity. Maps on the right-hand side show existing models of the relative abundance index (RAI) for that species of wild ungulate (Wild pig, feral goat, axis deer, or mouflon sheep) reprinted with permission from Risch et al., 2020, 2022, 2025, and in prep. Darker colors indicate higher predicted abundances of wild ungulates in natural conditions with no management.....38

Figure 3.2. Box plots of the predicted relative abundance index (RAI) of wild pigs on the island of Hawai‘i (n = 2,193), Maui (n = 622), O‘ahu (n = 684), and Kaua‘i (n = 306), within tax map key (TMK) land parcels categorized by general land management goals: Sensitive Conservation Areas (blue), Priority Hunting Areas (yellow), and All Other Areas (grey). ANOVA p-values are reported on each figure (significant p = <0.05).....40

Figure 3.3. Box plots of the predicted relative abundance index (RAI) of mouflon sheep on the island of Hawai‘i (n = 2,193), black-tailed deer on Kaua‘i (n = 306), and feral goats and axis deer on Maui (n = 622), within tax map key (TMK) land parcels categorized by general land management goals: Sensitive Conservation Areas (blue), Priority Hunting Areas (yellow), and All Other Areas (grey). Graphs are arranged clockwise from the top, starting with mouflon sheep on Hawai‘i, followed by black-tailed deer on Kaua‘i, and feral goats and axis deer on Maui. Silhouettes of each wild ungulate species are included to correspond with their respective graphs. ANOVA p-values are reported on each figure (significant p = <0.05).....41

Chapter 1: Introduction

Invasive wild ungulates pose significant ecological and economic challenges worldwide, but particularly in island ecosystems, with impacts on both native and agriculture lands (Kramer et al., 2006; Risch et al., 2022; Thinley et al., 2017; Widén et al., 2023). These species contribute to habitat alteration and biodiversity loss, resulting in cascading ecosystem effects. In Hawai‘i, ungulates such as axis deer (*Axis axis*), mouflon sheep (*Ovis musimon*), feral goats (*Capra hircus*), and wild pigs (*Sus scrofa*) are widespread, influencing both conservation areas and agricultural lands (Duffy & Lepczyk, 2021; Lepczyk & Duffy, 2019; Li, 2020). Overgrazing by these species reduces vegetation on the landscape, increases sediment runoff, and facilitates the spread of invasive plant species, ultimately threatening the sustainability of ranching and native ecosystems (Weller et al., 2011, 2018). Despite widespread recognition of these impacts, a key research gap remains in understanding how wild ungulates affect forage resources in ranchlands and how their distribution varies across different land-use classifications (Marchiori et al., 2012; Shwiff et al., 2024). Addressing these gaps is critical for informing management strategies that accounts for land managers goals to sustain Hawai‘i’s ecosystems.

Chapter 2 of this thesis examined the relationship between wild ungulate presence and forage availability across ranchlands on the island of Hawai‘i and Maui. Using a combination of game cameras, grazing exclusion cages, and vegetation surveys, this study quantified how wild ungulate activity correlates with changes in plant biomass and identified key environmental drivers that influence forage availability. By assessing wild ungulate preferences in plant communities and determining whether their presence significantly reduces forage, this chapter provides insight into how ungulates affect the sustainability of ranching operations.

Beyond direct impacts on vegetation, understanding how wild ungulates are distributed across different land-use designations is critical for effective management. Land parcels in Hawai‘i are designated and managed for various purposes, including conservation and hunting with different management priorities. While conservation areas aim to protect native ecosystems, hunting areas are managed to allow persistence of game animal populations. Chapter 3 evaluated predicted wild ungulate abundance across different land management classifications using spatial models from Risch et al. 2020, 2022, and 2025 with GIS layers from the Hawai‘i Statewide GIS Program. By analyzing wild distribution in relation to land-use designations, this chapter identified areas where these species are most abundant under unmanaged conditions and assessed whether “Sensitive Conservation Areas”, “Priority Hunting Areas”, or “All Other Areas” are disproportionately impacted. Statistical analyses compared predicted abundance across land types, revealing patterns that can inform targeted management strategies, such as fencing and removal. Together, these findings offer a comprehensive understanding of how wild ungulates interact with both vegetation availability and land-use designations, providing valuable information for managers.

Chapter 2

Wild Ungulate Impacts on Ranchlands in the Hawaiian Islands

Abstract

Invasive wild ungulates pose significant global concerns due to their impact on ecosystem functions and competition with native species. Many island systems lack large native predators to control wild ungulate populations, which intensifies these adverse effects, particularly on agricultural lands. Across the Hawaiian Islands, approximately one million acres of ranchland are dedicated to beef production, yet the overabundance of axis deer (*Axis axis*), mouflon sheep (*Ovis musimon*), and feral goats (*Capra hircus*) has led to overgrazing, increased sediment runoff, the proliferation of invasive plants, and declining ecosystem health—threatening the sustainability of generational ranching. This study examined the relationship between the abundance of wild ungulates and the availability of forage on ranchlands across the islands of Hawai‘i and Maui. Additionally, we assessed wild ungulate preferences in plant community composition. We employed game cameras, grazing exclusion cages, and line-transect sampling to measure wild ungulate detections, vegetation loss, and plant community composition. Elevation emerged as the primary environmental driver describing the availability of forage both with (AICc = 1885.8, weight = 0.53) and without wild ungulate presence (AICc = 3688.11, weight = 0.36), with models including grazing ungulates as a comparable alternative (Δ AICc = 0.51, weight = 0.28). While higher wild ungulate detections were associated with reduced plant biomass, the relationship was not statistically significant ($p = 0.26$). Wild ungulates were detected across all plant community types, consistent with their generalist and highly adaptable nature. Although wild ungulate presence was not the top predictive model, vegetation loss was recorded at 66% of study sites, aligning with recent reports from ranchers. These findings underscore the ecological impact of wild ungulates on forage resources, highlight

their widespread expansion across ranchlands, and emphasize the need for site-specific management strategies to mitigate their effects.

Introduction

Invasive wild ungulates negatively impact native ecosystems and agricultural lands (Kardol et al., 2014; Leopold & Hess, 2017; Shwiff et al., 2024; Valente et al., 2020; Widén et al., 2023), but how these impacts translate into the loss of vegetative biomass remains less understood. Across many ecosystems, invasive ungulates cause widespread damage through their feeding behaviors, trampling, and other disturbances, but quantifying these effects in terms of vegetation biomass and forage loss remains challenging (Myserud, 2006; Rong et al., 2014; Wiesmair et al., 2017). For agricultural lands, the consequences are equally dire, as invasive ungulates often consume or destroy crops, reduce the availability of forage for livestock, and degrade land productivity (Francesco et al., 2019; Marchiori et al., 2012; Valente et al., 2020; Widén et al., 2022, 2023). Globally, the presence of invasive ungulates has led to economic losses and increased costs for land management and restoration (Drimaj et al., 2023; Gordon et al., 2004; Khattak et al., 2022; Sorensen et al., 2015). Quantifying these effects is critical for understanding the scale of the problem and for designing targeted management strategies to mitigate their impacts.

Island ecosystems are highly vulnerable to the impacts of invasive ungulates due to their evolutionary isolation and the presence of species that lack adaptations to grazing pressure (Fritts & Rodda, 1998; Reaser et al., 2007; Vourc'h et al., 2001; Yelenik, 2018). In places like the Hawaiian Islands and Galápagos Islands, invasive ungulates have dramatically altered native plant communities, often favoring the spread of invasive plants and resulting in potentially

irreversible changes to the landscape (Cruz et al., 2009; Duffy & Lepczyk, 2021). Impacts include overgrazing (Leopold & Hess, 2017), altering plant species composition (Banko et al., 2013; DiTomaso et al., 2010), and causing soil erosion (Cole & Litton, 2014; Spear & Chown, 2009). This loss of ground cover prevents rainwater catchment within watersheds (Dunkell et al., 2011) and runoff leads to sedimentation of coral reefs, harming coastal health (Strauch et al., 2016).

In the Hawaiian Islands, ungulates were introduced over several centuries, with some species brought as livestock and others for game purposes (Duffy & Lepczyk, 2021; Hess, 2016; Tomich, 1986). With no natural predators except humans, these populations have proliferated in the warm climate of these semi-tropical islands (Sinclair, 2023), causing significant harm to native habitats and agricultural lands (Hess et al., 1999; Shwiff et al., 2024; Weller et al., 2011). While the ecological impacts of wild ungulates have been well documented, their effects on agricultural lands remain understudied in the Hawaiian Islands (Li, 2020). In particular, few studies have quantified the extent of forage loss attributable to wild ungulates in the Hawaiian Islands, leaving significant gaps in our ability to predict and manage these impacts.

Ranchlands in the Hawaiian Islands provide an ideal system to explore these relationships. Across the Hawaiian islands, 20% (765,579 acres) of land is dedicated to ranching (Perroy & Collier, 2020). Ranching has been culturally significant since the introduction of the *paniolo* (Hawaiian cowboy) tradition in the 1800s and continues to be a generational livelihood (Spickard, 2000). The sustainable management of cattle on these lands is essential for grassland management, watershed protection, and food security (Bremer et al., 2021). However, even with practices like rotational grazing and intensive water management, wild ungulates have reportedly degraded managed grasslands, forcing ranchers to reduce their livestock by 25–30% (pers.

comm. Greg Friel and Kristin Mack-Almasin). This dual impact on ecosystems and ranch operations underscores the urgent need for solutions. In this study, we investigated the relationship between wild ungulate relative abundance and forage loss on ranchlands on the islands of Hawai‘i and Maui, focusing on vegetation biomass and cover by species. We addressed the following questions: (1a) Which environmental drivers, such as rainfall and elevation, influence forage production on ranchlands with and without wild ungulate grazing? (1b) If wild ungulates have an influence on forage production, what is the direct relationship to forage loss? (2) Does the vegetation cover composition influence the predicted abundance of wild ungulates on ranchlands?

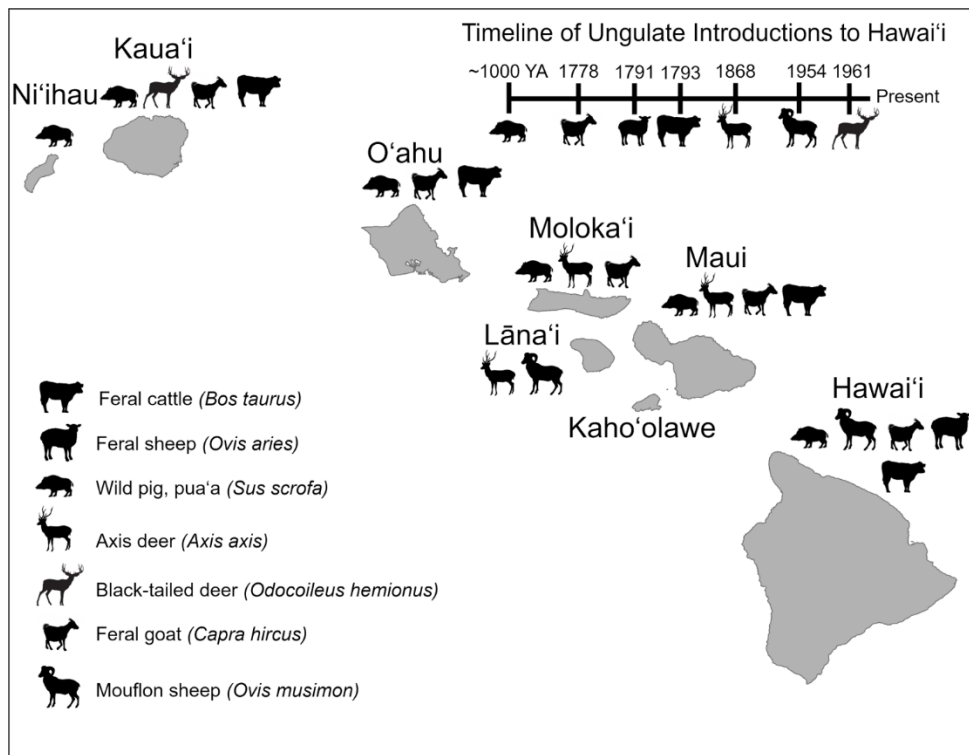


Figure 2.1. Wild ungulate species across the Hawaiian Islands and timeline of historical introductions from Shwiff et al. 2024. All wild ungulates are introduced and have become invasive in Hawai‘i with no natural predators besides humans (Duffy & Lepczyk, 2021).

Methods

Study Area. A variety of ungulates have been introduced across the Hawaiian Islands, with multiple species present on the two islands included in this study: Hawai‘i and Maui. On the island of Hawai‘i, wild pigs (pua‘a; *Sus scrofa*), mouflon sheep (*Ovis musimon*), feral sheep (*Ovis aries*), and feral goats (*Capra hircus*) have naturalized populations (Duffy & Lepczyk, 2021). The island of Maui hosts populations of wild pigs, axis deer (*Axis axis*), and feral goats (Figure 1). Wild pigs are commonly found in multiple ecosystems and are drawn to areas with supplemental food resources or fruiting trees, and are generalist feeders (Eisenberg 1981; Nogueira-Filho et al. 2009; Risch et al. 2022). On the island of Hawai‘i, wild pigs are commonly found in native forests and grasslands (Nogueira-Filho et al., 2009; Stone, 1985); on Maui, they are concentrated in mid- to high-elevation forested areas (Risch et al., 2020). In grassland regions of Hawai‘i Volcanoes National Park, grasses account for 50% of their diet (Baker, 1975). Feral goats are grazers and browsers depending on the availability of forage (Chynoweth et al., 2013). On both islands, feral goats are often found in dry lowland areas that are sparsely vegetated and range from coastal to sub-alpine areas (Chynoweth et al., 2013; Risch et al., 2022). On the island of Hawai‘i, mouflon sheep are concentrated around Mauna Kea and extend into the northern slopes of Mauna Loa (Ikagawa, 2013b; Judge et al., 2017a). Ikagawa (2013) estimated that mouflon occupy an area of 3,640 km², ranging from 550 meters in elevation to the summit of Mauna Kea (~3,660 meters). Axis deer on Maui are found in mid- to low-elevation shrublands and agricultural lands, with their range often overlapping with ranchlands (Risch et al., 2020). A survey conducted between late 2021 and early 2022 estimated a population of 46,743 axis deer, occupying 32% by area and occurring up to an elevation of 2,150 meters (Hess et al., 2022).

Site locations. Four ranches agreed to host study sites, two on the island of Hawai‘i and two on Maui, representing 47% of the total ranching area on the island of Hawai‘i and 42% of the total ranching area on Maui (Perroy & Collier, 2020). On the island of Hawai‘i, Ranch A is located on the southeastern slope of the island. Ranch A consists of 29,000 acres of ranch land from sea level up to 5,000 ft and is part of a Cooperative Game Management Area (CGMA) which is a lease agreement with the State of Hawai‘i Department of Land and Natural Resources (DLNR). Ranch A receives around 1,500 mm of annual rainfall. Ranch B is located in Waimea on the northern region of the island of Hawai‘i. Ranch B consists of around 230,000 acres spanning from 2,000 to 8,000 feet above sea level and receives around 760 mm of annual rainfall. On Maui, Ranch C is located upcountry on the leeward slope of the Haleakalā volcano. This ranch consists of around 30,000 acres of land that range from sea level up to around 4,000 ft in elevation and annual rainfall spans from 430 mm to 4,750 mm. Ranch D is also located on the leeward slopes of Haleakalā. Ranch D contains around 18,000 acres of land, some of which are leased from the State of Hawai‘i and private owners. Ranch D has an average annual rainfall of 890 mm.

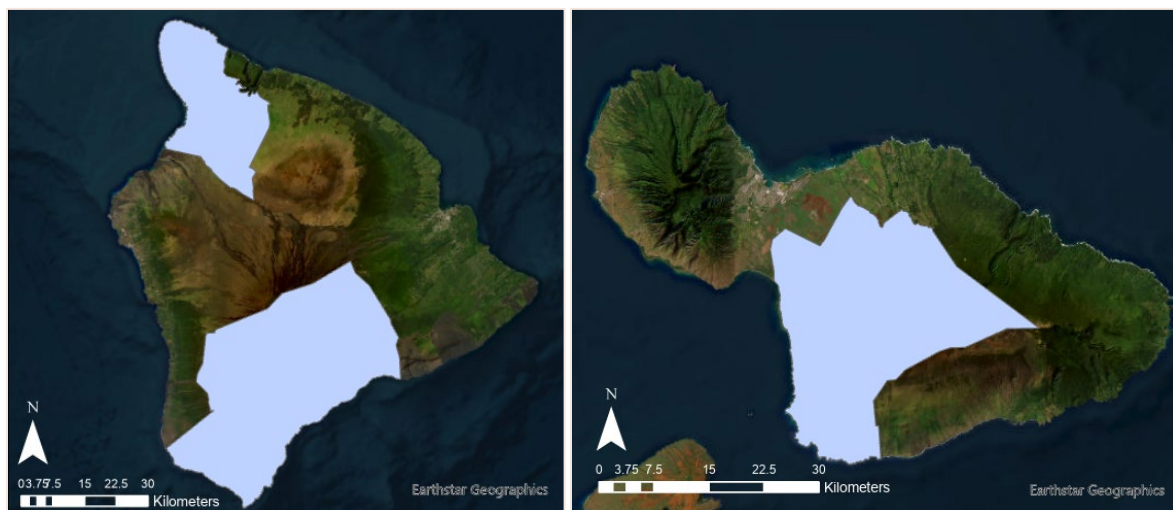


Figure 2.2. Study locations on the islands of Hawai‘i (left) and Maui (right). Areas are generalized by *moku* (historic Hawaiian land division roughly correlating to watersheds) from the Hawai‘i Statewide GIS Program layer “Moku” for the privacy of the ranches.

Site selection. Survey locations were selected in coordination with the ranch managers in areas where managed livestock had been rotated out or were absent and where wild ungulates had been previously sighted. Survey points were then randomly selected within the parcel at a minimum of 100 meters apart. Due to accessibility considerations, points were in proximity to access roads. Research equipment (described below) was in the field for a minimum duration of thirteen days to minimize interference with rotational grazing operations.

Wild Ungulate Detections. The following methods to capture the relative abundance index (RAI) for wild ungulates were derived from Risch et al. (2022). Each experimental plot consisted of six motion-activated game cameras (Bushnell Trophy Cams, Bushnell, Overland Park, KS) to detect wild ungulate activity. Cameras were arranged in a rectangular grid (two lines of three cameras), spaced 50 meters apart (Figure 2). Cameras were mounted onto nearby tree trunks when available or attached to t-posts anchored in the ground. To maximize the likelihood of detecting ungulates when they were in the area, cameras were angled toward areas with visible trails, tracks, or signs of damage. Cameras were set to take two consecutive photos after being triggered and then reset after three seconds.

Photos were organized by ranch site, point, and camera. The object detection model MegaDetector (Microsoft, 2020) was used in conjunction with Timelapse (<https://saul.cpsc.ucalgary.ca/timelapse/>) to identify photos with animals (Celis et al., 2024; Fennell et al., 2022; Leorna & Brinkman, 2022). Photo-viewing software Timelapse was used in conjunction with MegaDetector to manually classify animals by species. In Timelapse, an episode is defined as a sequence of images captured within a specified time span, representing an event such as animal movement through the area. For this study, episodes were generated using a one-minute time threshold. The total number of individual animals within each episode was

recorded and used to quantify relative abundance metrics. The highest number of individuals recorded within an episode was divided by the number of camera trap nights to calculate the relative abundance index (RAI) (O'Brien et al., 2003; Palmer et al., 2018).

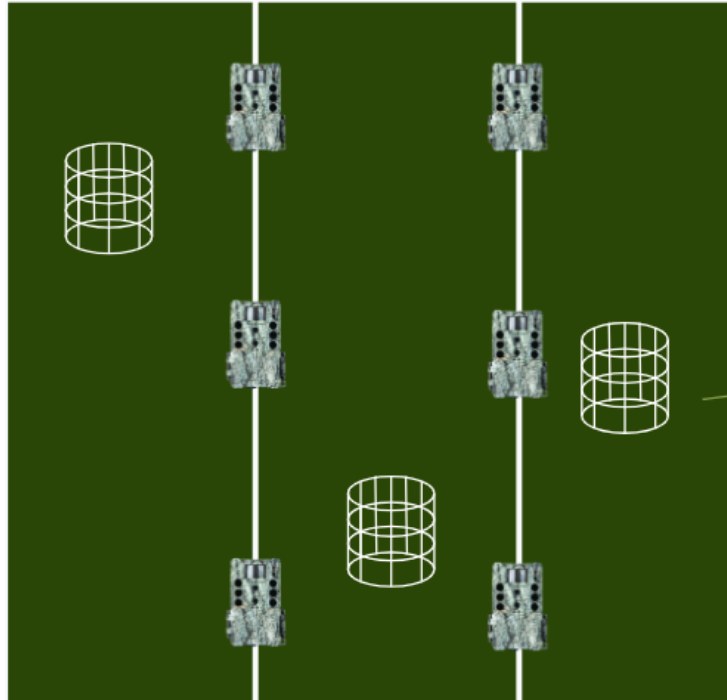


Figure 2.3. Example of a game camera (6) and grazing exclusion cage (3) arrangement at one site. Game cameras are set 50 meters apart on two imaginary transect lines while the grazing exclusion cages are set up on the outside and inside of the camera array.

Grazing/biomass. Vegetation utilization by wild ungulates was quantified by comparing grazed areas (outside exclusion cages) to ungrazed areas (inside exclusion cages) (Bonham et al., 2004; Klingman et al., 1943). Three individual one m² grazing exclusion cages were randomly placed along three transects: two outside the camera array and one within the array, at the start of each monitoring period. These exclusion cages remained in place for the duration of the game camera monitoring. Rainfall at each point was measured using rain gauges placed at one of the point's exclusion cages and measured at the end of the monitoring period.

Forage biomass samples were collected from inside and outside the exclusion cages following methods adapted from Thorne and Stevenson (2007). A 0.22 m² (1.67 m

circumference) sampling hoop was randomly placed near each exclusion cage to collect samples from outside exclusion cages, and samples from inside exclusion cages were collected from the center of the exclusion cage. Both the exclusion cages and sampling hoops were positioned in areas with grassier vegetation or in areas representative of the predominant vegetation.

Vegetation biomass was measured by clipping live vegetation at ground level within the hoop and weighing it in a paper bag using a spring scale to determine the mass of fresh vegetation.

One sample was collected at the beginning of the survey period prior to placing cages, and at the end of the survey period three samples were collected from inside the exclusion cages and three from outside. To determine dry weight values, the vegetation samples were oven-dried at 65°C for three days and then reweighed at facilities on each respective island. The dry weight measurements were converted to pounds per acre using hoop size conversion (dry weight grams x 40 = lbs/acre), and then to kilograms per hectare to estimate the average available forage production. Wild ungulate grazing pressure was calculated by determining the average difference in forage biomass (kg/hectare) between the inside and outside samples of each grazing exclusion cage at each point. All values were averaged at each point. The initial samples collected were compared to samples at the end of the survey to ensure the forage collection was within a reasonable range for data integrity.

Plant Cover. At the start of the wild ungulate monitoring period, the line-point intercept method was conducted to assess ground cover. Three 100-meter transects were placed on the outsides and middle of the game camera array using a tape measure and at every meter, a pin was utilized to record the species at each intercept (100 points per transect) (Bonham et al., 2004; Elzinga et al., 1999). At every point, the number of detections of each species on a transect was averaged and converted into a percent cover and percent composition of foliar cover by species.

Each plant species was categorized by grass, forb, shrub, litter, or bare ground. Litter refers to dried and dead plant material, while bare ground is defined as any surface lacking plant cover, such as exposed soil or rock. Species were identified in the field using iNaturalist and confirmed using the Hawai‘i Range & Pasture Field Identification Guide and Weeds of Hawai‘i’s Pastures and Natural Areas when possible (CTAHR: *Weeds of Hawaii’s Pastures and Natural Areas; An Identification and Management Guide*, n.d.; *Hawaii/Pacific Islands Area | Field Office Technical Guide | NRCS - USDA*, n.d.; *iNaturalist*, 2024). For each transect, the elevation and compass direction were recorded.

Analysis. As wild ungulate community composition varies by island and location (Duffy & Lepczyk, 2021; Tomich, 1986), we grouped ungulates for analysis by either “all ungulates” or “grazing ungulates” for subsequent analyses; if the number of detections of a wild ungulate species was adequate, we also ran individual models for each species.

The following analyses were conducted in R 4.1.1 (R Core Development Team, 2021). A linear mixed-effects model was implemented using the *lme4* package to assess the relationship between forage samples inside the exclusion cage (kg/ha) and the fixed effects of rainfall and elevation, with site included as a random effect. To identify the best-fit model among all possible combinations, the *MuMIn* package was used to rank models based on Akaike’s Information Criterion (AIC) (Bartoń, 2023). The same approach was applied to examine the relationship between forage samples inside and outside the exclusion cage (kg/ha), with fixed effects of wild grazing ungulates RAI (feral goats, feral sheep, axis deer, and mouflon sheep), rainfall, and elevation, and site as a random effect. Forage samples inside the exclusion cage were assigned an RAI of zero, as they represent forage availability without exposure to wild ungulates.

To further assess wild ungulate relationships with forage availability, a linear regression analysis was conducted using the *stats* package to examine the relationship between average forage biomass loss (kg/ha) and RAI, including all wild ungulate species detected across islands (wild pigs, feral goats, axis deer, feral sheep, and mouflon sheep).

To evaluate the relationship between grazing wild ungulates RAI and percent cover of grass, forb, shrub, litter, bare ground, and rainfall, a Generalized Linear Model (GLM) framework was used. Model selection was performed using the *glmulti* package which automated model selection based on AIC values and Akaike's weights (Calcagno & de Mazancourt, 2010).

To assess the relationship between forage production and the presence of wild ungulate species, a linear mixed-effects model was fit using the *nlme* package. Forage production (kg/ha) was the response variable, and the dominant wild ungulate species was included as a fixed categorical predictor. Species categories included axis deer, feral goats, mouflon sheep, wild pigs, and a "none" category representing the forage samples without wild ungulate exposure (inside the exclusion cage). For each forage sample collected outside an exclusion cage, the wild ungulate species with the highest RAI at the corresponding site was assigned as the dominant species. The "none" category consisted of forage samples collected from within exclusion cages, which were not exposed to wild ungulates. To account for variation among sampling locations, "site" was included as a random effect. Model predictions were visualized using *ggplot2*, and standard errors were calculated from the variance-covariance matrix of the fixed effects to generate 95% confidence intervals.

Results

Surveys were conducted from June 2023 to March 2024. In 2023, a total of 17 sites were surveyed: 5 on Hawai'i Island and 12 on Maui. In 2024, 18 sites were surveyed: 10 on Hawai'i Island and 8 on Maui. In total, 15 sites on Hawai'i island and 20 sites on Maui were surveyed. Three sites at Ranch D were retrieved after the 13-day period due to the catastrophic fires that began on Maui on August 8, 2023; these sites were not affected by the fires. Additionally, two study sites were established in fire-affected areas at Ranch C following a wildfire event.

On the island of Hawai'i where there are populations of wild pigs, mouflon sheep, feral sheep, and feral goats we detected all species except the feral sheep. Wild pigs were detected at 73% of the sites ($n = 11$), with 368 photos captured, 50 episodes recorded, and a maximum group size of 3 individuals. mouflon sheep were also detected at 73% of the sites ($n = 11$), with 11,190 photos, 1,516 episodes, and a maximum group size of 52 individuals, the highest recorded species detected on the island of Hawai'i. Feral goats were expected to be seen at 27% of sites ($n = 4$) based on distribution models but were only detected at 13% of sites ($n = 2$), with a total of 92 photos taken, 5 episodes, and a maximum group size of 15 individuals.

On Maui, all expected wild ungulates were detected including wild pigs, feral goats, and axis deer. Wild pigs were detected at 75% of the sites ($n = 15$), with 3,336 photos, 176 episodes, and a maximum group size of seven individuals. Feral goats were found at 5% ($n = 1$) of the sites, consistent with expectations based on species distribution models, resulting in 1,622 photos, 179 episodes, with a maximum group size of 6. Axis deer were detected at 95% of the sites ($n = 19$), generating a substantial 92,152 photos. There were 4,637 episodes recorded and the maximum group size for axis deer was 127 individuals, the highest recorded across all sites.

Table 2.1. Detections of wild ungulates on the island of Hawai‘i and Maui. On the island of Hawai‘i, detections include wild pigs, feral goats, mouflon sheep, and feral sheep, while on Maui, detections include wild pigs, feral goats, and axis deer. For each wild ungulate species, the table presents the number of sites where they were detected, the total number of photos, the number of episodes (defined as a sequence of photos captured within a one-minute time span), and the maximum group size observed in a single photo.

Island	Common Name	Scientific Name	# of Sites (%)	# of Photos	Episodes	Max Group Size
Hawai'i	Wild Pig	<i>Sus scrofa</i>	11 (73%)	368	50	3
	Feral Goat	<i>Capra hircuws</i>	2 (13%)	92	5	15
	Mouflon Sheep	<i>Ovis musimon</i>	11 (73%)	11190	1516	52
	Feral Sheep	<i>Ovis aries</i>	0 (0%)	0	0	0
Maui	Wild Pig	<i>Sus scrofa</i>	15 (75%)	3336	176	7
	Feral Goat	<i>Capra hircuws</i>	1 (5%)	1622	179	6
	Axis Deer	<i>Axis axis</i>	19 (95%)	92152	4637	127

A linear mixed-effects model was fitted to assess the effects of elevation (m) and rainfall (mm) on forage production (kg/ha) for samples collected from inside exclusion cages (i.e., without exposure to wild ungulates), with site included as a random intercept. Model selection revealed that the top model included only elevation (m) as a fixed effect, with site as a random effect (Table 2; AICc = 1885.79 weight = 0.53), while models incorporating rainfall received less support ($\Delta\text{AICc} \geq 1.91$). The following linear mixed-effects model evaluated the effects of elevation (m), rainfall (mm), and wild ungulate abundance ($\text{RAI}_{\text{grazing}}$) on forage production (kg/ha) across all samples, including those from both inside and outside exclusion cages. Elevation was identified as the strongest predictor of forage production through model selection (Table 3; AICc = 3688.11, weight = 0.36). The second-best model, which included both elevation and $\text{RAI}_{\text{grazing}}$, received similar support (Table 3; $\Delta\text{AICc} = 0.51$, weight = 0.28).

Table 2.2. Summary of linear mixed-effects model results for the effect of elevation (m) and rainfall (mm) on forage production (kg/ha) without exposure to wild ungulates (samples from inside exclusion cage) with random intercept for site. The top model was elevation (AICc = 1885.79 weight = 0.53), with other models showing less support ($\Delta\text{AICc} \geq 1.91$).

Model	AICc	delta	weight
Forage ~ Elevation + (1 Site)	1885.79	0.00	0.53
Forage ~ 1 + (1 Site)	1887.70	1.91	0.20
Forage ~ Elevation + Rainfall + (1 Site)	1888.00	2.21	0.18
Forage ~ Rainfall + (1 Site)	1889.44	3.65	0.09

Table 2.3. Summary of linear mixed-effects model results for the effect of elevation (m), rainfall (mm), and wild ungulate abundance ($\text{RAI}_{\text{grazing}}$) on forage production (kg/ha) with and without the exposure to wild ungulates (all samples from inside and outside exclusion cages) with random intercept for site. The top model was elevation (AICc = 3688.11, weight = 0.36) with the second model adding $\text{RAI}_{\text{grazing}}$ ($\Delta\text{AICc} = 0.51$, weight = 0.28) showing additional support as a predictor of forage production.

Model	AICc	delta	weight
Forage ~ Elevation + (1 Site)	3688.11	0.00	0.36
Forage ~ Elevation + $\text{RAI}_{\text{grazing}}$ + (1 Site)	3688.62	0.51	0.28
Forage ~ Elevation + Rainfall + (1 Site)	3690.04	1.93	0.14
Forage ~ Elevation + $\text{RAI}_{\text{grazing}}$ + Rainfall + (1 Site)	3690.52	2.42	0.11
Forage ~ 1 + (1 Site)	3692.16	4.05	0.05
Forage ~ $\text{RAI}_{\text{grazing}}$ + (1 Site)	3692.77	4.67	0.03
Forage ~ Rainfall + (1 Site)	3694.02	5.92	0.02
Forage ~ $\text{RAI}_{\text{grazing}}$ + Rainfall + (1 Site)	3694.69	6.58	0.01

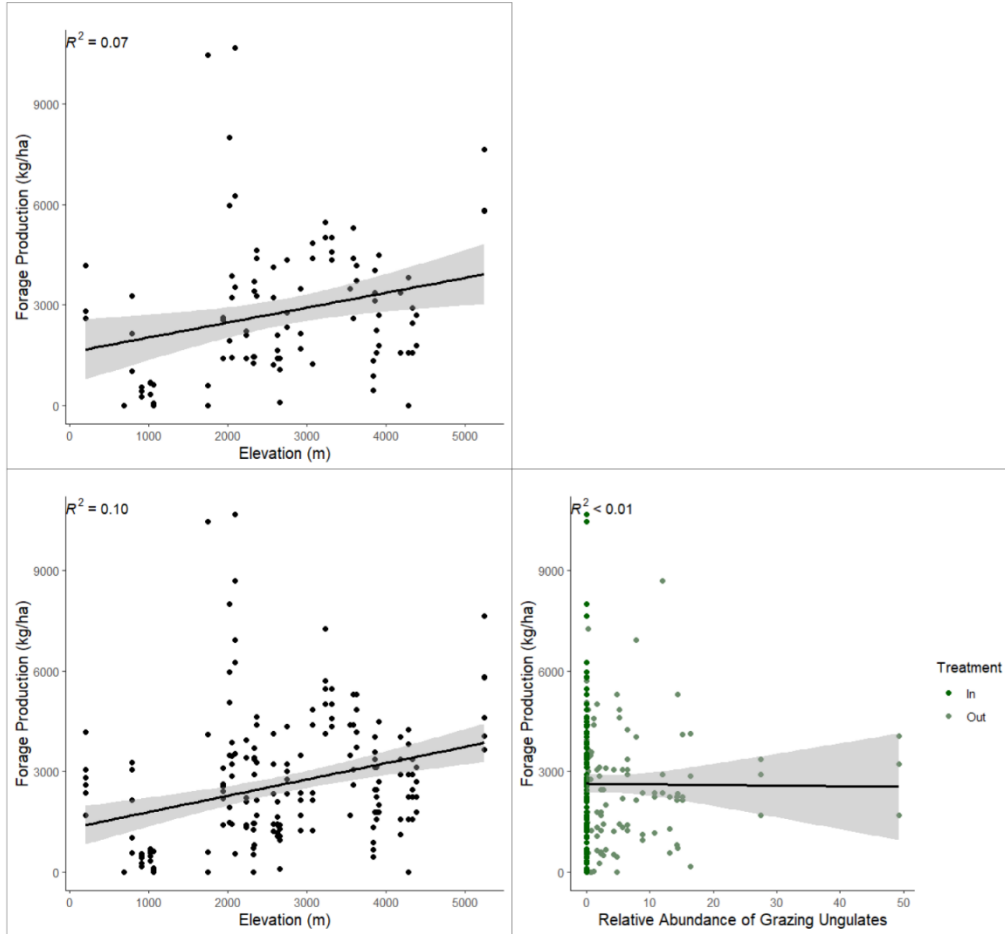


Figure 2.4. The top left graph shows the top model for forage production from samples inside the exclusion cage plotted against elevation (Estimate = 0.44, $t = 2.08$, $p = 0.05$). The bottom left is the top model for all forage samples, where elevation is the sole fixed predictor of forage production (Estimate = 0.49, $t = 2.59$, $p = 0.01$). The bottom right graph displays the second-best model for all forage samples, illustrating forage production as a function of the relative abundance of wild grazing ungulates (RAI_{grazing}) (Estimate = -15.96, $t = -1.27$, $p = 0.21$).

Linear regressions were utilized to assess relationships between average vegetation biomass (kg/ha) and wild ungulate RAI. Feral goats and feral sheep were not assessed individually as they occurred at none or at a small number of sites (Table 2.1). The relationship between wild ungulates RAI and the forage loss showed a slight positive trend (Figure 2.5; Intercept = 212.43, SE = 183.92; Slope = 17.79, SE = 15.49, $t = 1.15$, $R^2 = 0.04$). On the island of Hawai‘i there was a negative trend between the total wild ungulates detected and forage loss (Figure 2.6; Intercept = 234.57, SE = 248.08; Slope = -50.44, SE = 30.47, $t = -1.66$, $R^2 = 0.17$)

and Maui had a positive relationship between the total ungulates detected and forage loss (Figure 2.6; Intercept = 446.18, SE = 235.34; Slope = 25.41, SE = 16.77, $t = 1.52$, $R^2 = 0.17$). For mouflon sheep on the island of Hawai‘i, there was a negative relationship between RAI and forage loss (Figure 2.6; Intercept = 352.35, SE = 376.84; Slope = -61.86, SE = 39.94, $t = -1.55$, $R^2 = 0.11$). There was a positive relationship between the RAI of axis deer and forage loss (Figure 2.6; Intercept = 451.57, SE = 231.78; Slope = 25.72, SE = 16.64, $t = 1.55$, $R^2 = 0.11$).

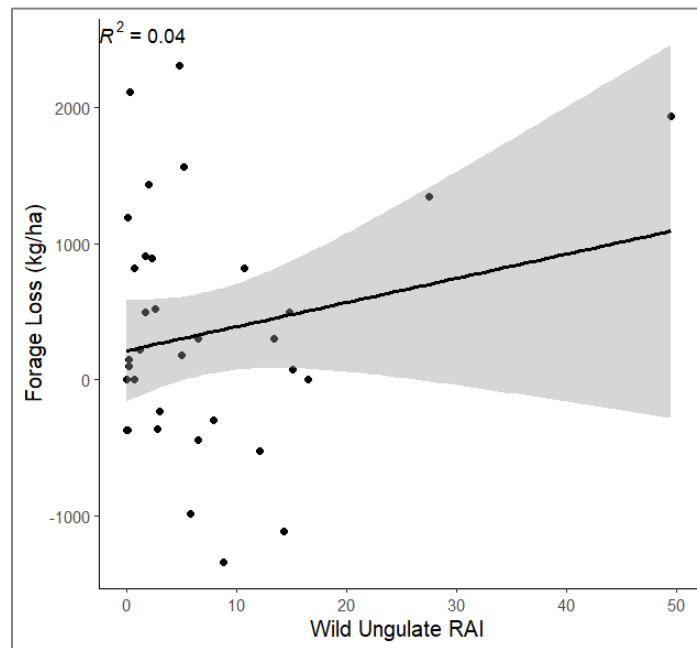


Figure 2.5. Linear regression of average forage loss (kg/ha) (inside exclusion cage – outside exclusion cage) as a function of total wild ungulate relative abundance index (RAI), which includes wild pigs, feral goats, axis deer, and mouflon sheep across all sites on Hawai‘i Island and Maui (Intercept = 212.43, SE = 183.92; Slope = 17.79, SE = 15.49, $t = 1.15$, $R^2 = 0.04$), but a slight positive trend is observed.

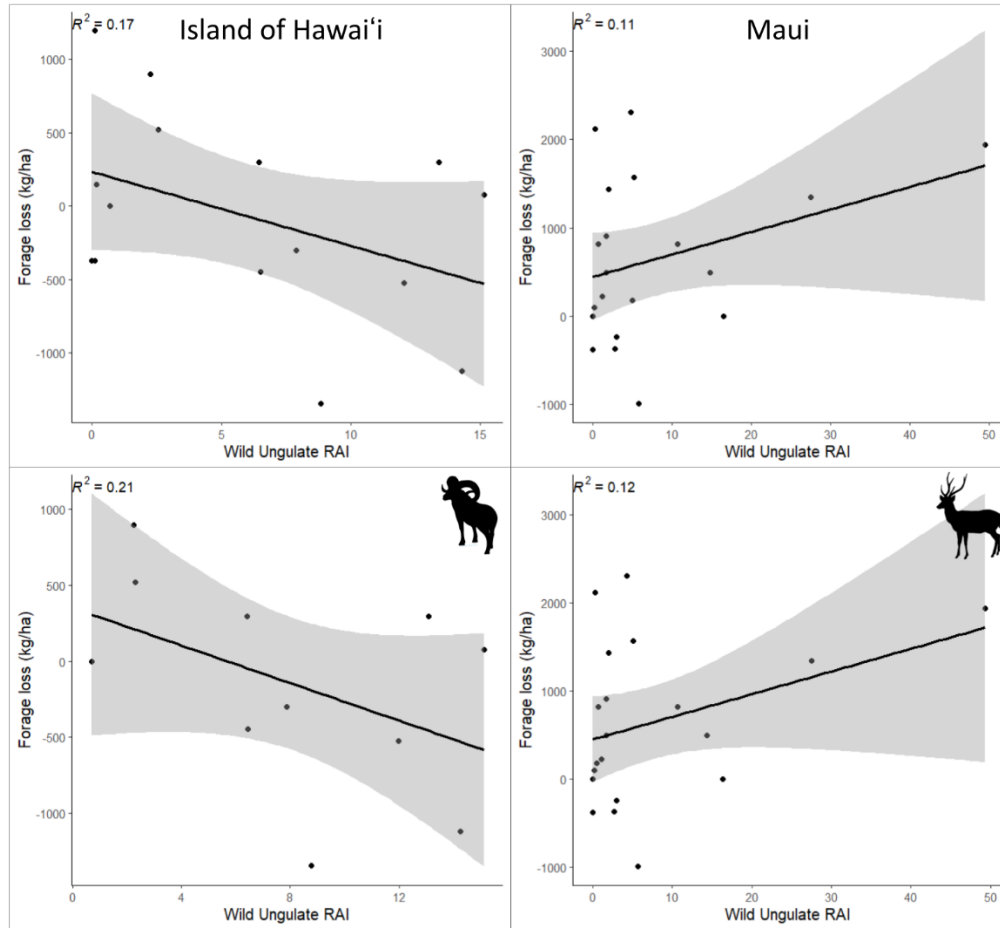


Figure 2.6. Linear regressions of the average forage loss (kg/ha) (inside exclusion cage – outside exclusion cage) and the relative abundance index (RAI) of wild ungulates an estimation of the number of wild ungulates detected. The two top panels show the relationship for all detected wild ungulates, including wild pigs, feral goats, and mouflon sheep on the island of Hawai'i (Intercept = 234.57, SE = 248.08; Slope = -50.44, SE = 30.47, $t = -1.66$, $R^2 = 0.17$) and wild pigs, feral goats, and axis deer on Maui (Intercept = 446.18, SE = 235.34; Slope = 25.41, SE = 16.77, $t = 1.52$, $R^2 = 0.17$). The bottom panels display species-specific relationships, with mouflon sheep on the island of Hawai'i (Intercept = 352.35, SE = 376.84; Slope = -61.86, SE = 39.94, $t = -1.55$, $R^2 = 0.11$) and axis deer on Maui (Intercept = 451.57, SE = 231.78; Slope = 25.72, SE = 16.64, $t = 1.55$, $R^2 = 0.11$).

Plant species were organized by functional group (grass, forb, shrub, and lichen) see Table A1 Appendix A. The automated model selection using the *glmulti* function evaluated 32 models of all possible combinations of wild grazing ungulates relative abundance (RAI_{grazing}) with predictor variables: grass, forb, shrub, bare ground cover, and rainfall. The model with the lowest AIC value was the null model ($RAI_{\text{grazing}} \sim 1$) with an AIC of 261.62 and 0.091 weight

(Table 4), indicating that none of the predictor variables had a significant effect on the relative abundance of wild grazing ungulates across study sites (weights = 0.0005 - 0.091).

Table 2.4. Generalized linear model result of all possible combinations of RAI_{grazing} (wild grazing ungulates detected: axis deer, mouflon sheep, feral goats) with predictor variables grass, forb, shrub, bare ground percent cover, and rainfall.

Model	AIC	Weight
$RAI_{\text{grazing}} \sim 1$	261.62	0.091
$RAI_{\text{grazing}} \sim 1 + \text{Shrub}$	261.74	0.086
$RAI_{\text{grazing}} \sim 1 + \text{Forb}$	262.15	0.070
$RAI_{\text{grazing}} \sim 1 + \text{Forb} + \text{Shrub}$	262.18	0.069
$RAI_{\text{grazing}} \sim 1 + \text{Shrub} + \text{Rainfall}$	262.60	0.056
$RAI_{\text{grazing}} \sim 1 + \text{Rainfall}$	262.84	0.049
$RAI_{\text{grazing}} \sim 1 + \text{Bare ground}$	263.04	0.045
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Shrub}$	263.26	0.040
$RAI_{\text{grazing}} \sim 1 + \text{Forb} + \text{Shrub} + \text{Rainfall}$	263.40	0.037
$RAI_{\text{grazing}} \sim 1 + \text{Grass}$	263.59	0.034
$RAI_{\text{grazing}} \sim 1 + \text{Forb} + \text{Rainfall}$	263.67	0.033
$RAI_{\text{grazing}} \sim 1 + \text{Shrub} + \text{Bare ground}$	263.74	0.032
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Forb}$	263.82	0.030
$RAI_{\text{grazing}} \sim 1 + \text{Bare ground} + \text{Rainfall}$	263.86	0.030
$RAI_{\text{grazing}} \sim 1 + \text{Forb} + \text{Bare ground}$	263.88	0.029
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Forb} + \text{Shrub}$	264.11	0.026
$RAI_{\text{grazing}} \sim 1 + \text{Forb} + \text{Shrub} + \text{Bare ground}$	264.11	0.026
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Shrub} + \text{Rainfall}$	264.42	0.022
$RAI_{\text{grazing}} \sim 1 + \text{Shrub} + \text{Bare ground} + \text{Rainfall}$	264.52	0.021
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Rainfall}$	264.63	0.020
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Bare ground}$	264.64	0.020
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Shrub} + \text{Bare ground}$	264.75	0.019
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Forb} + \text{Rainfall}$	265.04	0.016
$RAI_{\text{grazing}} \sim 1 + \text{Forb} + \text{Bare ground} + \text{Rainfall}$	265.13	0.016
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Forb} + \text{Shrub} + \text{Rainfall}$	265.40	0.014
$RAI_{\text{grazing}} \sim 1 + \text{Forb} + \text{Shrub} + \text{Bare ground} + \text{Rainfall}$	265.40	0.014
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Bare ground} + \text{Rainfall}$	265.69	0.012
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Forb} + \text{Bare ground}$	265.82	0.011
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Shrub} + \text{Bare ground} + \text{Rainfall}$	265.91	0.011
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Forb} + \text{Shrub} + \text{Bare ground}$	266.10	0.010
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Forb} + \text{Bare ground} + \text{Rainfall}$	267.03	0.006
$RAI_{\text{grazing}} \sim 1 + \text{Grass} + \text{Forb} + \text{Shrub} + \text{Bare ground} + \text{Rainfall}$	267.40	0.005

A linear mixed-effects model was used to assess differences in predicted forage production (kg/ha) by wild ungulate species presence. The model revealed that forage production was significantly lower at sites dominated by axis deer compared to ungulate-free exclusion plots (Table 2.5; $\beta = -686.09$, SE = 244.70, $p = 0.0056$). Predicted forage production was highest in areas without wild ungulate exposure (“none”), with an estimated mean of 2808.76 ± 262.28 kg/ha. Among the species, plots dominated by axis deer had the lowest predicted forage production (2122.66 ± 310.22 kg/ha), followed closely by feral goats (2127.60 ± 363.19 kg/ha). Wild pigs were associated with the highest predicted forage production among the wild ungulate-exposed plots, estimated at 3615.92 ± 1024.31 kg/ha along with mouflon sheep (2929.26 ± 613.61 kg/ha). These predictions reflect species-specific differences in grazing pressure relative to ungulate-free conditions.

Table 2.5. Summary of fixed effects from the linear mixed-effects model assessing predicted forage production (kg/ha) across wild ungulate species. The model includes “site” as a random effect. The reference category is forage samples collected inside exclusion cages with no wild ungulate exposure (“none”). Estimates represent the difference in predicted forage production relative to this baseline.

Predictor	Estimate	Std. Error	DF	t-value	p-value
None	2808.76	262.28	171	10.71	<0.001
Axis deer	-686.09	244.7	171	-2.80	0.0056
Mouflon sheep	120.49	309.12	171	0.39	0.6972
Feral goat	-681.16	583.23	171	-1.17	0.2445
Wild pig	807.15	1006.41	171	0.8	0.4237

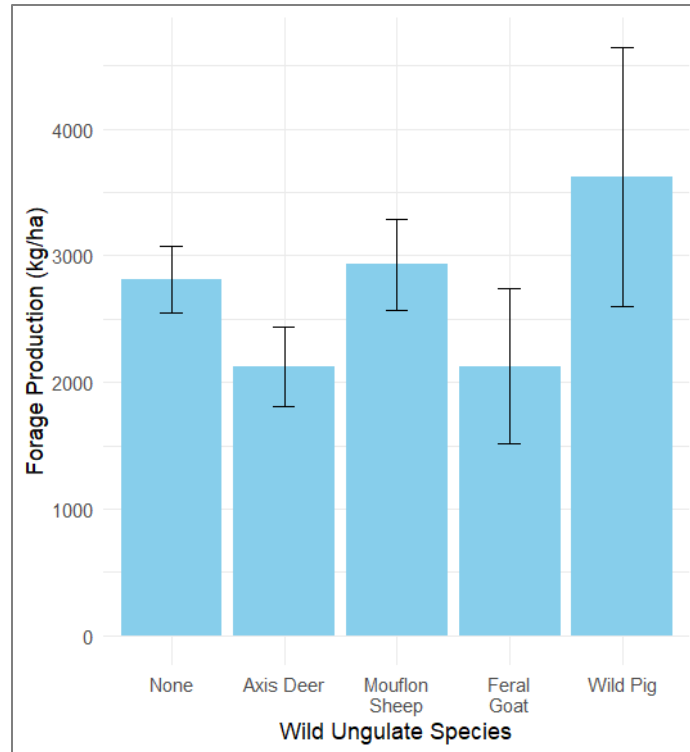


Figure 2.7. Predicted forage production (kg/ha) across wild ungulate species categories based on a linear mixed-effects model with "Site" as a random effect. Forage production was lowest in areas dominated by axis deer and feral goats when compared to forage production without exposure to wild ungulates ("none") and highest in areas dominated by wild pigs and mouflon sheep. Error bars represent ± 1 standard error of the predicted means.

Discussion

This is the first field study to examine the relationship between forage loss and wild invasive ungulates on ranchlands in the Hawaiian Islands. We found substantial vegetation loss at 66% of the study sites, consistent with substantial losses reported by ranchers in a recent study of economic impacts on livestock production (Shwiff et al. 2025). Further, wild ungulates were detected at sites where ongoing impacts from drought and wildfires resulted in a lack of forage availability for livestock, suggesting that wild ungulates may continue to degrade pastures long after they are unsuitable for ranch production.

Elevation emerged as the primary driver of forage production in both models, highlighting its strong influence on vegetation growth across sites (Table 2 & 3). The top model

for forage production inside exclusion cages included only elevation as a fixed effect, suggesting that, in the absence of wild ungulates, elevation has a strong impact on forage availability (Carlyle et al., 2014; Wu et al., 2024; Zhang et al., 2023). This is likely due to environmental differences at varying elevations such as temperature (K. Yang et al., 2022; Y. Yang et al., 2023), soil fertility (Khosravi Aqdam et al., 2023), and vegetation structure (Bora et al., 2021; Han et al., 2022). The strong influence of elevation on forage production in this study aligns with findings from research on native plant cover and fire dynamics in Hawaiian ecosystems (D'Antonio et al., 2000). This study similarly identified elevation as the primary environmental driver of vegetation responses, whereas rainfall did not systematically explain variation in plant cover. When assessing forage production across all samples inside and outside exclusion cages, elevation remained the strongest predictor.

Wild ungulate abundance appeared in the second-best model suggesting that grazing pressure may also influence forage availability, although to a lesser extent than elevation. This result aligns with previous studies demonstrating that wild ungulate grazing reduces forage biomass alongside other environmental factors (Frank et al., 2016; Ibañez-Alvarez et al., 2022; K. Kramer et al., 2006). The relatively close model weights between the top two models indicate some uncertainty regarding the relative influence of grazing compared to elevation, suggesting further investigation into potential interactions between these factors. Rainfall, while often considered a key factor in plant productivity (Gibson-Forty et al., 2016; Heisler-White et al., 2009), did not significantly improve model performance (Table 2 & 3), but we note that there has been a multi-year drought which may have influenced study results at some sites due to severe soil alteration.

At sites where grazing ungulates were detected on the islands of Hawai‘i and Maui (n = 32), 66% had forage loss (Appendix Table 2). Losses per site ranged from 74.72 kg/ha to 1942.81 kg/ha in areas with preferred cattle forage. To put this into context, in two weeks ungulates consumed the food needed for between 6 and 161 animal units (AU) (450 kg cow) for one day assuming one AU consumes 12 kg of dry matter per day (Heitschmidt & Stuth, 1991; Holechek, 1989; Scarnecchia, 1990; USDA, 2003). These results align with reports of ranchers reducing stocking rates or no longer rotating cattle through certain pastures due to impacts from invasive wild ungulates (Shwiff et al. 2025).

Multiple factors such as rainfall, drought, and soil health interact with wild ungulate abundance to affect forage availability for ranching. Additionally, some sites were in states of regrowth following fire damage (Ranch C, sites 3 and 4), were dominated by non-preferred vegetation (Ranch D sites 4 and 7), or lacked vegetation due to earlier impacts of wild ungulates and drought (Ranch C, site 4; Ranch D, site 10), likely influencing visitation rates by invasive wild ungulates. Despite these conditions, wild ungulates were present, suggesting their ability to persist in areas unsuitable for cattle, and exacerbating the continued alteration of pastureland.

Wild grazing ungulates (feral goats, axis deer and mouflon sheep), did not show a preference for specific vegetation types—such as grass, forbs, shrubs, or bare ground—and rainfall was not a significant predictor of their relative abundance. These findings suggest that these introduced wild grazing ungulates are opportunistic generalists, highly adaptive to varying environments (Barroso et al., 2000; Freschi et al., 2021; Newman et al., 1995; Rogosic et al., 2007; White et al., 2023). Wild ungulates may also be limited in their ability to move to areas with preferred vegetation due to barriers such as fencing or urban development.

Undesirable plant species covered more than 25% of pasture area at 31% of sites (11 out of 35 sites) (*Hawaii/Pacific Islands Area | Field Office Technical Guide | NRCS - USDA*, n.d.). Fireweed (*Senecio madagascariensis*), a known invasive and toxic pasture weed, was present at 69% of sites (24 out of 35 sites) (Haselwood et al. 1983, Le Roux 2010). These weeds compete with preferred grasses such as Kikuyu grass (*Pennisetum clandestinum*) (Fukumoto & Lee 2003). Due to unwanted grazing pressure from wild ungulates on ranchlands, grasses become suppressed, allowing noxious weeds and toxic forbs to grow in place (Leopold & Hess 2016, Perkins et al. 2018). Additionally, 11% of sites (4 out of 35 sites) had bare ground cover exceeding 35%, suggesting a shift toward highly altered pastureland and soil erosion.

Predicted forage production was significantly lower in areas dominated by axis deer compared to forage production without exposure to wild ungulates, indicating a measurable impact of this species on forage availability. Specifically, axis deer were associated with a 686 kg/ha reduction in predicted forage production relative to protected areas. Feral goats also showed reduced forage production, with a difference of 681 kg/ha compared to forage production without exposure to wild ungulates, although this difference was not statistically significant. These findings suggest that both axis deer and feral goats may exert consistent grazing pressure that suppresses forage recovery, and therefore these species may have the most impact on ranches. In contrast, forage production in areas with mouflon sheep and wild pigs was not significantly different from ungulate-free areas, and in some cases, predicted forage was even higher. This unexpected pattern may reflect site-specific environmental factors, such as higher rainfall, soil fertility, or less recent grazing pressure. These results emphasize the importance of considering both species-specific impacts and local site conditions when evaluating wild ungulate effects on rangeland productivity. Previous studies have indicated that grazers reduce

forage production and cause significant vegetation damage when overabundant or introduced (Marchiori et al., 2012). These findings highlight the need for targeted management strategies for the wild ungulate species that are of greatest impact on ranches.

Study limitations included relatively small sample sizes for feral goats and feral sheep (Table 2.1). Additionally, the short data collection period (two weeks), limited by rotational grazing schedules, likely captured only a snapshot of the complex interactions between wild ungulates and vegetation, potentially missing seasonal variations in forage dynamics or wild ungulate behavior. Ranchers have observed ungulates moving away from certain areas after heavy rainfall (pers. Comm. Lani Petrie.). Future studies should address these limitations by increasing the number of study sites, extending data collection across multiple seasons, and integrating data such as GPS tracking of wild ungulate movement, vegetation recovery rates, and soil health metrics to provide a more comprehensive understanding of these interactions.

Alongside the impacts caused by wild ungulates, climate change presents an additional and growing challenge for ranchers (Joyce et al., 2013; Ojima et al., 2020). As climate change progresses, environmental stressors such as rising temperatures, prolonged periods of drought, reduced rainfall, and increased risk of wildfires are expected to intensify (Briske et al., 2015; D'Adamo et al., 2021; Wonkka et al., 2019). These changes can impact forage growth, decrease pasture quality, and strain water resources—further complicating land and livestock management and increasing financial strains (Shwiff et al., 2024; Turner et al., 2024).

This study advances understanding of the complex relationships between invasive wild ungulates and forage loss, and points toward interactions among ecological factors beyond wild ungulate abundance alone. Further, these results highlight the need for targeted removal of wild ungulates to reduce impacts to local ranch production. Long-term research is crucial to capture

the cumulative impacts of ungulates on forage loss and the environmental factors driving their movement, such as vegetation structure or rainfall patterns. Future studies should also explore wild ungulate impacts across diverse habitats, including native forests and agricultural crops, to develop effective management strategies for mitigating their widespread effects.

Chapter 3

Invasive Ungulates in the Crosshairs: A Comparison of Management Goals and Predicted Abundance in the Hawaiian Islands

Abstract

Invasive wild ungulates are a major ecological and economic concern worldwide, as they contribute to habitat degradation, biodiversity decline, and agricultural losses. Across the Hawaiian Islands, non-native wild ungulates naturally vary in abundance based on environmental factors like vegetation and rainfall. Management goals also vary across landscapes, presenting challenges for coordinated efforts to mitigate wild ungulate impacts on endangered species. This study examined the relationship between predicted wild ungulate abundance and land management designations. We first categorized land parcels using layers from the Hawai‘i Statewide GIS portal, including “TMK Parcel,” “State Land Use Districts,” and “Reserves,” classifying them as: (1) Sensitive Conservation Areas, (2) Priority Hunting Areas, or (3) Other Areas. We then used existing spatial models predicting the abundance of wild pigs (*Sus scrofa*), feral goats (*Capra hircus*), mouflon sheep (*Ovis aries*), axis deer (*Axis axis*), and black-tailed deer (*Odocoileus hemionus columbianus*) to estimate mean wild ungulate abundance in each parcel under unmanaged conditions. Statistical analyses (ANOVA with Tukey’s HSD post hoc tests, where appropriate) were conducted to determine whether predicted wild ungulate abundance differed across management areas. Results indicate that wild pigs had significantly lower predicted abundance in Other Areas compared to Sensitive Conservation Areas on Hawai‘i Island ($p < 0.001$) and Maui ($p = 0.002$). On Maui, feral goats were more abundant in Priority Hunting Areas than in Sensitive Conservation Areas ($p = 0.05$). Axis deer were more abundant in Other Areas compared to Sensitive Conservation Areas ($p < 0.001$), while mouflon sheep had higher abundance in Sensitive Conservation Areas compared to both Priority Hunting Areas ($p =$

0.01) and Other Areas ($p < 0.001$). Additionally, mouflon sheep were more abundant in Priority Hunting Areas than in Other Areas ($p = 0.05$). These findings highlight areas where wild ungulates are predicted to be most abundant under natural conditions, providing insights into where targeted management strategies such as fencing and removal may be most needed if not currently implemented. The higher predicted abundance of wild pigs and mouflon sheep in conservation lands suggests that, in the absence of management, these areas will experience higher impacts from these species than other areas and highlights the importance of maintaining fencing and removal strategies. Conversely, the lower abundance of axis deer in conservation areas, combined with high abundance predictions in Other Areas, suggests that private, ranch, or agricultural lands are more likely to experience impacts from this species, aligning with current observations. Further investigation into landowner management objectives in areas not managed for game or conservation is essential for advancing collaborative management strategies for wild ungulates.

Introduction

Animals valued as game for food and recreational hunting have been introduced globally outside their historic ranges, providing predictable food resources for human communities but causing catastrophic ecological damage (Carpio et al., 2017; Comte et al., 2025). Today, policies often mandate contradictory management goals for these animals both as a food resource and as an invasive species, presenting social and environmental challenges for achieving these mandates. In the absence of complete eradication, differing management practices occur in a patchwork across the landscape, with some areas designated for hunting and others for

conservation, resulting in localized reductions or eradications, and still other areas with unclear objectives and/or a lack of active management.

Collaborative management of invasive ungulates across landscapes is critical to restoring native ecosystems, sustainable agricultural production, and minimizing impacts to human health and survival (Ballari et al., 2019; Hughey & Hickling, 2006; Widén et al., 2023). Invasive feral pigs consume native species, engage in behaviors such as rooting which lead to soil erosion and contamination of water, and facilitate the spread of invasive species (Beasley et al., 2018; Nogueira-Filho et al., 2009; Risch et al., 2022; Strauch et al., 2016), leading to cascading trophic effects across native ecosystems (Cole & Litton, 2014; C. J. Kramer et al., 2024). Invasive ungulates decrease agricultural productivity by competing for forage, disrupting water pipes and other infrastructure, and directly predating on livestock (Bleier et al., 2017; Katayama et al., in prep; Shwiff et al., 2024; Thinley et al., 2017; Widén et al., 2023), threatening food production systems. Further, invasive ungulates can impact human health through the spread of diseases such as Brucellosis (Motsi et al., 2013; Muñoz et al., 2010), and car strikes (Beasley et al., 2014; Kim et al., 2023).

In addition to hunting, diverse management tools to control invasive wild ungulates are available, and are typically selected based on land manager goals, cost, and policy (Martínez & Martín, 2017; Snow et al., 2024). Areas designated as ecologically sensitive may be fenced and invasive ungulates completely removed from inside the fenced area, providing ungulate-free zones in which native ecosystem restoration or agricultural production, for example, can take place (Hart et al., 2020; Hess, 2016; Kardol et al., 2014; Thinley et al., 2017). Other areas may be designated for hunting (e.g., game management areas), potentially contributing to food provisioning, recreational, and ecological goals (Kesch et al., 2015; Roekel et al., 2024). Further,

hunting for recreational, food provisioning, or commercial purposes may take place on private and public lands outside of designated hunting areas (Rowland et al., 2023; Small et al., 1991; Webb et al., 2011). Outside of fenced areas and designated hunting areas a variety of additional tools may be employed such as aerial shooting, poison baiting, snares or traps, and hormonal treatments (Cruz et al., 2009; Gürtler et al., 2023; Irvine & Thorley, 2024; Patton et al., 2007; Rubino & Williams, 2014).

Decisions regarding which management tools to employ for invasive wild ungulate management should take into consideration not only the sensitivity of ecosystems and the efficacy of various removal and exclusion methods, but also the natural abundance of the invasive ungulates (Brondum et al., 2017; Ikagawa, 2013a), as this may influence the degree of effort required to achieve management goals. Wild ungulate abundance varies across the landscape based on factors such as rainfall, vegetation, temperature, and food availability (Risch et al., 2020, 2022, 2025). Hunters are likely to prefer the placement of designated hunting areas in locations with a high potential abundance of ungulates (Black & Jensen, 2018; Byrd et al., 2017), providing an ecological benefit through reduced invasive wild ungulate populations by hunters. When ecosystems are particularly sensitive to invasive wild ungulates, fencing may be necessary to completely protect ecosystems from the impacts of ungulates, whether or not the invasive ungulates are in low or high abundance (Dobson et al., 2019). However, in sensitive areas with environmental characteristics that support a high carrying capacity of invasive ungulates, the incursion pressure on fences may be high, necessitating additional hunting or knockdown pressure outside of the fence to maintain an ungulate-free zone inside the fence.

In this study we aimed to evaluate the relationship between known land management goals and the predicted natural abundance of wild ungulates in the absence of management. We

conducted this evaluation in the Hawaiian Islands where different islands contain varying assemblages of invasive wild ungulates (See Figure 1 from Chapter I). Similar to other regions around the world, these species are valued as food resources as well as for cultural and recreational purposes (Luat-Hū'eu et al., 2021; Luat-Hū'eu et al., 2023), but also cause substantial damage to native species and ecosystems (Adams, n.d.; Anderson, 2003; Banko et al., 2013; Hess et al., 2022; Mueller-Dombois & Spatz, 1975; Nogueira-Filho et al., 2009). State agencies are mandated to provide hunting opportunities, while simultaneously protecting native species and ecosystems. To achieve these potentially conflicting goals, sensitive areas are designated for fencing and local eradication, and less sensitive areas are designated for hunting. However, outside of areas specifically designated for fencing or hunting, management goals and actions to achieve them vary considerably.

Within the past decade, relative abundance models were developed for the islands of Hawai'i (feral pigs, mouflon sheep), Maui (feral pigs, axis deer), O'ahu (feral pigs), and Kaua'i (feral pigs, black-tailed deer) (Risch et al., 2020, 2022, 2025, and in prep). To date, these models have not been utilized to evaluate relative abundance in designated hunting and conservation areas. Thus, in this study we aimed to answer the following question: In the absence of management actions (e.g., hunting or fencing), how does the predicted abundance of wild ungulates vary across three land management classifications: "Sensitive Conservation Areas", "Priority Hunting Areas", and "All Other Areas"?

Methods

Spatial analyses were conducted for the islands of Hawai'i, Kaua'i, Maui, and 'Oahu using ArcGIS Pro (Version 3.0.2, Redlands, CA: Environmental Systems Research Institute,

Inc., 2022). These islands were selected due to the existing data available for predicted wild ungulate distribution. The following layers were downloaded from the Hawai‘i Statewide GIS portal: “TMK Parcels,” “State Land Use Districts,” “Agricultural Land Use Baseline – 2020 Update,” and “Reserves.” The “Tax Map Key (TMK)” parcel for each respective island was utilized as the base layer to identify property boundaries. The “State Land Use Districts Boundaries” (SLUD) layer contained broad categories of land use, including agricultural, conservation, rural, and urban areas. The “Reserves” layer included data on various reserve types, preserves, parks, and the respective managing agencies.

For computational simplicity, parcels with a land area under 50 acres were removed from the TMK layer. To add attribute data from other layers to the TMK layer, the geoprocessing tool “Spatial Join” was used, with the option “largest overlap” selected. This ensured that TMK parcels were categorized by the overlapping polygon with the largest area. A new field labeled “Key Type” was then created to store the main category for each TMK parcel. Categories were added to the “Key Type” field in a hierarchical order, with the “Reserves” layer field “Type” as the highest priority, and finally the “ludcode” from the “State Land Use Districts”. This joining order ensured that the most specific categories were prioritized.

Each parcel was assigned a group of wild ungulate management goals, reflecting the broad desired management goals based on land designation and related assumptions. A new field, “Management Goals,” was created to store these values. Desired wild ungulate management goal groups by parcel type were categorized as “Sensitive Conservation Areas”, “Priority Hunting Areas”, and “All Other Areas”. Sensitive Conservation Areas were defined as areas with a high degree of management for native species and ecosystems such as State of Hawai‘i Natural Area Reserve Systems (NARS), which are considered to be very sensitive to

impacts from wild ungulates and are often fenced for protection. Priority Hunting Areas were defined as areas managed by the state for public hunting such as Game Management Areas (GMA). All Other Areas were any land types that did not have defined wild ungulate management goals. See Table 1 in the Appendix for a detailed summary of land types and assigned categories of wild ungulate management goals.

In addition, to accurately represent areas managed by the state of Hawai'i Division of Forestry and Wildlife (DOFAW), layers with information regarding which areas are designated for conservation resources and hunting management were incorporated into the base TMK layer. These layers, obtained from DOFAW, can be accessed on the DOFAW Lands and Management Classifications web page (Division of Forestry and Wildlife | Lands & Management Classifications). For DOFAW-managed lands, the C-1 (High Conservation Resources) and H-1 (Active Hunting Management) classifications were selected (Appendix Table 1). The C-1 class represents areas with high levels of native biological resources and intensive management to control wild ungulates, assigned to "Sensitive Conservation Areas". In contrast, the H-1 class designates areas where public hunting is prioritized to maximize sustainable yield while minimizing environmental impacts, thus assigned to "Priority Hunting Areas". Although these layers are based on TMK parcels, they do not perfectly align with the base TMK layer. To address this, a "Spatial Join" was conducted using the "Have their center in" option to prevent over-selection of polygons. Following the spatial join, polygons were manually reviewed, and wild ungulate management goals were recategorized for areas not fully selected during the initial join. Parcels partially covered by C-1 or H-1 areas, or containing both classifications, were visually reassigned based on the classification that encompassed majority of the parcel.

Next, we compared the predicted natural relative abundance of feral pigs under an assumption of no management (e.g., feral pigs carrying capacity based on environmental determinants of distribution) within each of the designated land types. To achieve this, we first downloaded raster layers of a relative abundance index (RAI) developed in previous studies (Risch et al., 2020, 2022, 2025). These layers include RAI distributions for feral pigs on the islands of Hawai‘i, Kaua‘i, Maui, and ‘Oahu, and mouflon sheep on the island of Hawai‘i, feral goats and axis deer on Maui, and black-tailed deer on Kaua‘i. The cell size of each raster layer was adjusted to 100 by 100 meters using the geoprocessing tool “Resample” with the bilinear sampling technique to enable averaging distribution values with the TMK parcel layer. To calculate the mean RAI raster value within each TMK polygon, the geoprocessing tool “Zonal Statistics as a Table” was applied with each TMK parcel layer and corresponding raster RAI distribution layer, setting the “statistics type” to “mean.” The resulting table was then joined to the main TMK parcel layer to allow comparisons between wild ungulate management goals and default relative abundance.

Analysis. The following analysis was conducted in R 4.1.1 (R Core Development Team, 2021). To determine whether the mean wild ungulate abundance estimates differed among Sensitive Conservation Areas, Priority Hunting Areas, and All Other Areas, a one-way ANOVA was performed using the *stats* package in R. If the ANOVA detected significant differences, Tukey’s HSD post hoc test was conducted to identify which groups differed. To visualize the results, *ggplot2* was used to generate boxplots for each wild ungulate species and island.

Results

Across the islands of Hawai‘i, Kaua‘i, Maui, and ‘Oahu, a total of 1,287,225 acres (43,716 to 964,762 per island) were identified as Sensitive Conservation Areas. Priority Hunting Areas covered 162,776 acres in total (2,877 to 119,965 acres per island), while All Other Areas spanned 2,013,435 acres (117,603 to 1,220,203 acres per island). On every island, "All Other Areas" had the largest total land area and frequency (Figure 1; Table 1).

The one-way ANOVA resulted in a significant effect among parcel management categories for some species on some islands: wild pigs on the island of Hawai‘i ($F(2, 2190) = 8.98, p = 0.0001$) and Maui ($F(2, 619) = 7.77, p = 0.0005$), feral goats on Maui ($F(2, 619) = 2.96, p = 0.05$), axis deer on Maui ($F(2, 619) = 10.44, p = 3.48e-05$), and mouflon sheep on Hawai‘i ($F(2, 2190) = 86.29, p = <2e-16$). No significant differences were detected among parcel categories for the following species/island combinations: wild pigs on O‘ahu ($F(2, 681) = 1.70, p = 0.18$), wild pigs on Kaua‘i ($F(2, 303) = 2.13, p = 0.12$), or black-tailed deer on Kaua‘i ($F(2, 303) = 0.23, p = 0.80$).

A Tukey’s HSD post hoc test was conducted for ANOVA results that were significant to identify pairwise differences between management areas. For pigs on Maui, abundance was significantly lower in All Other Areas compared to Sensitive Conservation Areas (mean difference = -3.89, 95% CI [-6.56, -1.22], $p = 0.002$). No other pairwise comparisons for pigs on Maui were significant (all p -values > 0.05). For axis deer on Maui, abundance was significantly higher in All Other Areas compared to Sensitive Conservation Areas (mean difference = 10.02, 95% CI [4.84, 15.93], $p = 0.0002$). No significant differences were found between other pairwise comparisons for axis deer (all p -values > 0.05). For feral goats on Maui, Priority Hunting Areas had a significantly higher abundance than Sensitive Conservation Areas (mean difference =

16.31, 95% CI [0.13, 32.49], $p = 0.05$), but no other comparisons were significant (all p -values > 0.05). For pigs on the island of Hawai‘i, abundance was significantly lower in All Other Areas compared to Sensitive Conservation Areas (mean difference = -1.56, 95% CI [-2.43, -0.70], $p = 0.00007$), but no other comparisons were significant (all p -values > 0.05). For mouflon sheep on the island of Hawai‘i, abundance was significantly lower in All Other Areas compared to Sensitive Conservation Areas (mean difference = -7.00, 95% CI [-8.27, -5.74], $p < 0.0001$), and Priority Hunting Areas had significantly lower abundance than Sensitive Conservation Areas (mean difference = -3.94, 95% CI [-7.17, -0.72], $p = 0.01$). Additionally, Priority Hunting Areas had significantly higher abundance than All Other Areas (mean difference = 3.05, 95% CI [0.04, 6.04], $p = 0.05$).

Across the islands, the relative abundance index (RAI) of wild ungulate species varied across the areas designated for various management goals. Wild pigs on the islands of Hawai‘i, Kaua‘i, and ‘Oahu, and mouflon sheep on the island of Hawai‘i had a higher predicted RAI in Sensitive Conservation Areas than in Priority Hunting Areas (Figure 2 and 3). Wild pigs, feral goats, and axis deer on Maui, and black-tailed deer on Kaua‘i were the only instances where the greatest median value was in Priority Hunting Areas (Figure 2 and 3). Although the median RAI was lower in some Sensitive Conservation Areas for feral goats and axis deer on Maui and black-tailed deer on Kaua‘i (Figure 3), there was substantial variability and a high number of outliers, suggesting that some Sensitive Conservation Areas were predicted to have higher RAI despite lower central values.

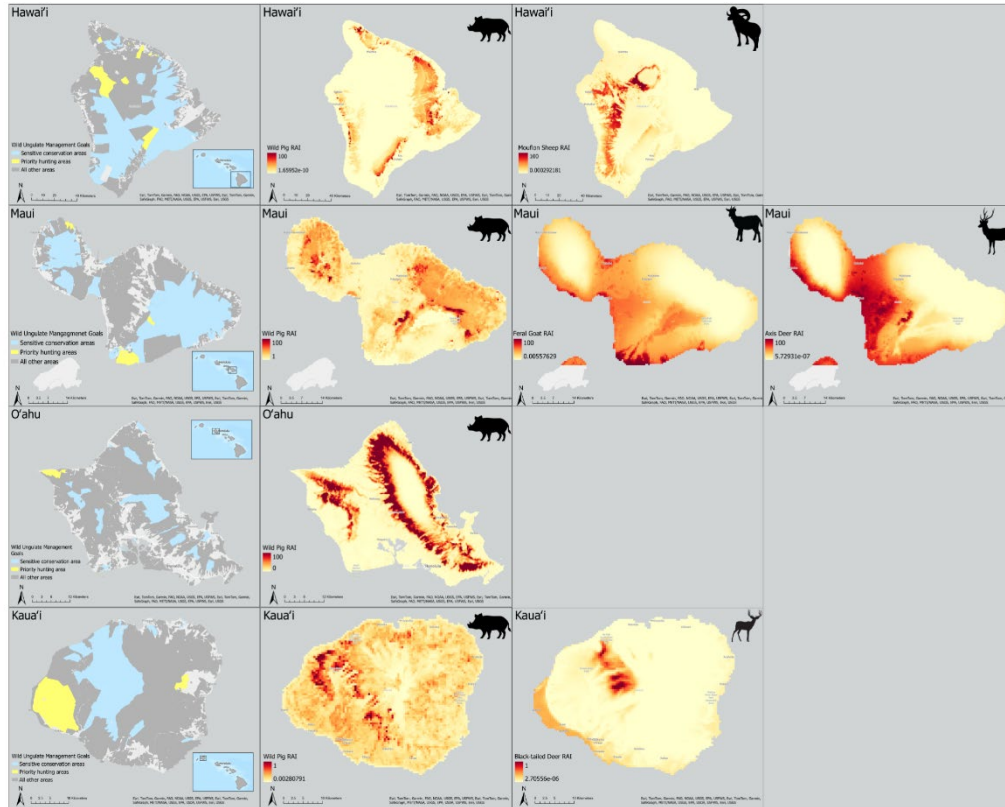


Figure 3.1. Maps of the island of Hawai‘i, Maui, O‘ahu, and Kaua‘i. Maps on the left-hand side show designated categories of parcels, Sensitive Conservation Areas (blue), Priority Hunting Areas (yellow), and All Other Areas (dark grey) where wild ungulate management goals are variable or unknown. Tax map key (TMK) parcel boundaries are hidden for visual simplicity. Maps on the right-hand side show existing models of the relative abundance index (RAI) for that species of wild ungulate (Wild pig, feral goat, axis deer, or mouflon sheep) reprinted with permission from Risch et al., 2020, 2022, 2025, and in prep. Darker colors indicate higher predicted abundances of wild ungulates in natural conditions with no management.

Table 3.1. Land area designated by Sensitive Conservation Areas, Priority Hunting Areas, and All Other Areas regarding wild ungulates on the islands of Hawai‘i, Kaua‘i, Maui, and ‘Oahu.

Island	Wild Ungulate Management Goal	Total Acres	Percent (%)	Frequency
Hawai‘i	Sensitive Conservation Areas	964,762	42	184
	Priority Hunting Areas	119,965	5	30
	All Other Areas	1,220,203	53	1,979
	Total	2,304,931	100	2,193
Maui	Sensitive Conservation Areas	177,768	45	97
	Priority Hunting Areas	9,620	2	8
	All Other Areas	207,940	53	517
	Total	395,328	100	622
O‘ahu	Sensitive Conservation Areas	43,716	15	42
	Priority Hunting Areas	2,877	1	5
	All Other Areas	250,022	84	637
	Total	296,615	100	684
Kaua‘i	Sensitive Conservation Areas	73,039	23	20
	Priority Hunting Areas	30,314	9	11
	All Other Areas	217,666	68	275
	Total	321,019	100	306

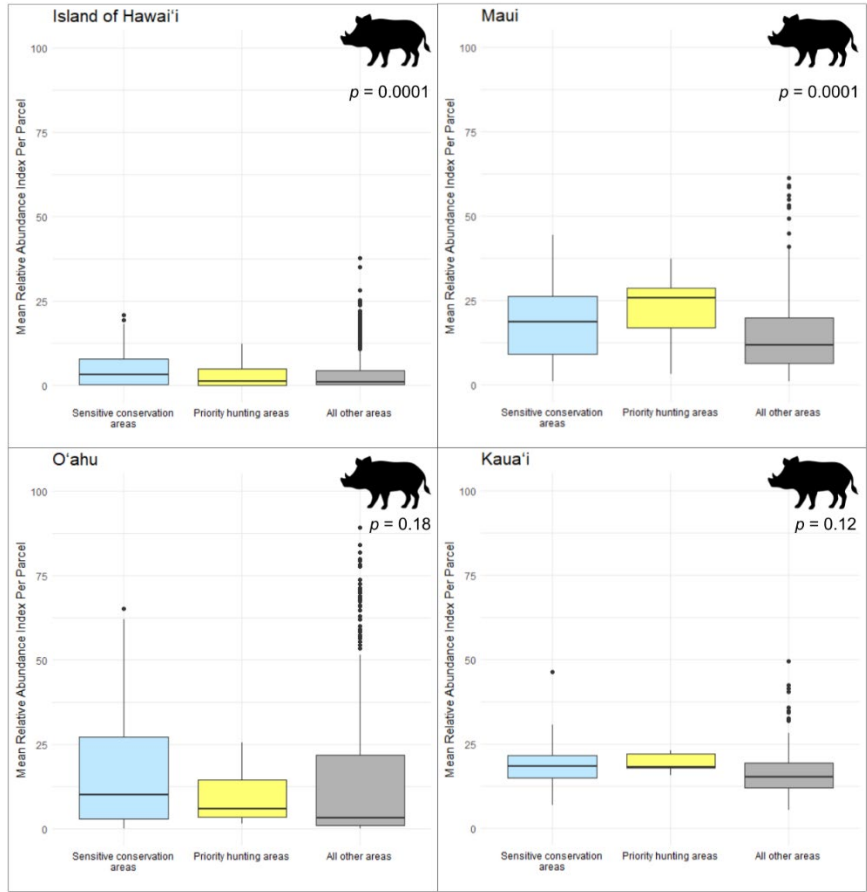


Figure 3.2. Box plots of the predicted relative abundance index (RAI) of wild pigs on the island of Hawai'i (n = 2,193), Maui (n = 622), O'ahu (n = 684), and Kaua'i (n = 306), within tax map key (TMK) land parcels categorized by general land management goals: Sensitive Conservation Areas (blue), Priority Hunting Areas (yellow), and All Other Areas (grey). ANOVA *p*-values are reported on each figure (significant *p* < 0.05).

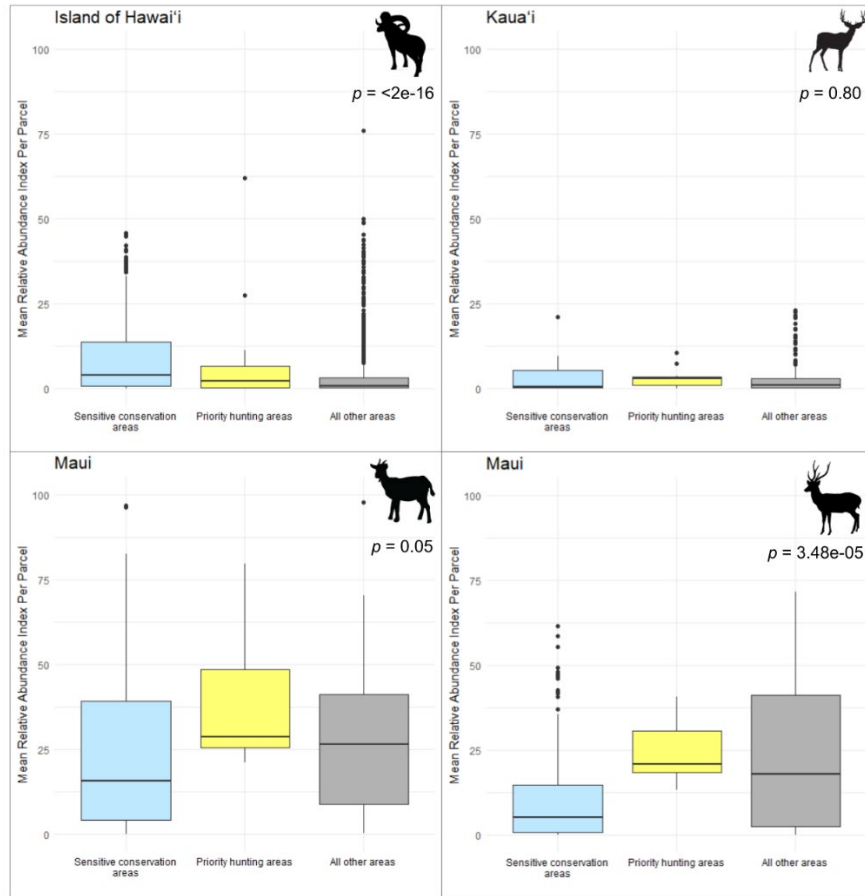


Figure 3.3. Box plots of the predicted relative abundance index (RAI) of mouflon sheep on the island of Hawai‘i (n = 2,193), black-tailed deer on Kaua‘i (n = 306), and feral goats and axis deer on Maui (n = 622), within tax map key (TMK) land parcels categorized by general land management goals: Sensitive Conservation Areas (blue), Priority Hunting Areas (yellow), and All Other Areas (grey). Graphs are arranged clockwise from the top, starting with mouflon sheep on Hawai‘i, followed by black-tailed deer on Kaua‘i, and feral goats and axis deer on Maui. Silhouettes of each wild ungulate species are included to correspond with their respective graphs. ANOVA p -values are reported on each figure (significant $p = <0.05$).

Discussion

In this study we aimed to compare the relative abundance of invasive wild ungulates in the absence of management actions between designated Priority Hunting Areas and Sensitive Conservation Areas. Our results highlight the importance of fencing in Sensitive Conservation Areas, as wild ungulate abundance was predicted to be higher in these areas on several islands compared with other categories. Our results also point to the importance of hunting pressure in game management areas, as feral goat and mouflon sheep abundances were predicted to be

higher in Priority Hunting Areas on some islands. Further, our results provide insights into potential differences in perceptions between private lands and those managed for hunting or conservation goals, as axis deer were predicted to be in higher abundance in areas outside of Priority Hunting and Sensitive Conservation lands.

Wild pigs had a significantly higher abundance in Sensitive Conservation Areas compared to All Other Areas on the island on Hawai'i ($p = 0.00007$) and Maui ($p = 0.002$) suggests that conservation lands may provide more favorable conditions for wild pigs, potentially due to increased cover and food availability in native plant-dominated areas (Risch et al., 2022).. Globally, wild pigs are recognized as an invasive species due to their adaptability, high reproductive rates, and omnivorous diet (Risch et al. 2021). In introduced environments, they cause substantial ecological damage by consuming native plants, invertebrates, and small vertebrates (Hegel et al., 2019; La Sala et al., 2023; Lavelle et al., 2017; Risch et al., 2021). Their rooting behavior disturbs soil structure, alters nutrient cycling, and facilitates erosion and the spread of invasive plant species (Brearley et al., 2024; Gray et al., 2020; Strauch et al., 2016). These impacts not only degrade habitat quality but also create direct competition with native wildlife (Carswell et al., 2024; Fay et al., 2023; O'Brien et al., 2019). As a result, many native species are threatened, with some already lost due to the extensive ecological disruption caused by wild pigs (Risch et al., 2021).

Similarly, axis deer on Maui were significantly more abundant in All Other Areas than in Sensitive Conservation Areas ($p = 0.0002$), indicating that lands designated for native species conservation may be less suitable for axis deer in the Hawaiian Islands. Importantly, our study demonstrates that axis deer are likely to be more abundant in land parcels not designated for conservation or hunting, such as ranchlands, leading to substantial impacts to agriculture,

ranching, and suburban gardens. Additionally, ranchlands may attract axis deer due to the availability of consistent water sources (Forsyth et al., 2019) and highly nutritious forage intended for livestock (Moe & Wegge, 1997; Watter et al., 2020). Unlike conservation and designated hunting areas, which are typically managed by a limited number of state or federal agencies, the responsibility of managing axis deer populations largely falls on a diverse network of landowners with potentially varying management priorities, capacities, and resources. To address these challenges, numerous efforts by private landowners and government agencies have been made since their introduction, which have had varying degrees of success. Examples include county efforts such as the Maui Axis Deer Task Force, county appropriated funds for ungulate deer fencing to private landowners, cooperative control efforts between DLNR and private landowners, and the emergence of United State Department of Agriculture (USDA) inspected wild meat to market businesses (e.g. Maui Nui Venison) (*01/13/22-Aerial Assessment of Moloka'i Axis Deer Illustrates the Extent of Overpopulation on Maui Nui*, 2022).

The significant difference in predicted feral goat abundance on Maui, with Priority Hunting Areas having higher populations than Sensitive Conservation Areas ($p = 0.05$), demonstrates potential benefits to hunters, in the form of increased hunting success, and potential benefits to the ecosystem, as hunters can help maintain goats at lower levels than would be supported by the ecosystem. On Pacific Islands, feral goats are found to prefer open, semi-arid landscapes (Chynoweth et al., 2013; Risch et al., 2022) which is consistent with the Priority Hunting Areas on Maui which are in lowland areas (yellow parcels; Figure 3.1). In island systems, feral goats are highly adaptable, as they are generalist foragers capable of exploiting a wide range of plant species and habitat types (Chynoweth et al., 2013; Hacker & Alemseged, 2013; Lu, 1988). Similar habitat associations have been documented globally, including in

Australia (Moseby et al., 2020) and the Galápagos Islands (Desender et al., 1999; Hamann, 1993), where feral goats have shown a strong preference for landscapes with short vegetation such as shrubland and abundant herbaceous cover. Although this type of landscape may be favored, feral goats have caused severe ecological impacts in introduced areas and thus are a concern for Sensitive Conservation Areas, even in lower abundance (Campbell & Donlan, 2005; Coblenz, 1978; Hess, 2016).

The most pronounced differences among parcel types were observed for mouflon sheep on the island of Hawai‘i. The significantly higher abundance of mouflon sheep in Sensitive Conservation Areas, compared to Priority Hunting Areas ($p = 0.01$) and areas outside of hunting and conservation areas ($p = 0.0001$), suggests that management efforts should be prioritized within conservation lands. This aligns with the historical proliferation of mouflon sheep on the slopes of Haleakalā following their introduction and highlights concerns similar to those raised in *Palila v. DLNR*, where extensive damage to native forest bird habitat prompted legal action (Banko et al., 2014; Ikagawa, 2013a; Judge et al., 2017b; *Palila v. Hawaii Department of Land and Natural Resources*, 1981). We note that the abundance estimates utilized in this study were derived solely from predictive models based on habitat and vegetation characteristics, and do not account for existing fencing or other management interventions implemented after *Palila v. DLNR* (Banko et al., 2014; Risch et al., 2020, 2022, 2025). However, the significantly higher predicted abundance in Priority Hunting Areas compared to other areas indicates that these locations have the potential to sustain larger populations, so hunting and other methods of control are critical to reduce ecosystem impacts of mouflon sheep.

We also evaluated the spatial arrangement of designated hunting and conservation areas. On the islands of Hawai‘i and Maui, several Priority Hunting Areas are located adjacent to

Sensitive Conservation Areas, underscoring the importance of fencing between these areas and the potential benefit provided by hunters in reducing incursion pressure along the fence lines. Although feral pigs on O‘ahu and Kaua‘i and black-tailed deer on Kaua‘i had no significant differences between land management parcel types, visually, we can see that high abundances are predicted in many conservation areas in the absence of fences or other management actions (Figure 1) (Risch et al., 2020, 2025). Thus, these areas may still experience substantial impacts from invasive ungulates if left unmanaged. Additionally, our results highlight the need for sustained management efforts, such as strategic fencing, increased hunting pressure, or targeted removal efforts to mitigate ecological damage.

Globally, our findings align with studies that examine the interplay between land management goals, species abundance, and ecological outcomes. For instance, research in the western United States and Australia has highlighted similar challenges, where private lands play a pivotal role in shaping wildlife dynamics (Taylor et al., 2025, 2025; Wilson et al., 2020, 2020). However, this study uniquely captures the cultural and geographic nuances of the Hawaiian Islands, where island ecosystems and endemic biodiversity are particularly vulnerable to the impacts of invasive ungulates. Wild ungulate management by the state has often focused only on state-managed lands (Ikagawa, 2013a), although this is not always the case. Further, private landowners may have a large degree of autonomy over their land but may be restricted in the types of management actions they can take due to regulatory or financial reasons (Benson, 2001).

Additionally, the findings reveal a significant research gap regarding the substantial portion of land with undefined management goals for wild ungulates, totaling 2,013,435 acres across the islands. This is particularly evident on private and agricultural lands, where economic impacts on operations result in substantial financial losses (Shwiff et al., 2024). Addressing this

gap by clarifying management goals could help alignment with state land management strategies, fostering more cohesive and effective approaches to wild ungulate management.

While this study provides valuable insights, it is important to acknowledge certain limitations. The analysis assumes that land designations—such as the Natural Area Reserves System (NARS), Wildlife Sanctuaries, and Game Management Areas (GMA)—serve as reasonable indicators for wild ungulate management goals. However, actual management practices may deviate from these generalizations, as individual land stewards may prioritize context-specific objectives. Additionally, some parcels may include multiple designated land uses, with Sensitive Conservation Area zones overlapping with Priority Hunting Areas. The use of RAI data from Risch et al. (2020, 2022, and 2024) for natural wild ungulate abundance presents another study limitation, as it does not account for current management interventions such as fencing, hunting efforts, or land use changes, and therefore represents predicted rather than actual abundances.

Despite these limitations, this study sheds light on the ecological and social dynamics of wild ungulate management in the Hawaiian Islands, offering a foundation for targeted, adaptive strategies. Future research should address areas outside of designated hunting and conservation lands by engaging large landowners across the Hawaiian Islands to better understand their objectives and constraints. Revising policies regarding wild ungulate management would require substantial legal and procedural changes (Ikagawa, 2013a), as well as careful consideration of stakeholder perspectives, including those of private landowners, state managers, and hunting groups. By addressing these challenges, Hawai'i can advance integrated approaches that balance ecological preservation with the effective stewardship of wildlife resources.

Chapter 4

Conclusions

Wild ungulate populations continue to be a growing concern and challenge for management globally, as their presence alters ecosystem functions, threatens biodiversity, and creates challenges with land-use priorities. In regions like Hawai'i, where large native predators are absent, wild ungulate populations have expanded unchecked, intensifying their impacts across landscapes. Researching their impacts is crucial for developing targeted management strategies that balance biodiversity conservation with the needs of ranchers and land managers. This study contributes to this effort by examining the relationship between wild ungulates and forage availability on Hawaiian ranchlands, as well as their predicted abundance across different land management designations.

Findings from Chapter 2 indicate that while wild ungulate presence was associated with reduced plant biomass, the relationship was not statistically significant, but vegetation loss was detected at 66% of sites indicating that losses may be site specific and further investigation is needed. Elevation emerged as a primary driver of vegetation availability, with grazing ungulates acting as a comparable alternative explanatory factor. These results align with rancher observations of widespread forage depletion, despite the lack of a strong statistical relationship. Additionally, ungulates were detected across all plant community types, reinforcing their generalist feeding behaviors. This chapter highlights the challenges in directly linking wild ungulate abundance to forage loss at a landscape scale, emphasizing the importance of site-specific factors in shaping grazing impacts.

Chapter 3 demonstrated that predicted wild ungulate abundance varied significantly across different land management classifications, providing key insights into where wild

ungulate impacts are likely most concentrated. Wild pigs and mouflon sheep were more abundant in Sensitive Conservation Areas, suggesting that these areas may provide preferred habitat conditions or limited hunting pressure, while axis deer were more prevalent in All Other Areas which are composed of agricultural and private lands. These findings suggest that wild ungulate management strategies must be tailored to land-use priorities, with conservation and game management lands potentially requiring increased fencing or removal efforts, and further research into management goals for agricultural and private lands.

Overall, this research contributes to the growing understanding of invasive wild ungulate dynamics across the islands of Hawai'i by linking their impacts on vegetation resources with broader landscape-scale distribution patterns. Future research should explore long-term monitoring of wild ungulate impacts and assess the effectiveness of different mitigation strategies in reducing wild ungulate pressure on key land-use areas.

Appendix: Detailed Data Tables

Table A1. List of all plant species scientific and common names that were found across study sites on the island of Hawai‘i and Maui organized by functional group (grass, forb, or shrub).

Functional Group	Scientific Name	Common Name
	<i>Anthoxanthum odoratum</i>	Sweet Vernal
	<i>Axonopus compressus</i>	Broadleaf Carpet Grass
	<i>Bromus catharticus</i>	Rescue Brome
	<i>Cenchrus ciliaris</i>	Buffel Grass
	<i>Cenchrus clandestinus</i>	Kikuyu Grass
	<i>Chloris virgata</i>	Feather Grass, Rhodes-Grass, Feather Windmill Grass
	<i>Cynodon dactylon</i>	Bermuda Grass
Grass	<i>Digitaria eriantha</i>	Pangola Grass
	<i>Digitaria insularis</i>	Sourgrass
	<i>Eragrostis pectinacea</i>	Carolina Lovegrass
	<i>Megathyrsus maximus</i>	Guinea Grass
	<i>Melinis repens</i>	Natal Redtop
	<i>Paspalum</i>	Paspalum
	<i>Schizachyrium condensatum</i>	Bushy Beard Grass or Bluestem
	<i>Stenotaphrum secundatum</i>	St. Augustine Grass
	<i>Sporobolus indicus</i>	West Indian Dropseed, Smutgrass, Rattail Grass
	<i>Abutilon grandifolium</i>	Hairy Indian Mallow, Hairy Abutilon
	<i>Amaranthus spinosus</i>	Spiny Amaranth
	<i>Asclepias physocarpa</i>	Balloon Plant
Forb	<i>Bidens pilosa</i>	Hairy Beggartick, Spanish Needle
	<i>Calyptracarpus vialis</i>	Straggler Daisy, Horseherb, Lawnflower
	<i>Chenopodium murale</i>	Nettleleaf Goosefoot
	<i>Conyza canadensis</i>	Horseweed, Maretail
	<i>Cyperus compressus</i>	Poorland Flatsedge

<i>Cyperus polystachyos</i>	Bunchy Sedge, Coast Flatsedge, Manyspike Flatsedge
<i>Desmodium incanum</i>	Kaimi Clover
<i>Erodium cicutarium</i>	Redstem Stork's Bill
<i>Helminthotheca echioides</i>	Bristly Oxtongue
<i>Hypochaeris radicata</i>	Catsear, Flatweed
<i>Indigofera hirsuta</i>	Hairy Indigo
<i>Indigofera suffruticosa</i>	Shrubby Indigo
<i>Kyllinga gracillima</i>	False-Green Kyllinga
<i>Lathyrus pratensis</i>	Meadow Pea
<i>Lotus corniculatus</i>	Birds Foot Trefoil
<i>Malva parviflora</i>	Cheeseweed Mallow
<i>Medicago lupulina</i>	Hop Clover, Yellow Trefoil
<i>Medicago polymorpha</i>	Bur Clover
<i>Macroptilium atropurpureum</i>	Purple Bush Bean, Siratro
<i>Mimosa pudica</i>	Hilahila, Sensitive Plant, Sleeping Grass
<i>Neonotonia wightii</i>	Tinaroo Glycine
<i>Nephrolepis cordifolia</i>	Kupu Kupu Fern
<i>Oxalis stricta</i>	Common Yellow Wood Sorrel
<i>Parthenium hysterophorus</i>	Ragweed Parthenium, False Ragweed, Santa Maria
<i>Senecio madagascariensis</i>	Madagascar Ragwort, Madagascar Fireweed, Variable Groundsel
<i>Sida fallax</i>	Yellow Ilima
<i>Trifolium dubium</i>	Lesser Trefoil, Suckling Clover, Little Hop Clover or Lesser Hop Trefoil
<i>Trifolium repens</i>	White Clover
<i>Triumfetta semitriloba</i>	Sacramento Bur
<i>Verbena litoralis</i>	Seashore Vervain, Oī
<i>Verbesina encelioides</i>	Cowpen Daisy, Golden Crownbeard

	<i>Abutilon grandifolium</i>	Hairy Indian Mallow, Hairy Abutilon
	<i>Eucalyptus obliqua</i>	Eucalyptus Tree
	<i>Lantana camara</i>	Largeleaf Lantana
Shrub	<i>Prosopis pallida</i>	Mesquite Tree
	<i>Rubus argutus</i>	Highbush Blackberry, Prickly Florida Blackberry
	<i>Solanum americanum</i>	Pōpolo, Glossy Nightshade
	<i>Solanum linnaeanum</i>	Apple of Sodom
Lichen	N/A	Foliose Lichen

Table A2. Summary of forage loss, vegetation change, and ungulate presence across study sites. The columns include site names, the dominant plant species at each site, and the average forage loss measured in kilograms per hectare (kg/ha). The gain or loss of vegetation is indicated as an increase or decrease in plant cover over the study period. Ungulates detected at each site are listed based on field observations and camera trap data. The relative abundance index (RAI) of grazing ungulates (RAI_{grazing}; axis deer, mouflon sheep, and feral goats) quantifies their presence at each site. The equivalent cattle loss (AU/Day) estimates the forage consumption by ungulates in terms of animal units per day (assuming one AU consumes 12 kg per day), providing a comparison to livestock grazing impacts.

Site	Dominant Plant Species	Average Forage Loss (kg/ha)	Gain/Loss of Vegetation	Ungulates Detected	RAI _{grazing}	Equivalent Cattle Loss (AU/Day)
Ranch A1	Kikuyu	74.72	Loss	Yes	15.12	6.23
Ranch A2	Kikuyu	-448.34	Gain	Yes	6.44	0.00
Ranch A3	Kikuyu	-1345.02	Gain	Yes	8.79	0.00
Ranch A4	Kikuyu	-298.89	Gain	Yes	7.87	0.00
Ranch A5	Kikuyu	-523.06	Gain	Yes	11.97	0.00
Ranch A6	Kikuyu	896.68	Loss	Yes	2.25	74.72
Ranch A7	Kikuyu	0.00	Gain	Yes	0.71	0.00
Ranch A8	Kikuyu	523.06	Loss	Yes	2.32	43.59
Ranch A9	Kikuyu	298.89	Loss	Yes	6.40	24.91
Ranch A10	Kikuyu	-1120.85	Gain	Yes	14.27	0.00
Ranch A11	Kikuyu and Kikuyu	298.90	Loss	Yes	13.08	24.91
Ranch B1	Rattail	1195.57	Loss	Yes	0.11	99.63
Ranch B2	Kikuyu	149.45	Loss	Yes	0.19	12.45
Ranch B3	Kikuyu	-373.62	Gain	No	0.00	0.00
Ranch B4	Kikuyu	-373.62	Gain	No	0.00	0.00
Ranch C1	Guinea grass	-988.00	Gain	Yes	5.62	0.00
Ranch C2	Guinea grass	-235.68	Gain	Yes	2.98	0.00

Ranch C3	Bare ground and litter	1.49	Loss	No	0.00	0.12
Ranch C4	Bare ground and litter	100.13	Loss	Yes	0.19	8.34
Ranch C5	Buffel grass	821.96	Loss	Yes	0.69	68.50
Ranch C6	Buffel grass	224.17	Loss	Yes	1.12	18.68
Ranch C7	Kikuyu	1569.20	Loss	Yes	5.12	130.77
Ranch C8	Kikuyu	821.96	Loss	Yes	10.66	68.50
Ranch C9	Kikuyu	1345.03	Loss	Yes	27.48	112.09
Ranch C10	Bermuda grass	1942.81	Loss	Yes	49.31	161.90
Ranch D1	Kikuyu	494.67	Loss	Yes	14.35	41.22
Ranch D2	Kikuyu	497.66	Loss	Yes	1.69	41.47
Ranch D3	Fire weed and Kikuyu	-366.15	Gain	Yes	2.66	0.00
Ranch D4	Sourgrass	1434.69	Loss	Yes	2.00	119.56
Ranch D5	Sourgrass and litter	2119.16	Loss	Yes	0.29	176.60
Ranch D6	Bare ground and litter	0.00	Gain	Yes	16.38	0.00
Ranch D7	Sourgrass	-375.11	Gain	Yes	0.03	0.00
Ranch D8	Litter and Sourgrass	911.03	Loss	Yes	1.64	75.92
Ranch D9	Kikuyu	2310.45	Loss	Yes	4.32	192.54
Ranch D10	Bare ground and litter	183.52	Loss	Yes	4.83	15.29

Table A3. Perceived wild ungulate management goals (Sensitive Conservation Areas, Priority Hunting Areas, and All Other Areas) of selected key land designation types grouped by ArcGIS layer name (Reserves, Department of Forestry and Wildlife (DOFAW) Management Guidelines, and State Land Use Designation). From the State Land Use District Boundaries layer, code Rural (R) was not included after <50 acres were removed from the analysis.

Land Management	GIS Layer and Land Category
Sensitive Conservation Areas	Reserves
	• Forest Reserve/Preserve (fr-p)
	• Land Trust (pvrt)
	• Marine Life Conservation District (mlcd)
	• National Area Reserve (nar)
	• National Park (np)
	• National Wildlife Refuge (nwr)
	• Nature Preserve (cnp)
• Private Preserve (prvt)	

	<ul style="list-style-type: none"> • Reserve (r) • The Nature Conservancy Preserve (tnc) • Wildlife Sanctuary (ws) (ws*) • Various Other Sanctuary (xs) • Other units managed by DOFAW (xxx) (Only Keauhou cooperative nene sanctuary)
	DOFAW Management Guidelines <ul style="list-style-type: none"> • C-1: High Conservation Resources

Priority Hunting Areas	Reserves <ul style="list-style-type: none"> • Game Management Area (gma) • Forest Reserve/Game Management Area (fr-gm) DOFAW Management Guidelines <ul style="list-style-type: none"> • H-1: Active Hunting Management
------------------------	---

All Other Areas	Reserves <ul style="list-style-type: none"> • Forest Reserve (fr) • Forest Reserve/ State Recreation Area (fr-sr) • Forest reserve/ Military Facility (fr-ml) • Forest Reserve/State Monument (fr-sm) • Forest Reserve / National Historical Park (fr-nhp) • Historic Preserve (hp) • National Historic Park (nhp) • National Historic Site (nhs) • National Memorial (nm) • Military (mil) • Office of Hawaiian Affairs (oha) • State Historical Park (shp) • State Monument (sm) • State Park (sp) • State Park - Other (sxp) and (sp-p*) • State Park Reserve (spr) • State Recreation Area (sra) • State Recreation Pier (srp) • State Scenic Shoreline (sss) • State Wayside (sw) • State Wilderness Park (swp) • Other units managed by DOFAW (xxx) (Maui motocross track and Kahuku motocross park (Oahu)) State Land Use Designation <ul style="list-style-type: none"> • Agriculture (A) • Conservation (C) • Urban (U)
-----------------	---

Literature Cited

- 01/13/22-Aerial Assessment of Moloka‘i Axis Deer Illustrates the Extent of Overpopulation on Maui Nui. (2022, January 13). Department of Land and Natural Resources.
<https://dlnr.hawaii.gov/blog/2022/01/13/nr22-005/>
- Adams, B. J. (n.d.). *Space Use and Annual Survival of Hybridized Mouflon Sheep in Hawaii and Comparing Estimates of Population Size Through Instantaneous Sampling and Photographic Capture-Recapture* [M.Sc., Brigham Young University]. Retrieved February 17, 2023, from
<https://www.proquest.com/docview/2430623818/abstract/3DFE27EDC26341B6PQ/1>
- Anderson, S. B. (2003). *Introduced axis deer (Axis axis) on Maui, Hawaii: History, current status, home range, grouping patterns, and a species account* [Ph.D., University of California, Davis].
<https://www.proquest.com/docview/305344750/abstract/6F66BC937D264A6APQ/1>
- Baker, J. K. (1975). *The Feral Pig in Hawaii Volcanes National Park*. 7.
- Ballari, S. A., Hendrix, B. D., Sample, M., & Nuñez, M. A. (2019). Management of invasive Pinaceae is imperiled by the lack of invasive ungulate control: Successful restoration requires multiple-species management. *Mammal Research*, 64(4), 535–542.
<https://doi.org/10.1007/s13364-019-00439-0>
- Banko, P. C., Camp, R. J., Farmer, C., Brinck, K. W., Leonard, D. L., & Stephens, R. M. (2013). Response of palila and other subalpine Hawaiian forest bird species to prolonged drought and habitat degradation by feral ungulates. *Biological Conservation*, 157, 70–77.
<https://doi.org/10.1016/j.biocon.2012.07.013>

- Banko, P. C., Hess, S. C., Scowcroft, P. G., Farmer, C., Jacobi, J. D., Stephens, R. M., Camp, R. J., Leonard, D. L., Brinck, K. W., Juvik, J. O., & Juvik, S. P. (2014). Evaluating the Long-Term Management of Introduced Ungulates to Protect the Palila, an Endangered Bird, and Its Critical Habitat in Subalpine Forest of Mauna Kea, Hawai'i. *Arctic, Antarctic, and Alpine Research*, *46*(4), 871–889. <https://doi.org/10.1657/1938-4246-46.4.871>
- Barroso, F. G., Alados, C. L., & Boza, J. (2000). Social hierarchy in the domestic goat: Effect on food habits and production. *Applied Animal Behaviour Science*, *69*(1), 35–53. [https://doi.org/10.1016/S0168-1591\(00\)00113-1](https://doi.org/10.1016/S0168-1591(00)00113-1)
- Bartoń, K. (2023). *MuMIn: Multi-Model Inference* (Version 1.47.5) [R]. <https://cran.r-project.org/web/packages/MuMIn/index.html>
- Beasley, J. C., Grazia, T. E., Johns, P. E., & Mayer, J. J. (2014). Habitats associated with vehicle collisions with wild pigs. *Wildlife Research*, *40*(8), 654–660. <https://doi.org/10.1071/WR13061>
- Beasley, J. C., Pitt, W. C., & Witmer, G. W. (2018). *Ecology and management of terrestrial vertebrate invasive species in the United States*. Taylor & Francis. <https://doi.org/10.1201/9781315157078>
- Benson, D. E. (2001). Survey of State Programs for Habitat, Hunting, and Nongame Management on Private Lands in the United States. *Wildlife Society Bulletin (1973-2006)*, *29*(1), 354–358.
- Black, K. E., & Jensen, W. F. (2018). Motivations and Satisfaction of North Dakota Deer Hunters During a Temporal Decline in Deer Populations. *Human–Wildlife Interactions*, *12*(3):427–443. digitalcommons.usu.edu/hwi

- Bleier, N., Kovács, I., Schally, G., Szemethy, L., & Csányi, S. (2017). Spatial and temporal characteristics of the damage caused by wild ungulates in maize (*Zea mays* L.) crops. *International Journal of Pest Management*, *63*(1), 92–100.
<https://doi.org/10.1080/09670874.2016.1227487>
- Bonham, C. D., Mergen, D. E., & Montoya, S. (2004). Plant Cover Estimation: A Contiguous Daubenmire Frame. *Rangelands*, *26*(1), 17–22. [https://doi.org/10.2111/1551-501X\(2004\)26\[17:PCEACD\]2.0.CO;2](https://doi.org/10.2111/1551-501X(2004)26[17:PCEACD]2.0.CO;2)
- Bora, Z., Angassa, A., Wang, Y., Xu, X., & You, Y. (2021). Effect of Elevation on the Density and Species Composition of Encroacher Woody Plants in Borana Rangeland, Southern Ethiopia. *Environmental Management*, *67*(6), 1075–1087.
<https://doi.org/10.1007/s00267-021-01458-x>
- Brearley, F. Q., Song, H., Tripathi, B. M., Dong, K., Zin, N. M., Abdul Rachman, A. R., Ickes, K., Adams, J. M., & Luskin, M. S. (2024). Wild pigs influence tropical forest soil microbial communities in a forest-agriculture mosaic landscape. *Forest Ecology and Management*, *572*, 122320. <https://doi.org/10.1016/j.foreco.2024.122320>
- Bremer, L. L., Nathan, N., Trauernicht, C., Pascua, P., Krueger, N., Jokiel, J., Barton, J., & Daily, G. C. (2021). Maintaining the Many Societal Benefits of Rangelands: The Case of Hawai‘i. *Land*, *10*(7), Article 7. <https://doi.org/10.3390/land10070764>
- Briske, D. D., Joyce, L. A., Polley, H. W., Brown, J. R., Wolter, K., Morgan, J. A., McCarl, B. A., & Bailey, D. W. (2015). Climate-change adaptation on rangelands: Linking regional exposure with diverse adaptive capacity. *Frontiers in Ecology and the Environment*, *13*(5), 249–256.

- Brondum, M. C., Collier, Z. A., Luke, C. S., Goatcher, B. L., & Linkov, I. (2017). Selection of invasive wild pig countermeasures using multicriteria decision analysis. *Science of The Total Environment*, 574, 1164–1173. <https://doi.org/10.1016/j.scitotenv.2016.09.155>
- Byrd, E., Lee, J. G., & Widmar, N. J. O. (2017). Perceptions of Hunting and Hunters by U.S. Respondents. *Animals : An Open Access Journal from MDPI*, 7(11), 83. <https://doi.org/10.3390/ani7110083>
- Calcagno, V., & de Mazancourt, C. (2010). glmulti: An R Package for Easy Automated Model Selection with (Generalized) Linear Models. *Journal of Statistical Software*, 034(i12). <https://ideas.repec.org/a/jss/jstsof/v034i12.html>
- Campbell, K., & Donlan, C. J. (2005). Feral Goat Eradications on Islands. *Conservation Biology*, 19(5), 1362–1374. <https://doi.org/10.1111/j.1523-1739.2005.00228.x>
- Carlyle, C. N., Fraser, L. H., & Turkington, R. (2014). Response of grassland biomass production to simulated climate change and clipping along an elevation gradient. *Oecologia*, 174(3), 1065–1073. <https://doi.org/10.1007/s00442-013-2833-2>
- Carpio, A. J., Guerrero-Casado, J., Barasona, J. A., Tortosa, F. S., Vicente, J., Hillstrom, L., & Delibes-Mateos, M. (2017). Hunting as a source of alien species: A European review. *BIOLOGICAL INVASIONS*, 19(4), 1197–1211. <https://doi.org/10.1007/s10530-016-1313-0>
- Carswell, B. M., Boyle, S. P., Brook, R. K., van Beest, F. M., & Vander Wal, E. (2024). Variation in spatiotemporal activity may reduce competitive interactions between invasive wild pigs (*Sus scrofa*) and native mammal species. *Canadian Journal of Zoology*, 102(4), 410–418. <https://doi.org/10.1139/cjz-2022-0145>

- Celis, G., Ungar, P., Sokolov, A., Sokolova, N., Böhner, H., Liu, D., Gilg, O., Fufachev, I., Pokrovskaya, O., Ims, R. A., Zhou, W., Morris, D., & Ehrich, D. (2024). A versatile, semi-automated image analysis workflow for time-lapse camera trap image classification. *Ecological Informatics*, *81*, 102578. <https://doi.org/10.1016/j.ecoinf.2024.102578>
- Chynoweth, M. W., Litton, C. M., Lepczyk, C. A., Hess, S. C., & Cordell, S. (2013). Biology and Impacts of Pacific Island Invasive Species. 9. *Capra hircus*, the Feral Goat (Mammalia: Bovidae). *Pacific Science*, *67*(2), 141–156. <https://doi.org/10.2984/67.2.1>
- Coblentz, B. E. (1978). The effects of feral goats (*Capra hircus*) on island ecosystems. *Biological Conservation*, *13*(4), 279–286. [https://doi.org/10.1016/0006-3207\(78\)90038-1](https://doi.org/10.1016/0006-3207(78)90038-1)
- Cole, R. J., & Litton, C. M. (2014). Vegetation response to removal of non-native feral pigs from Hawaiian tropical montane wet forest. *Biological Invasions*, *16*(1), 125–140. <https://doi.org/10.1007/s10530-013-0508-x>
- Comte, S., Bengsen, A. J., Botterill-James, T., Brausch, C., Bryant, S. L., Dickson, C. R., Hamer, R., Hamilton, D. G., Seaman, J., Taylor, P., & Forsyth, D. M. (2025). Impacts of Recreational Hunting on an Introduced Population of Fallow Deer (*Dama dama*) in Tasmania, Australia. *Ecological Management & Restoration*, *26*(1), e70001. <https://doi.org/10.1111/emr.70001>
- Cruz, F., Carrion, V., Campbell, K. J., Lavoie, C., & Donlan, C. J. (2009). Bio-Economics of Large-Scale Eradication of Feral Goats From Santiago Island, Galápagos. *The Journal of Wildlife Management*, *73*(2), 191–200. <https://doi.org/10.2193/2007-551>
- CTAHR: *Weeds of Hawaii's Pastures and Natural Areas; An Identification and Management Guide*. (n.d.). Retrieved September 12, 2024, from <https://www.ctahr.hawaii.edu/invweed/weedsHI.html>

- D'Adamo, F., Ogutu, B., Brandt, M., Schurgers, G., & Dash, J. (2021). Climatic and non-climatic vegetation cover changes in the rangelands of Africa. *Global and Planetary Change*, 202, 103516. <https://doi.org/10.1016/j.gloplacha.2021.103516>
- D'Antonio, C. M., Tunison, J. T., & Loh, R. K. (2000). Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral Ecology*, 25(5), 507–522. <https://doi.org/10.1046/j.1442-9993.2000.01079.x>
- Desender, K., Baert, L., Maelfait, J.-P., & Verdyck, P. (1999). Conservation on Volcán Alcedo (Galápagos): Terrestrial invertebrates and the impact of introduced feral goats. *Biological Conservation*, 87(3), 303–310. [https://doi.org/10.1016/S0006-3207\(98\)00078-0](https://doi.org/10.1016/S0006-3207(98)00078-0)
- DiTomaso, J. M., Masters, R. A., & Peterson, V. F. (2010). Rangeland Invasive Plant Management. *Rangelands*, 32(1), 43–47. <https://doi.org/10.2111/RANGELANDS-D-09-00007.1>
- Dobson, A. D. M., Milner-Gulland, E. J., Ingram, D. J., & Keane, A. (2019). A Framework for Assessing Impacts of Wild Meat Hunting Practices in the Tropics. *Human Ecology*, 47(3), 449–464. <https://doi.org/10.1007/s10745-019-0075-6>
- Drimaj, J., Skoták, V., Kamler, J., Plhal, R., Adamec, Z., Mikulka, O., & Janata, P. (2023). Comparison of Methods for Estimating Damage by Wild Ungulates on Field Crops. *Agriculture*, 13(6), Article 6. <https://doi.org/10.3390/agriculture13061184>
- Duffy, D. J., & Lepczyk, C. A. (2021). The Historical Ecology of Game Species Introductions in Hawai'i. *Pacific Science*, 75(1). <https://doi.org/10.2984/75.1.1>
- Dunkell, D. O., Bruland, G. L., Evensen, C. I., & Litton, C. M. (2011). Runoff, Sediment Transport, and Effects of Feral Pig (*Sus scrofa*) Exclusion in a Forested Hawaiian Watershed. *Pacific Science*, 65(2), 175–194. <https://doi.org/10.2984/65.2.175>

- Elzinga, C. L., Salzer, D. W., & Willoughby, J. W. (1999). Measuring and Monitoring Plant Populations. *Journal of Range Management*, 52(5), 544. <https://doi.org/10.2307/4003786>
- Fay, A. S., Zenas, S. J., Smith, M. D., & Ditchkoff, S. S. (2023). Impacts of wild pigs on acorn availability as a food source for native wildlife. *Wildlife Research*, 50(12), 1123–1130. <https://doi.org/10.1071/WR22146>
- Fennell, M., Beirne, C., & Burton, A. C. (2022). Use of object detection in camera trap image identification: Assessing a method to rapidly and accurately classify human and animal detections for research and application in recreation ecology. *Global Ecology and Conservation*, 35, e02104. <https://doi.org/10.1016/j.gecco.2022.e02104>
- Forsyth, D. M., Pople, A., Woodford, L., Brennan, M., Amos, M., Moloney, P. D., Fanson, B., & Story, G. (2019). Landscape-scale effects of homesteads, water, and dingoes on invading chital deer in Australia's dry tropics. *Journal of Mammalogy*, 100(6), 1954–1965. <https://doi.org/10.1093/jmammal/gyz139>
- Francesco, R., Fabio, B., Roberto, F., Pierre, E. A. J., & Leonardo, C. (2019). Geographical Relationship between Ungulates, Human Pressure and Territory. *Applied Spatial Analysis and Policy*, 12(4), 847–870. <https://doi.org/10.1007/s12061-018-9272-8>
- Frank, D. A., Wallen, R. L., & White, P. J. (2016). Ungulate control of grassland production: Grazing intensity and ungulate species composition in Yellowstone Park. *Ecosphere*, 7(11), e01603. <https://doi.org/10.1002/ecs2.1603>
- Freschi, P., Fascetti, S., Riga, F., Rizzardini, G., Musto, M., & Cosentino, C. (2021). Feeding Preferences of the Italian Roe Deer (*Capreolus capreolus italicus* Festa, 1925) in a Coastal Mediterranean Environment. *Animals*, 11(2), Article 2. <https://doi.org/10.3390/ani11020308>

- Fritts, T. H., & Rodda, G. H. (1998). The Role of Introduced Species in the Degradation of Island Ecosystems: A Case History of Guam. *Annual Review of Ecology and Systematics*, 29(1), 113–140. <https://doi.org/10.1146/annurev.ecolsys.29.1.113>
- Gibson-Forty, E. V. J., Barnett, K. L., Tissue, D. T., & Power, S. A. (2016). Reducing rainfall amount has a greater negative effect on the productivity of grassland plant species than reducing rainfall frequency. *Functional Plant Biology*, 43(4), 380. <https://doi.org/10.1071/FP15174>
- Gordon, I. J., Hester, A. J., & Festa-Bianchet, M. (2004). REVIEW: The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, 41(6), 1021–1031. <https://doi.org/10.1111/j.0021-8901.2004.00985.x>
- Gray, S. M., Roloff, G. J., Kramer, D. B., Etter, D. R., Vercauteren, K. C., & Montgomery, R. A. (2020). Effects of Wild Pig Disturbance on Forest Vegetation and Soils. *The Journal of Wildlife Management*, 84(4), 739–748. <https://doi.org/10.1002/jwmg.21845>
- Gürtler, R. E., Ballari, S. A., Maranta, A. A., & Cohen, J. E. (2023). Controlling the abundance of invasive exotic wild boar (*Sus scrofa*) improves palm-tree conservation in north-eastern Argentina. *European Journal of Wildlife Research*, 69(2), 1–15. <https://doi.org/10.1007/s10344-023-01668-0>
- Hacker, R. B., & Alemseged, Y. (2013). Incorporating farmed goats into sustainable rangeland grazing systems in southern Australia: A review. *The Rangeland Journal*, 36(1), 25–33. <https://doi.org/10.1071/RJ13035>
- Hamann, O. (1993). On vegetation recovery, goats and giant tortoises on Pinta Island, Galápagos, Ecuador. *Biodiversity & Conservation*, 2(2), 138–151. <https://doi.org/10.1007/BF00056130>

- Han, W., Chen, L., Su, X., Liu, D., Jin, T., Shi, S., Li, T., & Liu, G. (2022). Effects of Soil Physico-Chemical Properties on Plant Species Diversity Along an Elevation Gradient Over Alpine Grassland on the Qinghai-Tibetan Plateau, China. *Frontiers in Plant Science*, *13*. <https://doi.org/10.3389/fpls.2022.822268>
- Hart, P. J., Ibanez, T., Uehana, S., & Pang-Ching, J. (2020). Forest regeneration following ungulate removal in a montane Hawaiian wet forest. *Restoration Ecology*, *28*(4), 757–765. <https://doi.org/10.1111/rec.13116>
- Hawaii/Pacific Islands Area | Field Office Technical Guide | NRCS - USDA. (n.d.). Retrieved September 11, 2024, from <https://efotg.sc.egov.usda.gov/#/state/HI/documents/section=1&folder=65126>
- Hegel, C. G. Z., Santos, L. R., Marinho, J. R., & Marini, M. Â. (2019). Is the wild pig the real “big bad wolf”? Negative effects of wild pig on Atlantic Forest mammals. *Biological Invasions*, *21*(12), 3561–3574. <https://doi.org/10.1007/s10530-019-02068-9>
- Heisler-White, J. L., Blair, J. M., Kelly, E. F., Harmony, K., & Knapp, A. K. (2009). Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Global Change Biology*, *15*(12), 2894–2904. <https://doi.org/10.1111/j.1365-2486.2009.01961.x>
- Heitschmidt, R. K., & Stuth, J. W. (1991). *Grazing management: An ecological perspective*. Timber Press.
- Hess, S. C. (2016). A Tour de Force by Hawaii’s Invasive Mammals: Establishment, Takeover, and Ecosystem Restoration through Eradication. *Proceedings of the Vertebrate Pest Conference*, *27*(27). <https://doi.org/10.5070/V427110564>

- Hess, S. C., Banko, P. C., Brenner, G. J., & Jacobi, J. D. (1999). Factors Related to the Recovery of Subalpine Woodland on Mauna Kea, Hawaii. *Biotropica*, 31(2), 212–219.
<https://doi.org/10.1111/j.1744-7429.1999.tb00133.x>
- Hess, S. C., Sprague, J., & Muise, J. (2022). Evidence for Irruptive Fluctuation in Axis Deer of Hawai‘i. *Proceedings of the Vertebrate Pest Conference*, 30(30).
<https://escholarship.org/uc/item/5vz709dw>
- Holechek, J. (with Pieper, R. D., & Herbel, C. H.). (1989). *Range management: Principles and practices*. Prentice Hall.
- Hughey, K. F. D., & Hickling, G. J. (2006). Ecologically based policy evaluation: Application to ungulate management in New Zealand. *Environmental Science & Policy*, 9(7), 639–651.
<https://doi.org/10.1016/j.envsci.2006.07.001>
- Ibañez-Alvarez, M., Baraza, E., Serrano, E., Romero-Munar, A., Cardona, C., Bartolome, J., & Krumins, J. A. (2022). Ungulates alter plant cover without consistent effect on soil ecosystem functioning. *Agriculture, Ecosystems & Environment*, 326, 107796.
<https://doi.org/10.1016/j.agee.2021.107796>
- Ikagawa, M. (2013a). Invasive ungulate policy and conservation in Hawaii. *Pacific Conservation Biology*, 19(4), 270. <https://doi.org/10.1071/PC130270>
- Ikagawa, M. (2013b). *Mouflon Sheep and Rare Plants on the Island of Hawai‘i, With an Analysis of State Ungulate Mangement*. University of Hawai‘i at Mānoa.
- iNaturalist*. (2024). iNaturalist. <https://www.inaturalist.org/>
- Irvine, R. L., & Thorley, J. L. (2024). Relative efficiency of hunting methods during an incomplete Sitka black-tailed deer eradication on Haida Gwaii, Canada. *Ecological Solutions and Evidence*, 5(1), e12312. <https://doi.org/10.1002/2688-8319.12312>

- Joyce, L. A., Briske, D. D., Brown, J. R., Polley, H. W., McCarl, B. A., & Bailey, D. W. (2013). Climate Change and North American Rangelands: Assessment of Mitigation and Adaptation Strategies. *Rangeland Ecology and Management*, *66*(5), 512–528. <https://doi.org/10.2111/REM-D-12-00142.1>
- Judge, S. W., Hess, S. C., Faford, J. K., Pacheco, D., & Leopold, C. R. (2017a). Monitoring Eradication of European Mouflon Sheep from the Kahuku Unit of Hawai'i Volcanoes National Park. *Pacific Science*, *71*(4), 425–436. <https://doi.org/10.2984/71.4.3>
- Judge, S. W., Hess, S. C., Faford, J. K., Pacheco, D., & Leopold, C. R. (2017b). Monitoring Eradication of European Mouflon Sheep from the Kahuku Unit of Hawai'i Volcanoes National Park 1. *Pacific Science*, *71*(4), 425–436. <https://doi.org/10.2984/71.4.3>
- Kardol, P., Dickie, I. A., St. John, M. G., Husheer, S. W., Bonner, K. I., Bellingham, P. J., & Wardle, D. A. (2014). Soil-mediated effects of invasive ungulates on native tree seedlings. *Journal of Ecology*, *102*(3), 622–631. <https://doi.org/10.1111/1365-2745.12234>
- Kesch, M. K., Bauer, D. T., & Loveridge, A. J. (2015). Break on Through to the Other Side: The Effectiveness of Game Fencing to Mitigate Human—Wildlife Conflict. *African Journal of Wildlife Research*, *45*(1), 76–87. <https://doi.org/10.3957/056.045.0109>
- Khattak, R. H., Teng, L., Mehmood, T., Ahmad, S., & Liu, Z. (2022). Impacts of the Wild Boar (*Sus scrofa*) on the Livelihood of Rural Communities in Pakistan and Understanding Public Attitudes towards Wild Boars. *Animals*, *12*(23), Article 23. <https://doi.org/10.3390/ani12233381>

- Khosravi Aqdam, K., Asadzadeh, F., Rezapour, S., & Nouri, A. (2023). Comparative assessment of soil fertility across varying elevations. *Environmental Monitoring and Assessment*, *195*(8), 1–15. <https://doi.org/10.1007/s10661-023-11610-1>
- Kim, K., Andersen, D., & Jang, Y. (2023). Predictive Modeling of Ungulate–Vehicle Collision in the Republic of Korea. *Biology*, *12*(8), Article 8. <https://doi.org/10.3390/biology12081068>
- Klingman, D. L., Miles, S. R., & Mott, G. O. (1943). The Cage Method for Determining Consumption and Yield of Pasture Herbage¹. *Agronomy Journal*, *35*(9), 739–746. <https://doi.org/10.2134/agronj1943.00021962003500090001x>
- Kramer, C. J., Boudreau, M. R., Powers, R., VerCauteren, K. C., Miller, R. S., & Brook, R. K. (2024). Potential landscape connectivity for invasive wild pigs (*Sus scrofa*) across the northern prairies of North America. *Biological Invasions*, *26*(8), 2525–2538. <https://doi.org/10.1007/s10530-024-03326-1>
- Kramer, K., Groot Bruinderink, G. W. T. A., & Prins, H. H. T. (2006). Spatial interactions between ungulate herbivory and forest management. *Forest Ecology and Management*, *226*(1), 238–247. <https://doi.org/10.1016/j.foreco.2006.01.037>
- La Sala, L. F., Burgos, J. M., Caruso, N. C., Bagnato, C. E., Ballari, S. A., Guadagnin, D. L., Kindel, A., Etges, M., Merino, M. L., Marcos, A., Skewes, O., Schettino, D., Perez, A. M., Condori, E., Tammone, A., Carpinetti, B., & Zalba, S. M. (2023). Wild pigs and their widespread threat to biodiversity conservation in South America. *Journal for Nature Conservation*, *73*, 126393. <https://doi.org/10.1016/j.jnc.2023.126393>
- Lavelle, M. J., Snow, N. P., Fischer, J. W., Halseth, J. M., VanNatta, E. H., & VerCauteren, K. C. (2017). Attractants for wild pigs: Current use, availability, needs, and future potential.

- European Journal of Wildlife Research*, 63(6), 1–14. <https://doi.org/10.1007/s10344-017-1144-z>
- Leopold, C. R., & Hess, S. C. (2017). Conversion of native terrestrial ecosystems in Hawai'i to novel grazing systems: A review. *Biological Invasions*, 19(1), 161–177. <https://doi.org/10.1007/s10530-016-1270-7>
- Leorna, S., & Brinkman, T. (2022). Human vs. machine: Detecting wildlife in camera trap images. *Ecological Informatics*, 72, 101876. <https://doi.org/10.1016/j.ecoinf.2022.101876>
- Lepczyk, C. A., & Duffy, D. J. (2019). Historical trends in Hawaiian game harvest and hunter participation in Hawai'i from 1946-2008. *PLoS One*, 14(8), e0219283–e0219283. <https://doi.org/10.1371/journal.pone.0219283>
- Li, Y. (2020). Impacts of Invasive Species on Agriculture in Hawaii. *Agricultural Research & Technology: Open Access Journal, Juniper Publishers Inc.*, 24(1), 12–14.
- Lu, C. D. (1988). Grazing behavior and diet selection of goats. *Small Ruminant Research*, 1(3), 205–216. [https://doi.org/10.1016/0921-4488\(88\)90049-1](https://doi.org/10.1016/0921-4488(88)90049-1)
- Luat-Hū'eu, K. K., Vaughan, M. B., & Price, M. R. (2023). Understanding local pig hunter values and practices as a means toward comanagement of feral pigs (*Sus scrofa*; pua'a) in the Hawaiian Islands. *Ecology & Society*, 28(2), 1–13. <https://doi.org/10.5751/ES-13679-280232>
- Luat-Hū'eu, K. K., Winter, K. B., Vaughan, M. B., Barca, N., Price, M. R., Luat-Hū'eu, K. K., Winter, K. B., Vaughan, M. B., Barca, N., & Price, M. R. (2021). Understanding the co-evolutionary relationships between Indigenous cultures and non-native species can inform more effective approaches to conservation: The example of pigs (pua'a; *Sus*

- scrofa) in Hawai‘i. *Pacific Conservation Biology*, 27(4), 442–450.
<https://doi.org/10.1071/PC20086>
- Marchiori, E., Sturaro, E., & Ramanzin, M. (2012). Wild red deer [*Cervus elaphus* L.] grazing may seriously reduce forage production in mountain meadows. *Italian Journal of Animal Science*, 11(1), e9. <https://doi.org/10.4081/ijas.2012.e9>
- Martínez, Á., & Martín, Á. J. (2017). A matrix system using quality classes can be applied for managing sustainable wild ungulates populations: Convergence below optimum capacity. *Ecological Engineering*, 108, 10–16. <https://doi.org/10.1016/j.ecoleng.2017.07.043>
- Microsoft. (2020). *AI for Earth camera trap image processing API. (4.1)* [Computer software]. Microsoft. <https://github.com/microsoft/CameraTraps/blob/main/megadetector.md>
- Moe, S. R., & Wegge, P. (1997). The effects of cutting and burning on grass quality and axis deer (*Axis axis*) use of grassland in lowland Nepal. *Journal of Tropical Ecology*, 13(2), 279–292. <https://doi.org/10.1017/S0266467400010452>
- Moseby, K. E., Read, J. L., & Andersen, G. E. (2020). Goat movement patterns inform management of feral goat populations in semiarid rangelands. *Wildlife Research*, 48(1), 44–54. <https://doi.org/10.1071/WR20042>
- Motsi, T. R., Tichiwangana, S. C., Matope, G., & Mukarati, N. L. (2013). A serological survey of brucellosis in wild ungulate species from five game parks in Zimbabwe. *Onderstepoort Journal of Veterinary Research*, 80(1), Article 1.
- Mueller-Dombois, D., & Spatz, G. (1975). The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. *Phytocoenologia*, 3(1), 1–29.
<https://doi.org/10.1127/phyto/3/1975/1>

- Muñoz, P. M., Boadella, M., Arnal, M., de Miguel, M. J., Revilla, M., Martínez, D., Vicente, J., Acevedo, P., Oleaga, Á., Ruiz-Fons, F., Marín, C. M., Prieto, J. M., de la Fuente, J., Barral, M., Barberán, M., de Luco, D. F., Blasco, J. M., & Gortázar, C. (2010). Spatial distribution and risk factors of Brucellosis in Iberian wild ungulates. *BMC Infectious Diseases*, *10*(1), 46. <https://doi.org/10.1186/1471-2334-10-46>
- Mysterud, A. (2006). The concept of overgrazing and its role in management of large herbivores. *Wildlife Biology*, *12*(2), 129–141. [https://doi.org/10.2981/0909-6396\(2006\)12\[129:TCOOAI\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2006)12[129:TCOOAI]2.0.CO;2)
- Newman, J. A., Parsons, A. J., Thornley, J. H. M., Penning, P. D., & Krebs, J. R. (1995). Optimal Diet Selection by a Generalist Grazing Herbivore. *Functional Ecology*, *9*(2), 255–268. <https://doi.org/10.2307/2390572>
- Nogueira-Filho, S. L. G., Nogueira, S. S. C., & Fragoso, J. M. V. (2009). Ecological impacts of feral pigs in the Hawaiian Islands. *Biodiversity and Conservation*, *18*(14), 3677. <https://doi.org/10.1007/s10531-009-9680-9>
- O'Brien, P., Vander Wal, E., Koen, E. L., Brown, C. D., Guy, J., van Beest, F. M., & Brook, R. K. (2019). Understanding habitat co-occurrence and the potential for competition between native mammals and invasive wild pigs (*Sus scrofa*) at the northern edge of their range. *Canadian Journal of Zoology*, *97*(6), 537–546. <https://doi.org/10.1139/cjz-2018-0156>
- O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, *6*(2), 131–139. <https://doi.org/10.1017/S1367943003003172>

- Ojima, D. S., Aicher, R., Archer, S. R., Bailey, D. W., Casby-Horton, S. M., Cavallaro, N., Reyes, J. J., Tanaka, J. A., & Washington-Allen, R. A. (2020). A climate change indicator framework for rangelands and pastures of the USA. *Climatic Change*, *163*(4), 1733–1750. <https://doi.org/10.1007/s10584-020-02915-y>
- Palila v. Hawaii Department of Land and Natural Resources, 639 Federal Reporter, Second Series (F.2d) 495 (9th Circuit Court of Appeals 1981).
- Palmer, M. S., Swanson, A., Kosmala, M., Arnold, T., & Packer, C. (2018). Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. *African Journal of Ecology*, *56*(4), 791–803. <https://doi.org/10.1111/aje.12566>
- Patton, M. I., Jöchle, W., & Penfold, L. M. (2007). Review of contraception in ungulate species. *Zoo Biology*, *26*(4), 311–326. <https://doi.org/10.1002/zoo.20154>
- Perroy, R., & Collier, E. (2020). *2020 Update to the Hawai‘i Statewide Agricultural Land Use Baseline* [Hawai‘i Department of Agriculture]. <https://drive.google.com/drive/folders/1XAqTQC8sq49uk-hZv-8UcgoZN3iesw0U>
- Reaser, J. K., Meyerson, L. A., Cronk, Q., De Poorter, M., Eldrege, L. G., Green, E., Kairo, M., Latasi, P., Mack, R. N., Mauremootoo, J., O’Dowd, D., Orapa, W., Sastroutomo, S., Saunders, A., Shine, C., Thrainsson, S., & Vaiutu, L. (2007). Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environmental Conservation*, *34*(2), 98–111. <https://doi.org/10.1017/S0376892907003815>
- Risch, D. R., Honarvar, S., & Price, M. R. (2022). Environmental drivers of seasonal shifts in abundance of wild pigs (*Sus scrofa*) in a tropical island environment. *Ecological Processes*, *11*(1), 55. <https://doi.org/10.1186/s13717-022-00395-9>

- Risch, D. R., Omick, J., Honarvar, S., Smith, H., Stogner, B., Fugett, M., & Price, M. R. (2025). Insights Into Ungulate Distributions Show Range Expansion, Competition, and Potential Impacts on a Sub-Tropical Island. *Pacific Science*, 78(2), 201–217.
<https://doi.org/10.2984/78.2.5>
- Risch, D. R., Ringma, J., Honarvar, S., & Price, M. R. (2020). A comparison of abundance and distribution model outputs using camera traps and sign surveys for feral pigs. *Pacific Conservation Biology*, 27(2), 186–194. <https://doi.org/10.1071/PC20032>
- Risch, D. R., Ringma, J., & Price, M. R. (2021). The global impact of wild pigs (*Sus scrofa*) on terrestrial biodiversity. *Scientific Reports*, 11(1), Article 1.
<https://doi.org/10.1038/s41598-021-92691-1>
- Roekel, K. M. van, Snijders, L., & Visscher, D. R. (2024). Spatiotemporal responses of ungulates to hunting in a fenced multi-use area. *Wildlife Research*, 51(11).
<https://doi.org/10.1071/WR24027>
- Rogosic, J., Estell, R. E., Skobic, D., & Stanic, S. (2007). Influence of secondary compound complementarity and species diversity on consumption of Mediterranean shrubs by sheep. *Applied Animal Behaviour Science*, 107(1), 58–65.
<https://doi.org/10.1016/j.applanim.2006.09.013>
- Rong, Y., Yuan, F., & Ma, L. (2014). Effectiveness of exclosures for restoring soils and vegetation degraded by overgrazing in the Junggar Basin, China. *Grassland Science*, 60(2), 118–124. <https://doi.org/10.1111/grs.12048>
- Rowland, M. M., Nielson, R. M., Wisdom, M. J., Clark, D. A., DiDonato, G. T., Hafer, J. M., Naylor, B. J., & Johnson, B. K. (2023). Success is dependent on effort: Unraveling

- characteristics of successful deer and elk hunters. *Wildlife Society Bulletin*, 47(2), e1414.
<https://doi.org/10.1002/wsb.1414>
- Rubino, E., & Williams, C. (2014). Methods for Population Control: A Case Study on the Axis Deer of Maui Island, HI. *Proceedings of the Vertebrate Pest Conference*, 26(26).
<https://doi.org/10.5070/V426110549>
- Scarnecchia, D. L. (1990). Concepts of Carrying Capacity and Substitution Ratios: A Systems Viewpoint. *Journal of Range Management*, 43(6), 553. <https://doi.org/10.2307/4002363>
- Shwiff, S. A., Auwelo, C. L., Caires, K., Friel, G., Katayama, L., Munoz, Z., Price, M. R., Risch, D., Shartaj, M., Steensma, K., Thorne, M., & Zifko, R. (1000). Economic estimates of invasive wild ungulate damage to livestock producers in Hawai'i. *Pest Management Science*, 81(1), 438–449. <https://doi.org/10.1002/ps.8446>
- Shwiff, S. A., Auwelo, C. L., Caires, K., Friel, G., Katayama, L., Munoz, Z., Price, M. R., Risch, D., Shartaj, M., Steensma, K., Thorne, M., & Zifko, R. (2024). Economic estimates of invasive wild ungulate damage to livestock producers in Hawai'i. *Pest Management Science*, 81(1), 438–449. <https://doi.org/10.1002/ps.8446>
- Sinclair, A. R. E. (2023). *Natural Regulation of Ecosystems in Protected Areas as Ecological Baselines*.
- Small, R. J., Holzward, J. C., & Rusch, D. H. (1991). Predation and Hunting Mortality of Ruffed Grouse in Central Wisconsin. *The Journal of Wildlife Management*, 55(3), 512–520.
<https://doi.org/10.2307/3808983>
- Snow, N. P., Smith, B., Lavelle, M. J., Glow, M. P., Chalkowski, K., Leland, B. R., Sherburne, S., Fischer, J. W., Kohen, K. J., Cook, S. M., Smith, H., VerCauteren, K. C., Miller, R. S., & Pepin, K. M. (2024). Comparing efficiencies of population control methods for

- responding to introductions of transboundary animal diseases in wild pigs. *Preventive Veterinary Medicine*, 233, 106347. <https://doi.org/10.1016/j.prevetmed.2024.106347>
- Sorensen, A. A., van Beest, F. M., & Brook, R. K. (2015). Quantifying overlap in crop selection patterns among three sympatric ungulates in an agricultural landscape. *Basic and Applied Ecology*, 16(7), 601–609. <https://doi.org/10.1016/j.baae.2015.05.001>
- Spear, D., & Chown, S. L. (2009). Non-indigenous ungulates as a threat to biodiversity. *Journal of Zoology*, 279(1), 1–17. <https://doi.org/10.1111/j.1469-7998.2009.00604.x>
- Spickard, P. (2000). [Review of *Review of Paniolo O Hawai'i: Cowboys of the Far West*, by E. Lee & P. Berry]. *The Public Historian*, 22(4), 81–83. <https://doi.org/10.2307/3379260>
- Stone, C. P. (1985). *Alien Animals in Hawai'i's Native Ecosystems: Toward Controlling the Adverse Effects of Introduced Vertebrates*.
- Strauch, A. M., Bruland, G. L., MacKenzie, R. A., & Giardina, C. P. (2016). Soil and hydrological responses to wild pig (*Sus scrofa*) exclusion from native and strawberry guava (*Psidium cattleianum*)-invaded tropical montane wet forests. *Geoderma*, 279, 53–60. <https://doi.org/10.1016/j.geoderma.2016.05.021>
- Taylor, M., Davison, A., & Harwood, A. (2025). Transdisciplinary pathways for wildlife conservation: A method for navigating socio-ecological systems on private lands. *People and Nature*, 7(3), 596–610. <https://doi.org/10.1002/pan3.10792>
- Thinley, P., Lassoie, J. P., Morreale, S. J., Curtis, P. D., Rajaratnam, R., Vernes, K., Leki, L., Phuntsho, S., Dorji, T., & Dorji, P. (2017). High relative abundance of wild ungulates near agricultural croplands in a livestock-dominated landscape in Western Bhutan: Implications for crop damage and protection. *Agriculture, Ecosystems & Environment*, 248, 88–95. <https://doi.org/10.1016/j.agee.2017.07.036>

- Tomich, P. Q. (1986). *Mammals in Hawaii: A synopsis and notational bibliography* (2nd ed., rev. Ed). Bishop Museum Press.
- Turner, D., Baldwin, K., Beckman, J., Nava, N. J., Tsiboe, F., Vaiknoras, K., & United States Department of Agriculture Economic Research Service. (2024). *Potential budgetary impacts of climate change on the Pasture, Rangeland, and Forage insurance plan*. U.S. Department of Agriculture, Economic Research Service.
<https://doi.org/10.32747/2024.8755000.ers>
- USDA. (2003). *National Range and Pasture Handbook | Natural Resources Conservation Service*. National Resources Conservation Service U.S. Department of Agriculture.
<https://www.nrcs.usda.gov/conservation-basics/natural-resource-concerns/animals/livestock/national-range-and-pasture-handbook>
- Valente, A. M., Acevedo, P., Figueiredo, A. M., Fonseca, C., & Torres, R. T. (2020). Overabundant wild ungulate populations in Europe: Management with consideration of socio-ecological consequences. *Mammal Review*, 50(4), 353–366.
<https://doi.org/10.1111/mam.12202>
- Vourc'h, G., Martin, J.-L., Duncan, P., Escarré, J., & Clausen, T. P. (2001). Defensive Adaptations of *Thuja plicata* to Ungulate Browsing: A Comparative Study between Mainland and Island Populations. *Oecologia*, 126(1), 84–93.
- Watter, K., Baxter, G., Brennan, M., Pople, T., & Murray, P. (2020). Seasonal diet preferences of chital deer in the northern Queensland dry tropics, Australia. *The Rangeland Journal*, 42(3), 211–220. <https://doi.org/10.1071/RJ20015>
- Webb, S. L., Dzialak, M. R., Wondzell, J. J., Harju, S. M., Hayden-Wing, L. D., & Winstead, J. B. (2011). Survival and cause-specific mortality of female Rocky Mountain elk exposed

- to human activity. *Population Ecology*, 53(3), 483–493. <https://doi.org/10.1007/s10144-010-0258-x>
- Weller, S. G., Cabin, R. J., Lorence, D. H., Perlman, S., Wood, K., Flynn, T., & Sakai, A. K. (2011). Alien Plant Invasions, Introduced Ungulates, and Alternative States in a Mesic Forest in Hawaii. *Restoration Ecology*, 19(5), 671–680. <https://doi.org/10.1111/j.1526-100X.2009.00635.x>
- Weller, S. G., Sakai, A. K., Clark, M., Lorence, D. H., Flynn, T., Kishida, W., Tangalin, N., & Wood, K. (2018). The effects of introduced ungulates on native and alien plant species in an island ecosystem: Implications for change in a diverse mesic forest in the Hawaiian Islands. *Forest Ecology and Management*, 409, 518–526. <https://doi.org/10.1016/j.foreco.2017.11.023>
- White, C. Q., Bush, J. P., & Sacks, B. N. (2023). Deer dietary responses to wildfire: Optimal foraging, individual specialization, or opportunism? *Molecular Ecology*, 32(24), 6953–6968. <https://doi.org/10.1111/mec.17185>
- Widén, A., Clinchy, M., Felton, A. M., Hofmeester, T. R., Kuijper, D. P. J., Singh, N. J., Widemo, F., Zanette, L. Y., & Crowsigt, J. P. G. M. (2022). Playbacks of predator vocalizations reduce crop damage by ungulates. *Agriculture, Ecosystems & Environment*, 328, 107853. <https://doi.org/10.1016/j.agee.2022.107853>
- Widén, A., Crowsigt, J. P. G. M., Dressel, S., Felton, A. M., Singh, N. J., & Widemo, F. (2023). Direct and indirect effects of food, fear and management on crop damage by ungulates. *Ecological Solutions and Evidence*, 4(3), e12266. <https://doi.org/10.1002/2688-8319.12266>

- Wiesmair, M., Otte, A., & Waldhardt, R. (2017). Relationships between plant diversity, vegetation cover, and site conditions: Implications for grassland conservation in the Greater Caucasus. *Biodiversity and Conservation*, 26(2), 273–291.
<https://doi.org/10.1007/s10531-016-1240-5>
- Wilson, G., Edwards, M., & Byron, N. (2020). Custodianship of wildlife on private land to support conservation – an Australian model. *The Rangeland Journal*, 42(5), 309–321.
<https://doi.org/10.1071/RJ20039>
- Wonkka, C. L., Twidwell, D., Allred, B. W., Bielski, C. H., Donovan, V. M., Roberts, C. P., & Fuhlendorf, S. D. (2019). Rangeland vulnerability to state transition under global climate change. *Climatic Change*, 153(1), 59–78. <https://doi.org/10.1007/s10584-018-02365-7>
- Wu, Y., Shao, C., Zhang, J., Liu, Y., Li, H., Ma, L., Li, M., Shen, B., Hou, L., Chen, S., Xu, D., Xin, X., & Liu, X. (2024). Elevation-Dependent Contribution of the Response and Sensitivity of Vegetation Greenness to Hydrothermal Conditions on the Grasslands of Tibet Plateau from 2000 to 2021. *Remote Sensing*, 16(1), Article 1.
<https://doi.org/10.3390/rs16010201>
- Yang, K., Guo, D., Hua, W., Pepin, N., Yang, K., & Li, D. (2022). Tibetan Plateau Temperature Extreme Changes and Their Elevation Dependency From Ground-Based Observations. *Journal of Geophysical Research: Atmospheres*, 127(3), e2021JD035734.
<https://doi.org/10.1029/2021JD035734>
- Yang, Y., You, Q., Zuo, Z., Zhang, Y., Liu, Z., Kang, S., & Zhai, P. (2023). Elevation dependency of temperature trend over the Qinghai-Tibetan Plateau during 1901–2015. *Atmospheric Research*, 290, 106791. <https://doi.org/10.1016/j.atmosres.2023.106791>

- Yelenik, S. G. (2018). Long-Term Impacts of Exotic Grazer Removal on Native Shrub Recovery, Santa Cruz Island, California. *Western North American Naturalist*, 78(4), 777. <https://doi.org/10.3398/064.078.0417>
- Zhang, X., Ye, M., Pan, X., He, Q., Chen, W., Zeng, G., & Li, M. (2023). Characteristics of Grassland Plant Community Change with Elevation and Its Relationship with Environmental Factors in the Burqin Forest Region of the Altai Mountains. *Diversity*, 15(10), Article 10. <https://doi.org/10.3390/d15101098>