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Ecological associations of nonnative ungulates on the Hawaiian Island of Lāna‘i

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Abstract: Sustained-yield hunting of introduced ungulates in the Hawaiian Islands often conflicts with the conservation of native species, but there is little reliable data to guide effective management. European mouflon sheep (*Ovis musimon*; mouflon) and axis deer (*Axis axis*; deer) were introduced on the island of Lāna‘i to provide additional hunting opportunities. Managers will require better information regarding the ecological associations of introduced ungulate species, relative to the habitats occupied, to resolve longstanding conflicts between native species conservation and sustained-yield hunting on islands. To address this information need, we modeled sheep and deer ecological associations, habitat-use, and suitability using data obtained from an intensive aerial survey completed in 2013 and temporally matching environmental data. In habitat suitability models evaluated by Receiver Operating Characteristic (ROC) metrics, predictor importance in a generalized linear model (GLM) of deer decreased in the following order: afternoon cloud cover, topographic slope, mean annual precipitation (MAP), elevation, normalized difference vegetation index (NDVI), and bare soil index. In a random GLM model of mouflon, predictor importance decreased in the following order: afternoon cloud cover, deer habitat suitability, NDVI, bare soil index, topographic slope, elevation, and MAP. Mouflon were restricted to lower elevation arid slopes, whereas deer were more broadly distributed throughout upland environments of the island. The presence of deer was also an important predictor for mouflon distribution, although mouflon was not an important predictor of deer, suggesting asymmetrical competition. Removal of the more abundant deer population may lead to an increase in abundance and distribution of mouflon without containment. This work represents the first habitat suitability analysis for all nonnative ungulates on any entire Hawaiian island. Our results are applicable to other islands where conflicts may arise with introduced ungulates, sustained-yield hunting, and native species conservation.

Key words: *Axis axis*, axis deer, European mouflon sheep, habitat suitability, Hawai‘i, Hawaii, invasive species, island conservation, Lāna‘i, Lanai, *Ovis musimon*, sustained-yield hunting

Principles of wildlife management used by resource management agencies rarely meet rigorous scientific standards, and thus the ability to manage wildlife populations for specific conservation objectives in the public interest is often limited (Artelle et al. 2018). Although many resource management agencies oversee introduced populations of sometimes overabundant game species, Hawai‘i, USA, is a special case because all large game animals are introduced ungulate species that are considered to be incompatible with native ecosystem conservation and are known to cause severe ecological degradation (Lepczyk et al. 2011, Leopold and Hess 2017). Introduced ungulates in Hawai‘i and other locations have no natural predators and few diseases; thus, they tend to become overabundant without intensive management or continuous high levels of hunting pressure (Caughley 1970).

Monitoring the abundance of cryptic animals is costly and often biased (Lancia et al. 1996).

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Abundance may also change rapidly, but habitat suitability may remain relatively stable and provide a more lasting basis for management, particularly for spatial aspects of land use planning (Duflot et al. 2018, Crawford et al. 2020). Such models can also be updated based on projected environmental change. Ungulate habitat suitability and ecological associations may therefore be useful to inform land use prioritization analyses and to resolve conflicts between native species conservation and sustained-yield hunting (Nelli et al. 2022). Basic information for nonnative game mammals such as comprehensive models of habitat suitability have not been developed for most species in the Hawaiian Islands. Such models could greatly aid in the conservation of both native biota and sustained-yield management of game mammals by providing ecological insights about habitat associations and species interactions.

Differences in habitat suitability may reflect areas of net productivity and population sinks (Pulliam and Danielson 1991). Areas with higher habitat suitability may contain more productive resources such as forage, thereby subsidizing greater abundance (Illius and O'Connor 2000). Such areas may require repeated removals of excess animals and incur greater costs for management. However, habitat suitability for nonnative animal species may be uncoupled from native plant communities because these plant and animal species did not evolve together. Introduced herbivores may exhibit little association with native or nonnative plant species, although some insular endemic plant species may be preferentially selected as forage because they lack chemical or physical defenses against herbivory (Bowen and Van Vuren 1997, Cubas et al. 2019). Introduced grasses may confound the ability to detect preferences for plant species if they have become widely interspersed throughout native plant communities. Thus, determining specific habitat associations or preferences of introduced animals in novel environments may be challenging and require new modeling approaches (Elith et al. 2006), particularly when comprehensive data on the environment and species of interest are scarce.

Historically, record keeping on the release and status of Hawaiian game animals has been fragmentary (Lepczyk and Duffy 2019). Although whole-island indices of relative abundance and distribution are available for some species on some islands (Risch et al. 2020), abundance and population dynamics of game species in Hawaiʻi is generally not rigorously studied or monitored on a regular basis except for total annual harvest in some cases, hindering the ability to designate hunting seasons or bag limits based on vital rates to achieve desired levels of abundance (Hess and Judge 2021). Hence, managers and biologists in Hawaiʻi have little reliable data on which to base management goals.

Game animals in Hawaiʻi have comparatively less economic value than native game species in other states. Hawaiʻi had the lowest per capita of licensed hunters and the second lowest gross expenditure on hunting licenses among the 50 states in 2020 (U.S. Census Bureau 2020, U.S. Fish and Wildlife Service 2020). Consequently, reinvestment in game management is relatively low, especially for overabundant domestic species that have become feral such as wild pigs (*Sus scrofa*), goats (*Capra hircus*), or sheep (*Ovis aries*), which occur throughout most Hawaiian Islands (Lepczyk et al. 2011). However, species that have never been domesticated, such as axis deer (*Axis axis*; deer) and European mouflon sheep (*O. musimon*; mouflon), are considered more desirable among game hunters (Lohr et al. 2014) and are limited to few islands: Hawaiʻi, Maui, Molokaʻi, and Lānaʻi (Hess 2008). Reported annual harvest of these 2 species on the island of Lānaʻi has increased approximately 10-fold over the period from the 1950s to the 2000s (Lepczyk and Duffy 2019), reflecting the island's increasing popularity as a hunting destination. Despite their popularity with hunters, deer have continued to grow in abundance over recent decades, threatening natural resources and infrastructure (Hess et al. 2022).

Our objectives were to use habitat suitability models to understand the ecological and climatic associations of 2 introduced ungulate species, mouflon and deer, on the island of Lānaʻi based on data from an intensive aerial survey conducted in 2013. We temporally matched survey data to environmental data that included climate, vegetation, and topographic variables. Because aerial surveys can provide a comprehensive snapshot of ungulate distribution across their spatial extent, we were primarily interested in models that could elucidate the factors associated with variation in habitat suitability across the entire island landscape. Because these ungulate species did not evolve with native plant species of Hawaiʻi, we expected habitat suitability to be generally related to environmental variables associated with climatic conditions similar to those found in their native distributional ranges rather than the plant communities and physiognomy of Lānaʻi. We also expected that competitive interactions between the 2 ungulate species may be an important factor influencing their distributions.

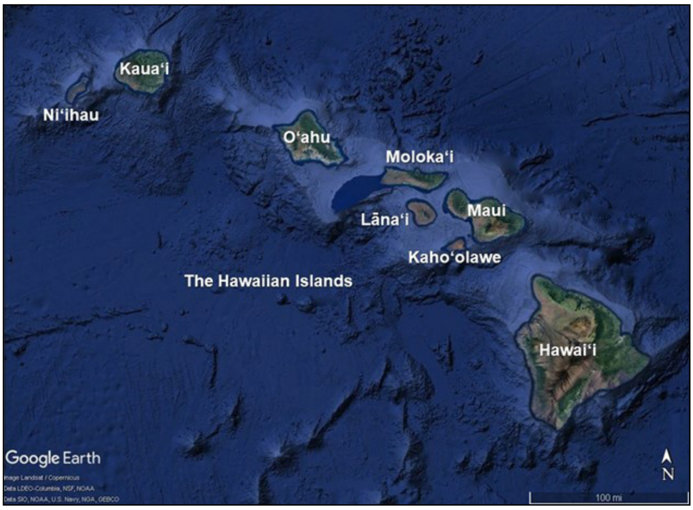

Figure 1. Habitat suitability modeling for axis deer (*Axis axis*) and European mouflon sheep (*Ovis musimon*) was conducted on the island of Lānaʻi, Hawaiʻi, USA.

Figure 2. An axis deer (*Axis axis*) among a group of European mouflon sheep (*Ovis musimon*) on the island of Lānaʻi, Hawaiʻi, USA (*photo courtesy of J. Muise*).

Study area

We conducted our study on the island of Lānaʻi (Figure 1). Lānaʻi is the sixth-largest Hawaiian island (364 km^2) with a maximum elevation of 1,026 m ASL and ~3,000 human inhabitants. Soil substrates are circa 1.25 million years old, and the island was connected intermittently to Maui, Molokaʻi, and Kahoʻolawe until 18,000 years ago. The island lies in the leeward rainshadow of the West Maui Mountains (1,764 m asl) and has an overall mean annual rainfall of approximately 550 mm, ranging between 380 mm in drier areas and >900 mm in the highest elevation areas (Giambelluca et al. 2013). It is therefore more arid and lacks environmental heterogeneity and extensive wet forests found on other larger Hawaiian islands but once had well-developed dry forests and shrublands with associated fauna (Hobdy 1993). The island has suffered a severe loss of native biodiversity due to ecological degradation, which Hobdy (1993) ascribed to the longstanding actions of abundant ungulates, including herbivory and hoof action. Patches of barren ground contribute to substantial upland erosion and coastal accretion. Numerous island endemic species are now extinct (Hobdy 1993).

Domestic pigs and goats that had been introduced by early European settlers and became feral were eradicated in the mid-1930s and 1981, respectively (Tomich 1986, Hobdy 1993). Pronghorn antelope (*Antilocapra americana*) were introduced in 1959 but disappeared by the mid-1980s (Tomich 1986). Deer that were introduced in 1920 and mouflon that were introduced in 1954 are the only 2 wild ungulate species that currently occur on the island (Hess and Jacobi 2011; Figure 2). In 1961, approximately 1,675 axis deer occupied ~9.5% of Lānaʻi (Graf and Nichols 1966), and >200 mouflon occupied ~3.5% of the island in 1968 (Kramer

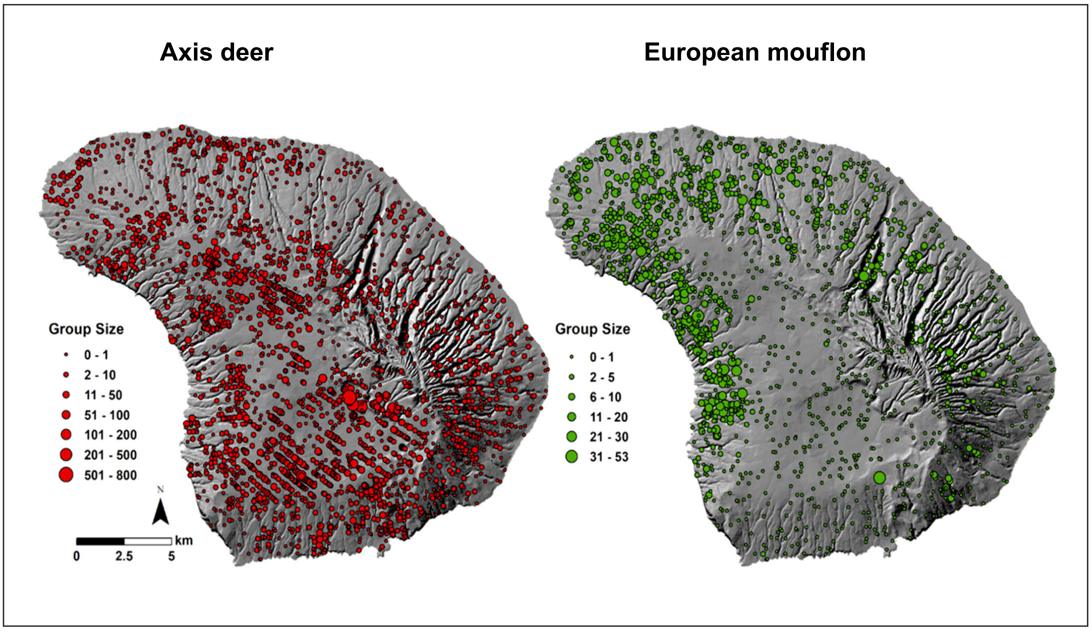

Figure 3. Aerial surveys of axis deer (*Axis axis*) and European mouflon sheep (*Ovis musimon*) conducted on the island of Lānaʻi, Hawaiʻi, USA, June 17–22, 2013.

1971). Both species were excluded from interior areas of the island until intensive agriculture was discontinued in 1992.

Methods

Ungulate data collection and processing

The aerial survey conducted in Lānaʻi in 2013 represents perhaps the only intensive effort to quantify all game animals on any of the Hawaiian Islands. During June 17–22, 2013, 1,305 km of transects were flown by helicopter covering the entire island on mornings until 3 hours after sunrise by J. Muise, KIA Hawaiʻi (Figure 3). All hunting activities were suspended during the surveys. Surveys of 252 km in length were conducted on 24 transects oriented East-West in the interior of the island and 1,053 km on 240 transects oriented radially on coastal slopes. Perpendicular distances to animal groups were recorded ≤160 m from the aircraft.

When possible, we used the number of animals detected at recorded points along the aerial survey as differing case weights in our models. Since not all modeling approaches considered allowed for case weight information, we considered each animal detected across the landscape as an individual presence point (i.e., essentially disaggregating aerial survey points with multiple animal detections). This approach effectively weighted our resulting models to areas with multiple animal detections. For background points, we generated points equal in number to the observations for each ungulate species randomly across the landscape but with the density of final points inversely proportional to the density of animal detections across the landscape using the spatialEco library in program R (Evans 2018, R Core Development Team 2017).

Predictors of ungulate habitat suitability

We first examined categorical variables of physiognomic vegetation zones, moisture zones, slope, and elevation. These variables revealed strong collinearity among potential predictors that limited their utility and were not considered further (Hess et al. 2020). We then identified multiple variables related to vegetation productivity and forage quality as suitable predictor variables for ungulate distribution models, including spectral indices from satellite images, climate, and topography.

Satellite spectral indices predictors. We used a WorldView-2 high resolution composite image generated from multiple flyovers in 2011 to generate predictors of ungulate habitat suitability in our models. While no specific dates were available for the images used in the composite, it is likely that most images were collected during a similar dry season period as the aerial surveys, as that is the narrow window of time when minimal cloud cover is present over the island. With this image, we calculated the normalized difference vegetation index (NDVI),

Table 1. Sources and spatial resolution of data used for candidate predictors used in habitat suitability models of axis deer (*Axis axis*) and European mouflon sheep (*Ovis musimon*) on the island of Lānaʻi, Hawaiʻi, USA. MAP = Mean annual precipitation; NDVI = normalized difference vegetation index.

Data sources	Type	Native resolution	Derived resolution	Source
MAP	Continuous	250 m	90 m	Giambelluca et al. (2013)
Cloud cover 1400 hours HST	Continuous	250 m	90 m	Giambelluca et al. (2014)
NDVI	Continuous	0.5 m	90 m	WorldView-2 imagery
Elevation	Continuous	10 m	90 m	National Oceanic and Atmospheric Administration (NOAA 2007)
Slope	Continuous	10 m	90 m	NOAA (2007)
Bare soil index	Continuous	0.5 m	90 m	WorldView-2 imagery

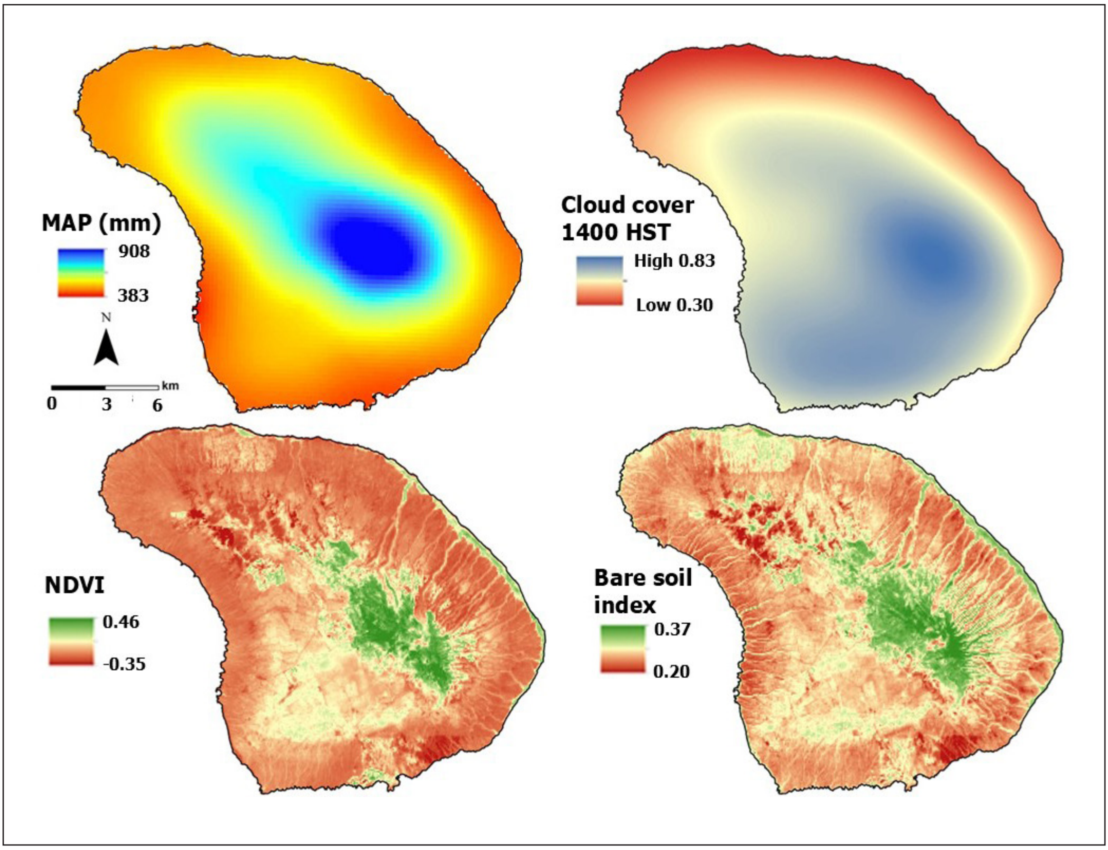

Figure 4. Climate and productivity layers used for habitat suitability modeling of axis deer (*Axis axis*) and European mouflon sheep (*Ovis musimon*) on the island of Lānaʻi, Hawaiʻi, USA. Predictors included mean annual precipitation (MAP), afternoon cloud cover at 1400 hours HST, normalized difference vegetation index (NDVI), and an index of bare soil cover.

and a bare soil index at 0.5 m resolution. These indices were calculated using standard formulas using the different spectral bands available (Rikimaru et al. 2002):

NDVI = (infrared - red)/(infrared + red)

Bare soil index = ((red + blue) - green)/((red + blue) + green)

To ensure that our results were not influenced by a temporal mismatch between survey (2013) and satellite (2011) data acquisition, we repeated the entire model building steps described using similar vegetation and bare soil metrics derived from a mosaic of coarser Landsat 8 satellite data collected during the exact month of the aerial survey, which showed very similar patterns. However, we did not use this as the basis of our final results, as the Landsat mosaic was not spectrally corrected and had more cloud coverage than the 2011 WorldView-2 data.

Climatic and topographic predictors. We considered several climate variables as potential predictors of ungulate habitat suitability. These included mean annual precipitation and mean cloud frequency at mid-afternoon (1400 hours HST) that likely reflected the time of greatest daily heat stress for plants and animals (Giambelluca et al. 2014). All predictor variables above were interpolated/aggregated to a 90-m spatial resolution that was coarse enough to represent the general habitat around animals observed during aerial surveys while also accounting for likely errors in recording exact locations of animals from aircraft (Table 1; Figure 4).

Habitat suitability modeling

Model type selection. Using the ungulate distribution data and predictors described above, we initially explored 4 approaches to modeling ungulate habitat suitability: (1) generalized linear models (GLM); (2) boosted logistic regressions, (3) bagged classification and regression trees (CART), and (4) random GLMs, a hybrid modeling approach that incorporates machine learning principles to GLM methods such as model ensembles based on data subsets using bagging and model feature selection (Song et al. 2013). After preliminary runs, however, 2 of the machine learning methods considered (boosted logistic regressions and bagged CART models) were dropped as they showed habitat suitability responding in complex ways to the variability of predictors considered, indicating model overfitting that made biological interpretation of these models challenging. Because the aerial surveys already provided a comprehensive snapshot of ungulate distribution across the island, our focus for developing these habitat suitability models was for inference rather than prediction. Therefore, we focused model building on GLM and random GLM modeling approaches, which generally yielded curvilinear modeled responses that allowed for easier model inference and biological interpretability of results. We performed all model building, validation, and projections using caret, a package in R for model creation that standardizes model building for >200 model types developed across multiple R packages (Kuhn 2008).

Inclusion of species interactions. To examine if possible competitive exclusion effects of other animal species helped define a species-suitable habitat, we fit habitat suitability models of each species using the habitat suitability of the other species as a potential predictor, along with all other environmental predictors described above (Araújo and Luoto 2007). This was done by creating models for the other species without interactions, and then fitting models for the subject species using the habitat suitability model from the other species as a predictor. The models with species interactions were then compared to models without species interactions in terms of accuracy, predictor responses, and resulting habitat suitability projections.

For each of these 2 species, we fit 4 candidate models: (1) a GLM without species interaction; (2) a GLM with species interaction; (3) a random GLM without species interaction; and (4) a random GLM with species interaction.

Model evaluation and exploration. For each model type considered, we trained and evaluated models based on 3 sets of 10-fold validation model runs where at each run 10% of the data was kept aside during model training to be used in model evaluation. Accuracy was calculated as the percent of data points correctly predicted as animal presence and absence. Sensitivity, a metric that describes the ability of a model to predict true positives, was calculated as the ratio of true positives divided by the sum

Table 2. Evaluation metrics for candidate habitat suitability models considered for axis deer (*Axis axis*) and European mouflon sheep (*Ovis musimon*) on the island of Lānaʻi, Hawaiʻi, USA. GLM = generalized linear model; ROC = Receiver Operating Characteristic.

Species	Model type	Species interaction	Accuracy	ROC	Sensitivity	Specificity
Axis deer[a]	GLM	--	0.69	0.74	0.68	0.71
Axis deer	GLM	Y	0.70	0.74	0.69	0.71
Axis deer	Random GLM	--	0.69	0.75	0.66	0.72
Axis deer	Random GLM	Y	0.70	0.75	0.68	0.72
Mouflon	GLM	--	0.70	0.75	0.64	0.75
Mouflon	GLM	Y	0.71	0.77	0.63	0.79
Mouflon	Random GLM	--	0.72	0.76	0.63	0.82
Mouflon[a]	Random GLM	Y	0.74	0.81	0.65	0.83

[a] Best model for each species

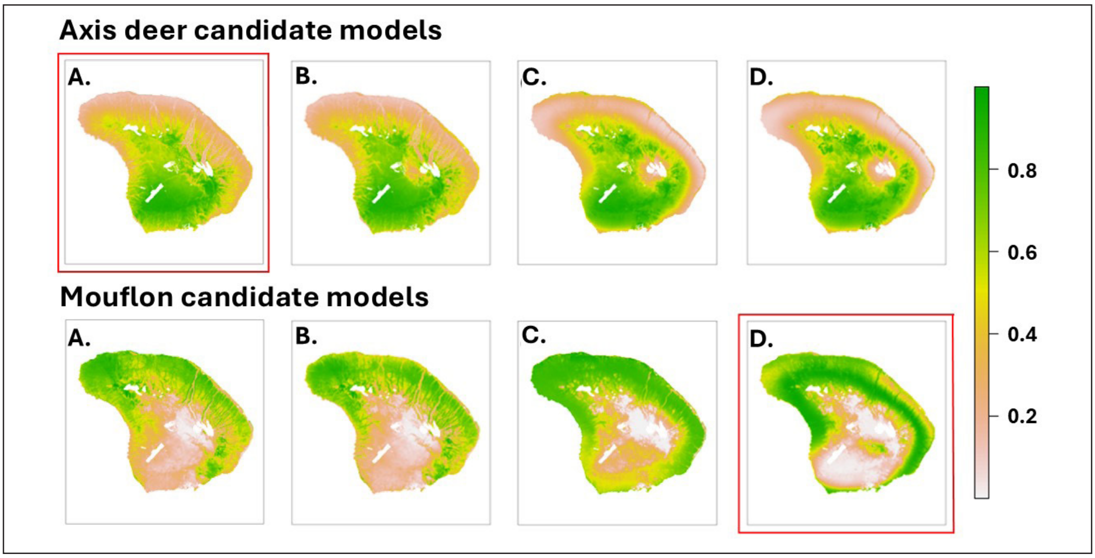

Figure 5. Candidate habitat suitability models for axis deer (*Axis axis*) and European mouflon sheep (*Ovis musimon*) on the island of Lānaʻi, Hawaiʻi, USA, corresponding to Table 1: generalized linear model (GLM) without species interaction (A); GLM model with species interaction (B); random GLM model without species interaction (C); random GLM model with species interaction (D). Red boxes indicate best models for each species; green indicates higher suitability; pink indicates lower suitability; white areas were excluded from analyses.

of true positives and false negatives. Specificity, a metric that describes the ability of a model to predict true negatives, was calculated as the ratio of true negatives divided by the sum of true negatives and false positives. Lastly, we also considered Receiver Operating Characteristic (ROC), a commonly used metric to evaluate model fit that integrates model sensitivity and specificity.

We developed response curves for each model, which allowed us to explore how ungulate suitability varied in response to each of the predictors from all candidate models considered. This allowed us to ensure models reflected biologically plausible species response to habitat variability. Response curves were generated for each predictor by fitting the projected models to values between the 5 and 95% quantiles of the predictor while holding all other predictors constant at their median values (Elith et al. 2006). Similar response curves where 2 predictors simultaneously varied were also developed to explore potential predictor interactions. An estimate of the relative variable importance to each habitat suitability model was also created using caret's variable importance estimates that scale values from 0 to 100.

Lastly, because many areas across the landscape had reduced animal densities due to other factors aside from habitat quality, we excluded these areas when building our ungulate habitat suitability models. These included developed areas such as Lānaʻi City, the airport, and fenced ungulate exclosures. Without doing so, areas that would otherwise be considered environmentally highly suitable for a species could be assigned artificially low habitat suitability values.

Results

Aerial surveys

There were 681 groups of mouflon consisting of 3,853 individuals and 1,878 groups of deer consisting of 13,070 individuals recorded with associated UTM coordinates during surveys. Analyses of these data indicated 5,800–7,800 mouflon and 17,600–19,500 deer (J. Muise, KIA Hawaiʻi, unpublished data). Although these data suggested there may be 2.3–3.4 times more deer than mouflon, removals of deer were 6.4 times greater than mouflon during 2015 to 2018 because of differences in reproduction and selective harvest to reduce deer abundance (J. Sprague, Pūlama Lānaʻi, unpublished data).

Habitat suitability modeling

For each species, model projections and response curves showed how habitat suitability varied across the landscape and how this variability was associated with variation in each predictor variable (Table 2; Figure 5; supplemental material). In general, deer suitability models changed little in accuracy or landscape projections with respect to modeling approach and configurations. Additionally, because species interactions in the deer habitat suitability model (i.e., including mouflon habitat suitability as a predictor) only resulted in a small increase in model accuracy and model sensitivity while increasing model complexity, the final habitat suitability model for deer was chosen as the GLM-based model with individual-weighted presence and no species interaction (Figure 6A). We chose the random GLM model with a species interaction term as the best habitat suitability model for mouflon, as the random GLM models generally had higher model specificity for the species, and the model including species interaction (i.e., using deer habitat suitability as a predictor) had the highest ROC scores (Table 2; Figure 6B).

For deer, predictors varied in importance in decreasing order: afternoon cloud cover, slope, MAP, elevation, NDVI, and bare soil index (Table 3). For mouflon, variable importance decreased in the following order: afternoon cloud cover, deer habitat suitability, NDVI, bare soil

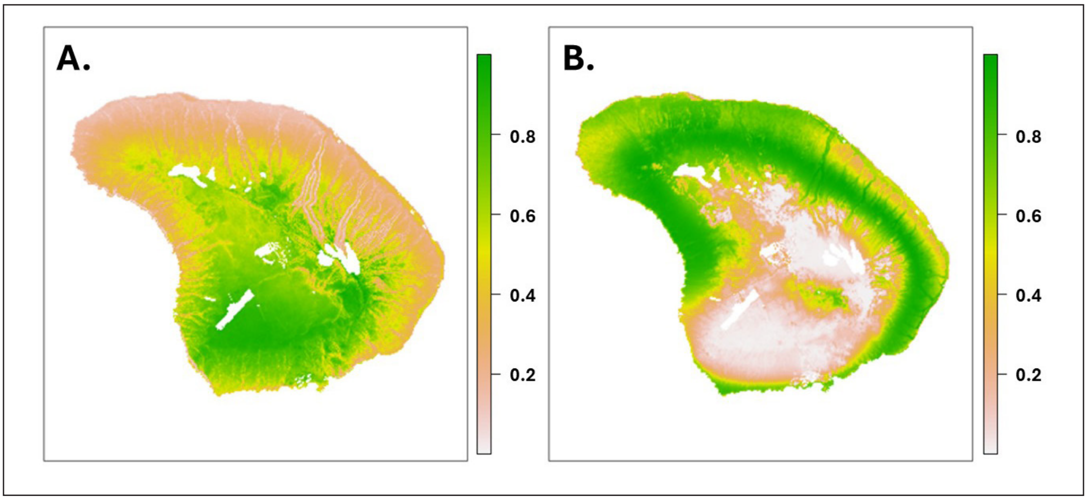

Figure 6. Final habitat suitability models for (A) axis deer (*Axis axis*) and (B) European mouflon sheep (*Ovis musimon*) on the island of Lānaʻi, Hawaiʻi, USA. Green indicates higher suitability; pink indicates lower suitability; white areas were excluded from analyses.

Table 3. Relative importance of variables for habitat suitability models of axis deer (*Axis axis*) and European mouflon sheep (*Ovis musimon*) on the island of Lānaʻi, Hawaiʻi, USA. Values are unitless ranging from 0–100, and relative to the most important variable for each species model (100). Continuous variables used in models include cloud cover at 1400 hours HST, interaction with ungulate species, slope and elevation derived from a digital elevation model, mean annual precipitation (MAP), and normalized difference vegetation index (NDVI) and an index of bare soil coverage derived from satellite imagery. GLM = generalized linear model.

Axis deer GLM		Mouflon random GLM	
Variable	Value	Variable	Value
Cloud	100	Cloud	100
Slope	87	Deer	87
MAP	66	NDVI	74
Elevation	37	Bare soil	59
NDVI	24	Slope	37
Bare soil	0	Elevation	31
--	--	MAP	0

index, slope, elevation, and MAP. Variable response curves showed how habitat suitability varied in response to predictor variability, thus allowing us to explore the underlying animal response to habitat variability (supplemental material).

Discussion

Our goal was to use habitat suitability models to understand the ecological and climatic associations of 2 introduced ungulate species. This work is the first analysis of habitat suitability for all nonnative ungulates on any entire Hawaiian island. Models indicate that environmental conditions on Lānaʻi offer broadly suitable habitat for deer, but suitable habitat was substantially more restricted for mouflon. Both mouflon and deer were habitat generalists and not strongly associated with any particular plant species or communities on Lānaʻi (Hess et al. 2020). We expected that these species should not have close associations with physiognomy, plant species, or plant communities outside their native distribution.

The native range of deer includes tropical and subtropical India, Sri Lanka, and Nepal (Anderson 2003). European mouflon are wild sheep derived from ancestors in Asia Minor but were brought to arid Mediterranean islands of Sardinia and Corsica by Neolithic people in an early attempt at domestication (Hess et al. 2017). While mouflon are from seasonally arid, temperate Mediterranean islands, deer originated from tropical and subtropical wet to semi-arid zones of India and are not found in arid environments. Deer also have broad habitat associations in their native range and are found in dry and wet deciduous forests, some thorn forests, and are also reported to avoid rugged terrain (Schaller 1967). This habitat generalism may have contributed to the success of their introductions throughout the world.

Lānaʻi lacks strong seasonality but has an annual dry period with few clouds; nonetheless, peak annual temperature stress is probably not as great as either the Mediterranean islands or India because of relatively cool ocean waters that surround the island and ameliorate the climate. Consequently, deer on Lānaʻi may be able to either forgo daily access to standing water that is necessary for survival in warmer climates or subsist on morning condensation, which is probably more common in the Hawaiian Islands. Nonetheless, deer are also known to use water troughs provided for game animals (J. Sprague, Pūlama Lānaʻi, unpublished data). We did not account for these or several other artificial sources of standing water, which likely influenced the distribution of deer, because the locations of available water were not known from the time of the aerial survey. Feral goats and sheep are not reliant on the availability of standing water in contrast to deer (Hess et al. 2017).

Plant communities of Lānaʻi may also be degraded such that habitats do not differ strongly with regard to some dominant invasive species (Hobdy 1993). Abundant nonnative grasses and other plants have invaded many areas and are now interspersed throughout native plant communities of the Hawaiian Islands (Leopold and Hess 2017). Many of these species were introduced to improve the productivity and nutritional forage quality for domestic herbivores and now dominate or co-dominate most native vegetation communities except less disturbed wet forests. Deer are broadly distributed on Lānaʻi but make heavy use of lands formerly used for intensive agriculture, which are now dominated by invasive nitrogen-fixing leguminous shrubs and trees such as mulga (*Acacia aneura*), haole koa (*Leucaena leucocephala*), and kiawe (*Prosopis* spp.), which were introduced throughout the Hawaiian Islands as nutritious fodder for domestic livestock.

Afternoon cloud cover, reflecting areas where plants and animals may occur during the time of greatest daily heat stress, was the most important predictor of habitat suitability for both ungulate species. Lānaʻi is known to have consistent afternoon cloud cover because of its location in the lee of the west Maui mountains (Giambelluca et al. 2014). In other studies, NDVI was an important predictor for herbivore distribution, as species follow seasonal green-up during migrations (Merkle et al. 2016). Ungulates on Lānaʻi may also move seasonally in response to changes in NDVI. Although we only had a snapshot of ungulate distribution, NDVI may also be used to predict changes in seasonal and annual distribution. Moreover, NDVI and other measures of climate and vegetative productivity in our models may be useful to project future ungulate distribution based on changing climate scenarios. In fact, recent historical analyses of satellite imagery across the archipelago have shown consistent decreases in NDVI over the last 4 decades (Madson et al. 2022).

The distribution of both ungulate species was influenced by elevation. In the case of mouflon, there was a strong peak elevation at approximately 400–500 m, which corresponded primarily to lower-elevation dry and arid areas. Mouflon were likely restricted to lower slopes because of competition from deer. In other parts of the world where mouflon have been introduced such as temperate areas of Europe, they are found primarily between 1,000 and 1,500 m elevation (Darmon et al. 2012). In contrast, our models suggested that deer would have used areas of higher elevation if they had been available on Lānaʻi. In their native range in Nepal, deer generally occur at <1,000 m elevation (Schaller 1967). However, they are abundant in higher elevation areas on neighboring Maui and have been reported at >2,100 m elevation on east Maui (Anderson 2003).

Our models suggested that asymmetrical competition influenced habitat suitability. Deer are numerically dominant, and models suggested they exclude mouflon from areas likely to be inhabited based on the distributional range of mouflon on Hawaiʻi Island (Hess et al. 2017). Mouflon generally occupied lower elevation dry and arid areas of Lānaʻi where deer do not occur in high abundance. However, mouflon occurred in high abundance up to 2,750 m elevation on Mauna Loa in the absence of ungulate competitors (Hess et al. 2006), and mouflon hybridized with domestic sheep occurred up to 2,900 m on Mauna Kea in the presence of feral goats (Scowcroft and Conrad 1988). Because mouflon originated from seasonally arid environments, they may only be able to successfully compete with deer in more arid environments of Lānaʻi. Furthermore, the pattern of competition in the model of mouflon distribution suggests that the order of introduction may have contributed to the current dominance by deer. Mouflon were introduced 34 years after deer, and limited information on abundance suggests there may have been at least several hundred deer at the time mouflon were introduced to the island. Pronghorn antelope were introduced 5 years after mouflon and likely had to contend with competition from mouflon, deer, and feral goats, which may have all been factors in their extirpation from Lānaʻi (Tomich 1986). Thus, removal of the more abundant deer population may lead to an increase in abundance and distribution of mouflon without containment (Gürtler et al. 2017).

The habitat suitability models we developed were unlike those for most other similar ungulates because we sought to use the models to understand the ecological and environmental associations of 2 ungulates using data that essentially represented a comprehensive island-wide snapshot in time. However, other factors have also been found to influence the distribution and habitat use of these and similar species, such as intraspecific and interspecific social interactions and niche overlap (Moe and Wegge 1994, Darmon et al. 2012, Bleyhl et al. 2018). While these processes undoubtedly affect aspects of group spacing and distribution, such effects may only be measurable with fine-scale data from much longer periods of study. Other studies have examined the effects of habitat fragmentation and human encroachment limiting suitable habitat of mountain ungulates (Paudel et al. 2015). We lacked data to address long-term demographic trends and social structure, but nevertheless environmental factors explained the majority of more coarse-scale distributional patterns we observed in these species on Lānaʻi.

Management implications

First, our work provides basic information necessary to understand and manage the landscape of an entire island for both sustained-yield hunting of introduced game species and the conflicting purpose of conservation of threatened and endangered native species. Where high suitability for game species and the spatial distribution of threatened and endangered native species overlaps substantially, the landscape can be managed to reduce this conflict. In areas where overlap with threatened and endangered species is low, sustained-yield hunting may be considered more appropriate. Fences may be used, for example, in conservation planning to exclude game species from areas that are important for threatened and endangered species while still allowing for sustained-yield game production in other areas. This habitat suitability modeling may also be used in more complex land use prioritization algorithms that account for other factors such as agriculture, energy production, or urban development to implement effective conservation strategies, which has been done for the island of Lānaʻi (Leopold et al. 2024). Our results are applicable to other islands where conflicts may arise with introduced ungulates, sustained-yield hunting, and native species conservation. Secondly, areas of high suitability, particularly for overabundant game species such as deer, may be identified for focused management removals to curtail overall abundance. However, if strong competition with deer limits mouflon and a substantial proportion of the deer population were removed, without containment, mouflon may eventually become numerically more abundant and occupy a greater area, warranting further management. Thus, our habitat suitability models may be important for understanding and managing these species-level interactions.

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Supplemental materials

Supplemental material can be viewed at https://digitalcommons.usu.edu/hwi/vol17/iss2/10.

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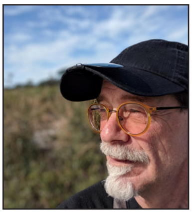

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