MODELING BREEDING HABITAT PREFERENCES OF TAHITI PETREL *PSEUDOBULWERIA ROSTRATA* ON TA‘Ū, AMERICAN SAMOA

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ABSTRACT

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Understanding the prevalence and use of breeding habitat of seabird species is important for evaluating appropriate conservation and management strategies. Seabirds are one taxonomic group for which we have relatively few species distribution studies, particularly on remote islands. To address this limitation, the goals of this study were to (1) build and use a species distribution model to identify which differences in habitat structure, physical characteristics, and environmental conditions affect Tahiti Petrel *Pseudobulweria rostrata* nesting presence on the island of Ta‘ū, American Samoa; and (2) evaluate how important nesting habitat characteristics can identify the fine-scale extent and location of suitable Tahiti Petrel breeding habitat throughout the summit region of Ta‘ū. We found that closed canopy cover and higher altitudes best predicted Tahiti Petrel nesting locations. We classified the summit montane rainforest habitat above 650 m by the presence of canopy species using supervised image classification. Of the 774.7 ha (7.474 km^2) of habitat classified, 63.8% was covered by canopy species, and a total of 254.1 ha (2.541 km^2) of montane habitat was classified as most suitable for Tahiti Petrel nesting. Closed canopy cover was higher on the leeward side of the summit (80.02%) compared to the windward side (46.50%). This difference is likely caused by a combination of prevailing winds and disturbances from storm events, which can significantly alter the amount and distribution of canopy vegetation. This pattern highlights the importance of considering breeding habitat availability when assessing the conservation needs of Tahiti Petrels.

Key words: spatial models, petrels, habitat survey, distribution models, tropical Pacific

INTRODUCTION

Seabirds are important upper trophic level predators that can provide a key link between terrestrial and marine ecosystems as they move nutrients from oceans to land via guano (Polis & Hurd, 1996). This movement can stimulate primary productivity, structure plant communities, and shape terrestrial food webs (Anderson & Polis, 1999; Croll et al., 2005; Hutchinson, 1950). In arid areas, seabirds transfer nutrients onto unproductive island ecosystems, thereby supporting high densities of arthropods (Polis & Hurd, 1996; Sánchez-Piñero & Polis, 2000). Even in temperate, more productive terrestrial ecosystems, the nutrients provided by seabirds lead to increased abundance of animals in multiple trophic levels, including invertebrates and lizards (Markwell & Daugherty, 2002). Hence, when seabirds are extirpated from islands or their populations are reduced, it may have a significant impact on the terrestrial ecosystem (Wardle et al., 2009). For example, extirpation of seabirds from islands can lead to lower soil fertility due to the loss of nutrient inputs, leading to cascading effects on belowground ecosystems (Fukami et al., 2006).

Pelagic seabirds are particularly vulnerable to threats, especially in the case of small breeding populations restricted to few breeding locations (Croxall et al., 2012). Among such species, Procellariiforms are particularly threatened (Baillie et al., 2004) due to habitat loss, invasive species, and climate change (Croxall et al., 2012; Doney et al., 2012; Grémillet & Boulinier, 2009). Climate change, because of reductions in cloud immersion, rainfall changes, and increases in hurricane frequency, is particularly impactful for the montane rainforests of high tropical islands where seabirds breed (Foster, 2001; Loope & Giambelluca, 1998).

The determination and classification of how species associate with each other and the environment have a long history, from the advent of wildlife-habitat relationships to increasingly complex statistical approaches that reveal how species interactions shape their distributions. For example, predictive habitat modelling uses resource selection functions to characterize the terrestrial niche of a species by linking its presence with surrounding ecological predictors (Guisan & Zimmermann, 2000). Predictive habitat models, niche models, and species distribution models (SDM) reflect the influence of limiting factors, disturbances, and resources on species (Algar et al., 2009; Guisan & Thuiller 2005; Wisz et al., 2013). SDMs, in particular, are a common method for capturing the variation in habitats, populations, and complexity of ecosystems (Franklin, 2010; Miller, 2010). These models have been used to determine the oceanic distribution of seabirds generally (Cleasby et al., 2020; Waggitt et al., 2020), as well as the terrestrial colony size and its distribution for many burrow-nesting Procellariiformes, including Cook’s Petrel *Pterodroma cookii*, Sooty Shearwater *Ardenna grisea*, Mottled Petrel *Pterodroma inexpectata*, and Hawaiian Petrel *Pterodroma sandwichensis* (Rayner et al., 2007; Scott et al., 2009; VanZandt et al., 2014).

Because habitat characteristics are valuable predictors for determining nesting locations and densities of seabirds, incorporating habitat information into conservation planning is important (Caughley, 1994; Rayner et al., 2007; Scott et al., 2009). Given this need, our goals were to (1) build and use a SDM to determine what differences in habitat structure, physical characteristics, and environmental conditions affect Tahiti Petrel *Pseudobulweria rostrata* nesting presence on the island of Ta‘ū, American Samoa; and (2) evaluate how the important nesting habitat characteristics of this species can identify the fine-scale extent and location of suitable habitat throughout the summit region of Ta‘ū. By addressing these goals, we provide estimates on the type and quality of habitat where Tahiti Petrel nests are found on Ta‘ū, which can help determine the importance of this habitat for the regional population of Tahiti Petrels.

METHODS

Study site

Field work was conducted on the island of Ta‘ū (14.2329°S, 169.4623°W), located in the Manu‘a group of islands, 128 km east of the main island of American Samoa, Tutuila (Fig. 1). The territory of American Samoa is located west of French Polynesia, and north of Tonga (Fig. 1). Ta‘ū, a high volcanic shield island reaching 980 m, is the highest point in the Samoan Islands and provides breeding habitat for a suite of Procellariiform species, including the Tahiti Petrel (Amerson et al., 1982; Stice & McCoy, 1968). The partial collapse of the peak resulted in a gentle, north-facing slope and a sharp, near-vertical slope to the south, descending nearly 600 m to a shelf comprised of caldera deposits and the ocean (Stice & McCoy, 1968). We focused field research within montane habitat above 650 m, which was previously identified as breeding habitat for Procellariiform seabird species, including Tahiti Petrel (Amerson et al., 1982; O’Connor & Rauzon, 2004; Pyle et al., 1990). The high montane region of Ta‘ū is split into two different zones, montane forest and summit scrub. The montane forest canopy is shorter than in the lowland forest and has a partially open (i.e., broken) canopy with dense ground cover underneath (Whistler, 1992); the summit scrub habitat has similar flora to the montane forest, but high winds and moisture keep the vegetation in a constant state of disturbance in which understory species dominate (Whistler, 1992). These zones of disturbed vegetation are dominated by understory species such as ferns and *Freycinetia* vines (Whistler, 1992). As a result of high levels of rainfall (~2,500 mm·y^{-1}) and periodic but often severe disturbance from high winds and hurricane damage, fewer tree species are found at higher elevations. The forest canopy is dominated by Cyathea tree ferns, and in the lower montane forest other tree species are found, including *Astronidium pickeringii*, *Syzygium samoense*, and *Weinmannia affinis* (Whistler, 1992).

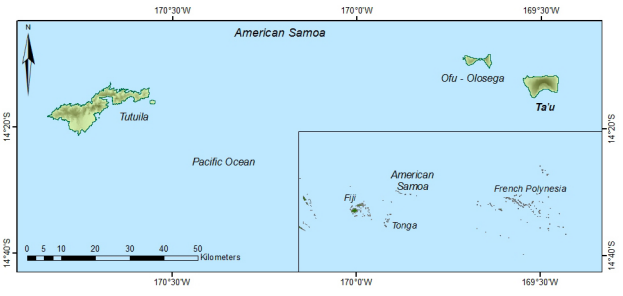

Fig. 1. Map of the main islands of American Samoa including Tutuila, Ofu-Olosega, and Ta‘ū. Inset shows American Samoa relative to other islands in the South Pacific Ocean.

Sampling design–control plots

To determine the relationship between habitat characteristics and the presence of Tahiti Petrels, we compared the characteristics of habitat surrounding petrel burrows (burrow habitat) with those of randomly available habitat (random control habitat) in the summit area on Ta‘ū. Random habitat control plots were selected using a random number generator that determined the distance in meters along the trail from the summit. A total of 32 habitat control plots were sampled during this study. Random survey sites were restricted to accessible habitat off the main trail to reduce habitat damage. At each randomly selected site, the habitat was characterized 3 m off the trail, on either the left or right side. Control plots that overlapped or were within 6 m of each other were not considered.

Petrel burrow plots

General search areas were determined using acoustic surveys from seven monitoring sites established for bird monitoring (Titmus, 2017) and where Tahiti Petrels had been identified by call (Titmus & Lepczyk, 2024). Areas surrounding the acoustic survey sites and along established trail areas were surveyed for the presence of recently used burrows or hollows. Search parameters that helped to indicate a burrow included the removal of leaves, mold, and litter from hollows under the roots of trees, or the presence of bare mud or clearly excavated soil (Fig. 2). Identified burrows were marked with flagging tape and their location was recorded with GPS (Garmin GPS Map 64, 3 m accuracy). A total of 25 petrel burrow plots (3-m radius around a burrow entrance) were identified and sampled during the study. The width, height, and depth of the burrow or hollow entrance, as well as the immediate vegetation, including closest tree species, were described at each burrow. Access and time for searching were limited on the leeward (west) side of the summit by a lack of permanent trails. Thus, searching effort was focused on the windward (east) side of the summit. None

Fig. 2. Tahiti Petrel *Pseudobulweria rostrata* burrow with a pair of dueting petrels present. The structure of the burrow is provided by the root structure of the overhead trees and the ground is free of vegetation.

of the identified burrows were occupied when found. For safety reasons, all burrow searches were conducted during the day when petrels would have been at sea. Remote infrared game cameras (Reconyx HF900) placed at the entrances of identified burrows confirmed that burrows were occupied at night (Fig. 2).

Sampling design

Between 28 July and 10 August 2016, we measured a suite of habitat variables at both random and burrow sites across the summit scrub region of Ta‘ū. Habitat attributes were measured at each site using a modified Braun Blanquet cover abundance scale (Braun-Blanquet, 1932). Vegetation was split into two distinct layers: ground cover (0–2 m from the ground) and canopy cover (> 2 m). Plots with a 3-m radius from either the center of the randomly selected location or the burrow entrance have been used in other studies, e.g., VanZandt et al. (2014). Within each circular plot, the percent cover provided by each type of plant form was estimated visually. Ground cover was identified to plant form, including grass, shrub, forb, fern, and moss, and also as two individual species, *Freycinetia storkii* and *Clidemia hirta*. The percent cover of litter, logs, rock, and bare ground was also estimated to characterize the dominant type of ground cover at each plot. Canopy trees and ferns (> 2 m tall) were identified to species and used to determine the prevalent canopy cover species. Canopy closure was measured using a convex crown densiometer (Forestry Suppliers Inc.) by averaging measurements taken in each of the four cardinal directions. Canopy closure was categorized as either open (< 25% cover) or closed (> 25% cover) based on widespread use of this threshold value (Hansen et al., 2010; VanZandt et al., 2014). In addition, we estimated the canopy height and counted numbers of both trees and tree ferns in each plot to determine the dominant canopy species. Geographic position, altitude, and aspect were determined from GPS. A Digital Elevation Model (United States Geological Survey, 2002) was used within a Geographic Information System (GIS; ArcMap, ESRI Inc.) to determine the slope at each plot site.

Species distribution model

To build our SDM, we determined the most important habitat variables that influence Tahiti Petrel nest site selection using a forward stepwise binomial logistic regression, with the burrows as the cases and the random plots as controls. Binomial logistic regression has been used to identify habitat features most closely correlated with the presence of animals, including seabirds, bats, and wolverines (Copeland et al., 2007; Ford et al., 2005; VanZandt et al., 2014). The environmental and habitat explanatory variables were first checked for multicollinearity based on the variance inflation factor (VIF ≥ 5). Where variables were significantly collinear, only one was chosen as an input into the logistic regression model. The logistic regression models were built using the independent explanatory variables of altitude, aspect, canopy cover type, dominant ground cover type, dominant canopy species, number of trees, and number of tree ferns. Logistic regression models were built with the logit-link function and conditional stepwise selection based on the significance of the score statistic. Models were evaluated for fit using the Hosmer-Lemeshow goodness of fit (GOF) test ($P > 0.05$ was considered a good model fit), and individual parameters were evaluated for significance using $P < .05$ as the cutoff value. The models with the highest explanatory power and number of significant variables were identified based on the lowest corrected Aikake Information Criterion (AICc), and the final model was chosen using model fit values (Hosmer-Lemeshow GOF). The logistic regression model was built using presence/absence of a Tahiti Petrel burrow as the dependent variable. Altitude (m), aspect, number of trees, and number of tree ferns were continuous independent variables. Canopy cover type, dominant canopy species, and dominant ground cover vegetation type were categorical independent variables. Results of the logistic regression model were used to determine the extent of suitable petrel habitat on Ta‘ū.

Determination of suitable habitat

Using the results of the logistic regression SDM modeling, we applied the results of the best model to map suitable Tahiti Petrel habitat using the presence of canopy cover. We classified the summit montane rainforest habitat > 650 m on Ta‘ū by vegetation type, distinguishing between tree cover from open ground cover. A high resolution 2012 United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) Orthoimage of Ta‘ū (USDA, n.d.) was analyzed using GIS (datum = WGS 1984; projection = Web Mercator) to classify the vegetation types present over the summit habitat. This satellite image contained multispectral bands with a resolution of 0.3 m that allowed for individual trees to be identified by shape and color. The image was first clipped to restrict analysis to altitudes > 650 m. The steep, south-facing cliff section was removed from the analysis due to significant shadowing that prevented accurate image classification. The image used was the most recent available and had the least cloud cover. Overall, we classified 774.72 ha (7.7472 km^2) of habitat; we were unable to classify 31.18 ha (0.3118 km^2) of the area because of cloud cover. The imagery was classified in GIS using a maximum likelihood supervised classification model to distinguish between open ground cover areas dominated by *Freycinetia* vines and ferns, and closed canopy areas where trees and tree ferns were present. Over 150 training areas were created based on identifiable features, classifying pixel color into four categories: trees, open ground cover, bare earth, and cloud cover. Results of the image classification were used to determine the surface area covered by each category. Image classification results were then compared to the assessments of canopy cover from field plots to determine whether the fit of the model was appropriate (Kirui et al., 2013; Lauer & Aswani, 2008; VanZandt et al., 2014). Due to inherent GPS position errors, the percent canopy cover of each field plot was compared to the estimated canopy cover from a larger 6-m radius plot on the classified image.

The habitat classification was then combined with the digital elevation model to create a weighted habitat suitability index within GIS. Both altitude and habitat type were binned into five categories from least suitable (5) to most suitable (1). Altitude values were binned into equal categories: 650–719 m (5, least suitable), 720–789 m (4), 790–859 m (3), 860–929 m (2), 930–998 m (1, most suitable). The four habitat type values were categorized as follows: Open (1, most suitable), Bare (3), Closed (5, least suitable), and Cloud (excluded from analysis). The final suitability index was weighted towards habitat type (0.75) due to its greater importance in determining burrow location. This analysis provided an assessment of the amount of likely suitable nesting habitat present over the summit of Ta‘ū.

RESULTS

Burrow site descriptions

A total of 25 Tahiti petrel burrows were found on the summit of Ta‘ū (Fig. A1 in Appendix, available on the website), with 16 located on the windward (east) side surrounding the Lata summit between 793 m and 966 m; nine burrows were found on the leeward (west) side close to the Olotania crater. All burrows were found within hollows underneath small trees or tree ferns, with the root structure providing an open space for nesting (Fig. A1 in Appendix). Typically, there was a single large, visible opening to each burrow, along with some smaller side openings. The most common tree species providing root structure to the petrel burrows was *Weinmannia affinis* (42%), followed by *Cyathea* tree ferns (36%), and *Astronidium pickeringii* (21%). Average burrow dimensions measured 47.4 ± 4.7 cm (mean ± standard error [SE]) wide, 40.5 ± 4.2 cm tall, and 79.2 ± 8.9 cm long. Average canopy cover at burrow sites was 67.8% ± 6.4%; 84% of plots had a closed canopy cover (> 25%). In comparison, average canopy cover at random sites was 22.2% ± 6.3%. Ferns were the most prevalent ground cover, accounting for the highest percent cover in 48% of the plots. The next most prevalent ground cover was *Freycinetia*, accounting for the highest percent cover in 28% of the plots. Within the 3-m plots, ferns provided an average cover of 26.5%, and *Freycinetia* provided an average cover of 24.0%.

Burrow habitat models

The final binary logistic regression model was built using the independent explanatory variables of altitude, aspect, canopy cover type, dominant ground cover type, dominant canopy species, number of trees, and number of tree ferns (Table 1). The best model included both canopy cover type and altitude and explained 52.4% of the variance, correctly predicting whether the plot would contain a petrel burrow 83.9% of the time (χ^2 = 27.74, *df* = 2, *P* < .001). Of the top models based on AICc values, the one-variable and three-variable models were poor fits (Hosmer–Lemeshow GOF, *P* ≤ .05; Table 1). Canopy cover was the most important variable in determining if a plot contained a burrow, with closed canopies much more likely to have a burrow present (Odds Ratio [OR] = 40.6, *df* = 1, *P* < .001). In addition, altitude also had a significant effect on whether a plot contained a petrel burrow, with higher altitudes more likely to have a burrow present (OR = 1.0, *df* = 1, *P* = .036). The ground cover type was not important for determining burrow location because burrows were overwhelmingly associated with closed canopies. The dominant canopy species was not important for determining burrow location because, regardless of species, the presence of taller trees or tree ferns provided structure for the burrows underneath.

TABLE 1
Goodness of fit and selection results for the best binary logistic models explaining Tahiti Petrel *Pseudobulweria rostrata* nesting habitat preferences

Model[a]	R^2	AICc	ΔAICc	*P*
Canopy type	0.441	10.6	0.0	<.001
Canopy height	0.131	43.8	33.1	.027
Canopy type + Altitude	0.524	51.1	41.3	**.894**
Canopy type + Canopy height	0.452	61.7	51.9	**.509**
Canopy type + Altitude + Dominant vegetation type	0.556	51.5	42.5	.037

[a] The selected best model was the two-variable model (Canopy type + Altitude) due to a high R^2 combined with a low Akaike Information Criterion (AICc) value for a model, which was well fitted using the Hosmer–Lemeshow Goodness of Fit test (*P*) shown in bold.

Habitat availability on Ta‘ū

Overall, we classified 774.72 ha (7.774 km^2) of habitat. Of the visible habitat, 494.22 ha (4.9422 km^2) was classified as tree-covered (63.79%), and 249.02 (2.4902 km^2) was classified as *Freycinetia* or fern-covered (32.14%; Fig. A2 in Appendix). All closed canopy cover habitat plots were within 3 m (GPS error) of tree classified pixels, and accuracy of estimated canopy cover in the classified plots was 84.5%, indicating that the supervised maximum likelihood classification was accurate. There was a clear difference in the habitat composition between the east and west sides of the summit habitat, with the west side containing a much higher percentage of trees (80.02%) than the east side (46.50%). Of the final habitat suitability index, 254.1 ha (2.541 km^2) (32.8%) of the total montane habitat on Ta‘ū was determined to be suitable for Tahiti petrel breeding (category 1 and 2; Fig. A3 in Appendix).

DISCUSSION

The presence of canopy species was the most important factor for determining the presence of Tahiti Petrel nests across the summit of Ta‘ū. Additionally, there was a large amount of variation in the distribution of canopy species across the summit habitat above 650 m, and this variation likely has a significant impact on the distribution of the petrels. Trees and canopy cover were the most important components of habitat for Tahiti Petrels.

A large difference was found in the amount of tree and tree fern cover between the east and west sides of the summit habitat above 650 m on Ta‘ū. Canopy cover on the west side was 80.0% *versus* 46.5% on the east side of the summit (Fig. A2 in Appendix), but reasons for the difference are unclear. Whistler (1992) characterized the entire area as summit vegetation but noted the difference between the vegetation on either side, describing the east side as summit scrub, with smaller, sparse tree coverage. In an in-depth vegetation survey of Ta‘ū, Cole et al. (1988) classified the entire summit area as moss forest, with no distinction between the east and west sides. Possible explanations for the observed variation in spatial habitat composition are differences in localized groundwater impoundment or prevailing wind conditions (Amerson et al., 1982; Bentley, 1975; Izuka 2005). The prevailing easterly trade winds may contribute to the stunted scrub habitat on the eastern windward side, while the lower wind conditions on the leeward side of the summit may allow for larger trees to grow.

All Tahiti Petrel burrows were found underneath the exposed root systems of trees and tree ferns within the summit montane habitat, a finding similar to those of previous studies at this colony (Amerson et al., 1982; O’Connor & Rauzon, 2004). Due to the Tahiti Petrel’s reliance on trees and tree ferns for suitable nesting habitat, and the general tendency for Procellariiform seabirds to exhibit high

nest site fidelity (Bried & Jouventin, 2001), changes in the amount of tree-covered habitat on Ta‘ū would likely affect the carrying capacity of the montane habitat, which in turn would impact breeding population size. Both American Samoa and Independent Samoa have been hit by many significant storms and hurricanes, including at least 39 hurricanes between 1831 and 1926 (Amerson et al., 1982). Most recently, in 2005, Ta‘ū was hit by hurricane Olaf, which caused significant structural damage to the island's forests (Webb et al., 2014). While the Tahiti Petrel population on Ta‘ū has likely adapted to the historic habitat disturbance frequency, any future increases in the amount of disturbance or long-term changes to the montane habitat structure could negatively impact the Tahiti Petrel population.

Conservation and management implications

Extensive research has documented the negative impacts of invasive animals, such as rats, cats, dogs, and mongooses, on Procellariiform populations (Croxall et al., 2012; Warham 1990). However, further research should focus on determining the direct impacts of habitat loss and change on populations, as this has been significant (Croxall et al., 2012; Dolman & Sutherland, 1995). Sub-tropical island breeding petrels are particularly susceptible to threats and extinction (Carlile et al., 2003; Warham, 1990), including the loss of habitat (BirdLife International, 2000). In addition, tropical hurricane intensity has been increasing over the last 30 years, which may lead to greater habitat loss for seabirds (Emanuel, 2005). Monitoring this loss is important for properly informing management plans.

The summit of Ta‘ū is home not only to Tahiti Petrels, but also to at least four other seabird species: Tropical Shearwater *Puffinus bailloni*, Herald Petrel *Pterodroma heraldica*, possibly Newell's Shearwater *Puffinus newelli*, and an unidentified petrel. As such, the summit provides an important location for seabird conservation. Based on our findings, we have several recommendations for future research and conservation. First, although separate habitat evaluations were not conducted for the other seabird species, it is important to assess how the amount of habitat available for Tahiti Petrels may be changing over time, using our study as a baseline. If changes are found to occur, understanding the drivers of the change will be key to determining if management actions are needed. Second, our SDM results could be used to predict Tahiti Petrel habitat on other nearby islands, such as Tutuila. Although it would be critical to evaluate these islands in more depth, an initial analysis could be carried out with our model. Third, our findings demonstrate the importance of trees and other forest canopy species in providing nesting habitat for Tahiti Petrels. Samoa lies within a region of the Pacific Ocean that experiences a low likelihood of hurricanes, with the number per year declining due to global warming (Goni et al., 2009). However, in western Polynesia and Melanesia, hurricanes are more frequent, and breeding habitat requirements for Tahiti Petrels and their population sizes are lower. Ironically, ocean productivity is enhanced by hurricanes (Hung & Gong, 2011), providing opportunities for smaller petrels that are more abundant and that forage lower in the food web. Specifically, Tahiti Petrels feed mostly on fish and squid in the eastern tropical Pacific Ocean, whereas smaller Pterodroma petrels tend to take more invertebrates as prey (Spear et al., 2007). Therefore, it is important to understand how climate change may influence hurricanes across the geographic range of Tahiti Petrels, particularly in terms of both habitat availability and food resources. This information may enhance our understanding of how the population size of Tahiti Petrels, as well as other petrel species, could be affected. Overall, our study emphasizes the importance of developing SDMs specifically for Tahiti Petrels, and for seabirds in general, as a first step in conservation planning.

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