

STUDIES OF ARTIFICIAL LIGHT, SEABIRD FALLOUT, AND HABITAT
SUITABILITY CONCERNING NEWELL'S SHEARWATER AND
HAWAIIAN PETREL CONSERVATION

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STUDIES OF ARTIFICIAL LIGHT, SEABIRD FALLOUT, AND HABITAT
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ABSTRACT

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The federally threatened Newell's Shearwater (*Puffinus newelli*; listed as endangered on the IUCN Red List) and endangered Hawaiian Petrel (*Pterodroma sandwichensis*) formerly nested throughout the main islands of the Hawaiian Archipelago. As a result of certain anthropogenic activities, breeding ranges of these species are now restricted to high-elevation regions of particular islands and numbers of Newell's Shearwaters are currently declining. I conducted large-scale GIS-based studies

of artificial light, seabird fallout, and habitat suitability concerning the conservation of these two seabirds. Models that I developed suggest that there are few to no portions of Kauai from which young birds could fledge and not view light on their post-natal nocturnal flights. Additionally, the spatial pattern of observed Newell's Shearwater fallout is consistent with the amount of light that fledglings may view along their first flights to and beyond the coastline, providing support for the idea that fledglings could be attracted back to land after reaching the ocean in numbers large enough to contribute significantly to island-wide fallout. Terrestrial habitat suitability models for both species on Kauai predict that a large portion of the interior of Kauai could be suitable for both of these species in the absence of anthropogenic threats. Habitat suitability models incorporating threats identified the mountains on the north-central portion of the island as the most isolated from a combination of anthropogenic disturbances, making it ideal for future surveys. Much of this region, however, is privately owned and not currently designated as a reserve. In addition, a moderate degree of overlap between habitat predicted to be suitable for both the Hawaiian Petrel and Newell's Shearwater suggests that some of the same larger tracts of land could potentially be managed jointly for both species. These studies provide information that is crucial for conservation biologists, federal and state employees, and private landowners because expanding efforts to further reduce artificial light output and control non-native predators, as well as management of additional lands as reserves, may be necessary for the protection and preservation of these two endemic tropical seabirds.

CHAPTER I

MODELING ARTIFICIAL LIGHT VIEWED BY FLEDGLING SEABIRDS

Introduction

Artificial light is increasing rapidly across the surface of our planet (Cinzano et al. 2001) and its impacts on organism ecology include numerous examples of interference with the typical behaviors of certain animals (Longcore and Rich 2004). Fledglings of certain small- to medium-sized shearwaters, petrels (Procellariidae), and storm-petrels (Hydrobatidae) are attracted to, and disoriented by, sources of anthropogenic light on their post-natal nocturnal flights to the ocean (Hadley 1961, Harrow 1965, King and Gould 1967, Imber 1975, Reed et al. 1985, Telfer et al. 1987, Le Corre et al. 2002, Rodriguez and Rodriguez 2009, Miles et al. 2010), though the reason for this behavior remains largely unknown. This disorientation can cause them to fall to the ground following exhaustion and/or crashing into manmade structures and vegetation (a phenomenon termed “fallout”). Once grounded, they are vulnerable to starvation, dehydration, predation by introduced mammals, and collisions with vehicles, which can result in large numbers of injured and dead individuals (Reed et al. 1985, Telfer et al. 1987, Le Corre et al. 2002, Rodriguez and Rodriguez 2009). Previous studies of light attraction exhibited by species at Reunion Island (Le Corre et al. 2002), in the Canary Islands (Rodriguez and Rodriguez 2009), and in Hawaii (Ainley et al. 2001, Griesemer

and Holmes, *in press*) suggest that light-induced fledgling mortality can affect recruitment and potentially play a significant role in population decline.

One of the most familiar examples of fallout occurs each autumn on the island of Kauai, Hawaii, as fledgling Newell's Shearwaters ('A'o [*Puffinus newelli*]), Hawaiian Petrels ('Ua'u [*Pterodroma sandwichensis*]), and Band-rumped Storm-Petrels ('Ake'ake [*Oceanodroma castro*]) take their maiden flights to sea (Reed et al. 1985, Telfer et al. 1987, Ainley et al. 2001). Between 1978 and 2009, more than 30,000 Newell's Shearwater fledglings were collected as fallout birds, in addition to over 300 Hawaiian Petrels and 20 Band-rumped Storm-Petrels (State of Hawaii, unpublished data). Notably, many fallout fledglings are never recovered, either due to predation and scavenging by introduced predators or birds simply landing in areas unlikely to be visited by the public. Consequently, the >30,000 Newell's Shearwaters collected have been estimated to represent from 93% to as little as 50% of actual fallout, suggesting ~32,250-60,000 fledglings may have actually been grounded due to the effects of anthropogenic light (Ainley et al. 2001). Kauai residents are encouraged to assist fallout birds by delivering them to aid stations for a veterinary examination, after which they are released if deemed to be in physical condition appropriate for fledging (Reed et al. 1985, Telfer et al. 1987, Rauzon 1991). Many individuals are located, banded, and released each season, but their fate after release is unknown (Duffy 2010).

Conservation efforts for seabirds would benefit significantly by using a spatially-explicit model to estimate the degree to which young birds fledging from regions of known and potential breeding habitat may be affected by anthropogenic light. A map of stationary night light intensity is insufficient, however, as it does not account for

fledgling movement. Such a model must account for the total intensity of light that can be viewed along a fledgling's entire path to the ocean because young birds fledging from dark breeding sites (in which no light can be viewed) may encounter artificial light subsequent to fledging and become disorientated.

I developed a GIS-based method to estimate the total intensity of artificial light that young procellariids and hydrobatids, fledging from any terrestrial region of interest, could potentially view along a least-cost path (with respect to topography) on their initial nocturnal flights to sea. Because an unknown threshold of light intensity may exist for attraction by birds to be exhibited (making the exact manner in which they would respond to various light intensities unknown), model birds traveled along least-cost paths based on topography, accumulating values of viewable light intensity along those paths, versus following paths based on movement toward light. Two models, developed using 2009 artificial light data from a satellite image, are presented for the island of Kauai and their relevance to the Newell's Shearwater is emphasized. I compare the proportion of two-dimensional surface area on Kauai covered by different categories of light intensity, including values of no light, calculated from four GIS layers: an artificial light intensity layer obtained from a satellite image, a layer accounting for the intensity of light that can be viewed from each island location, and the two models that account for light viewed along hypothesized fledgling flight paths. This allowed a comparison of the coverage of three types of dark area on Kauai: area with no night light output, area from which artificial light could not be viewed, and area from which birds could fledge and not view artificial light along their flight paths. In addition, I present the island-wide pattern of Newell's Shearwater fallout on Kauai that occurred from 1998 to 2008 and compare it to

the developed models. I then discuss possible applications of this modeling approach for taxa other than seabirds for which light is a significant threat, as well as its potential use for modeling other threats to ecological systems.

Methods

I used ArcGIS 9.3.1 (ESRI, Redlands, CA) and digital layers of the island of Kauai to develop two models. One model represents the total intensity of artificial light a fledgling procellariid or hydrobatid could view along the topographically least-cost path from every location on the island to the coastline (the ‘island’ model) and the other represents these same paths to the coastline extended to 10 km offshore (the ‘extended flight’ model). This required the extension of a Digital Elevation Model (DEM) past the coastline (i.e., converting ocean to land), a layer of the total intensity of artificial light viewable from each pixel of this extended DEM (a viewable light intensity layer), and two models that summed all pixels of viewable light along topographically least-cost paths from the destination (the coastline for the ‘island’ model and 10 km past the coastline for the ‘extended flight’ model) back to each starting location (each DEM pixel). Figure 1.1 outlines the steps involved in the development of the layers and models produced in this study. To provide repeatable steps for future use, the GIS-based processes are described in substantial detail in the Appendix.

Model assumptions

Both models required a set of assumptions concerning the flight behavior of fledgling procellariids and hydrobatids and if they can view light originating from the land once at sea. The ‘island’ model included four assumptions. First, fledglings followed the path of least topographical resistance (i.e., major drainages) from their natal sites to

the ocean, as suggested for fledgling movements based on observed concentrations of fallout birds on Kauai (Telfer et al. 1987, Podolsky et al. 1998). Second, fledglings viewed light from 100 m above ground level, though this height differs from 100 m for sloped terrain because of the manner in which viewing light above ground level was modeled in this study. Third, once fledglings descended to, or were already at or below, 100 m in elevation they flew a straight path to the ocean, avoiding geographic features >100 m in elevation along their path. This assumption allowed birds to discontinue following rivers once they descended to 100 m, which is likely more realistic based on personal observations of adults flying straight paths over lowland regions near the coast when returning to breeding sites. And finally, fledglings no longer viewed artificial light when they traveled beyond the coastline. The ‘extended flight’ model included the first, second, and third assumptions from the ‘island’ model plus an additional one, that fledglings could view light emanating from the island until they traveled to 10 km beyond the coastline.

Viewable artificial light intensity layer

A layer of stable average artificial night light intensity from 2009 for the earth (developed from a satellite image with 911.25 x 911.25 m resolution; pixel values ranging from 0-63 relative units) was obtained from the National Geophysical Data Center (<http://www.ngdc.noaa.gov/dmsp/downloadV4composites.html>) and the island of Kauai was clipped for further analysis (Fig. 1.2). Light originating from the sun, moon, aurora, and ephemeral sources (e.g., wildfires) were not included in this light intensity layer. All data included originated from sources of artificial light, including persistent sources such as gas flares, on cloud-free nights. Because these light intensities represent

an average over an entire year, using this layer required the assumption that yearly average light intensities are a good approximation of light conditions on any night during the fledging period (e.g., October-November for Newell's Shearwater; Telfer et al. 1987). Light intensity pixels with values from 1-63 were then converted to points and the point layer was clipped so that all light points fell within the island boundary.

A previous study estimated that adult Newell's Shearwaters on Kauai flew at a mean height of ~125 m (ranging from 8 to 750 m) above ground level with considerable variation among sites (Day and Cooper 1995). One limitation of the GIS methods I used is that, at each pixel on the extended DEM, fledglings remained at ground level; therefore, to account for height of both fledgling flight and light sources while developing this viewable light intensity layer, I raised the height of all light points to 100 m above ground level. For birds at ground level at the same elevation as light sources, raising the height of light sources above ground level allows birds to view light in an identical manner to raising birds the same height while keeping light sources at ground level; however, this relationship is not identical when birds and/or light sources are on sloped terrain. Therefore, this approach is considered an attempt to approximate the manner in which fledglings view light sources from realistic flight heights (Day and Cooper 1995) above the ground. I then generated a raster layer highlighting which light points were viewable from each pixel of the extended DEM of Kauai, correcting for the curvature of the earth. Because of software limitations, multiple output layers were produced; all output layers were summed to generate a layer of the total intensity of artificial light viewable in 360° from each pixel of the extended DEM (i.e., a viewable light intensity layer; Fig. 1.3).

Input layers for models

As input for the final model step, I reclassified the extended DEM of Kauai so that no pixel values were <100 m to achieve the assumption that fledglings fly a straight path to the ocean once they descend to, or are already at or below, 100 m in elevation. The two models required clipping smaller layers from the reclassified extended DEM and the viewable light intensity layer. For the 'island' model, I clipped the extended DEM and light intensity layer to the size of the island of Kauai. For the 'extended flight' model, I clipped the extended DEM and light intensity layer to 10 km beyond the coastline of Kauai.

Development of final model layers

I used several tools from the TauDEM Version 5.0 toolset (Tarboton 2010) to develop the final layer for both models. I raised pits (low-elevation pixels that are completely surrounded by higher-elevation pixels and interfere with flow paths) in the DEMs for both models and created a flow direction raster from these pit-removed DEMs. I then used both the flow direction and viewable artificial light intensity layers to generate a layer of the intensity of all light viewable along the topographically least-cost path from every DEM pixel on the island either to the coastline (for the 'island' model; Fig. 1.4) or to 10 km past the coastline (for the 'extended flight' model; Fig. 1.5). To accomplish this, the software generated topographically least-cost paths from each DEM pixel to the destination (the coastline for the 'island' model and 10 km past the coastline for the 'extended flight' model) and summed pixels of viewable light along these paths from the destination back to all possible starting locations (each DEM pixel). This included light behind the flight direction of the bird; therefore, pixel values of this layer

should be considered the total possible intensity of light that could be viewed along the path. In addition, the same individual lights are viewed in a series of consecutive pixels along a flight path, compounding their contribution to final cumulative light values. I consider this representative of the potential continual influence of particular light sources on the probability of attracting and disorienting fledglings.

Model limitations

Limitations of this modeling method include its lack of account for light attenuation (the decay in light intensity with increasing distance from the source), potential effects of wind speed and direction on fledgling movement patterns, effects of temporary weather conditions (e.g., local cloud cover and precipitation) on viewable light, or variation in the lunar cycle (which is known to affect fallout rates; Reed et al. 1985, Telfer et al. 1987, Ainley et al. 2001, Rodriguez and Rodriguez 2009, Miles et al. 2010). In addition, the light intensity pixels from the 2009 layer are 911.25 x 911.25 m in resolution, and each pixel was converted to a single point 100 m above ground level at the center of the original pixel; therefore, some variability in the horizontal and vertical distribution of lights was undoubtedly lost. In reality, individual lights in some locations could be distributed such that additional pockets of dark space may exist, through which some fledglings could fly to sea without viewing artificial light. Additionally, the 2009 night light layer contains artificial sky lighting (i.e., additional glow caused by refraction by water and dust molecules suspended in the air), which is most noticeable in proximity to cities (Elvidge et al. 2007), and this may inflate light intensity values to some extent in areas surrounding urban sites on Kauai.

Light intensity summary

From the 2009 night light intensity layer, I noted the single highest light intensity pixel value for Kauai and for the remainder of the Hawaiian archipelago for comparison. I also compared the proportion of two-dimensional surface area on Kauai covered by different categories of total light intensity calculated from the 2009 artificial light intensity layer, the 2009 viewable light intensity layer, the ‘island’ model, and the ‘extended flight’ model. I reclassified the pixel values for all four layers into groups as follows: 0, 1-250,000, 250,001-500,000, etc.; the last category contained values from 1,750,001 to 5,611,830. I then divided the number of pixels within pixel categories by the total pixels for the island, yielding the proportion of the island covered by the different light intensities. The category containing only values of zero allowed us to compare the proportion of area on Kauai covered by three types of dark area: area with no night light output (from 2009 artificial light intensity layer), area from which artificial light could not be viewed (from the viewable light intensity layer), and areas from which birds could fledge and not view artificial light along their paths (from both the ‘island’ and ‘extended flight’ models).

Results

Light intensity values for Kauai from the original 2009 night light layer range from 0 to 55 (relative units; Fig. 1.2). The highest light intensity value for Kauai within a single 911.25 x 911.25 m pixel (= 55) approaches the highest value for the entire planet (= 63), which is recorded for many major metropolitan areas of the earth (e.g., Tokyo, Los Angeles), including Honolulu on the island of Oahu (the nearest main Hawaiian island southeast of Kauai). Figure 1.3 displays the intensity of light viewable from each

location (i.e., DEM pixel) on Kauai, as well as over the ocean near the shoreline, and demonstrates the pervasiveness of artificial light in the interior of the island not illustrated by the original satellite image. Viewable light intensity values in Figure 1.3 range from 0 to 5957 relative units; the highest value of viewable light intensity occurs on the island.

Summing viewable light values along topographically least-cost paths hypothesized for post-natal fledgling flights yielded cumulative viewable light values ranging from 0 to 1,575,440 for the ‘island’ model (Fig. 1.4) and from 85,460 to 5,611,830 for the ‘extended flight’ model (Fig. 1.5). The intensity of artificial light progressively increased, both in value and proportion of Kauai covered (Table 1.1), from the original 2009 night light layer to the ‘extended flight’ model (in which birds could view light along paths to 10 km past the coastline). Notably, with respect to fledgling seabirds, the ‘island’ model yielded only 3.2% of the island’s total two-dimensional surface area “unaffected” by artificial light (i.e., that from which young birds could fledge and not view artificial light) and the ‘extended flight’ model yielded no “unaffected” portions of the island (Table 1.1).

Discussion

Model results highlight that fledging shearwaters, petrels, and storm-petrels on Kauai are likely exposed to artificial light beyond regions depicted by a satellite image alone. The practical value of this modeling effort lies in allowing managers to assess potential light exposure, and hence risk, to these fledglings from different colony sites on Kauai. The exact manner in which birds would respond to this light is unknown, however, as a threshold of intensity may be required for attraction and disorientation to

occur. Given that the terrestrial activities of procellariids and hydrobatids (i.e., flights over land) are nocturnal and that the eye of the Manx Shearwater (*P. puffinus*; a close relative of the Newell's Shearwater) was shown to be adapted for nocturnal vision (Martin and Brooke 1991), faint light, as perceived by strictly diurnal animals, could be amplified when viewed by these fledglings, making even low-intensity light sources possible threats.

The 'island' model, incorporating realistic assumptions concerning fledgling movement to the shoreline, suggests that there are very few regions on Kauai from which young procellariids and hydrobatids could successfully fledge without potentially viewing artificial light along their paths to the ocean. The 'extended flight' model, however, which allows birds to view light offshore, suggests that there are no such areas on the island. The large increase in minimum and maximum cumulative viewable light intensity yielded by the 'extended flight' model, compared to the 'island' model, arose from the expanded visual field birds experienced once over the ocean. This allowed fledglings to view distant lights along the coastline not previously visible when traveling along their terrestrial paths. Though it is not known how these birds respond to viewing lights on the land once they are at sea, previous authors suggested that birds can be attracted by light back to the shore (Podolsky et al. 1998), making a model with this assumption likely more appropriate for estimating the cumulative threat posed by artificial light.

Notably, the north shore region of Kauai contains the highest number of Newell's Shearwater fallout records summed from 1998-2008 (Fig. 1.6), a time during which the approximate geographical distribution of artificial light, relative to other portions of the

island, did not change compared to 2009. This region, however, did not yield the highest light intensity values from the 2009 night light satellite layer, the viewable light layer, or the 'island' and 'extended flight' models. Most remaining Newell's breeding sites are known from the northwestern portion of the island (Hawaii Division of Forestry and Wildlife, unpublished data). Thus, the high volume of fallout on the north shore is expected to be a function of high fledgling productivity within northwestern watersheds and, therefore, a large number of fledglings from northwestern colonies being exposed to artificial light originating from the north shore (i.e., north shore lights viewed from the ground or air surrounding northwestern mountain peaks or once offshore north of Kauai [Fig. 1.3]). The Newell's Shearwater is currently exhibiting a population decline on Kauai (Griesemer and Holmes, *in press*), and given that fallout can hinder population growth (Ainley et al. 2001), minimization of light attraction will play a crucial role in the recovery of this species, particularly on the north shore. In addition, though lesser numbers of Hawaiian Petrels and Band-rumped Storm-Petrels are found annually, any reduction in successful fledging of these long-lived seabirds with low fecundity could have significant long-term impacts on their populations, especially in concert with the continuous threat of predation by introduced mammals.

Researchers and managers may use the layers stemming from these models as a first step in assessing the level of impact of artificial light on individual breeding colonies of the Newell's Shearwater on Kauai. Examining light pixel values from original satellite images (e.g., Fig. 1.2) within areas will be valuable for managers because it provides an assessment of risk to birds at sites of light sources. By comparison, modeling viewable light and fledgling movement as I have done in this study allows managers to assess the

threat that light poses to birds originating from known breeding colonies, as well as regions where breeding activity is suspected. Summing light pixel values from original satellite images within individual watersheds can also provide a simple and rapid assessment of potential risk to fledglings that does not require complex modeling. Summing light by watershed, however, does not account for light that can be viewed originating from neighboring watersheds, and thereby may depict some watersheds as “dark” when they may contain fledglings that could view light along their flight paths. Risk assessment at the colony scale will become increasingly important for managers of threatened and endangered burrowing shearwaters and petrels on Kauai and other islands when determining where to allocate limited resources to protect birds.

The modeling method described here can be applied to related taxa in other locations. The 2009 night light layer I used is available for the entire planet from the National Geophysical Data Center, providing current artificial light data for other locations, particularly islands, where the threat of light attraction and fallout is significant. As light layers from this source are available for a period spanning 18 years (1992-2009), light conditions could be modeled as well to investigate changes during the past two decades. In addition, the assumptions considered herein could be modified to incorporate behavioral information specific to other seabird species (i.e., varying the height of fledgling flight and the elevation at which fledglings fly straight paths to the ocean). Light intensities could also be altered on base satellite images to examine how proposed artificial light reduction goals or projections of future night light output might affect particular regions and breeding sites after accounting for seabird movement. Light attenuation could be accounted for as well through use of an attenuation formula, a map

of two-dimensional distance from each light source (used as a proxy for actual three-dimensional distance from light sources), and the 'Raster Calculator' to adjust light intensities as they decay with distance. However, this may require each light point, which could range from hundreds to thousands, to be modeled individually.

Methods presented herein could also be used to estimate the threat of light altering the behaviors of non-seabird taxa, particularly migratory passerines and hatchling marine turtles, traveling through or breeding in human-populated regions (e.g., Cochran and Graber 1958, Witherington 1992, Salmon et al. 1995, Jones and Francis 2003, Bird et al. 2004, Tuxbury and Salmon 2005, Baker and Richardson 2006, Stone et al. 2009, Keenan et al. 2007, Kempnaers et al. 2010). Maps of viewable light intensity would provide such an estimate in some cases and could be developed using light layers at resolutions finer than the layer used to develop these models (i.e., those displaying individual light sources). Furthermore, elements of the technique described here (or alterations thereof) could be used to spatially model other point-source threats to ecological systems, such as sound and air pollution. Movements that differ from the downhill, least-cost paths employed in this study (e.g., long-distance migration routes of passerines) could be modeled as well, but this would require different methods for the final step of model development than those presented in this paper. Spatially assessing threats at large scales may require developing multiple layers due to computer and software limitations.

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Table 1.1. The proportion of two-dimensional surface area on Kauai covered by artificial light intensity categories from four layers: a 2009 night light intensity layer (obtained from a satellite image), a layer of light intensity viewable from each island location (developed using the 2009 night light layer), and our 'island' (representing the total possible light intensity fledglings could view along topographically least-cost paths to the coastline) and 'extended flight' models (representing the total possible light intensity fledglings could view along the same paths as in the 'island' model extended to 10 km offshore).

Light Intensity (relative units)	Artificial Light	Viewable Artificial Light	'Island' Model	'Extended Flight' Model
0	0.615	0.288	0.032	0.000
1 - 250,000	0.385	0.712	0.794	0.088
250,001 - 500,000	0.000	0.000	0.102	0.073
500,001 - 750,000	0.000	0.000	0.012	0.142
750,001 - 1,000,000	0.000	0.000	0.041	0.030
1,000,001 - 1,250,000	0.000	0.000	0.012	0.252
1,250,001 - 1,500,000	0.000	0.000	0.008	0.047
1,500,001 - 1,750,000	0.000	0.000	8.311x10 ⁻⁵	0.071
1,750,001 - 5,611,830	0.000	0.000	0.000	0.296

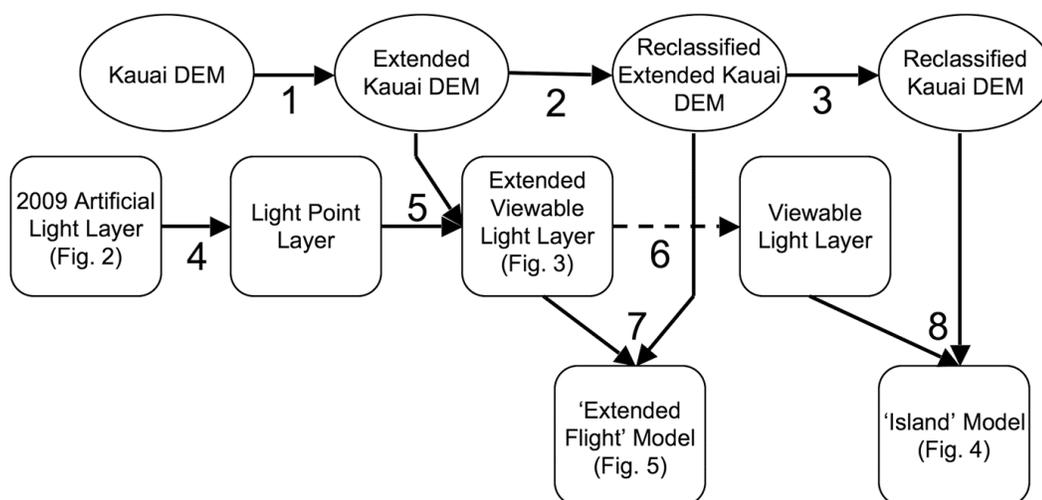


Fig. 1.1. Flowchart of GIS layers developed in this study and the steps involved in their production: (1) a Digital Elevation Model (DEM) of Kauai was extended 11 km beyond the coastline to produce an extended DEM, (2) all pixels of the extended Kauai DEM <100 m in elevation were reclassified to 100 m so that fledgling seabirds flew straight paths to their destination once at or below 100 m, (3) the reclassified extended DEM was clipped to match the extent of the original Kauai DEM, (4) pixels of an artificial night light layer (from a satellite image) were converted to points raised 100 m above ground level to account for height of fledgling flight, (5) the extended Kauai DEM and light point layer were used to develop a layer of the total intensity of light that could be viewed from each extended DEM pixel (i.e., an extended viewable light layer that accounts for light that can be viewed offshore), (6) the extended viewable light layer was clipped to match the extent of the original Kauai DEM, (7) to develop the 'extended flight' model, both the reclassified extended Kauai DEM and extended viewable light layer were clipped to 10 km beyond the coastline and pixel values from the 10 km extended viewable light layer were summed along topographically least-cost paths from each fledgling destination (10 km beyond the coastline) back to all possible starting locations (every pixel of the 10 km reclassified extended DEM), and (8) to develop the 'island' model, pixel values from the viewable light layer were summed along topographically least-cost paths from each fledgling destination (the coastline) back to all possible starting locations (every reclassified DEM pixel).

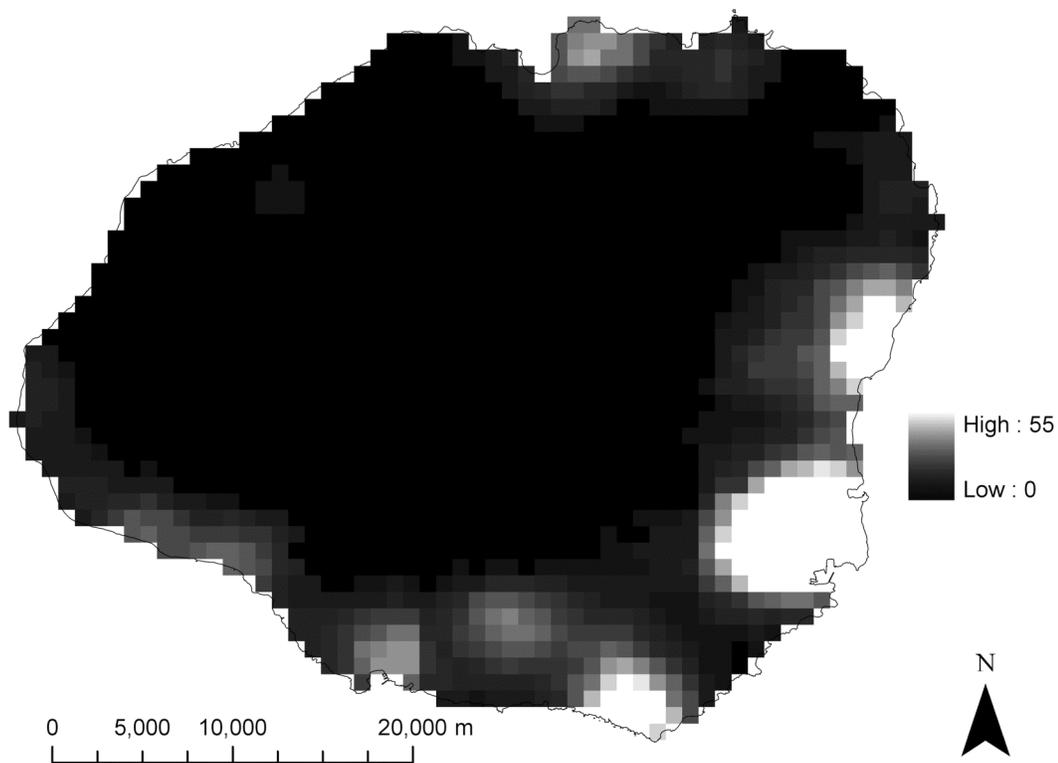


Fig. 1.2. Map of Kauai illustrating the stable average artificial night light intensity for 2009. Light intensity pixels (911.25 x 911.25 m in resolution) are not in complete overlap with the island boundary (outlined in black).

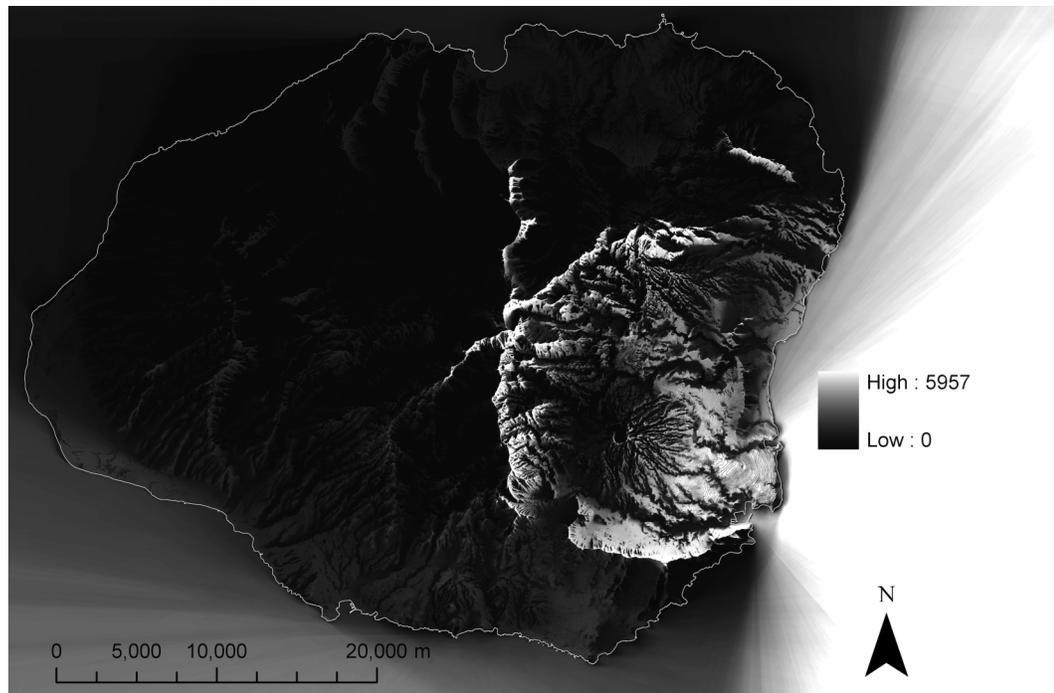


Fig. 1.3. Map of Kauai (10 x 10 m resolution) and nearby ocean illustrating the total intensity of artificial light (for 2009) viewable in 360° from each island and ocean pixel (i.e., from each extended DEM pixel). Light viewable from the ocean is included to show light intensity near the coastline that fledgling procellariids and hydrobatids could potentially view past the island boundary (outlined in white). The highest viewable light intensity value occurs on the island.

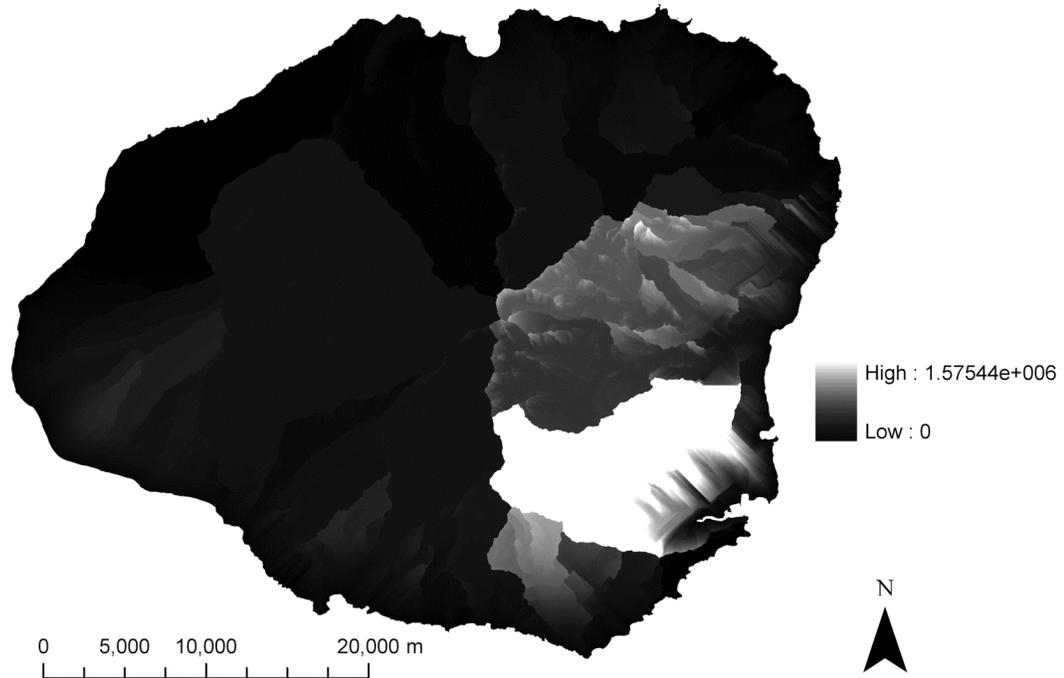


Fig. 1.4. Map of Kauai (10 x 10 m resolution) illustrating the total intensity of artificial night light (for 2009) a fledgling procellariid or hydrobatid could potentially view if it followed the topographically least-cost path from any point on the island until descending to 100 m above sea level (asl), at which point it flew a straight path toward the ocean (avoiding obstacles > 100 m asl and only viewing light until it reached the coastline).

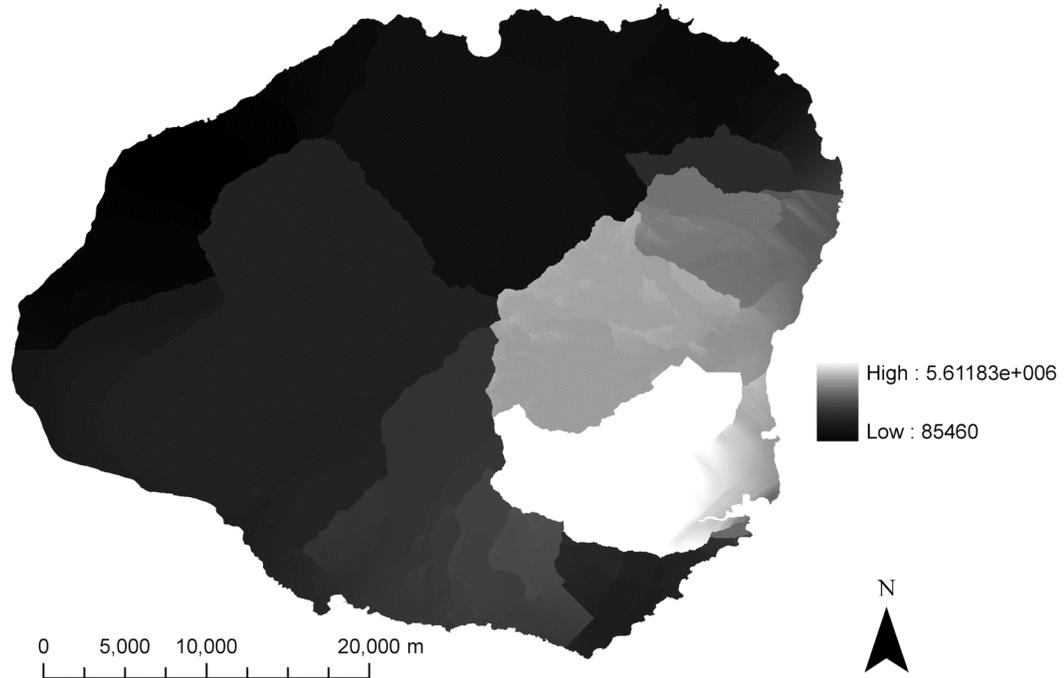


Fig. 1.5. Map of Kauai (10 x 10 m resolution) illustrating the total intensity of artificial night light (for 2009) a fledgling procellariid or hydrobatid could potentially view if it followed the topographically least-cost path from any point on the island until descending to 100 m above sea level (asl), at which point it flew a straight path to 10 km beyond the coastline (avoiding obstacles > 100 m asl and only viewing light until it traveled 10 km beyond the coastline).

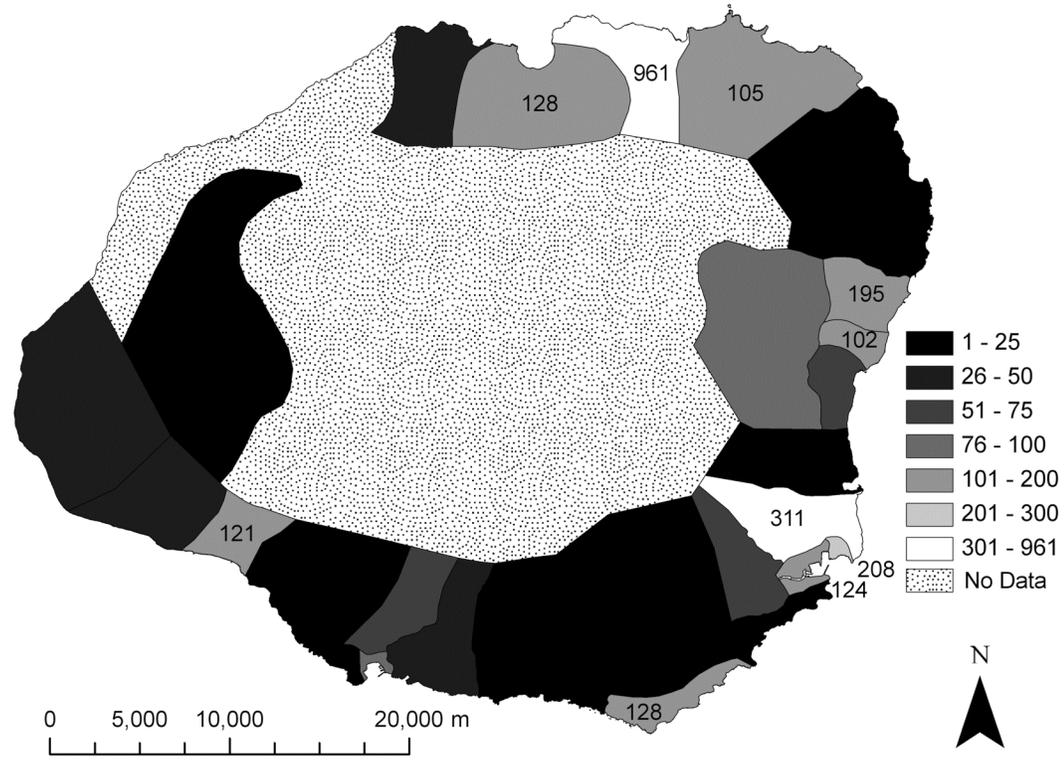


Fig. 1.6. Newell's Shearwater fledgling fallout summed by sector on Kauai from 1998-2008 (Hawaii Division of Forestry and Wildlife unpublished data). Fledglings without a sector location identified are not included. The number of fledglings is labeled in sectors with >100 known fledgling recoveries. All fallout data were obtained from Hawaii Division of Forestry and Wildlife. Data were collected by Hawaii Division of Forestry and Wildlife from 1998-2005, by Kauai Island Utility Cooperative from 2006-2007, and by Kauai Humane Society in 2008.

Appendix

Summary of GIS methods

I used ArcGIS 9.3.1 (ESRI, Redlands, CA) and digital layers of the island of Kauai to develop two models. One model represents the total intensity of artificial light a fledgling procellariid or hydrobatid could view along the topographically least-cost path from every location on the island to the coastline (the ‘island’ model) and the other represents the same paths to the coastline extended to 10 km offshore (the ‘extended flight’ model). The tool used for the final step of model development requires that its input layers have completely overlapping extents; however, preliminary development of one of the model input layers resulted in the two input layers for the final model step having slightly non-overlapping extents. To correct for this, I first extended a Digital Elevation Model (DEM) of the island of Kauai 11 km past the coastline, developed a layer of artificial light intensity viewable in 360° from each pixel of this extended DEM, and clipped smaller layers for the ‘island’ and ‘extended flight’ models from the larger 11 km extended layers, snapping each clipped viewable light intensity layer to its companion clipped DEM to achieve complete overlap. Below, I describe the GIS-based model-building process in substantial detail to provide repeatable steps for future use.

Extended DEM

I extended a DEM of Kauai (10 x 10 m resolution) from the Hawaii Coastal Geology Group (www.soest.hawaii.edu/coasts) 11 km from the coastline (i.e., which converted ocean ≤ 11 km offshore to land). First, I reclassified the DEM so that all numeric pixel values were converted to values = 0 and all ‘NoData’ pixels remained ‘NoData’ pixels. This reclassified DEM was converted to a polygon using the ‘Raster to

Polygon' Tool. A buffer of 11,000 m surrounding the island polygon was then created using the 'Buffer' Tool and converted to a raster layer (10 x 10 m resolution) with pixel values = 0 using the 'Feature to Raster' Tool. I combined the original DEM and new raster layer using ArcCatalog to create an unmanaged raster catalog containing both layers; the 'Raster Catalog to Raster Dataset' Tool was then used to combine these layers, extending the coastline of the Kauai DEM by 11 km.

Viewable artificial light intensity layer

A layer of stable average artificial night light intensity from 2009 for the earth (obtained from a satellite image with 911.25 x 911.25 m resolution; pixel values ranging from 0-63 relative units) was obtained from the National Geophysical Data Center (<http://www.ngdc.noaa.gov/dmsp/downloadV4composites.html>). I projected the layer in North American Datum (NAD) 1983 Zone 4 using the 'Project Raster' Tool and clipped out the island of Kauai using the 'Clip' Tool and a shapefile of the boundary of Kauai obtained from the USGS Hawaii Data Clearinghouse website (<http://hawaii.wr.usgs.gov/>) (Fig. 1.2). This clipped layer was reclassified so that pixel values = 0 were converted to 'NoData' and all other pixels were equal to their original light intensities. The light intensity pixels with values from 1-63 were then converted to points using the 'Raster to Point' Tool and this point layer was clipped using the Kauai boundary shapefile so that all light points fell within the island boundary. To account for the height of both fledgling flight and light sources while developing this viewable light intensity layer, I raised the height of all light points to 100 m above ground level by creating an 'OFFSETA' field within the attributes table of the light point layer and setting values = 100 using the 'Field Calculator'.

I then used the ‘Observer Points’ Tool and the 11 km extended Kauai DEM, correcting for the curvature of the earth (with a refractory coefficient = 0.13), to generate a raster layer highlighting which light points were viewable from each extended DEM pixel. Because of the inability of the ‘Observer Points’ Tool to handle a large number of points, I segmented the light point layer into many smaller layers (containing ≤ 10 points of equal light intensity). I added a light intensity field to the attributes table of each observer points output layer, in which I tallied the number of lights viewable from each point and multiplied them by their light intensity values using the ‘Field Calculator’; this yielded a raster layer of additive (viewable) light intensity based only on each separated light point layer. All Observer Points outputs were then summed using the ‘Weighted Sum’ Tool, with each layer weighted equally, to generate a layer of the total intensity of artificial light viewable in 360° from each pixel of the extended DEM (i.e., a viewable light intensity layer; Fig. 1.3).

Input layers for models

As input for the final model step, I reclassified the 11 km extended DEM of Kauai so that no pixel values were < 100 m to achieve the assumption that fledglings travel a straight path to the ocean once they descend to, or are already at or below, 100 m in elevation. The two models required clipping smaller files from both the reclassified extended DEM and the viewable light intensity layer as input for model development. For the ‘island’ model, I created a polygon from the original Kauai DEM by first reclassifying all pixel values = 0 and then converting the new raster layer to a polygon using the ‘Raster to Polygon’ Tool (without simplification so that the polygon matched the pixelated raster shape exactly). I then used this polygon to clip the 11 km extended

DEM and light intensity layer to the size of the island of Kauai. For the ‘extended flight’ model, I added a 10,000 m buffer to the polygon created from the Kauai DEM using the ‘Buffer’ Tool. I then converted this file to a raster layer (10 x 10 m resolution) using the ‘Polygon to Raster’ Tool and converted this raster back to a polygon (without simplification) using the ‘Raster to Polygon’ Tool. This polygon was used to clip the 11 km extended DEM and light intensity layer to 10 km beyond the coastline of Kauai. Clipping for both models resulted in slightly non-overlapping extents between the two clipped layers (i.e., the DEM had slightly fewer rows and columns than the viewable light intensity layer). Therefore, I clipped the DEM a second time, using the ‘Snap Raster’ feature (located in the ‘General Settings’ tab under ‘Environments’) to snap the extent of the DEM to that of the clipped viewable light intensity layer so that the two overlapped completely. Snapping raster layers to one another may not be required in all cases to attain complete overlap of input layers, and other methods likely exist to achieve this goal.

Development of final model layers

I used several tools from the TauDEM Version 5.0 toolset (Tarboton 2010) to develop the final layer for both models. This toolset requires that all input raster layers be in TIFF format; therefore, the clipped reclassified DEMs and viewable light intensity layers to be used for both models were converted to TIFF files. I used the ‘Pit Removal’ Tool to raise pits in the DEMs for both models and used the ‘D-Infinity Flow Direction’ Tool to create a flow direction raster from these pit-removed DEMs. I then used the ‘Reverse Accumulation’ Tool, with both the flow direction and viewable artificial light intensity layers as input, to complete the final model layer. This tool summed pixel values

of a cost layer (e.g., viewable artificial light intensity) along topographically least-cost (downhill) paths from the target destination of fledgling seabirds (i.e., the lowest elevation pixels along the edge of the DEM) back to all pixels higher in elevation (i.e., the possible starting locations of fledgling seabirds). Because the cost layer for the models was the total intensity of light viewable in 360° from each pixel, the ‘Reverse Accumulation’ Tool added the intensity of all viewable light along each path, including light behind the bird. As the input layers for the ‘island’ model had the same extent as the unaltered Kauai DEM, the ‘Reverse Accumulation’ output was the final ‘island’ model. To complete the ‘extended flight’ model (i.e., so that it had the same extent as the ‘island’ model), I clipped out the island of Kauai from the 10 km extended cumulative light intensity layer using a shapefile created from the Kauai DEM, snapping it to the ‘island’ model raster. Despite snapping the ‘extended flight’ model to the ‘island’ model output, the raster files did not contain the same number of pixels; I consider this slight difference negligible for comparison of the two models.

CHAPTER II

USING OBSERVED SEABIRD FALLOUT RECORDS TO INFER PATTERNS OF ATTRACTION TO ARTIFICIAL LIGHT

Introduction

Artificial light is becoming a prevalent nocturnal feature of our planet (Cinzano et al. 2001) and documented cases of its effects on the natural activities of organisms are on the rise (Longcore and Rich 2004). Fledglings of certain seabird species, particularly in the families Procellariidae (shearwaters and petrels) and Hydrobatidae (storm-petrels), are attracted to artificial light on their maiden flights to the ocean (Hadley 1961, Harrow 1965, King and Gould 1967, Imber 1975, Reed et al. 1985, Telfer et al. 1987, Le Corre et al. 2002, Rodriguez and Rodriguez 2009, Miles et al. 2010), though the cause of this attraction remains unknown. As these birds approach light sources they can become disoriented and fall to the ground following physical exhaustion or collision with manmade structures and vegetation, a phenomenon known as ‘fallout’. While many of these downed birds are found alive and released each year through public rescue efforts, recent studies suggest that light-induced mortality may still significantly decrease long-term population recruitment (Ainley et al. 2001, Le Corre et al. 2002, Rodriguez and Rodriguez 2009, Fontaine et al. 2011, Griesemer and Holmes 2011, Rodriguez et al. 2012b).

Perhaps the most well known example of fallout occurs each autumn on the island of Kauai in the Hawaiian Archipelago (Reed et al. 1985, Telfer et al. 1987, Ainley et al. 2001) during the fledging season of the Newell's Shearwater (*Puffinus newelli*), a species listed as 'threatened' under the Endangered Species Act and 'endangered' on the IUCN Red List (IUCN 2012). More than 30,000 Newell's Shearwater fledglings have been found as victims of fallout on Kauai during the past few decades (Griesemer and Holmes 2011), and thousands of other young shearwaters, petrels, and storm-petrels from different islands around the world are downed by light annually (e.g., Le Corre et al. 2002, Miles et al. 2010, Fontaine et al. 2011, Rodrigues et al. 2012, Rodriguez et al. 2012b). Despite this large number of fallout observations, certain elements of this phenomenon remain unknown, including the locations along the path from nest to the ocean from which fledglings are consistently drawn off course and downed by artificial light (i.e., if light viewable from natal colonies and/or light viewed along flight routes to the ocean is regularly involved in fallout). In addition, an extremely small number of individuals (compared to the tens of thousands of birds that have been rescued worldwide) have returned as repeat victims of fallout a short time after having been rescued, banded, and released at coastal sites (Podolsky et al. 1998, Fontaine et al. 2011). This suggests that a few individuals can indeed be drawn back to land from the ocean, but it remains unknown if many birds can be attracted back to land after first reaching the sea (without human intervention) such that they contribute significantly to total island-wide fallout (as suggested by Podolsky et al. [1998]).

An improved understanding of how attraction to artificial light results in the pattern of observed fallout exhibited by young seabirds is important for future seabird

conservation efforts worldwide because it would aid in further assessing the severity of threat that artificial light poses to these birds. The information necessary to directly measure patterns of fledgling movement in relation to the distribution of artificial light could potentially be acquired by fitting a large number of nestlings at breeding colonies with radio or satellite transmitters and monitoring flight paths leading to fallout locations. However, many seabird species whose fledglings are negatively affected by artificial light only breed in isolated and mountainous terrain of oceanic islands; thus, the locations of very few nests are usually known, often rendering such a large-scale effort unrealistic. This is especially true of the Newell's Shearwater, as fewer than ~20 active natural burrows are currently documented (State of Hawaii, *unpublished data*).

An indirect method, however, offers a more feasible and less invasive approach to estimate the pattern of fledgling fallout caused by attraction to artificial light. In this study, I compared observed numbers of Newell's Shearwater fallout victims within established regions (known as 'fallout sectors') on Kauai to fallout expected from a series of hypothetical models containing basic assumptions concerning flight paths and attraction to light. These comparisons included models incorporating bird movement and the ability of birds to view light once at sea, allowing us to test where along presumed flight paths (from natal site to the sea) that attraction can occur and, importantly, if these young birds could potentially be attracted back to land after reaching the ocean in numbers large enough to contribute significantly to island-wide fallout. Herein, I discuss the likely causes behind observed fallout on Kauai in the context of my hypothetical models followed by a discussion of future research objectives to support the protection of these seabirds from the detrimental effects of artificial light.

Methods

Fallout records

Citizens of Kauai are encouraged to deliver seabirds found as victims of fallout to one of a number of aid stations on the island (Reed et al. 1985, Telfer et al. 1987, Rauzon 1991) and the pick-up location for many of these birds is recorded. I obtained a shapefile of 33 ‘fallout sectors’ (regions with defined boundaries, ranging in size from 1236.68 to 96925.81 km², in which fledglings found as victims of fallout are tallied each year) and Newell’s Shearwater fallout records on Kauai from 1998 to 2009 from the Save Our Shearwaters program (Hawaii Division of Forestry and Wildlife). Fallout data were collected by the Hawaii Division of Forestry and Wildlife from 1998 to 2005, by Kauai Island Utility Cooperative from 2006 to 2007, and by the Kauai Humane Society in 2008 and 2009. Fallout records were summed by fallout sector such that all observations of birds with no known pick-up location were not included in total sums. Peak fledging season is from October to November, but some fledglings also depart in September and December (Telfer et al. 1987); therefore, I included only birds found from September to December because birds identified as fledglings during other times of year are expected to be misidentified adults. For the 2009 data, information on Newell’s Shearwater age (i.e., hatch-year vs. adult) was not available. Because the vast majority (~98%) of Newell’s Shearwater recoveries from 1998 to 2008 collected from September through December were identified as fledglings (unpublished data), all birds from 2009 were considered fledglings for the purposes of this study. Additionally, a few birds (n = 29) were also found within two fallout sectors (sectors 33 and 35) that were not available for spatial analysis; thus, these birds and sectors were not included in this study, yielding

3181 birds (i.e., fallout records). One fallout sector (fallout sector 2) contained a large number of fledglings relative to the other fallout sectors ($n = 1045$; approximately one-third of the island-wide total) (Fig. 2.1); therefore, analyses were conducted without input from fallout sector 2, yielding a total of 2136 birds available for analysis.

Artificial light layers

A geographic information system (GIS) layer of artificial light intensity for the earth, excluding light originating from the sun, moon, and aurora, was obtained for both 1998 and 2009 from the National Geophysical Data Center (<http://www.ngdc.noaa.gov/dmsp/downloadV4composites.html>). Stable average light layers were used for both years, meaning that light from ephemeral sources (such as wildfires) was identified and replaced with values of zero. Pixel values for both layers ranged from 0 to 63 relative units. The 1998 and 2009 layers were developed from satellite images with 913.47 x 913.47 m resolution and 911.25 x 911.25 m resolution, respectively. All contributing light originated from artificial light sources on cloud-free nights, including persistent sources such as gas flares. Pixels of this satellite layer also contain some artificial sky glow (i.e., illumination caused by the refraction and scattering of light by water, dust, and other molecules suspended in the air); this sky glow is most apparent close to cities (Elvidge et al. 2007) and may somewhat inflate light intensity pixel values in the vicinity of urban sites and incorrectly depict dark areas very near urban light sources with lighted pixels. These light intensities represent an average over an entire year; therefore, any reduction in light output during the Newell's Shearwater fledging season is not completely accounted for, meaning that using this layer required

the assumption that yearly average light intensities are a suitable approximation of light conditions during the fledging period of the species.

Both the 1998 and 2009 light layers were clipped by a shapefile of Kauai extended to 10 km past the shoreline of the island. Mean light intensity from 1998 and 2009 was obtained for each fallout sector, as well as the proportion of cover of light pixels within each sector. Mean light values were only calculated using fallout sector pixels representing light; dark pixels were not included in the calculation. Because summary statistics within polygons are only performed on pixels whose centroids (i.e., pixel centers) fall within the polygon boundary, the pixel size for each light layer was resampled to 10 x 10 m so that calculations of mean values were more representative of pixel cover within the irregular shapes of the fallout sectors.

Mean light intensity values within fallout sectors from 1998 and 2009 were compared using Pearson's correlation coefficient (Pearson's r), as were the proportions of cover of light pixels within sectors between the two years. Because fallout sectors are arbitrary sampling units, P -values for each of these correlation coefficients were determined using randomization tests (based on 1000 reshuffled 1998 datasets [resampled without replacement] compared to the 2009 data); see the analyses subsection further discussion on randomization tests. Mean light intensities for both years were strongly correlated ($r = 0.95$, $P = <0.001$), as were proportions of cover of light pixels within those sectors ($r = 0.89$, $P = <0.001$); therefore, 2009 light was used to weight estimates of expected fallout within sectors calculated from the hypothetical models. The slight differences in pixel sizes between the original 1998 and 2009 layers (mentioned above) were considered negligible for these analyses. In addition, slight differences in light

intensity values in certain locations between 1998 and 2009, as well as minor differences in the proportion of fallout sectors covered by light between these years, were considered unimportant because of the large scale of this study and the fact that mean light intensity values were used as relative weights in calculations of expected numbers of downed fledglings within fallout sectors.

Suitability of light layer pixel size for fallout research

In this study, the satellite layer pixels from 2009 were 911.25 x 911.25 m in size and these pixels displayed light intensity as a yearlong average output. Because each pixel represents an average value over such a large area, pixel values likely reflect a combination of different light intensities (some of which may be greater than the actual pixel value) and numbers of light sources. Despite whether pixel values represent the actual light intensity being emitted by lights or the numbers of lights within the pixel area (or both), this satellite layer is suitable for research investigating the threat that light may pose to fledgling seabirds (e.g., Chapter I), as well as the relationship between light and seabird fallout (e.g., Rodrigues et al. 2012, Rodriguez et al. 2012), on a large scale. Even if one considers the extreme assumption that all light sources on the island emit a light intensity equal to 63 relative units (the highest pixel value for the planet), meaning that differences in pixel values were only due to the number of lights within the pixel area, it is highly likely that pixel-sized areas with more light sources can attract more fledglings than areas with fewer lights. Such a large pixel size, however, precludes use of this light layer for investigating how light intensity emitted from individual light sources affects fledgling fallout.

Model overview

Expected fallout numbers in this study were calculated for eight hypothetical models: a sector area model (based only on the two-dimensional surface area of each fallout sector), a light area model (based only on the two-dimensional surface area of the lighted portion of each fallout sector), a light intensity model (based only on light emitted from sources within fallout sectors), a stationary model (accounting for light potentially viewed by fledglings only from known Newell's Shearwater activity sites), an island movement model (accounting for light potentially viewed by fledglings while flying over land from Newell's Shearwater activity sites through watersheds to the coastline), and three ocean movement models (extending the island movement model to one of three distances beyond the shoreline in a cumulative manner).

For all models, fallout sectors were the unit of observation and an overall weight was calculated for each fallout sector in order to derive expected fallout numbers for each sector. For the sector area model, this weight was based only on the two-dimensional surface area of each fallout sector. For the light area model, this weight was based only on the two-dimensional surface area of the lighted portion of each sector. For the light intensity model, this weight was based only on the mean intensity of light being emitted from light sources within each sector. For all other models, this weight was based on more complex factors, including the mean artificial light intensity for that fallout sector. These weights were converted to proportions (of the island-wide total for all fallout sector weights) that were then used to calculate the expected number of fallout birds for each sector; calculation of weights in this manner assumes a linear relationship between light intensity and seabird fallout. The proportion for each sector was then multiplied by

the total island-wide observed fallout without fallout sector 2 ($n = 2136$) to generate expected numbers for that sector. The treatment of viewable light in certain models, model types and their assumptions, model limitations, and analyses are described below, and development of layers for pixel summaries and calculation of expected numbers from the hypothetical models are described in the Appendix.

Treatment of viewable light in particular models

Weights for the stationary, island movement, and ocean movement models were based in part on lighted portions of fallout sectors that could be viewed from locations on the island that the birds may encounter (locations depending on particular model assumptions). To accomplish this, viewsheds (analyses that highlight the landscape viewable from a feature) would ideally be conducted from each location that a fledgling could potentially visit (raised to a biologically relevant flight height). However, fledglings could potentially visit millions of locations (i.e., 10 x 10 m pixels of a digital elevation model [DEM] of this island). Thus, I used a surrogate measure that is much less analytically intensive, yet very appropriate for such a landscape-scale analysis. This measure involved generating viewshed layers from the perimeter of the lighted portion of each fallout sector (i.e., from the perspective of the fallout sector) to highlight the areas of the island that could be viewed from the lighted portion of the fallout sector; see the Appendix for details of viewshed layer development.

A limitation of this method is that at each pixel of the DEM (used as an input layer for viewshed analyses), fledglings were forced to view light from ground level. Therefore, when birds are at the same elevation as light sources, raising the height of light sources above the ground is equivalent to raising birds the same height while

keeping light sources on the ground. However, this relationship is not always identical when birds and/or light sources are on sloped terrain with rugged topography. For example, a bird flying (and viewing light from above ground level) near a ridgeline that separates the bird and a particular light source could potentially view that light source. However, because the light source is positioned above ground level (and the bird is positioned at ground level), the viewshed analysis from the perspective of the light source may not necessarily indicate that a bird at this location could view that light source. Despite this limitation, I consider this measure a very suitable approximation of the area from which birds could view light sources existing in particular fallout sectors.

Sector area model

Expected numbers from this model were based only on the two-dimensional surface area of each fallout sector. This model tested the hypothesis that greater numbers of birds are observed in larger fallout sectors (regardless of the geographical coverage of light sources, light intensity being emitted by light sources, or how distance from light sources to birds could potentially affect the probability of attraction). A proportion of the total area of Kauai covered by all fallout sectors was calculated for each sector and multiplied by the observed total fallout ($n = 2136$).

Light area model

Expected numbers from this model were based only on the two-dimensional surface area of the lighted portion of each fallout sector. This model tested the hypothesis that greater numbers of birds are grounded by artificial light in fallout sectors containing a greater coverage of lighted terrain (regardless of the light intensity being emitted by light sources within sectors or how distance between light sources and birds could

potentially affect the probability of attraction). A proportion of the total lighted area within all fallout sectors was calculated for each sector and multiplied by the observed total fallout ($n = 2136$).

Light intensity model

Expected numbers from this model were based only on the mean value of 2009 artificial light within fallout sectors, a value calculated only from lighted portions of fallout sectors (i.e., dark pixels were not included in the calculation). This model tested the hypothesis that birds are attracted to sectors with a greater mean intensity of artificial light, regardless of the location on the island from which particular birds originated (i.e., their natal sites); thus, this model contains some general assumptions pertaining to fledgling movement that are described in the discussion section. Additionally, this model did not account for how distance between light sources and birds could potentially affect the probability of attraction. A proportion of the total light within all fallout sectors was calculated for each fallout sector and multiplied by the observed total fallout ($n = 2136$).

Stationary model

This model assumed that birds could only be attracted by artificial light at (or in the air above) known Newell's Shearwater activity sites (assumed to be their natal sites). The Kauai Endangered Seabird Recovery Project provided a shapefile of the estimated boundaries of these sites (see the Appendix for treatment of this shapefile). Expected numbers from this model were based on several factors, beginning with the two-dimensional surface area of all known Newell's Shearwater activity sites viewable from the lighted portions of each fallout sector. An assumption of this measure was that this surface area positively correlated with the number of breeding Newell's Shearwaters and,

therefore, with the number of fledglings available to be attracted to fallout sectors. If a Newell's Shearwater site fully or partially overlapped with a viewshed (suggesting that at least some of the site could be viewed), the entire two-dimensional area for that site was factored into the expected number calculation for that fallout sector. This accounted for the possibility that young Newell's Shearwaters may circle their natal colony aloft before departing, in which case a fledgling taking flight from any part of a breeding site could view light emanating from that sector.

To calculate the overall weight for each fallout sector, the two-dimensional surface area of each Newell's Shearwater site that could be viewed from the lighted portion of that fallout sector was divided by the mean distance from that Newell's Shearwater site to the nearest boundary of the lighted portion of that sector (based on two-dimensional surface area). For each sector, these values were then summed and the summed value was multiplied by the mean intensity of artificial light emanating from that sector to obtain the overall weight for that sector. A proportion of the total for all fallout sectors was then calculated for each sector and multiplied by the observed island-wide fallout ($n = 2136$).

Many areas of Kauai, including some Newell's Shearwater activity sites, were viewable from the lighted portions of more than one fallout sector. Accounting for the distance from Newell's Shearwater sites to lighted portions of sectors, as well as the mean artificial light intensity within those sectors, appropriately weighted the calculations of expected numbers for each sector, relative to one another. Both of these measures accounted for instances in which lights from more than one fallout sector were viewed from a single Newell's Shearwater site (i.e., when a certain site was viewed by

lighted portions of more than one fallout sector) by directly relating to the likelihood that birds could be attracted from that site to each sector.

Island movement model

Expected numbers of fallout birds calculated from this model were based on several factors and assumptions. As adult Newell's Shearwaters likely follow topographic depressions (e.g., river valleys) to reach the ocean (Telfer et al. 1987, Podolsky et al. 1998), these models assumed that fledglings fly topographically least-cost paths (i.e., following depressions such as watersheds) to the sea. To simulate downhill movement, watershed boundaries were redefined to be equal to or lower in elevation than the highest elevation pixel from a Newell's Shearwater site within that watershed (see the Appendix for details). Another assumption was that the proportion of the redefined watershed area viewable from the lighted portion of a particular fallout sector was positively correlated with the likelihood that fledglings from that watershed would be attracted to arrive in that sector (this was a less analytically intensive surrogate measure for the lighted portions of each fallout sector viewable from every location that a fledgling could visit on their flight to the coastline). Under this assumption, birds from known Newell's Shearwater sites could view light emanating from fallout sectors, but only from portions of sites viewable from the lighted portions of each sector. This differed slightly from the stationary model, which assumed that birds could view light from an entire activity site, whether that site overlapped fully or only partially with a fallout sector viewshed. However, the area of Newell's Shearwater activity sites viewable from a particular fallout sector is likely to be substantially smaller than the area of a watershed viewable from that sector, and, therefore, the island movement model builds upon the stationary model because it

accounts for light that can be viewed from Newell's Shearwater sites, as well as light potentially viewed by birds as they travel to the coastline.

To calculate the overall weight for each fallout sector from this model, weights for each redefined watershed were first calculated. The total Newell's Shearwater site area within that watershed was multiplied by the proportion of that watershed viewable from the lighted portion of each fallout sector and then divided by the mean two-dimensional distance from all viewable pixels (within the watershed) to the nearest boundary of the lighted portion of that sector. For each fallout sector, these watershed weights were then summed and this summed value was multiplied by the mean intensity of artificial light emanating from that sector. Accounting for mean distance and artificial light intensity in this manner appropriately weighted calculations of expected numbers of fledglings for each fallout sector, relative to one another, in the event that a particular location in a watershed was viewable from more than one sector. A proportion of the total for all fallout sectors was then calculated for each fallout sector and multiplied by the observed island-wide fallout ($n = 2136$).

Ocean movement models

Like the island movement model, expected numbers of fallout birds calculated from these models were based on several factors and assumptions. Each model extended the island movement model out to one of three distances beyond the watershed coastline (which allowed birds to view light from the ocean and potentially be attracted back to land). The distance categories of ocean regions were 0-1, 1-5, and 5-10 km in all directions from the coastline and only included areas of ocean surface (see the Appendix). The assumptions of the land-based portion of each of these models were the

same as those of the island movement model, with the additional assumptions that birds were allowed to fly any direction from the coastline (as long as they remained over the ocean) and that the proportion of an ocean region viewable from the lighted portion of a particular fallout sector was positively correlated with the likelihood that fledglings from that ocean region would be attracted to that sector.

Calculating expected numbers from each of these models required multiple steps. For each redefined watershed, the proportion of that watershed viewable from the lighted portion of each fallout sector was divided by the mean two-dimensional distance from all viewable pixels (within the watershed) to the nearest boundary of the lighted portion of that sector to calculate a watershed weight. Likewise, the proportion of each ocean region viewable from the lighted portion of each fallout sector was divided by the mean two-dimensional distance from all viewable pixels (within the ocean region) to the nearest boundary of the lighted portion of that sector (see Fig. 2.2) to calculate a weight for that region. The watershed weights were added to the weights for the individual ocean region(s) of interest before being multiplied by the Newell's Shearwater site area within the watershed, ensuring that ocean movement model weights were additive in the calculation. For example, in the ocean movement model extending to 10 km past the coastline, the watershed weight was added to the weight for each of the three ocean regions. The total two-dimensional area of Newell's Shearwater activity sites within the watershed was then multiplied by this additive weight. For each fallout sector, these values were then summed and the summed value was multiplied by the mean intensity of artificial light emanating from that sector. A proportion of the total for all fallout sectors

was then calculated for each fallout sector and multiplied by the observed island-wide fallout ($n = 2136$).

Calculating weights in this additive manner was appropriate for dark watersheds (i.e., those from which no light can be viewed) that led into regions of ocean from which light could be viewed. Likewise, it appropriately weighted watersheds from which light could be viewed that led into ocean regions from which light could not be viewed. Additionally, when light could be viewed from the major portion of a watershed that led into one or more ocean regions from which light could also be viewed, a total weighted value > 1 was produced, which inflated the value of Newell's Shearwater site area within that watershed. However, these weights were used to calculate a proportion of the island-wide total fallout for all fallout sectors and, thus, were ultimately relative. Therefore, watersheds with weighted values > 1 were appropriately weighted because birds from those watersheds who could view light from both the watershed and its associated ocean regions were hypothesized to be more likely affected by light (and attracted to a particular fallout sector) than are birds traveling through more space from which light could not be viewed.

Model limitations

Because the stationary and movement models contain only basic assumptions, I anticipated that several factors unaccounted for in the models would generate expected numbers for various fallout sectors that differed somewhat from observed numbers. First, though two-dimensional Newell's Shearwater site area is likely to be more or less positively correlated with the number of breeding adults (and, thus, the number of fledglings), some variation in numbers of fledglings produced at activity sites was

expected. In addition, the models did not account for the locations of multiple unknown breeding sites. The models also did not account for the possibility that fledglings could be attracted toward a particular lighted region and subsequently be drawn away from that trajectory toward a different lighted region. Finally, factors such as weather conditions may influence the direction of fledgling movement but were not factored into model calculations.

Analyses

Observed fallout numbers were compared to fallout numbers expected from each of the eight hypothetical models using two measures of relationship. Pearson's correlation coefficient (Pearson's r) was used to measure the linear relationship between the observed and expected numbers. In addition, the mean fallout sector ratio (MFSR) for each observed and expected pair within a fallout sector was used to further assess how well the pattern of fallout expected from the models matched the observed pattern. MFSR was calculated as the minimum (of the observed and expected value) divided by the maximum (of the observed and expected value) so that the ratio would indicate the difference between the observed and expected numbers without being affected by the direction of the difference (i.e., observed and expected values of 50 and 100, respectively, give the same MFSR as do values of 100 and 50). Because fallout sectors are arbitrary sampling units, I devised a randomization test to assess the significance of r and MFSR.

I used a series of randomization tests to calculate the probability that measures for these observed and expected comparisons (Pearson's r and MFSR) could have been produced solely by random pairing of observed and expected fallout values. I randomly assigned (without replacement) each observed fallout value to one of the expected values

and compared those fallout numbers (using r and MFSR as before). I repeated this process 1000 times for each model. This yielded a sampling distribution of 1000 values for each measure (r and MFSR). Essentially, the randomization test created the distributions of r and MFSR values that would be obtained if observed fallout numbers were randomly distributed to any sector and then compared to the expected numbers for that sector. For each of the hypothetical models, I compared the actual values of Pearson's r and MFSR to the two respective sampling distributions. For both measures, P -values were determined as the proportion of the sampling distribution that was greater than or equal to the actual values. These tests were conducted using Program R version 2.15.1 (R Core Team 2012).

Results

Based on the two measures of relationship considered in this study, several hypothetical models generated expected numbers consistent with the observed pattern of Newell's Shearwater fallout. Expected numbers from both the sector area and light area models exhibited very low (and non-significant) correlations with the observed data, as well as the lowest MFSRs (Table 2.1). Positive (and significant) correlations between observed and expected numbers were achieved for all other models, but only the ocean movement models and the light intensity model exhibited MFSRs that differed significantly from random (Table 2.1). The ocean movement and light intensity models yielded the highest correlation coefficients and MFSRs, with numbers from the light intensity model exhibiting the strongest positive linear relationship with the observed data (Table 2.1). Though expected numbers generated from the stationary and island movement models were moderately (and significantly) correlated with observed fallout,

when considering both measures of relationship simultaneously, the ocean movement models and the light intensity model generated expected numbers more consistent with observed fallout.

Discussion

Fledgling movement and viewable light

Overall, my results suggest that the spatial pattern of observed seabird fallout is consistent with the amount of light that fledglings may view along their first flights to and beyond the coastline. Moreover, it appears that the observed pattern of fallout cannot be explained merely by fallout sector area or the physical area covered by light sources within sectors. Though only one species, the Newell's Shearwater, was examined in this study, the general similarity of the fallout phenomenon in other locations and the close relatedness of many species affected by fallout both suggest that the findings of this study are likely relevant to many of the shearwaters, petrels, and storm-petrels that are attracted to artificial light in other parts of the world. Good support was shown for the ocean movement models and the light intensity model when fallout sector 2 was removed from analyses. As distance from the coastline increased for the ocean movement models (allowing birds to view light from increasingly more area), stronger positive correlations between observed and expected numbers were observed (with values of r ranging from 0.547 to 0.631), progressively approaching the value obtained for the light intensity model ($r = 0.765$). And though there was some deviance from this pattern in values of MFSR among the ocean movement models, the light intensity model, again, exhibited the highest value.

Expected numbers from the light intensity model were based only on the mean intensity of light within fallout sectors; however, given known information related to mechanics of light attraction and the biology of the species, this model carries assumptions of bird movement that were not previously discussed. First, fledglings likely follow river valleys and other topographical depressions from their high-elevation natal sites to the ocean (Telfer et al. 1987, Podolsky et al. 1998) and, therefore, should generally continue to do so prior to viewing light (which may draw them off course from their initial trajectory). In addition, from a stationary perspective (i.e., without considering bird movement), it was recently shown that light could not be viewed from approximately 30% of the island of Kauai (Chapter I), and these dark locations mostly included regions in the interior and northwestern portion of the island where many known Newell's Shearwater activity sites are located. Given this additional information concerning viewable light on Kauai, the expected behavior of the species in the absence of light, and the results of this study, it appears likely that many birds could successfully reach the coastline and ocean, where they are then exposed to a range of light intensities emanating from multiple fallout sectors (spanning a large portion of the island) and are more likely to be attracted to sectors with greater light intensities and/or greater densities of light sources. Therefore, these results provide support for the idea that fledglings could indeed be attracted back to land after reaching the ocean in numbers large enough to contribute significantly to island-wide fallout.

These findings build upon the results of a recent study, in which light intensity was positively correlated with the number of downed fledgling shearwaters near breeding sites (Rodrigues et al. 2012). Additionally, these results support a recent GIS-based study

that modeled the relative intensity of light that fledglings could view on their post-natal maiden flights to and beyond the coastline, which estimated that there are few to no portions on Kauai from which young seabirds could fledge and not view at least some artificial light (Chapter I). Consequently, these findings are disconcerting because they suggest that birds fledging from “dark” breeding sites (i.e., those from which no light can be viewed) could be drawn off course by light along their journey to the sea, and even those flying through “dark” watersheds may still not be safe once they reach the ocean.

Susceptibility to light attraction and future research

Fallout caused by attraction to artificial light is thought to be a contributing factor to the decline of several procellariid and hydrobatid species (Ainley et al. 2001, Le Corre et al. 2002, Rodriguez and Rodriguez 2009, Fontaine et al. 2011, Rodriguez et al. 2012b), and my findings further underscore the severity of the threat that anthropogenic light poses to these birds. Annual public participation in the rescue of fledglings downed by lights has resulted in thousands of birds reaching the ocean that would otherwise not have arrived there, and reduction in light use through awareness campaigns has undoubtedly prevented many instances of light-induced mortality (e.g., Ainley et al. 2001, Le Corre et al. 2002, Rodriguez and Rodriguez 2009, Fontaine et al. 2011, Rodriguez et al. 2012b). Methods to reduce overall light output, including attaching shields to bright light sources (which prevents direct upward radiation; Reed et al. 1985) and simply decreasing total light output (King and Gould 1967, Miles et al. 2010), have been shown to reduce total fledgling fallout in local areas. However, in these instances, young Newell’s Shearwaters were still attracted to areas in which many of the brighter lights were shielded (Reed et al. 1985) and fledgling Manx Shearwaters (*P. puffinus*) were still attracted when most lights

were turned off or shielded during a period of very diminished moonlight, suggesting that certain species are still attracted to very weak lighting (Miles et al. 2010). Though rescue efforts for downed fledglings appear to save many birds annually, it is estimated that some birds still perish due to fallout because they are never found (Ainley et al. 2001). Furthermore, it is unknown if the experience of fallout leaves rescued fledglings unscathed enough to survive their first few weeks of pelagic life (Ainley et al. 2001, Le Corre et al. 2002, Rodriguez and Rodriguez 2009, Rodriguez et al. 2012a). Thus, while the continuation of these rescue and light reduction efforts is crucial, populations could still be declining due to the effects of anthropogenic light despite these measures, albeit at a slower rate.

Rescue of downed seabirds accompanied by reduction in artificial light output, though clearly important, may not be the ultimate solution to this problem because long-term recruitment of new breeders to the population could still be hindered by light-induced mortality. Therefore, additional research on light types and intensities that may be associated with decreased fallout may be necessary (Rodriguez and Rodriguez 2009). For example, though some species are apparently attracted to weak lighting (Miles et al. 2010), a threshold of light intensity could potentially be required for attraction to light to occur (below which fledglings may disregard light and safely reach the ocean), though the possible existence of such a threshold has not been investigated. Perhaps more importantly, manipulating the wavelength of light (i.e., altering its color) to investigate its effects on fallout could be a promising area of research, as light with shorter wavelengths (i.e., green and blue light) has been shown to significantly reduce the impact of light on the behavior of nocturnally migrating passerines relative to white light or light with

longer wavelengths (Poot et al. 2008). Supporting this idea, King and Gould (1967) reported that no Newell's Shearwater fledglings were downed after bright white ground lights were replaced by subdued colored lights at a particular location on Kauai in the 1960s. Given the results of this study and previous fallout research, studies investigating the effects of light wavelength and/or intensity on fallout may be an important next step in the conservation of these birds.

Conclusion

The results of this study are important for shearwater and petrel conservation worldwide because they provide evidence for the locations of fledgling attraction to light and further highlight the severity of this phenomenon by demonstrating that fledglings may indeed be attracted to land from the ocean on an island-wide scale versus only a few isolated occurrences of previously rescued individuals being recaptured. It seems doubtful that nocturnal light use will ever be fully eliminated on islands during the fledging seasons of these long-lived seabirds, and without additional research, a comprehensive understanding of the relationship between the various forms of visible light and seabird attraction may elude us. Therefore, in addition to shielding light sources, reducing total light use, and increasing public involvement in assisting downed fledglings (all of which are necessary at this time), studies investigating the intensities and types of light that are potentially useful for human purposes and safe for fledgling seabirds may be crucial. The more that is known about the mechanics of seabird attraction to light, the greater the likelihood that conservation biologists can influence government officials and citizens to initiate measures that will further reduce or eliminate the detrimental effects of anthropogenic light on these charismatic animals.

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Table 2.1. Results of comparisons of expected fallout numbers from eight hypothetical models to total Newell's Shearwater fallout observed on Kauai, Hawaii from 1998 to 2009. Shown are results from randomization tests of Pearson's correlation coefficient (r) and the mean fallout sector ratio (MFSR) of expected and observed numbers within each fallout sector (see text for explanation of MFSR). Models are arranged by decreasing values of r .

Model	r	$P(r)$	MFSR	$P(\text{MFSR})$
Light intensity	0.765	<0.001	0.442	0.006
Ocean movement to 10 km	0.631	<0.001	0.431	0.009
Ocean movement to 5 km	0.601	<0.001	0.432	0.007
Ocean movement to 1 km	0.547	0.003	0.430	0.012
Island movement	0.483	0.003	0.368	0.220
Stationary	0.445	0.013	0.373	0.157
Light area	-0.050	0.587	0.318	0.879
Sector area	-0.171	0.833	0.328	0.730

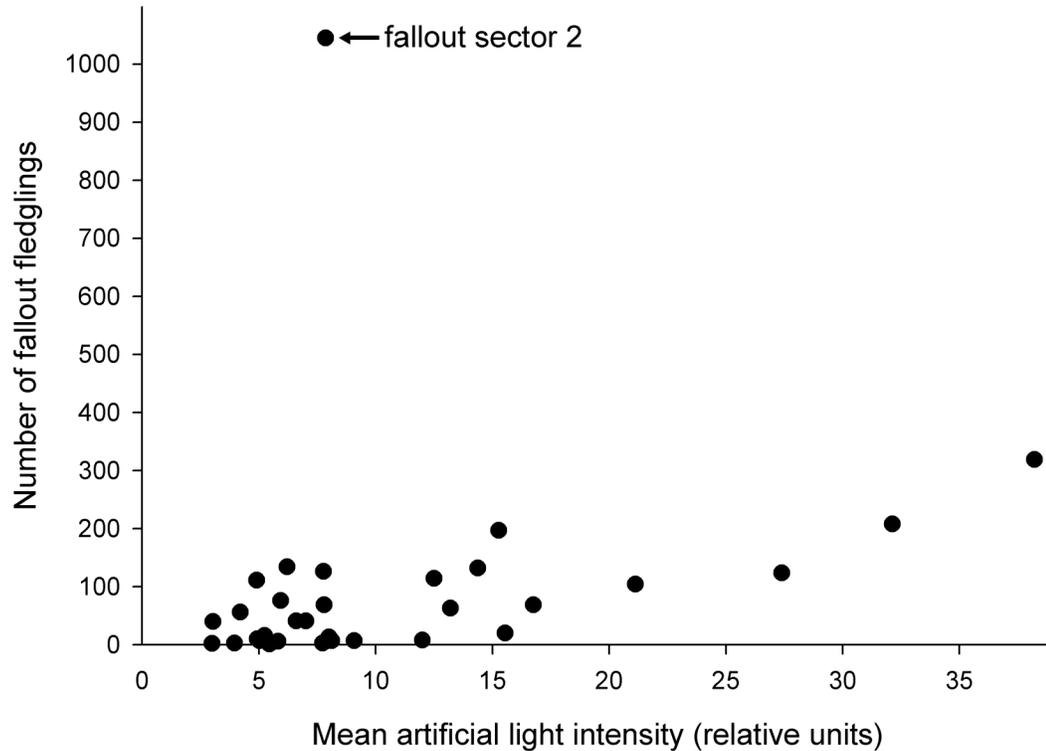


Figure 2.1. Fledging Newell's Shearwaters found as victims of fallout plotted by mean artificial light intensity from 2009 within fallout sectors ($n = 33$) on the island of Kauai, Hawaii. Fledglings were summed by fallout sector from 1998 to 2009. Because artificial light attracts and/or disorients fledglings, mean light calculations excluded dark areas. Fledglings were observed in all fallout sectors, though fewer than 5 individuals were found in particular sectors. Fallout sector 2 is labeled to highlight the exceptionally large number of fledglings observed there during the study period.

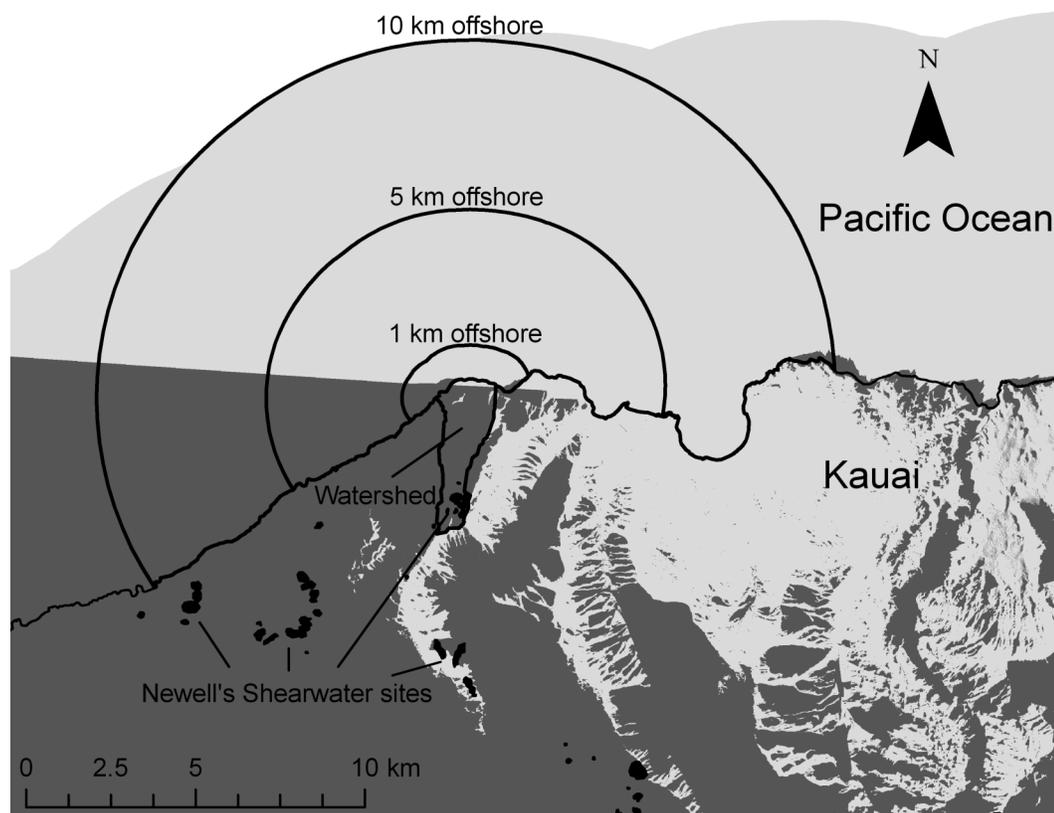


Figure 2.2. A single watershed and its associated ocean regions used in the calculation of expected fallout numbers from ocean movement models in this study. Areas shaded in dark gray represent regions of land and ocean that cannot be viewed from the lighted portion of a particular fallout sector (not shown in this figure for simplicity). Areas colored in lighter gray represent regions of land and ocean that can be viewed from the lighted portion of that fallout sector. Black polygons represent Newell's Shearwater activity sites (some of which are labeled); additional sites are present on the remaining (unseen) portion of the island. A watershed (containing Newell's Shearwater sites) and its associated ocean regions extending one of three distances past the coastline are displayed. In the ocean movement models, fledglings were assumed to travel downhill paths through their natal watersheds to the coastline (with an equal chance of flying through any portion of the watershed at or lower in elevation than the highest Newell's Shearwater site pixel in the watershed). Upon reaching the coastline, fledglings had an equal likelihood of traveling in any direction over the ocean only. These assumptions carry the additional assumption that the proportion of watershed or ocean region viewable from the lighted portion of the fallout sector, as well as the mean distance from all viewable pixels within the watershed or ocean region to the lighted portion of that fallout sector, are positively correlated with the likelihood of attracting a fledgling to that sector.

Appendix

Layers containing polygons (representing the two-dimensional boundaries of Newell's Shearwater activity sites, watersheds, and regions of ocean) were used and developed in this study so that pixel summaries within the boundaries of these polygon features could be performed. The values generated from these pixel summaries were then used to weight calculations of expected numbers within fallout sectors under different hypothetical models.

Newell's Shearwater activity sites

The Kauai Endangered Seabird Recovery Project provided a shapefile containing polygons of Newell's Shearwater sites of activity on Kauai. After deletion of redundant polygons, 59 Newell's Shearwater site polygons were available for analysis. I used the 'Add AREA/PERIMETER Fields to Table' Tool in Hawth's Analysis Tools (Beyer 2004) to calculate the two-dimensional surface area of each site polygon, and these values were used as the basis for calculating expected numbers in the stationary, island movement, and ocean movement models.

Viewshed layer development

A shapefile of Kauai fallout sectors was obtained from the Save Our Shearwaters program (Hawaii Division of Forestry and Wildlife). A copy of the fallout sector shapefile was clipped by a shapefile of Kauai representing areas with no artificial light cover from 2009 (so that the area of the clipped fallout sectors matched that of artificial light cover within the sector). The original large pixel size of the night light layer (911.25 x 911.25 m) resulted in some light-clipped fallout sectors containing small sector sections very near the coastline that were separated from the main fallout sector polygon. Because

these polygons overlapped with regions of no light, they were trimmed from the main fallout sector polygon. Small regions of the main fallout sector polygon not in overlap with light (because of the manner in which the layer was clipped) were not trimmed and remained as part of the main polygon; contributions of these small regions to viewsheds were likely negligible.

To aid in estimating how Newell's Shearwater fledglings may have arrived in particular fallout sectors (i.e., from what locations fledglings are attracted by light such that birds are downed in particular sectors), viewshed analyses were conducted from the perimeter of each light-clipped fallout sector to establish which locations on the island could be viewed from the lighted portion of each sector. Conducting viewsheds in this manner, therefore, results in an estimation of the locations on this island from which lights in particular fallout sectors could be viewed. A previous study estimated that adult Newell's Shearwaters on Kauai flew at a mean height of 125 m (with a range of 8-750 m) above ground level with considerable variation among sites (Day and Cooper 1995). Therefore, each light-clipped fallout sector polygon was converted to a polyline (outlining the light-clipped fallout sector perimeter) and this polyline was raised to 100 m above ground level (a general approximation of 125 m). A viewshed was then conducted from each raised perimeter to simulate birds viewing light emanating from each fallout sector from a realistic flight height.

The resulting output viewshed layers for each fallout sector, which were composed of pixels, were reclassified using the 'Reclassify' Tool such that all pixels viewable from the light-clipped fallout sector perimeter had a value of one and all pixels not viewable had a value of zero. A digital elevation model (DEM) of Kauai extended to

10 km past the coastline was used as input for the viewshed analyses so that regions of ocean within 10 km of the coastline viewable from each fallout sector were highlighted; see the Appendix in Chapter I for details concerning the development of such an extended DEM. Curvature of the earth was accounted for in viewshed analyses with a refractory coefficient = 0.13.

Watersheds redefined by elevation for the island movement model

A copy of the extended 10 km DEM of Kauai was reclassified such that, within watersheds containing known Newell's Shearwater activity sites, pixels higher in elevation than the highest elevation pixel within activity sites were converted to values of zero while all elevation values equal to or lower in elevation than that highest elevation pixel were converted to values of one. Elevation pixels within watersheds containing no activity sites were all reclassified to values of one. To reclassify the DEM in this watershed-specific manner, each individual watershed was first saved as a shapefile. The DEM was then reclassified once for each watershed containing one or more known Newell's Shearwater activity sites ($n = 14$), masking the reclassification by the watershed of interest. This masking resulted in individual DEMs for each of these 14 watersheds. For each of these DEMs, values of zero were converted to shapefiles, these shapefiles were pasted into a new shapefile (containing no features), and all of these polygons were joined into a single polygon. This joined polygon was then used to clip a copy of the original watershed layer. This clipped (redefined) watershed layer was then used in summaries of pixels for the island movement model and ocean movement models. Redefining watershed boundaries by elevation in this manner corresponds to an assumption that fledglings fly least-cost downhill paths (following topographical

depressions such as watersheds) to the ocean (Telfer et al. 1987, Podolsky et al. 1998, Chapter I), ensuring that areas within watersheds higher in elevation than known Newell's Shearwater activity sites did not factor into calculations of the proportion of watersheds viewable from lighted portions of fallout sectors or mean two-dimensional distance from those viewable areas to those sectors.

Ocean region polygons for the ocean movement models

The ocean movement models incorporated regions of ocean 0-1 km, 1-5 km, and 5-10 km past the coastline to the island movement model. Ocean polygons actually developed for these distances were generated as 0-1 km, 0-5 km, and 0-10 km, and pixel summaries from these polygons were then used to calculate summary values for the 0-1 km, 1-5 km, and 5-10 km distance categories. To develop these ocean polygons, a copy of the watershed shapefile was generated and all individual watershed polygons within that layer were dissolved so that only one polygon (that of the island boundary) remained. This polygon layer was then converted to a polyline layer representing the coastline of Kauai. Each individual watershed from the original watershed layer was then exported as an individual layer and each watershed was used to clip the coastline layer. This resulted in individual polyline coastline layers for each watershed. These watershed coastlines were then merged into a single layer containing each watershed coastline using the 'Merge (Data Management)' Tool.

A buffer layer for each ocean distance category (0-1 km, 0-5 km, and 0-10 km) was then produced using the 'Buffer' Tool with the new watershed coastline layer as input. This resulted in a layer containing a buffer of 0-1 km, 0-5 km, or 0-10 km from the coastline of each watershed. Because buffers are generated out to a specified distance in

all directions from a feature, these buffers not only extended out to the ocean, but extended inland as well. Therefore, the buffers were clipped by the polygon of the boundary of Kauai (the layer produced by merging the watersheds) so that the buffers only covered regions of ocean. All buffers from the same distance category were then joined into a single layer (resulting in three ocean buffer layers). These buffers were used to calculate the proportion of ocean viewable from the lighted portion of each fallout sector on the island, as well as the mean two-dimensional distance from the viewable pixels within each ocean buffer to the lighted portion of each of those sectors.

Distance from viewable pixels to lighted portions of fallout sectors

Artificial light varied among fallout sectors in proportion of the sector covered. The 'Euclidean Distance' Tool was used to calculate the two-dimensional distance from the lighted portion of each fallout sector (i.e., from each light-clipped fallout sector polygon) to every 10 x 10 m DEM pixel on the island, as well as those extending to 10 km past the coastline. This was accomplished by expanding the output extent of the 'Euclidean Distance' Tool to the boundary of a 10 km extended DEM of Kauai. A polygon layer was developed from the 10 km extended DEM (using the 'Raster to Polygon' Tool with the 'Simplify Polygon' box left unchecked) so that the 10 km boundary could be used to clip the Euclidean distance outputs from each of the fallout sectors. Values of mean Euclidean distance were calculated only for pixels viewable from each light-clipped fallout sector and these distances were used to weight values of Newell's Shearwater activity site area. Because weighting involved dividing values of Newell's Shearwater area by values of mean distance, values of zero from the Euclidean distance layers were converted to values of one using a Con statement in the 'Raster

Calculator'. Each fallout sector distance layer was then multiplied by its corresponding reclassified fallout sector viewshed layer (composed to values of either zero or one) so that pixels not viewable from the fallout sector had distance values of zero and only those pixels that were viewable from the fallout sector retained their original distance values.

Pixel summaries for hypothetical models

The proportion of pixels within each redefined watershed and ocean region viewable from the lighted portion of each fallout sector was calculated using output from the 'Thematic Raster Summary' Tool (Beyer 2004), a tool that provides a total count of pixels with discrete values (e.g., viewable and non-viewable) within the boundaries of a polygon. A combination of techniques was used to calculate the mean distance from only the viewable pixels within watersheds and ocean regions to the lighted portion of each fallout sector. First, the value of total distance (i.e., the sum of all distance pixels) within each redefined watershed and ocean region polygon was obtained using the 'Zonal Statistics ++' Tool (Beyer 2004). Second, this value was divided by the count of viewable pixels obtained from the thematic raster summary. Three types of ocean regions (0-1 km, 0-5 km, and 0-10 km from each watershed coastline) were developed and used in pixel summaries. For ocean regions, values for only 0-1 km, 1-5 km, and 5-10 km past the coastline were obtained by subtracting values obtained for the region closer to the coastline from those of the region farther from the coastline (e.g, values for the 0-1 km region were subtracted from values for the 0-5 km region). Values equal to these could have also been achieved using ocean regions that were clipped to those preferred sizes before pixel summaries were generated (i.e., using ocean buffers 0-1 km, 1-5 km, and 5-10 km in size for pixel summaries).

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CHAPTER III

HABITAT SUITABILITY MODELING FOR THE NEWELL'S SHEARWATER, AN ENDANGERED SEABIRD ENDEMIC TO THE HAWAIIAN ISLANDS

Introduction

Large-scale habitat alteration, hunting pressure, and release of non-native predators contributed to widespread avian extinction and extirpation in the Hawaiian Archipelago during the past 1500 years (Olson and James 1982, Duffy 2010). Persisting endemic taxa, including the Newell's Shearwater (*Puffinus newelli*), or 'A'o, are now confined to breeding in remnant patches of high-elevation habitat. This seabird, considered by some to be a subspecies (*P. auricularis newelli*) of the Townsend's Shearwater (*P. auricularis*), is listed as endangered on the IUCN Red List (IUCN 2011) and considered federally threatened under the US Endangered Species Act. Ornithological radar surveys reveal that numbers of Newell's Shearwaters have declined sharply during the past two decades (Day et al. 2003, Griesemer and Holmes 2011) on Kauai, where ~90% of the world population breeds (Ainley et al. 1997). In addition, few active breeding sites are confirmed based on recent surveys in the mountains of central and northwestern Kauai and the species appears to be experiencing a breeding range contraction on this island (State of Hawaii, unpublished data). Previous observations documented that remnant breeding sites of Newell's Shearwaters are characterized by

steep slopes, a thick understory of native ferns and an open canopy of scattered native trees (Ainley et al. 1997). Little more is known of this species' habitat characteristics and inaccessible terrain and expensive on-ground surveys make wide-ranging search efforts difficult. Predictive habitat suitability modeling, therefore, is a practical approach to investigating environmental factors hypothesized to be important for the terrestrial activities of the Newell's Shearwater, which allows the extent of remaining suitable habitat to be estimated to aid conservation efforts for this species.

Many techniques exist for developing habitat suitability models and these procedures typically involve a suite of environmental variables that potentially influence taxon distribution (Guisan and Zimmermann 2000). A challenge arises in regression-based suitability modeling when environmental variables are correlated with one another, some to moderate and high degrees (i.e., multicollinearity is present), complicating our understanding of their individual importance as model parameters (Quinn and Keough 2002, Graham 2003). Principal components analysis (PCA) has been used to develop suitability models in various ways (e.g., Osborne and Tigar 1992, Robertson et al. 2001, Rotenberry et al. 2006). PCA extracts new composite variables known as principal components (PCs) from linear combinations of all original variables, and these new variables are statistically uncorrelated with one another. Scores calculated from these PCs can be used as independent variables in regression analyses, eliminating the problematic effects caused by predictor variable correlation (Quinn and Keough 2002, Graham 2003). In addition, statistical issues associated with low sample size can be alleviated through the loading of correlated environmental variables onto the same principal components, which reduces the number of potentially important independent variables to be included

in regression-based analyses while accounting for patterns of relationship among the original variables.

In this study, I developed two terrestrial habitat suitability models for the Newell's Shearwater on Kauai. The first model was derived from abiotic and biotic environmental variables using a method based on PC regression (Hotelling 1957, Kendall 1957) that directly incorporates PC scores into suitability layers in a GIS framework (e.g., Osborne and Tigar 1992, Buckland and Elston 1993, Gates and Donald 2000, Suarez-Seoane et al. 2002, Di Cola et al. 2008). The second model combined anthropogenic threats with the environmental variable model to reflect human-induced pressures that may degrade otherwise suitable habitat. The major goals in this study were: (1) to delineate relationships between environmental variables and known Newell's Shearwater distribution on Kauai, (2) to narrow future searches for breeding sites on Kauai by identifying unsearched areas with a high probability of containing Newell's Shearwater habitat, and (3) to obtain estimates of the quantity of predicted suitable habitat available in major categories of land designation and ownership. Herein, I emphasize the strengths of using PC regression in habitat suitability modeling procedures and discuss its applicability when few presence observations are available compared to the number of environmental variables to be tested as possible model predictors.

Methods

Shearwater activity sites, random sites, and environmental variables

Using ArcGIS 9.3.1 (ESRI, Redlands, CA), I obtained mean values of remotely sensed environmental variables associated with both Newell's Shearwater activity sites and a large number of randomly selected pseudo-absence sites on Kauai, and differences

in mean values between these two site types were compared using PC logistic regression (see the next subsection for details concerning PC regression). Random pseudo-absence sites were used because true absence locations for Newell's Shearwaters (i.e., areas known conclusively to not contain the species) were not available and recent studies have demonstrated that informative regression-based ecological models are produced when presence sites are compared to a large number (i.e., thousands) of random pseudo-absence locations (Wisz and Guisan 2009, Barbet-Massin et al. 2012).

A GIS shapefile containing polygons of Newell's Shearwater activity sites was provided by the Kauai Endangered Seabird Recovery Project (State of Hawaii). Activity sites are defined as areas where breeding birds have been observed or where presence of breeding individuals is strongly suspected based on acoustic surveys documenting consistent localized calling activity and/or other evidence of bird presence (i.e., feathers or seabird guano). To reduce the risk of pseudo-replication (i.e., falsely treating one occupied site as two), I combined sites within a distance of ≤ 175 m from one another (based on two-dimensional surface area) into one site, resulting in 35 Newell's Shearwater activity sites for the purpose of this study. This distance was based on visual clusters of Newell's Shearwater polygons. To assess the appropriateness of clustering at this scale, I used the modeling procedure described below with polygons combined into larger activity sites (i.e., polygons within watersheds and polygons ≤ 1 km from one another within a watershed; $n = 17$ activity sites). The main contributors to the final model were the same environmental variables found to be most important in the final model based on the ≤ 175 m grouping (unpublished data), suggesting that the model was not sensitive to cutoff distance. Random pseudo-absence points ($n = 5000$) were

generated using the ‘Generate Random Points’ Tool (Beyer 2004) and stipulated to be above 200 m in elevation (slightly higher than the lowest elevation of all known abandoned breeding sites) and at least 25 m from all Newell’s Shearwater activity site boundaries. To develop random pseudo-absence sites, a buffer extending 25 m from each random point was generated using the ‘Buffer’ Tool, creating a circular polygon (50 m in diameter) centered on each point that did not overlap with activity sites; this size of these polygons corresponds approximately to the size of the smallest individual activity site polygon.

I consulted studies of burrowing procellariiforms and other burrowing animals to develop a list of environmental variables to include in the modeling procedure (Table S3.1 in Appendix A). Most variables were hypothesized to provide structure appropriate for nesting or to facilitate access to (and departure from) sites, although some may also influence the presence of introduced predators. Environmental variables included: elevation, slope, northness and eastness (linear variables related to aspect [Roberts 1986, Guisan et al. 1999]), distance to nearest ridge and distance to nearest drainage (both based on three-dimensional surface area), wind speed at 30 m in altitude, % native vegetation cover, % woody vegetation canopy cover, vegetation height, and % rock fragment composition within 0-76.2 cm soil depth (or from 0 cm to bedrock <76.2 cm). Potential effects of these variables on Newell’s Shearwater habitat are presented in Table S3.1 in Appendix A and methods for the treatment and development of remotely sensed layers depicting these environmental variables are discussed in Appendix B.

Principal components regression

For each activity and random site, I used the ‘Zonal Statistics ++’ Tool (Beyer 2004) to generate mean values of each environmental variable (from all pixels within a site). Because % native vegetation cover was categorical (non-native pixels = 0, native pixels = 1), the mean for each site represented the percent of pixels = 1. I initially compared mean values of environmental variables from Newell’s Shearwater activity sites with those from random sites using logistic regression. This allowed us to remove (from further consideration) variables that appeared to be poor predictors ($P > 0.20$) of Newell’s Shearwater terrestrial habitat, yielding four significant variables (Table 3.1). However, the model containing eastness was only significant at $P = 0.192$; therefore, eastness was not included in subsequent analyses. I then conducted a PCA (Pearson 1901, Hotelling 1933) on the dataset comprised of the three remaining environmental variables, based on a correlation matrix, to obtain three principal components (PCs) representing unique linear combinations of each of the three original variables now uncorrelated with one another. I retained all three PCs for subsequent model-building steps because even components representing small amounts of the total variance in the original predictor variable dataset can have strong effects on response variables in subsequent regressions (i.e., PC regression), though they are often inappropriately discarded (Jolliffe 1982, Hadi and Ling 1998). To obtain clear relationships between factor loadings on different PCs, I applied a varimax rotation (Kaiser 1958) to the three PCs. I then calculated scores for each varimax-rotated PC (z-transformed values of the original environmental variables multiplied by their loadings for that rotated PC from a correlation matrix). These scores were then used as new predictor variables in a series of logistic regressions (Hotelling

1957, Kendall 1957, Quinn and Keough 2002) with the response variable coded as random sites = 0 and activity sites = 1. Because of the disparity in sample size between activity sites (i.e., presence sites; $n = 35$) and random pseudo-absence sites ($n = 5000$), random sites were case-weighted in all logistic regression analyses to reduce the effective sample size to simulate an equal number of presence and random sites (Wisz and Guisan 2009, Barbet-Massin et al. 2012).

To identify the best combination of PCs as predictor variables for the final habitat suitability model, I compared several logistic regression models. I first conducted three separate regressions where the single predictor variable in each regression was one of the three PCs and removed (from further consideration) PCs that appeared to be poor predictors ($P > 0.20$) of Newell's Shearwater terrestrial habitat. This liberal α -level of 0.20 reduced the number of candidate models without relying on an arbitrarily low α -level (e.g., 0.05; Palma et al. 1999). Akaike's information criterion, corrected for small sample size (AIC_c ; Sugiura 1978), and Akaike weights (Burnham and Anderson 2002) were used to compare models containing additive combinations of the single PCs retained in the previous step. The model with the lowest AIC_c value and highest Akaike weight was selected as the final model. Nagelkerke r^2 , a coefficient of determination for logistic regression, was used to assess model fit (Nagelkerke 1991). Ranges and standard errors of mean values for each environmental variable were calculated to describe activity and random sites in terms of original variables (Table 3.1). The PCA, calculation of PC scores, and logistic regressions were conducted using JMP version 8.0.1 (SAS Institute Inc., Cary, NC) and calculations of ranges and standard errors of mean environmental

variable values were conducted using R version 2.10.0 (R Development Core Team 2009).

Contribution of original environmental variables

Because each original variable is included in each PC, each variable contributes (to some degree) more than once in a model containing more than one PC. In this situation, it is often difficult to keep track of the total effect of each original environmental variable. Therefore, I calculated the regression coefficients from the final model in terms of the original variables. These calculations involve multiplying the matrix of original variable loadings for each PC in the regression model by the vector of regression coefficients for each PC (Jackson 1991, Morzuch and Ruark 1991).

Alternatively, as I demonstrate in this study, the equation can be derived as: $\chi_j = \gamma_{1j}\beta_1 + \gamma_{2j}\beta_2 + \dots \gamma_{nj}\beta_n$ for all $j = 1$ to n , where χ_j = the regression coefficient in terms of the original environmental variable (j), γ_{nj} = the factor loading for the original environmental variable (j) on the independent variable (PC_n), and β_n = the regression coefficient for PC_n from the regression equation. The sign of each original variable regression coefficient (i.e., the sign of each χ_j) indicates the direction of the relationship between the original variable and the response variable. I also calculated the total proportional contribution (i.e., importance) of each original environmental variable to the final model by dividing the absolute value of each original variable regression coefficient by the sum of all absolute values.

Habitat suitability model development

PCs contributing to the final logistic regression model were used to produce the habitat suitability model in a GIS framework. PC score layers were developed separately

for each significant PC by z-transforming each original predictor variable layer, multiplying it by its factor loading for that particular PC, and adding it to the other transformed predictors (see Roberston et al. [2001]) using the ‘Raster Calculator’ in ArcGIS 9.3.1. Each PC score layer was then inserted as a digital layer into the logistic regression equation as the independent variable (e.g., Osborne and Tigar 1992, Buckland and Elston 1993, Gates and Donald 2000) using the ‘Raster Calculator’ to produce the final habitat suitability model displayed as a map of Kauai. The output of this model is the predicted probability of each pixel in supporting the terrestrial activities of Newell’s Shearwaters based on the environmental conditions of the pixel.

Model with anthropogenic threats

Two threats to Newell’s Shearwaters are fledgling attraction to artificial light (Reed et al. 1985, Telfer et al. 1987, Ainley et al. 2001) and predation by introduced predators. Feral cats (*Felis catus*; Medina et al. 2011) and rodents (Jones et al. 2008) are known mammalian predators of seabirds introduced to Kauai; however, direct measures of their abundance in different habitats on Kauai do not exist. Because more mammalian predators may exist closer to human disturbance (i.e., trails, roads [references within May and Norton (1996); Delgado et al. 2001], development, and agriculture [Chalfoun et al. 2002, Shake et al. 2011]), I used a proxy measure of distance from these disturbances to estimate the potential for introduced predator presence. I consider this a useful measure for cats (likely the major predator of seabirds on Kauai); this may also be a somewhat appropriate measure for introduced Barn Owls (*Tyto alba*), which sometimes prey upon seabirds (Byrd and Telfer 1980). This measure, however, may be unsuitable for estimating rodent presence. I combined GIS layers depicting these threats with the

environmental variable model (see Appendix B) to develop a second model identifying regions predicted to contain structurally suitable habitat where fledglings would likely be less susceptible to artificial light attraction (Chapter I) and less likely to experience predator-related threats associated with human disturbance. Lack of account for the placement of power lines (a known source of mortality [Podolksy et al. 1998]) and the likelihood of rodent presence is expected to be a limitation of this model.

Habitat suitability model processing

To make the habitat suitability model layers more interpretable and appropriate for pixel summaries, both model layers (with and without threats) were resampled to 50 x 50 m pixel resolution (2500 m²), allowing one pixel to fully encompass the smallest Newell's Shearwater activity site polygon (1708.38 m²), reclassified into probability categories of 0.10 (i.e., 0-0.10, >0.10-0.20, etc.), and resampled back to 10 x 10 m resolution (which retained the data resolution of the 50 x 50 m pixel size); this resampling process facilitates more appropriate pixel summaries for landowner polygons that are smaller than 50 x 50 m (see section below). Layers were resampled using the 'Resample' Tool with the 'NEAREST' (nearest neighbor assignment) Resampling Technique and layers were reclassified using the 'Reclassify' Tool.

Land ownership and reserve designation

A shapefile of landowners holding at least 404.7 ha on an individual Hawaiian island (updated in 2009 for Kauai) and a shapefile of habitat reserves (updated in 2011) were obtained from the Hawaii Statewide GIS Program (<http://hawaii.gov/dbedt/gis/>). I used these layers to develop a GIS layer (Fig. 3.1) with five land ownership and designation categories (government reserves, government non-reserves, private reserves,

private non-reserves, and other land [i.e., non-reserve lands owned by those with <404.7 ha]; see Appendix B). I then calculated the proportion of area covered by categories of probability (from 0.0-0.1 to >0.9-1.0) from the two models (the environmental variable model both with and without threats) within each land type using the ‘Thematic Raster Summary’ Tool (Beyer 2004).

Results

Both PC1 and PC3 were significant at the cutoff α -level of $P \leq 0.20$. Therefore, model comparison and selection involved each of these single variable models plus their additive combination. The best-fit logistic regression model ($y = e^{-1.40 + 1.36(PC1) + 1.53(PC3)} / (1 + e^{-1.40 + 1.36(PC1) + 1.53(PC3)})$), according to model selection (Table 3.3), contained PC1 and PC3 as predictor variables and exhibited a good fit to the data (Nagelkerke $r^2 = 0.49$). Slope loaded strongly onto PC3 and % native vegetation loaded strongly onto PC1 (loadings >0.90); % rock fragment composition within the soil loaded moderately onto PC3 (Table 3.2) due to its significant positive relationship with slope in this study. Signs of regression coefficients in terms of the original variables, as well as proportional contributions of these variables to the final model, suggest that the probability that a site on Kauai could be a Newell’s Shearwater activity site increases with steeper slopes, more native vegetation, and greater coverage of rock fragments in the soil (Table 3.4; see Table 3.1 for variable means and ranges); original logistic regressions strongly suggest that the other environmental variables examined in this study may be of little importance. The environmental variable model suggests that a large portion of the mountainous interior of Kauai is potentially suitable habitat for Newell’s Shearwater (Fig. 3.2). When combined with the anthropogenic threats, however, the model identifies a much more restricted

portion of the island as structurally suitable habitat in which the anthropogenic threats that I examined are thought to be reduced (Fig. 3.3). In addition, the majority of regions of the island that may contain suitable habitat and reduced threats occur within privately owned land not designated as reserve land (Table 3.5).

Discussion

The habitat suitability models produced in this study will be useful in aiding future conservation efforts for the Newell's Shearwater in the Hawaiian Islands. I uncovered important information regarding the significance of habitat characteristics associated with known Newell's Shearwater activity sites, defined the extent and location of habitat predicted to be suitable for the species, and calculated estimates of the proportion of suitable habitat within major categories of land differing in ownership type and reserve status. Calculating regression coefficients in terms of the original environmental variables (Jackson 1991; Morzuch and Ruark 1991), as well as proportional variable contributions, revealed the total effect of each of the original variables in the final environmental model. These values, in concert with means and ranges of the original habitat variables (Table 3.1), are informative for defining the habitat of the Newell's Shearwater and they facilitate comparisons with previous observations for this and other species.

Newell's Shearwaters have been observed breeding in rocky volcanic soil on steep slopes (Ainley et al. 1997), similar to my findings based on remotely sensed data. Steep slopes may facilitate access to (and departure from) breeding sites, provide proper drainage during precipitation events to prevent burrow flooding (Schramm 1986, Stokes and Boersma 1991, Brandt et al. 1995, Catry et al. 2003, Rayner et al. 2007), and/or

represent locations difficult to access by non-native predators. Steep slopes may also be linked to burrow stability through their association with rocky substrates on Kauai. In this study, % rock composition in the soil exhibited a positive correlation with slope and soils of activity sites generally contained a greater coverage of rock fragments (including boulders) and areas of exposed bedrock than those of random sites. Typical soil profiles of Kauai soil map units suggest that many soils of the mountainous interior are composed of at least a moderate amount of fine soil particles, which is positively related to burrow stability in other species (Stokes and Boersma 1991, Carter 1997, Holmes et al. 2003, Kintigh and Andersen 2005), and rocks within this soil may provide additional benefits to these seabirds, increasing the sturdiness of burrow walls (Stokes and Boersma 1991) and supplying roofs to burrows (Wingate 1964, Brandt et al. 1995, Bourgeois et al. 2008, Le Roux et al. 2011).

The breeding sites of Newell's Shearwaters have also been observed to contain a thick understory of uluhe fern (*Dicranopteris linearis*) and an open canopy of scattered ohia trees (*Metrosideros polymorpha*) (Ainley et al. 1997). In this study, Newell's Shearwater activity sites and random sites were generally characterized by mean vegetation height values ranging from >0-5 to 5-10 m and by 60-70% woody vegetation canopy cover (Table 3.1). These values suggest a widespread coverage of woody vegetation with openings in the canopy, similar to that previously observed. Though Newell's Shearwaters may indeed benefit from this structural arrangement of woody shrubs and trees (Ainley et al. 1997), my analyses suggest that it does not influence the clustered distribution of these birds on Kauai. Activity sites, however, were covered by more native vegetation than random sites, suggesting that non-native vegetation provides

less suitable habitat. Invasive plants alter the three-dimensional structure of Hawaiian forests (Asner et al. 2008), which can affect seabird habitat use. For example, young strawberry guava (*Psidium cattleianum*) plants can form nearly impenetrable stands of vegetation, limiting opportunities for seabirds to burrow and physically access the ground (Duffy 2010); this species is associated with at least one abandoned Newell's Shearwater colony on Kauai.

The model based only on abiotic and biotic environmental variables suggests that a large portion of the interior of Kauai may be potential habitat for the Newell's Shearwater and this model exhibited a good fit to the distributional data. Recent searches for this species conducted in the mountains of the central and northwestern sections of the island revealed that Newell's Shearwater activity sites are scattered through portions of these regions with high predicted suitability values, but are not widespread in coverage. This result may therefore reflect other variables not related to structural components of the habitat, including intrinsic factors (such as social attraction [Podolsky and Kress 1989] and site fidelity), as well as factors that negatively affect seabird populations (including terrestrial anthropogenic threats [e.g., Ainley et al. 2001, Keitt et al. 2002]). Though intrinsic factors were not modeled in this study, the second version of the environmental variable model spatially incorporated major terrestrial threats to predict structurally suitable habitat most isolated from these threats relative to other portions of the island.

According to the model incorporating terrestrial threats, some current Newell's Shearwater activity sites (e.g., in Limahuli Preserve) are located in areas with predicted probabilities in the >0.20-0.30 range and likely represent sites on the edge of suitable

range. Therefore, other areas with similar predicted values could harbor additional activity sites, despite their seemingly low values. Importantly, this model highlights a particular region with appropriate topographic and vegetation structure that is the most isolated from certain human disturbances on Kauai (with predicted probabilities ranging from >0.60 to 0.90), making it a promising candidate for long-term persistence of breeding colonies. This area exists in the mountains of the north-central region of the island, north of Mount Waialeale, south of Hanalei, east of the Wainiha River, and west of the Hanalei River; this region only partially overlaps with Halelea and Wainiha Reserves. In addition to this region possibly containing breeding Newell's Shearwaters, it could be investigated as a site for future stimulation of breeding colony formation (Podolsky and Kress 1989). Structurally suitable habitat on the northwestern portion of Kauai is predicted to be the least affected by artificial light (unpublished data), suggesting that additional on-ground searches should be conducted in this region to confirm the locations of breeding sites, in concert with expanding efforts to control introduced predators (as in Limahuli Preserve). Furthermore, much of the structurally suitable habitat in the interior of Kauai can increase in overall suitability if efforts to control introduced predators become widely established and artificial light output is limited during the fledging season of this species.

I acknowledge that some private lands on Kauai may be managed for the conservation of native species without being officially recognized as reserves; however, the summary of habitat in categories of suitability within land types was conducted using information concerning landownership (government versus private) and official reserve status. The environmental variable model suggests that the largest portion of land in most

categories of probability is government-owned and designated as reserve land; the second largest portion is privately owned and not designated as reserve land. In the model incorporating threats, however, the largest portion of land in all but one category with predicted probability values >0.20 (a range of values that characterizes many active Newell's Shearwater sites) is privately owned and not designated as reserve land. In addition, the region of the island with the highest predicted probability of containing Newell's Shearwater habitat that is most isolated from certain anthropogenic threats (Fig. 3.3) exists in one area that is unprotected (i.e., not a reserve). This information is critical for discussions between conservation biologists, federal and state employees, and private landowners concerning future searches for this species, possible induced formation of new breeding colonies, efforts to control non-native predators, and management of additional lands as reserves (which may be necessary for protection and preservation of this species). Moreover, this same region may also be important because potentially suitable habitat for the Newell's Shearwater is likely to be suitable for some of Kauai's other rare taxa (e.g., Hawaiian Petrels [*Pterodroma sandwichensis*] and certain plants of conservation concern) because of its physical isolation from directly disturbed land. Habitat suitability models for species of conservation concern may benefit greatly by accounting for isolation from anthropogenic disturbances to identify regions more likely to resist degradation induced by human activities.

Habitat suitability modeling based on PC regression (e.g., Osborne and Tigar 1992, Buckland and Elston 1993, Gates and Donald 2000, Suarez-Seoane et al. 2002, Di Cola et al. 2008), as applied in this study, is appealing for several reasons: (1) using PC scores as independent variables in regression analyses removes the problematic effects of

predictor correlation on interpretation of individual variable importance (Quinn and Keough 2002, Graham 2003) (2) the number of possible explanatory models requiring investigation can be vastly reduced when a large number of environmental variables are seemingly important to taxon distribution (Osborne and Tigar 1992, Rushton et al. 2004), and (3) it allows each variable to contribute to the final model (by contributing to each PC in the model) without actually being included as an individual model parameter. The loading of correlated environmental variables onto the same PCs reduces the number of potentially important independent variables to be included in regression analyses, making this method of habitat suitability modeling particularly appropriate when the sample size of presence sites is low. In a greater context, the technique of PC regression may be a valuable tool for conservation biologists faced with the challenge of developing habitat suitability and distribution models for a wide range of threatened and endangered species in which data are limited due to rarity.

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Table 3.1. Means, standard errors (SE), and ranges (minimum and maximum values) for the means of abiotic and biotic variables from Newell's Shearwater activity sites and random sites on Kauai, Hawaii. 'Ridge' and 'Drainage' = distance (m) to nearest ridge or drainage (based on three-dimensional surface area), respectively, 'Wind' = wind speed (m/s) at 30 m in altitude, 'Native veg' = % native vegetation cover, 'Woody veg' = % woody vegetation cover, 'Veg height' = vegetation height on an ordinal scale, and 'Rock comp' = % rock fragment composition within 76.2 cm soil depth (or to bedrock <76.2 cm).

	Newell's Shearwater				Random			
	Mean	SE	Min	Max	Mean	SE	Min	Max
Elevation	711.47	33.82	283.68	1127.35	639.69	4.76	201.57	1568.00
Slope*	40.20	1.48	24.59	63.15	27.36	0.20	0.00	73.24
Eastness [†]	-0.20	0.09	-0.97	0.81	-0.02	0.01	-1.00	1.00
Northness	0.09	0.10	-0.96	0.96	-0.03	0.01	-1.00	1.00
Ridge	15.85	0.95	4.74	31.17	14.83	0.15	1.00	142.00
Drainage	71.74	4.89	27.44	140.79	63.1	0.65	4.55	287.68
Wind	3.85	0.32	1.27	7.72	4.22	0.02	0.76	11.92
Native veg*	0.85	0.04	0.00	1.00	0.44	0.01	0.00	1.00
Woody veg	6.53	0.20	4.27	8.71	6.03	0.03	0.00	10.00
Veg height	1.70	0.09	1.00	2.77	1.86	0.01	0.00	3.00
Rock comp*	49.24	4.42	32.61	100.00	33.95	0.51	0.00	100.00

* Mean values from Newell's Shearwater activity sites and random sites differ significantly ($P < 0.05$); all other variables (aside from eastness) did not differ significantly ($P > 0.20$)

[†] Mean values from Newell's Shearwater activity sites and random sites differ significantly at $P = 0.192$

Table 3.2. Loadings (contributions based on correlations) of the four original abiotic and biotic environmental variables onto three varimax-rotated principal components (PCs). Variable abbreviations are listed in Table 3.1.

Variable	PC1	PC2	PC3
Slope	0.10	0.31	0.95
Native veg	0.99	0.05	0.09
Rock comp	0.05	0.95	0.30

Table 3.3. Results of model selection. Reported are the models, number of model parameters (K), Akaike's information criterion (corrected for small sample size [AIC_c]), change in AIC_c (δAIC_c), and Akaike weight.

Model	K	AIC_c	δAIC_c	Akaike weight	Nagelkerke r^2	P
PC1 + PC3	3	71.22	0.00	0.9982	0.49	<0.0001
PC3	2	84.42	13.19	0.0014	0.28	<0.0001
PC1	2	86.71	15.48	0.0004	0.25	0.0002

Table 3.4. Regression coefficients in terms of the original environmental variables and total proportional contributions of each original variable to the best-fit logistic regression model (selected using AIC_c). Signs of regression coefficients indicate the directional relationship of the original environmental variables to a site being suitable for Newell's Shearwater terrestrial activity. Variable abbreviations are listed in Table 3.1.

Variable	Regression coefficient	Proportional contribution
Slope	1.58	0.44
Native veg	1.49	0.41
Rock comp	0.53	0.15

Table 3.5. Proportion of land within categories of predicted suitability for two models in categories of land designation on Kauai, Hawaii. One model is based solely on environmental variables and the other incorporates anthropogenic threats into the environmental variable model. PR = 'private reserve', PNR = 'private non-reserve', GR = 'government reserve', GNR = 'government non-reserve', and O = 'other land'. Proportions in some categories of habitat suitability do not sum exactly to one due to rounding.

Suitability	Model without threats					Model with threats				
	PR	PNR	GR	GNR	O	PR	PNR	GR	GNR	O
0.0-0.1	0.00	0.37	0.20	0.18	0.25	0.00	0.35	0.34	0.12	0.17
>0.1-0.2	0.00	0.40	0.42	0.08	0.10	0.06	0.48	0.42	0.00	0.03
>0.2-0.3	0.01	0.39	0.47	0.06	0.08	0.16	0.48	0.30	0.00	0.06
>0.3-0.4	0.02	0.34	0.55	0.04	0.05	0.22	0.41	0.29	0.00	0.07
>0.4-0.5	0.03	0.31	0.60	0.02	0.04	0.26	0.36	0.37	0.00	0.01
>0.5-0.6	0.04	0.30	0.62	0.01	0.03	0.13	0.52	0.36	0.00	0.00
>0.6-0.7	0.04	0.31	0.62	0.01	0.02	0.02	0.75	0.22	0.00	0.00
>0.7-0.8	0.04	0.30	0.63	0.01	0.02	0.00	1.00	0.00	0.00	0.00
>0.8-0.9	0.04	0.33	0.59	0.00	0.03	0.01	0.99	0.00	0.00	0.00
>0.9-1.0	0.10	0.44	0.43	0.00	0.03	NA	NA	NA	NA	NA

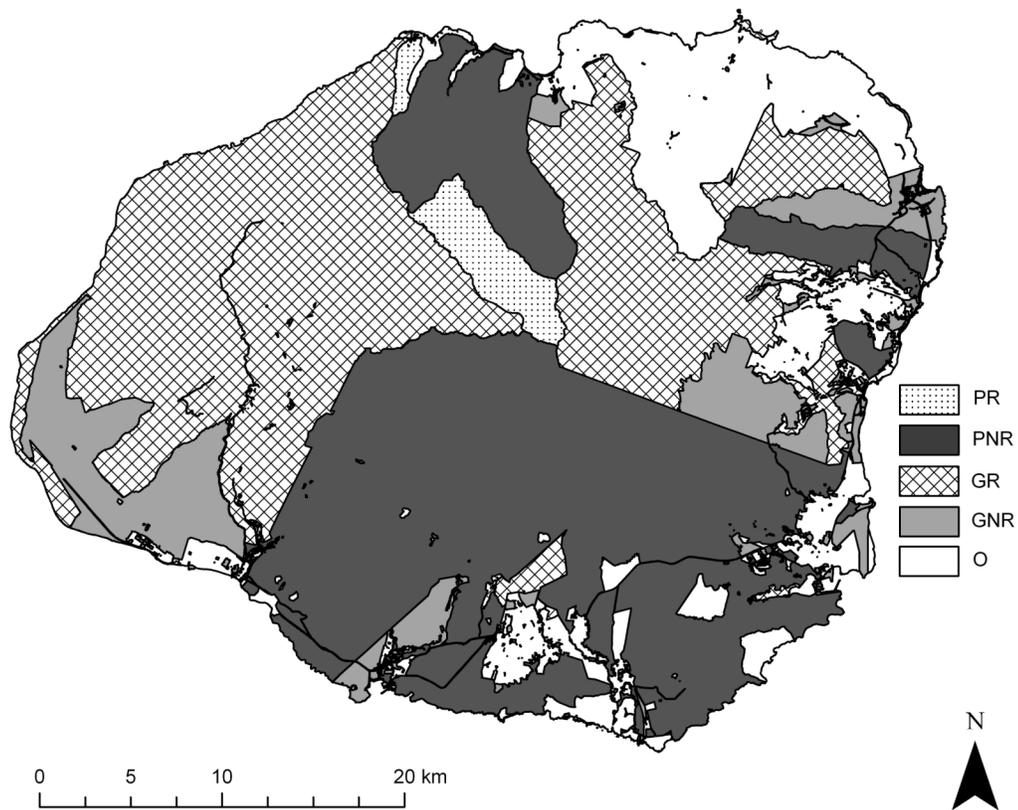


Fig. 3.1. The island of Kauai in five categories of land designation. In the figure legend, PR = 'private reserve', PNR = 'private non-reserve', GR = 'government reserve', GNR = 'government non-reserve', and O = 'other land'.

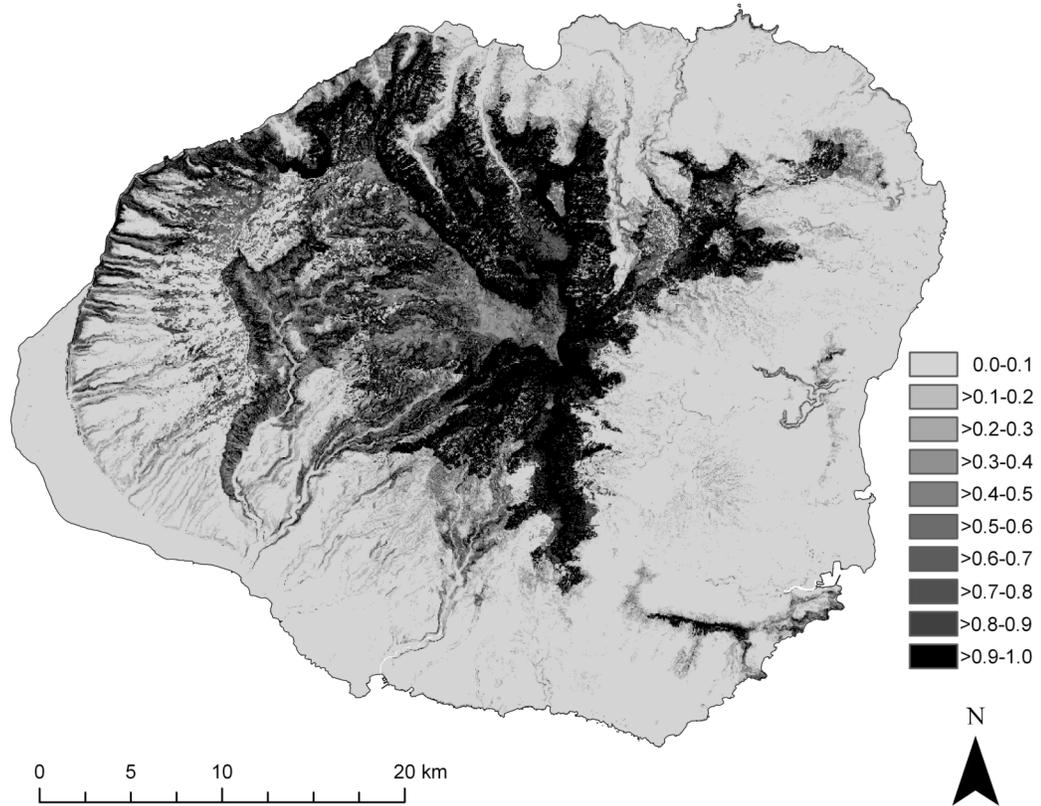


Fig. 3.2. The island of Kauai in categories of predicted suitability for Newell's Shearwater terrestrial activity based on abiotic and biotic environmental variables.

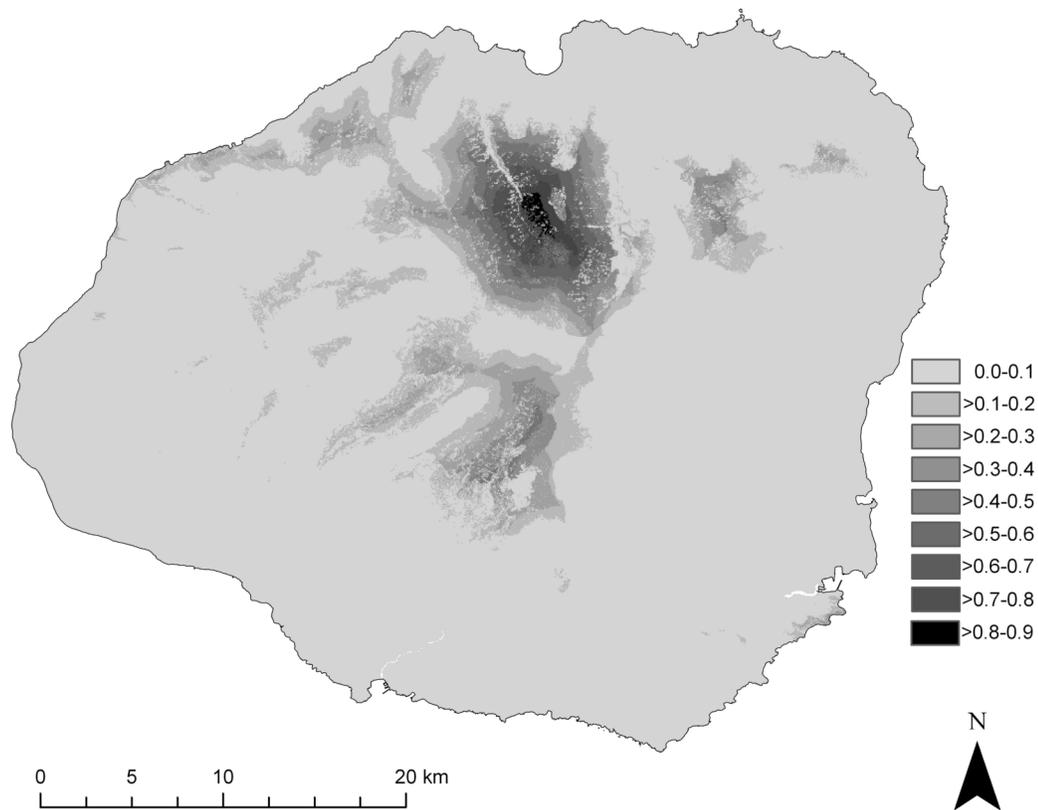


Fig. 3.3. The island of Kauai in categories of predicted suitability for Newell's Shearwater terrestrial activity based on abiotic and biotic environmental variables combined with threats (terrestrial anthropogenic disturbance and the risk of possible fledgling attraction to artificial light).

Appendix A

Table S3.1. Potential effects of abiotic and biotic environmental variables on Newell's Shearwater terrestrial habitat.

Environmental variable	Potential effects on terrestrial habitat
Elevation	Newell's Shearwaters were likely historically uncommon at lower elevations (Olson and James 1982); introduced predators are likely more abundant at lower elevations (Olson and James 1982, Harrison 1990, Rayner et al. 2007)
Slope	Steeper slopes could facilitate access to (and departure from) breeding sites and provide drainage during precipitation events (Schramm 1986, Stokes and Boersma 1991, Brandt et al. 1995, Catry et al. 2003, Rayner et al. 2007)
Northness and eastness (linear variables related to aspect)	Direction of breeding site slope may be associated with prevailing wind direction, which may facilitate taking flight (Shulz et al. 2005), or thermal conditions appropriate for nesting
Distance to nearest ridge and distance to nearest drainage (based on three-dimensional surface area)	Habitat on or near ridges may facilitate accessibility to breeding sites (Shulz et al. 2005, Rayner et al. 2007) and habitat farther from drainages is less likely to accumulate water during precipitation and may be more accessible to birds
Wind speed at 30 m altitude	Particular wind speeds aloft may facilitate access to and departure from breeding sites (see Bourgeois et al. [2008])
% Native vegetation cover	Native vegetation may provide appropriate vegetative structure to facilitate access to breeding sites (Asner et al. 2008, Duffy 2010) and structural root components crucial for burrow stability (Gillham 1961, Brandt et al. 1995, Ainley et al. 1997, Underwood and Bunce 2004, Bancroft et al. 2005)
% Woody vegetation canopy cover	Lower shrub and tree cover may be associated with breeding site access (as this species is found in open forest [Ainley et al. 1997] and in Waimea Canyon on slopes with little vegetation [Wood et al. 2002]) and burrows may be located at the base of woody vegetation for burrow stability (Gillham 1961, Brandt et al. 1995, Ainley et al. 1997, Underwood and Bunce 2004, Bancroft et al. 2005)
Vegetation height	Greater vegetation height in may be associated with trees suitable for climbing and launching to achieve flight (Ainley et al. 1997, Sullivan and Wilson 2001)

% Rock fragment composition from 0-76.2 cm soil depth (or 0 cm to bedrock <76.2 cm)	Larger rock fragments (Wingate 1964, Brandt et al. 1995), crevices in exposed bedrock (Brandt et al. 1995) and greater rock fragment composition in soil (Stokes and Boersma 1991, Brandt et al. 1995, Bourgeois et al. 2008, Le Roux et al. 2011) may provide stability to burrows
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Appendix B

Treatment and development of remotely sensed environmental variable layers

I used a Digital Elevation Model (DEM) of Kauai (10 x 10 m resolution) obtained from the Hawaii Coastal Geology Group (www.soest.hawaii.edu/coasts) to generate a slope raster layer for the island using the 'Slope' Tool in ArcGIS 9.3.1 (ESRI, Redlands, CA). I then created an aspect raster layer from the DEM using the 'Aspect' Tool. Because aspect is a circular variable (ranging from 0°-360°), it was reclassified as two linear variables, northness (a gradient varying from south [-1] to north [1]) and eastness (a gradient varying from west [-1] to east [1]), using the 'Raster Calculator'. Northness = cosine (aspect in radians) and eastness = sine (aspect in radians); this allowed interpretable mean values to be calculated for each site (Roberts 1986, Guisan et al. 1999).

I developed a flow direction raster layer (which determines the direction water would flow) using the Kauai DEM and the 'Flow Direction' Tool and subsequently generated a flow accumulation raster from the flow direction layer using the 'Flow Accumulation' Tool. The flow accumulation raster layer was reclassified to produce a ridge layer (values = 0 flow accumulation were reclassified as 'ridges') and drainage layer (values ≥ 100 flow accumulation were reclassified as 'drainages'; i.e., pixels with ≥ 100 pixels flowing into them from higher elevations were considered drainages). This value of 100 was based on trials in which flow accumulation values reclassified as 'drainages' were varied and the resulting layers were placed over a DEM (Jenson and Domingue 1988) zoomed to a familiar abandoned Newell's Shearwater breeding site to examine which values yielded the most realistic representation of drainages. The ridge

and drainage layers were then used to generate two layers, one of distance to the nearest ridge and one of distance to the nearest drainage (both based on three-dimensional surface area), using the 'Path Distance' Tool with the Kauai DEM as the 'input surface raster'. Maps of mean annual wind speed (m/s) at 30 m in altitude (200 x 200 m resolution; produced by AWS Truewind) were obtained from the Hawaii Statewide GIS Program (<http://hawaii.gov/dbedt/ert/winddata/winddata.html>).

A soil shapefile for Kauai was obtained from the USGS Soil Data Mart (<http://soildatamart.nrcs.usda.gov/>). Polygons of the same soil type were merged using the 'Merge' Function in 'Editor' and the shapefile was converted to a raster layer (10 x 10 m resolution) using the 'Feature to Raster' Tool. Using soil map unit information for Kauai available from the USGS Soil Data Mart, I reclassified soil type into a new variable: % rock fragment composition within the soil from 0-76.2 cm soil depth; soils with a depth to bedrock of <76.2 cm were characterized only from 0 cm to bedrock <76.2 cm. To construct the layer of % rock fragment composition, I developed two initial layers. First, I reclassified soils based on % rock fragment composition as follows: no rock fragments = 0, no modifier before rock fragment size description (e.g., "stony" [15-35% fragment cover]) = 25, the modifier "very" (e.g., "very gravelly" [35-60% fragment cover]) = 50, the modifier "extremely" (e.g., "extremely cobbly" [60-90% fragment cover]) = 75 and exposed bedrock (assumed to be 100% rock cover) = 100. To account for more than one layer of soil with differing rock fragment compositions, I calculated the % depth covered by the soil band(s) containing rocks between the surface and 76.2 cm depth (or between the surface and bedrock <76.2 cm) and reclassified soil type based on these values. I then multiplied these two reclassified layers together to yield the

general % rock fragment composition within soil 0-76.2 cm in depth or from 0 cm to bedrock <76.2 cm. Bedrock <76.2 cm below the soil surface was not factored into % rock fragment cover because exposed bedrock is weathered and more likely to provide small-scale topographic features suitable for nesting (e.g., Brandt et al. 1995), whereas bedrock under the soil surface and unexposed to intense weathering may not. Only one soil type contained layers with rock fragments that differed in their modifier (i.e., they differed in overall % rock composition); this was accounted for in the development of the % rock fragment composition layer. Because reclassification of Kauai soils was based on the typical profile for a soil map unit, minor soil components were not considered.

I used a preclassified land cover layer, a vegetation height layer and a vegetation canopy cover layer of Kauai (30 x 30 m resolution) from the Landscape Fire and Resource Management Planning Tools Project (www.landfire.gov) to develop three vegetation variables. The land cover layer was reclassified into native vegetation (= 1) and non-native vegetation and other land cover types (= 0) to create a native vegetation layer. Vegetation height was reclassified as an ordinal variable combining preclassified categories of height as follows: (a) open water, developed land and cultivated crops = NoData, (b) barren land = 0, (c) herb height 0->1 m, shrub height 0->3 m and forest height 0-5 m = 1, (d) forest height 5-10 m = 2 and (e) forest height >10 m = 3. Combining height categories in this manner required the assumption that herbs >1 m and shrubs >3 m are <5 m in height. To create a woody vegetation canopy cover layer, I reclassified the vegetation canopy cover as follows: (a) open water, developed land and cultivated crops = NoData, (b) barren land and herb cover = 0 and (c) shrub and tree

canopy cover into values from 2-10, so that >10-20% shrub or tree cover = 2, >20-30% = 3, etc.; no data were available for shrub or tree canopy cover in the 0-10% range.

All layers not projected in North American Datum (NAD) 1983 Zone 4 were converted to this projection using the 'Project' Tool. All reclassifications were performed using the 'Reclassify' Tool. All rasters not 10 x 10 m in resolution were converted to 10 x 10 m for analysis to generate mean predictor values for all variables based on identical pixel sizes.

Development of model with anthropogenic threats

Two threats to Newell's Shearwater are fledgling attraction to artificial light and close proximity to human disturbance. I combined GIS layers depicting these threats with the terrestrial habitat model (based on abiotic and biotic environmental variables) to develop a second model identifying regions of predicted habitat where fledglings would likely be less susceptible to artificial light attraction and less likely to experience the threats associated with human disturbance. For the artificial light threat, I used a GIS layer for the island of Kauai of the total intensity of artificial light a fledgling seabird could view if it traveled a least-cost path, based on topography, from any location on the island to 10 km past the coastline (Chapter I). For distance to nearest human disturbance, I developed a layer depicting distance to the nearest trail, road, developed land or agricultural land (based on three-dimensional surface area).

I obtained two USGS road shapefiles, one classified as 'major roads' and the second as 'other roads', for Kauai from the Hawaii Statewide GIS Program (<http://hawaii.gov/dbedt/gis/>). A buffer of 0.5 m surrounding all roads within each road layer was generated using the 'Buffer' Tool, transforming both road layers into a layer of

merged road and trail polygons. I used the preclassified land cover layer of Kauai (30 x 30 m resolution) from the Landscape Fire and Resource Management Planning Tools Project (www.landfire.gov) to generate a polygon layer of developed and agricultural land by highlighting those land cover categories in the attributes table and using the 'Raster to Polygon' Tool to convert the highlighted land types to polygons (without polygon simplification). The developed and agricultural land and both trail and road polygon layers were merged using the 'Merge' Tool, and all individual polygons were then merged using the 'Merge' Function in 'Editor'. I used this shapefile to generate a raster layer of distance to nearest road (10 x 10 m resolution), based on three-dimensional surface area, using the 'Path Distance' Tool with the Kauai DEM as the 'input surface raster'.

The threat layers of artificial light and distance to nearest human disturbance were combined with the terrestrial habitat model to identify regions of predicted habitat where fledglings would likely be less susceptible to artificial light attraction and less likely to experience the threats associated with human disturbance. To combine these layers, I first reclassified them into proportions by dividing each layer by its highest pixel value using the 'Raster Calculator'. Because greater values of distance to the nearest terrestrial human disturbance may be associated with decreased risk of threat to Newell's Shearwaters, proportional values of this layer were equivalent to threat risk (on a scale from 0-1). Greater values of artificial light, however, are likely associated with higher risk that fledglings will be intercepted by light on their nocturnal fledging flights. I therefore inverted the pixel values of the proportional night light layer so that the highest values represented the lowest risk and hence lowest threat. Both threat layers and the

habitat suitability layer then were multiplied using the ‘Raster Calculator’ to produce a second suitability layer accounting for these potential threats.

Development of land ownership and designation layer

A shapefile of large government and private landowners in the main Hawaiian Islands, holding at least 404.7 ha on an individual island (updated for Kauai in 2009), and a shapefile of designated habitat reserves (updated in 2011) were obtained from the Hawaii Statewide GIS Program (<http://hawaii.gov/dbedt/gis/>). I used the ‘Create Layer From Selected Features’ option in ArcGIS 9.3.1 (ESRI, Redlands, CA) to create both a large landowner and a reserve layer for Kauai from these layers. One copy of each layer was produced so that each copy of the same layer could be edited differently (using the ‘Merge’, ‘Clip’, and ‘Explode’ Functions in ‘Editor’) to create layers of different types. All government land polygons in the large landowner layer were merged into one group and all private land polygons were merged into another group using the ‘Merge’ Function. These government and private land polygons were then split into two separate layers using the ‘Create Layer From Selected Features’ option. I used the reserve layer to clip both the government and private land layers using the ‘Clip’ Function, and both the government and private land layers were then used to clip the reserve layer using the ‘Clip’ Function. This produced four individual landowner layers (government reserves, government non-reserves, private reserves, private non-reserves). For this analysis, I considered Limahuli Preserve (a privately owned reserve containing several Newell’s Shearwater activity sites) in northwestern Kauai as a reserve though the shapefile of reserves did not. Small remnant polygons along former boundaries of clipped polygons were deleted using the ‘Explode’ Function to separate all polygons in the layer and

deleting them individually; the remaining polygons were merged using the 'Merge' Function. These four landowner layers were merged using the 'Overlay' Tool.

The combination of these layers left portions of Kauai without landowner designation (i.e., non-reserve lands owned by those with <404.7 ha). To fill these regions, I used a polygon of the boundary of Kauai obtained from the Hawaii Statewide GIS Program (<http://hawaii.gov/dbedt/gis/>). The merged four-landowner layer was then used to clip the island boundary layer to produce a layer of smaller landowners (which I termed 'other land') using the 'Clip' Function. Finally, this layer was combined with the four-landowner layer using the 'Overlay' Tool, yielding a layer with five land ownership categories (the four previously mentioned as well as 'other land').

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CHAPTER IV

HABITAT SUITABILITY MODELING FOR THE ENDANGERED HAWAIIAN PETREL WITH COMMENTS ON PREDICTED HABITAT OVERLAP WITH THE NEWELL'S SHEARWATER

Introduction

Anthropogenic activities in the main islands of the Hawaiian Archipelago, including habitat alteration and introduction of non-native predatory mammals, has led to the extinction of many native avian taxa and restricted the ranges of most extant native birds to high elevations (Kirch 1982, Olson and James 1982, Cuddihy and Stone 1990, Duffy 2010). Most breeding colonies of the endangered Hawaiian Petrel, or `Ua`u (*Pterodroma sandwichensis*), at lower elevations were likely extirpated even before the arrival of European settlers (Olson and James 1982). At present, breeding sites of this species remain on Maui (Simons 1985, Brandt et al. 1995), Hawaii (Harrison 1990, Hu et al. 2001), Lanai (Hirai 1978, Simons and Hodges 1998), and Kauai (Day and Cooper 1995, Ainley et al. 1997), and the species may also still breed on Molokai (Simons and Hodges 1998).

Hawaiian Petrels currently nest in two distinct habitats: high-elevation xeric terrain on Maui (Simons 1985, Brandt et al. 1995) and Hawaii (Richardson and Woodside 1954, Hu et al. 2001) and wet montane forest on Lanai (Hirai 1978) and Kauai

(Gon 1988, Ainley et al. 1997). On Maui (Simons 1985, Brandt et al. 1995) and Hawaii (Richardson and Woodside 1954, Hu et al. 2001), breeding sites are characterized by sparse vegetation and large rock features (e.g., boulders, rock outcrops, and lava flows). On Lanai (Hirai 1978) and Kauai (Gon 1988, unpublished Kauai Endangered Seabird Database), however, breeding sites contain a thick cover of uluhe fern and scattered native trees. The apparent commonalities between these two habitats are high elevation, habitat features that may provide stability to breeding burrows, and isolation from human disturbance and development (which may be correlated with the likelihood of introduced predator presence). Additional habitat features may be important for the terrestrial activities of Hawaiian Petrels and a complete island-wide census of the locations associated with these activities (including currently unknown sites) remains a critical recovery action. A large portion of the mountainous interior of most of the main Hawaiian islands, however, is difficult to access because of steep terrain, making these endeavors costly and difficult.

In this study, I used GIS-based methods (as in Chapter III) to develop two terrestrial habitat suitability models for the Hawaiian Petrel on the island of Kauai to aid in improving knowledge of important habitat characteristics for the species on Kauai and of the regions where additional breeding sites may occur. The first model was based on abiotic and biotic environmental variables and developed using a method of habitat suitability modeling based on principal components regression that incorporates principal component (PC) scores into suitability layers in a GIS framework (e.g., Osborne and Tigar 1992, Buckland and Elston 1993, Palma et al. 1999, Gates and Donald 2000, Chapter III). The second model was produced by combining the first model with two GIS

layers depicting potential anthropogenic threats to the species (Chapter III). The main objectives in the development of these models were to outline the relationships between environmental variables and sites of Hawaiian Petrel terrestrial activity (i.e., those characterized by breeding and/or consistently vocalizing Hawaiian Petrels) on Kauai, to identify regions with a high likelihood of containing habitat suitable for Hawaiian Petrels, and to estimate the extent of potentially suitable habitat in major categories of land designation and ownership. In addition, I calculated the degree of overlap between the two Hawaiian Petrel suitability models and corresponding models from a recent study of the Newell's Shearwater (*Puffinus newelli*; Chapter III) and combined the corresponding models for each bird to produce a model identifying regions of Kauai that may contain habitat suitable for both species. The use of PC regression is discussed as a valuable method in the context of habitat suitability modeling when data concerning taxon distribution are limited and the degree of large-scale overlap between highly suitable habitat predicted for Hawaiian Petrels and Newell's Shearwaters is discussed from a management perspective.

Methods

Presence sites, absence sites, and environmental variables

Mean values of remotely sensed environmental variables (calculated from pixels) within sites of Hawaiian Petrel activity (i.e., presence sites) on Kauai and sites centered on randomly selected former survey locations (in which no Hawaiian Petrels were observed) were extracted using ArcGIS 9.3.1 (ESRI, Redlands, CA). Differences in these values between these site types were assessed using logistic regression and PC logistic regression, which formed the basis of habitat suitability modeling for this species. The

Kauai Endangered Seabird Recovery Project (KESRP) provided a GIS shapefile containing polygons defining the boundaries of terrestrial sites of Hawaiian Petrel activity observed since 2006. Activity sites were considered areas where nesting Hawaiian Petrels have been observed or where the presence of breeding individuals is suspected based on consistent and localized calling activity and/or other evidence of bird presence (i.e., seabird feathers or guano). To reduce the risk of incorrectly treating one activity site as two or more, I combined all polygons whose boundaries were within a two-dimensional distance of 175 m from one another (a distance based on visual clusters of sites), resulting in 13 Hawaiian Petrel activity sites (some of which were clusters of multiple sites in close proximity to one another). To test the appropriateness of grouping Hawaiian Petrel polygons ≤ 175 m from one another, I used the modeling procedure described below with activity sites based on grouping polygons ≤ 600 m from one another (yielding 7 activity sites). Because of a mismatch in numbers (7 activity sites and 13 random absence sites), sites were case-weighted during logistic regression such that activity sites were given a weight = 1 and random sites were given a weight = 7/13. The main contributors to this final model were the same as those found to be important based on the ≤ 175 m grouping (unpublished data), except that three-dimensional distance to the nearest drainage was a minor contributor to the final model (due to its correlation with wind speed in this instance). This suggests that the final model was not sensitive to cutoff distance.

Known Hawaiian Petrel activity sites on Kauai mostly encompass ridge tops. Random points, therefore, were selected from a shapefile of point locations on ridges previously surveyed by KESRP that did not overlap with known Hawaiian Petrel activity

sites; these points were selected (equal in number to activity sites [$n = 13$]) using the ‘Create Random Selection’ Tool (Beyer 2004). To produce a layer of random sites for comparison with Hawaiian Petrel activity sites, Hawaiian Petrel activity site polygons were copied and their polygon centroids were centered onto the random points (within 0.5 m) so that the shape and two-dimensional surface area of random site polygons matched that of activity sites. Though some random sites were composed of multiple unconnected polygons jointly centered on a previously surveyed point, a mean of 92% of two-dimensional random site area fell within the boundaries of auditory coverage from previous surveys (as determined by survey coverage polygons provided by KESRP). This suggests that these random sites can be considered absence sites for the purposes of this study. Furthermore, mean three-dimensional distance to nearest ridge calculated for absence sites was <4 m greater than that of Hawaiian Petrel activity sites, suggesting that random sites centered on former survey points on ridges generally matched the ridge characteristics of activity sites (data not shown).

Variables known or suspected to influence the breeding habitat of burrowing procellariiforms, as well as burrow stability in other animals, guided model development. In general, most variables were associated with burrow stability, access to breeding sites, and/or the likelihood of introduced predator presence. These remotely sensed variables included: elevation, slope, northness and eastness (linear variables related to aspect [Roberts 1986, Guisan et al. 1999]), three-dimensional distance to nearest drainage, wind speed at 30 m in altitude, % native vegetation cover, % woody vegetation canopy cover, vegetation height, and % rock fragment composition within 0-76.2 cm soil depth (or from 0 cm to bedrock <76.2 cm).

Methods for the production of GIS layers representing these 10 environmental variables and their potential effects on Hawaiian Petrel terrestrial habitat are identical to those presented in the appendices of a recent study of the Newell's Shearwater on Kauai (Chapter III). Methods of model production applied in this study are also very similar to those used in the previous Newell's Shearwater study (Chapter III), except that three-dimensional distance to nearest ridge was not investigated because the locations of Hawaiian Petrel activity sites may be biased toward ridge tops and random sites were centered on ridges. In addition, PC regression in the present study was performed on the original unrotated PCs versus varimax-rotated PCs. The repeated methods of model production are summarized in the following subsection; see Chapter III and associated appendices for more comprehensive methods relevant to this study.

Habitat suitability modeling

For each Hawaiian Petrel activity site and absence site, I calculated mean values for 9 of the 10 environmental variables. Percent native vegetation cover was categorical (non-native pixels = 0, native pixels = 1); therefore, the mean for each site represented the percent of pixels with a value = 1. Mean values of each environmental variable for activity sites were compared with those within absence sites using logistic regression (Table 4.1). Because small sample sizes (as in this study) can result in biased estimates of regression coefficients when using logistic regression, parameter estimates were calculated using Firth's bias adjustment (Firth 1993). Ranges and standard errors of means for the environmental variables were also calculated to aid in describing activity and random sites in terms of the original variables (Table 4.1). Variables significant at P

≤ 0.20 were retained for inclusion in a PCA, yielding three variables to be used in further analysis.

A PCA (Pearson 1901, Hotelling 1933) was conducted on the environmental variable dataset (comprised of the three retained variables), based on a correlation matrix, to obtain three principal components (PCs), uncorrelated linear combinations of all three original variables. All three PCs were retained for subsequent analyses. I calculated scores for each PC and these scores were used as independent variables (Hotelling 1957, Kendall 1957, Quinn and Keough 2002) in a series of logistic regressions (with Firth's bias adjustment [Firth 1993]) to identify the best combination of PCs (used as predictors) for the final habitat suitability model. I conducted three separate regressions where the single predictor variable was one of the three PCs. Model significance was tested at a liberal α -level of 0.20 to reduce the number of candidate models for further comparison while avoiding an arbitrarily low α -level (Palma et al. 1999). Only one PC was significant at $P \leq 0.20$ (see Results). Nagelkerke r^2 , a coefficient of determination for logistic regression, was used to assess model fit (Nagelkerke 1991). The PCA, calculation of PC scores, and logistic regressions were conducted using JMP version 8.0.1 (SAS Institute Inc., Cary, NC) and calculations of ranges and standard errors of mean environmental variable values were conducted using R version 2.10.0 (R Development Core Team 2009).

To assess the effect of each original environmental variable to the final model, regression coefficients from the model were calculated in terms of the original variables (the sign of the coefficient indicates the direction of effect). In these calculations, the matrix of loadings for each original variable on each PC in the regression model is

multiplied by the vector of regression coefficients for each PC (Jackson 1991, Morzuch and Ruark 1991); more direct equations are given in Chapter III. I also calculated the total relative contribution of each original variable to the final model by dividing the absolute value of each original variable regression coefficient by the sum of absolute values for all coefficients.

To portray the suitability model based on environmental variables as a GIS layer, a PC score layer was developed for the significant PC (Roberston et al. 2001) and inserted as the independent variable into the logistic regression equation for the final model (e.g., Osborne and Tigar 1992, Buckland and Elston 1993, Gates and Donald 2000, Suarez-Seoane et al. 2002, Di Cola et al. 2008, Chapter III). This produced a GIS layer in which each pixel represented the predicted probability of supporting Hawaiian Petrel terrestrial activity based on the environmental conditions of the location represented by the pixel. A major threat to procellariids (including the Hawaiian Petrel) is the attraction of fledglings to sources of artificial light during their first flights to the ocean (Reed et al. 1985, Telfer et al. 1987, Ainley et al. 2001, Chapter I). In addition, introduced predators pose a significant threat to burrowing seabirds, and these predators may be more prevalent closer to trails, roads (references within May and Norton [1996], Delgado et al. 2001), and developed and agricultural lands (Chalfoun et al. 2002, Shake et al. 2011). A second version of the environmental variable model was developed that spatially incorporated both of these threats. Thus, this model identified areas of the island containing habitat predicted to be structurally suitable for Hawaiian Petrels, in which birds would potentially be less susceptible to the combination of fledgling attraction to artificial light and predator-related threats associated with directly disturbed land (relative

to other portions of the island). See Chapter III for further discussion on the adequacy of these GIS layers in spatially defining major threats to this species on Kauai and Appendix B in Chapter III for detailed methods concerning the development of this second model in a GIS framework.

Land ownership and reserve designation

To make the habitat suitability model layers more appropriate for pixel summaries, GIS layers for both models (with and without threats) were resampled to a 50 x 50 m pixel resolution (50 m is slightly larger than the width of most Hawaiian Petrel activity site polygons) and reclassified into probability categories of 0.10 (i.e., 0-0.10, >0.10-0.20, etc.). These reclassified layers were then resampled back to 10 x 10 m resolution, which retained the 50 x 50 m data resolution while allowing for more accurate pixel summaries within land ownership polygons with lengths and/or widths much smaller than 50 m. I then calculated the proportion of area within five land ownership types covered by categories of probability (from 0.0-0.1 to >0.9-1.0) from both model layers (i.e., the environmental variable model with and without threats). I used a shapefile of landowners holding at least 404.7 ha on an individual Hawaiian island (updated in 2009 for the island of Kauai) and a shapefile of habitat reserves (updated in 2011) to develop this layer of ownership categories (government reserves, government non-reserves, private reserves, private non-reserves, and other land [i.e., non-reserve lands owned by those with <404.7 ha]; see Appendix B in Chapter III).

Overlap between predicted habitat for the Hawaiian Petrel and Newell's Shearwater

Two habitat suitability models were previously developed for the Newell's Shearwater on Kauai, one based on abiotic and biotic environmental variables and the

other incorporating threats, using identical methods to those used in this study (Chapter III). I calculated the degree of overlap between the environmental variable suitability model for the Hawaiian Petrel and the same model for the Newell's Shearwater, and between the models incorporating threats for both species. To calculate overlap, both Hawaiian Petrel models were first converted to shapefiles using the 'Raster to Polygon' Tool (with the 'simplify polygons' box unchecked so that the original pixelated shape of the model was retained and exactly matched that of the Newell's Shearwater models). All polygons (which were based on pixels within identical categories of predicted probability) were then dissolved using the 'Dissolve (Data Management)' Tool so that there were 10 polygon categories corresponding to the 10 categories of predicted suitability. For each model type (i.e., for both the environmental variable model and the model incorporating anthropogenic threats), pixels within the 10 categories of predicted probability for the Newell's Shearwater were summed within polygons of suitability categories from the Hawaiian Petrel models using the 'Thematic Raster Summary' Tool (Beyer 2004). I then calculated proportional overlap between all combinations of pixel types in probability categories of 0.10 from >0.6-1.0.

Combined suitability models for the Hawaiian Petrel and Newell's Shearwater

The two habitat suitability models for the Hawaiian Petrel (with and without threats) were combined with their corresponding Newell's Shearwater suitability models developed in Chapter III. For combination, the original suitability models were multiplied by one another using the 'Raster Calculator' (i.e., the environmental variable models for both species were multiplied, as were the models incorporating threats). These combined

suitability models were then reclassified into probability categories of 0.10 using the ‘Reclassify’ Tool.

Results

The only logistic regression model significant at $\alpha < 0.20$ contained PC1 as the single predictor variable ($\chi^2 = 28.79$, $P < 0.0001$) and this model ($y = e^{-1.56 + 3.87(PC1)} / (1 + e^{-1.56 + 3.87(PC1)})$) exhibited a good fit to the data (Nagelkerke $r^2 = 0.88$). Wind speed at 30 m above ground, elevation, and % native vegetation cover contributed largely to PC1 (and thus to the final model) (Table 4.3). Regression coefficients calculated in terms of these original variables suggest that the probability that a pixel on Kauai could be a Hawaiian Petrel activity site increased with increasing wind speed at 30 m above the ground, elevation, native vegetation cover.

The model containing only abiotic and biotic environmental variables predicts a large portion of the interior of Kauai to be highly suitable for Hawaiian Petrels (Fig. 4.1). Most land from this model with predicted suitability values of >0.10 - 0.90 is privately owned and not designated as an official reserve; government reserves make up the second largest portion of land within suitability values of >0.10 - 0.90 and the largest portion of land with suitability values >0.90 was found within government owned reserves (Table 4.4). The model incorporating terrestrial anthropogenic threats, however, predicts a greatly reduced portion of Kauai to be highly suitable for Hawaiian Petrels (based on abiotic and biotic environmental variables) that is also isolated from the two major anthropogenic disturbances examined in this study (Fig. 4.2). Most land from this model with predicted suitability values >0.20 is privately owned non-reserve land (Table 4.4). The degree of overlap between categories of predicted suitability for the Newell’s

Shearwater and Hawaiian Petrel was moderate for suitability values of >0.90-1.00 from the two environmental variable models (Table 4.5; Fig. 4.3) and high for suitability values >0.70 from the models incorporating threats (Table 4.5; Fig. 4.4). Regions of predicted habitat overlap from the environmental variable models and models incorporating threats are displayed in categories of probability in Figs. 4.3 and 4.4, respectively.

Discussion

Principal components regression and limited distributional data

This study demonstrates the utility of PC regression in habitat suitability modeling for rare species with a small sample of observations relative to the number of possible influential environmental variables. PC regression condensed the three major contributors to the final model (wind speed at 30 m above ground level, elevation, and native vegetation cover) into a single PC. Though the sample size of Hawaiian Petrel activity sites was small, the regression coefficient for this single predictor was estimated with a small standard error, which would not have been possible with each of the three original variables being included as individual model parameters. Other modeling techniques (i.e., those based on maximum entropy [Phillips et al. 2006]) have been shown to produce models with good predictive power when the sample size of presence locations for a taxon is small (Pearson et al. 2007, Wisz et al. 2008). For researchers preferring to develop habitat suitability models using regression techniques when distributional data are limited, however, ordination-based methods such as PC regression, and perhaps partial least squares regression (which can be applied with fewer observations than candidate variables [Carrascal et al. 2009, Skarpaas et al. 2011]), may

be applicable if multiple variables appearing to influence taxon distribution contribute moderately or strongly to the same PC axis (or axes). If the suite of potentially relevant environmental variables cannot be condensed to one or a few PCs, however, the number of candidate variables may not be supported numerically (see Barry and Elith [2006]) and other methods, including those based on maximum entropy or variable elimination, may be required.

Hawaiian Petrel habitat characteristics

Absence sites in this study were centered on previous survey locations on ridges that did not overlap with Hawaiian Petrel activity site polygons, which reduced possible ridge-based bias between activity and absence sites. Though the comparison between activity and absence sites was confined to sites on (and near) ridgelines, 74% of Kauai is less than 20 m from the nearest ridge and 21% is between 20 and 40 m from the nearest ridge, with approximately identical values for habitat with predicted suitability values of $>0.9-1.0$ from the environmental variable model (data not shown). These values suggest that model predictions presented in this study (on a 50 x 50 m scale) are likely valid for much of the island.

Regression coefficients calculated for the original environmental variables show that Hawaiian petrel activity sites are higher in elevation, contain more native vegetation, and are characterized by higher wind speeds aloft than randomly distributed sites on ridges in the mountains of Kauai. Hawaiian Petrel activity sites were characterized by a mean wind speed at 30 m aloft of just over 8 m/s (with a range of $\sim 6.5-10$ m/s), whereas random sites had a mean wind speed of ~ 4.5 m/s (with a range of $\sim 2-9$ m/s). Though the GIS layer used in this study depicts mean wind speed over an entire year, it is expected

that areas with greater wind speeds aloft also contain higher winds during the Hawaiian Petrel breeding season. Wind speed is important for gadfly petrels (a group consisting mostly of the *Pterodroma* petrels), in that stronger winds are associated aerial activity (e.g., Spear and Ainley 1997, Haney 1987, Adams and Flora 2010). At sea, gliders (including large gadfly petrels such as the Hawaiian Petrel) are found in areas with stronger winds than species exhibiting other types of flight (Spear and Ainley 1997). Haney (1987) observed Black-capped Petrels (*Pterodroma hasitata*) in flight only beyond a particular threshold of wind speed (versus birds sitting on the ocean surface), with more flying birds observed at wind speeds of 11-27 knots (5.5-13.8 m/s) and peak numbers at 17-21 knots (8-10.7 m/s). Petrels are also aerially active over land, commonly circling above their breeding colonies upon returning from foraging trips (Warham 1990). Given the association between larger gadfly petrels and stronger winds at sea, greater wind speeds above breeding sites may, perhaps, aid species such as the Hawaiian Petrel by facilitating landing and taking flight (see Bourgeois et al. [2008]), as well as reducing the energetic costs of circling aloft and performing aerial displays.

While winds greater than the minimum average wind speed calculated for Hawaiian Petrel sites in this study exist at lower elevations (along the eastern coast and in the southern portion of the island), all known Hawaiian Petrel activity sites on Kauai occur in high-elevation areas characterized by these wind conditions. All but two random sites were above 350 m in elevation; however, these two lower-elevation sites (with mean elevations of ~58 and 189 m) did not heavily influence the final model because eliminating them as random sites produced almost identical results, with elevation being a strong contributor to the model (unpublished data). Hawaiian Petrels once nested at

much lower elevations before the introduction of predatory mammals to Hawaii (Olson and James 1982), but their breeding colonies are now confined to the mountainous interior of particular islands. Elevation, therefore, is likely important in the environmental variable model because high-elevation sites containing Hawaiian Petrels are expected to reflect appropriate wind conditions combined with lower densities of non-native mammalian predators (e.g., feral cats) than locations found at lower elevations, as well as the most intact remnant native vegetation.

The results of this study show that native vegetation is prevalent within Hawaiian Petrel sites on Kauai (~80-100% cover within sites) and is a significant predictor of suitable habitat on the island, in conjunction with higher elevations and wind speeds. In xeric alpine habitat on Maui (Simons 1985, Brandt et al. 1995) and Hawaii (Richardson and Woodside 1954, Hu et al. 2001), however, a thick covering of native vegetation appears unnecessary for the Hawaiian Petrel, as birds there often nest under boulders, rock outcrops, and lava flows, or in sturdy habitat features (e.g., lava tubes and cracks), in addition to excavating burrows under sparsely distributed shrubs. It is possible that Hawaiian Petrel sites on Kauai contain more native vegetation merely because it is more prevalent at higher elevations than non-native vegetation (though non-native vegetation can still be found above 1400 m on Kauai [unpublished data]). However, on Kauai, native vegetation may also be associated with habitat structure appropriate for seabirds, as opposed to that provided by certain exotic species in Hawaii with the capacity to change three-dimensional forest structure (Asner et al. 2008). Introduced strawberry guava (*Psidium cattleianum*), for example, can form stands of vegetation thick enough to prevent seabirds from physically accessing potential nesting sites (Duffy 2010).

Therefore, a thick cover of native vegetation in forested areas may facilitate seabird activities associated with breeding.

Model predictions and land category summaries

The environmental variable model suggests that a large portion of the interior of Kauai may be habitat suitable for the terrestrial activity of Hawaiian Petrels based on the variables considered in this study. Aside from predictions that some suitable habitat may exist in the extreme southern portion of the island, this finding is comparable to that of a recent study that predicted habitat suitable for the Newell's Shearwater (Chapter III), though much more highly suitable habitat is predicted for the Hawaiian Petrel. Recent surveys suggest that sites of Hawaiian Petrel activity are not at all common in the mountainous interior of Kauai; however, this is to be expected as factors other than habitat structure can potentially influence the distribution of nesting petrels, such as conspecific social attraction (Podolsky and Kress 1989), site fidelity, and terrestrial anthropogenic threats (e.g., Ainley et al. 2001; Keitt et al. 2002). For example, some sites near the southern coast are predicted to be suitable based on abiotic and biotic environmental variables (Fig. 4.1); however, these birds are likely absent from this region because of human-induced pressures, including the expected prevalence of introduced predators. Almost half of the land with predicted suitability values from this model of >0.10 - 0.90 is privately owned land without official designation as a reserve. In addition, slightly more than half of the land with probability values >0.90 exists within government reserves, but $\sim 40\%$ is still privately owned, non-reserve land.

The environmental variable model incorporating two major terrestrial threats, however, predicts a much reduced portion of Kauai as containing structurally suitable

habitat that is more isolated with respect to both fledgling attraction to artificial light and a proxy measure for the likelihood of introduced predator presence. According to this model, most known Hawaiian Petrel activity sites are found in land with predicted suitability values in the >0.20-0.40 range, suggesting that regions with suitability values >0.20 may support additional unknown breeding sites. At least 46% the land within categories of predicted suitability >0.20 is private land that is not designated as a reserve, including 56% of land with suitability values >0.60-0.70 and 100% of land with values >0.70 existing in one region in the north-central portion of the island (Fig. 4.2), a region expected to be potentially important for the Newell's Shearwater as well (Chapter III). Though it is likely that even this remote region is not completely isolated from the effects of artificial light (see Chapter I) or introduced predators, it appears to be the region where the combination of these threats is minimized. These findings are important for the conservation of the Hawaiian Petrel because they suggest that much of the habitat predicted to be highly suitable for the species that is the most isolated from major human-related threats occurs on privately owned land. As found for the Newell's Shearwater (Chapter III), however, the environmental variable model (which does not incorporate anthropogenic threats) suggests that if efforts to control predators and to eliminate nocturnal light use during crucial fledging times are broadly established, a large portion of the interior of Kauai could potentially become habitat suitable for this species.

Habitat overlap with the Newell's Shearwater: implications for joint management

The overlap analysis conducted in this study suggests that, on the 50 x 50 m scale of this study (i.e., larger than a microhabitat scale surrounding individual burrows), there is a moderate degree of overlap in habitat predicted to be highly suitable for the Hawaiian

Petrel and Newell's Shearwater on Kauai, including the isolated region in the mountains of the north-central portion of the island. This overlap suggests that protection for both species could perhaps be achieved by managing some of the same larger areas on the island, similar to the current situation in Upper Limahuli Preserve where both species are found. It appears that breeding sites of these species remain separate when in close proximity on Kauai (unpublished data), which is likely related to social attraction and perhaps species-specific small-scale habitat differences (Warham 1990). Future habitat studies will be important in examining environmental features associated with breeding sites of these species on a much finer scale than that of this study. The results of this study provide information that will be valuable in future conservation efforts for both the Hawaiian Petrel and Newell's Shearwater. One major challenge is likely to be the protection of suitable habitat for these seabirds located within privately owned lands lacking predator control, making this study important for both conservation biologists and private landowners. Modeling the regions containing habitat predicted to be highly suitable for these species, as well as other taxa of conservation concern in Hawaii, may become increasingly important for maximizing the use of funding through the concentration of predator control efforts in key locations and in the design and foundation of new nature reserves.

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Table 4.1. Means, standard errors (SE), and ranges (minimum and maximum values) for the means abiotic and biotic variables from Hawaiian Petrel activity sites and random sites on Kauai, Hawaii. 'Drainage' = three-dimensional distance (m) to nearest ridge or drainage, respectively, 'Wind' = wind speed (m/s) at 30 m in altitude, 'Native veg' = % native vegetation cover, 'Woody veg' = % woody vegetation cover, 'Veg height' = vegetation height on an ordinal scale, and 'Rock comp' = % rock fragment composition within 76.2 cm soil depth (or to bedrock <76.2 cm).

	Activity site				Absence site			
	Mean	SE	Min	Max	Mean	SE	Min	Max
Elevation*	1087.32	48.81	772.22	1255.30	661.33	97.17	57.74	1374.11
Slope	29.21	2.26	9.00	40.03	32.55	3.86	14.96	65.53
Eastness	0.03	0.13	-0.88	0.68	-0.02	0.10	-0.86	0.49
Northness	0.04	0.10	-0.49	0.56	0.18	0.16	-0.74	0.90
Drainage	95.24	11.44	33.14	167.33	77.71	13.78	35.82	185.54
Wind*	8.17	0.32	6.45	10.00	4.74	0.48	2.15	9.01
Native veg*	0.96	0.02	0.81	1.00	0.53	0.12	0.00	1.00
Woody veg	6.81	0.40	4.18	8.18	5.93	0.62	0.03	9.00
Veg height	2.24	0.14	1.23	2.86	1.95	0.23	0.00	3.00
Rock comp	45.76	7.22	18.00	100.00	42.32	7.90	0.00	99.32

* Variable means differ significantly between activity and absence sites ($P < 0.001$)

Table 4.2. Loadings (contributions based on correlations) of the three original abiotic and biotic environmental variables onto three principal components (PCs). Variable abbreviations are the same as those in Table 4.1.

Variable	PC1	PC2	PC3
Elevation	0.86	-0.24	-0.46
Wind	0.84	-0.34	0.42
Native veg	0.76	0.65	0.05

Table 4.3. Regression coefficients in terms of the original environmental variables and total relative contributions of each original variable to the significant logistic regression model. Signs of regression coefficients indicate the directional relationship of the original environmental variable to a site being suitable for Hawaiian Petrels. Variable abbreviations are identical those in Table 4.1.

Variable	Regression coefficient	Relative contribution
Elevation	3.31	0.35
Wind	3.26	0.34
Native veg	2.92	0.31

Table 4.4. Proportion of land within categories of predicted suitability for Hawaiian Petrels from two models in categories of land designation on Kauai, Hawaii. One model is based solely on environmental variables and the other incorporates anthropogenic threats into the environmental variable model. PR = 'private reserve', PNR = 'private non-reserve', GR = 'government reserve', GNR = 'government non-reserve', and O = 'other land'.

Suitability	Model without threats					Model with threats				
	PR	PNR	GR	GNR	O	PR	PNR	GR	GNR	O
0.0-0.1	0.00	0.34	0.30	0.16	0.20	0.01	0.36	0.12	0.17	0.34
>0.1-0.2	0.03	0.46	0.23	0.09	0.20	0.07	0.45	0.00	0.02	0.45
>0.2-0.3	0.03	0.49	0.24	0.10	0.14	0.14	0.53	0.00	0.05	0.28
>0.3-0.4	0.03	0.51	0.28	0.05	0.13	0.13	0.52	0.01	0.07	0.27
>0.4-0.5	0.03	0.53	0.29	0.02	0.12	0.26	0.47	0.00	0.03	0.24
>0.5-0.6	0.04	0.58	0.27	0.01	0.11	0.20	0.46	0.00	0.00	0.34
>0.6-0.7	0.04	0.53	0.31	0.01	0.11	0.04	0.56	0.00	0.00	0.41
>0.7-0.8	0.05	0.50	0.33	0.01	0.11	0.00	1.00	0.00	0.00	0.00
>0.8-0.9	0.05	0.43	0.41	0.01	0.10	0.00	1.00	0.00	0.00	0.00
>0.9-1.0	0.06	0.38	0.53	0.00	0.03	NA	NA	NA	NA	NA

Table 4.5. Proportional overlap (in categories of 0.10 from >0.60-1.00) between two habitat suitability models for the Hawaiian Petrel (the environmental variable model and the environmental variable model incorporating terrestrial anthropogenic threats) and two models developed using identical methods for the Newell's Shearwater on Kauai, Hawaii. No category of >0.9-1.0 was available from the Newell's Shearwater model with threats.

		Model without threats			
		Hawaiian Petrel			
		>0.6-0.7	>0.7-0.8	>0.8-0.9	>0.9-1.0
Newell's	>0.6-0.7	0.03	0.03	0.04	0.06
	>0.7-0.8	0.04	0.04	0.04	0.07
Shearwater	>0.8-0.9	0.07	0.07	0.08	0.11
	>0.9-1.0	0.22	0.30	0.36	0.47
		Model with threats			
		Hawaiian Petrel			
		>0.6-0.7	>0.7-0.8	>0.8-0.9	>0.9-1.0
Newell's	>0.6-0.7	0.63	0.10	0.01	NA
	>0.7-0.8	0.03	0.76	0.17	NA
Shearwater	>0.8-0.9	0.01	0.06	0.81	NA

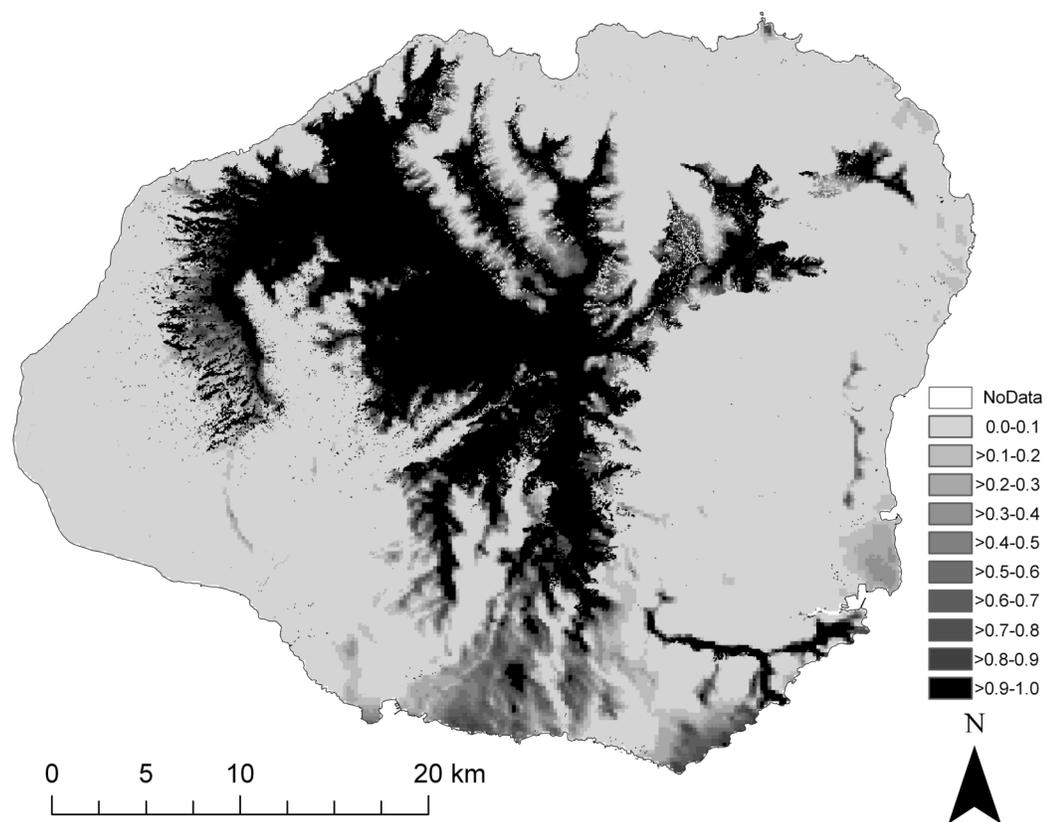


Figure 4.1. The island of Kauai in categories of predicted suitability for Hawaiian Petrel terrestrial activity based on abiotic and biotic environmental variables.

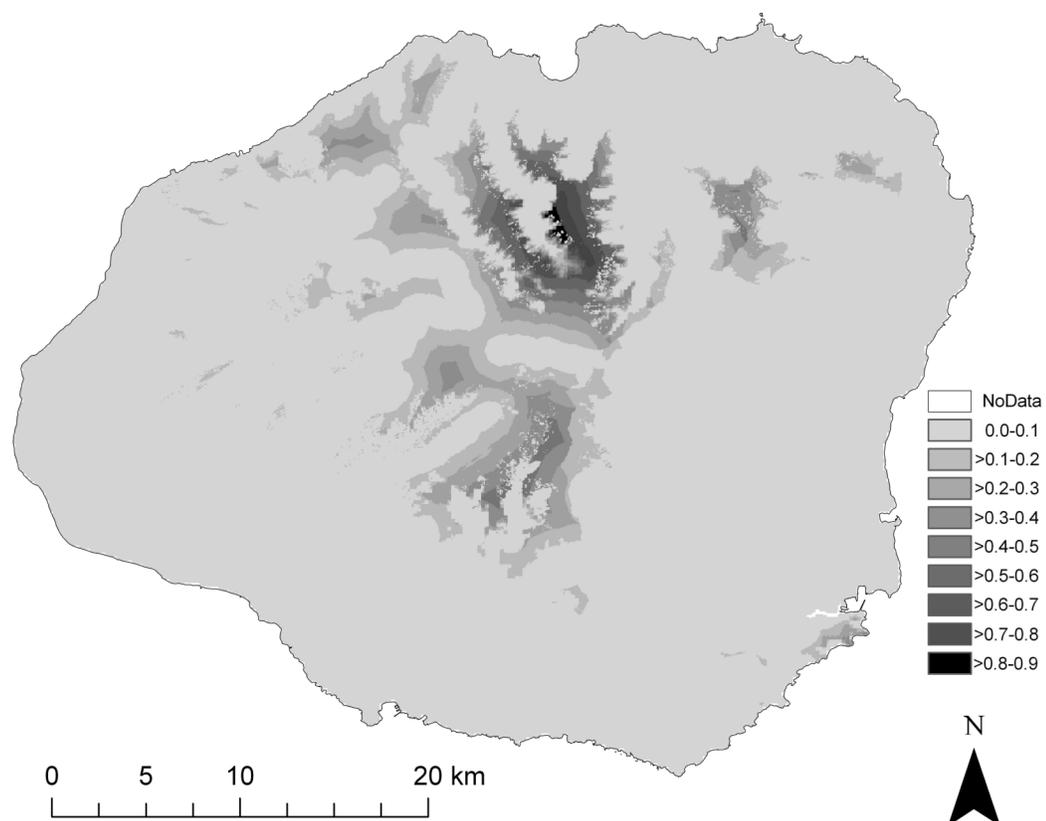


Figure 4.2. The island of Kauai in categories of predicted suitability for Hawaiian Petrel terrestrial activity based on abiotic and biotic environmental variables combined with threats (terrestrial anthropogenic disturbance [a proxy for introduced predator presence] and the risk of possible fledgling attraction to artificial light).

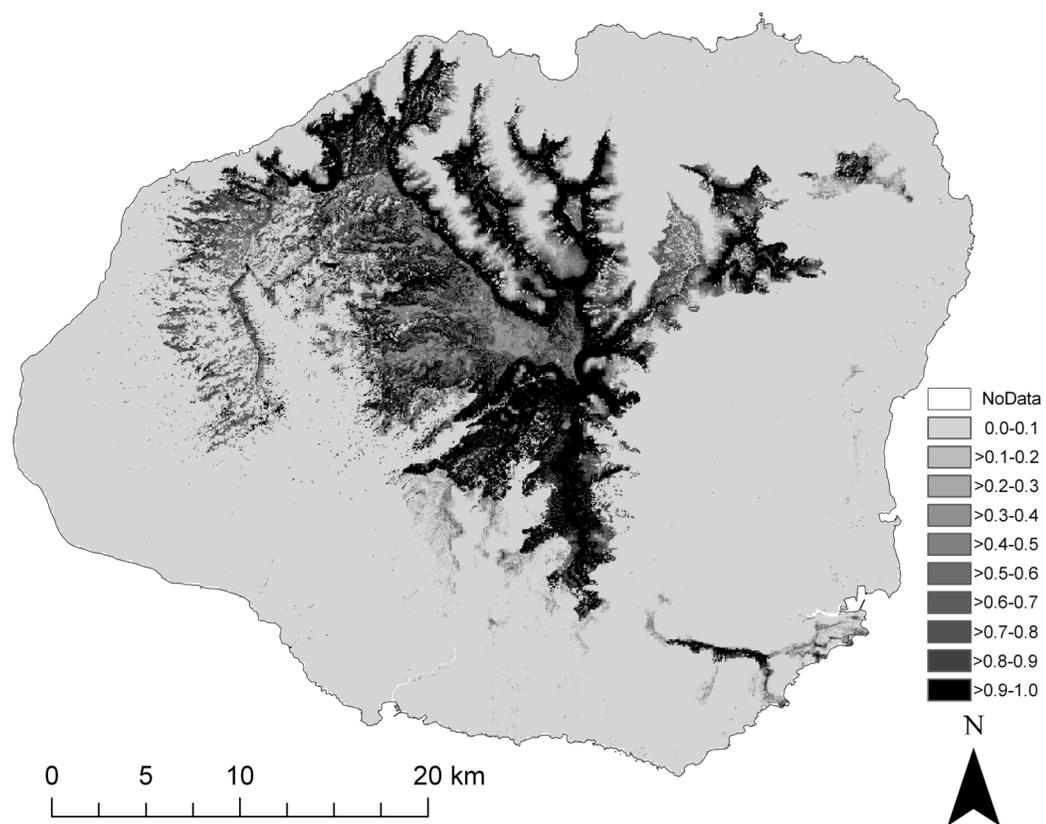


Figure 4.3. The island of Kauai in categories of predicted suitability for the terrestrial activity of both the Hawaiian Petrel and Newell's Shearwater, based on abiotic and biotic environmental variables.

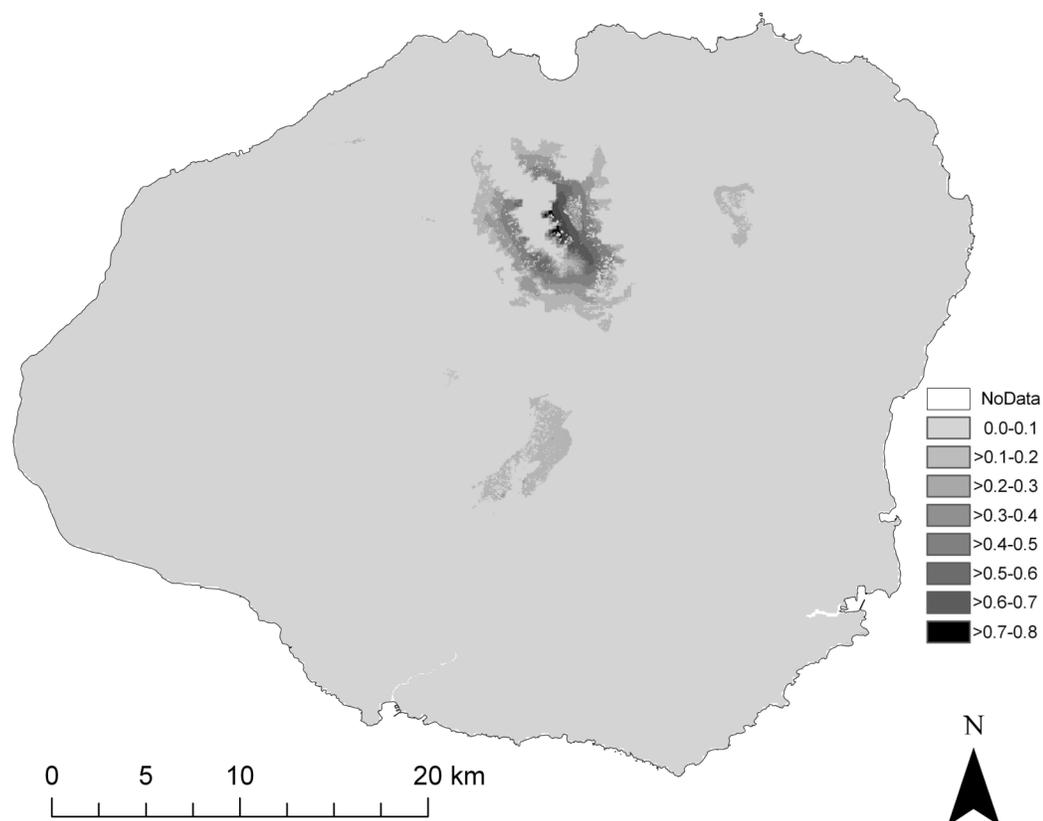


Figure 4.4. The island of Kauai in categories of predicted suitability for the terrestrial activity of both the Hawaiian Petrel and Newell's Shearwater, based on abiotic and biotic environmental variables combined with threats (terrestrial anthropogenic disturbance [a proxy for introduced predator presence] and the risk of possible fledgling attraction to artificial light).

CHAPTER V

SMALL-SCALE HABITAT CHARACTERISTICS ASSOCIATED WITH NEWELL'S SHEARWATER AND HAWAIIAN PETREL BURROWS ON KAUAI

Introduction

After the arrival of humans to the Hawaiian Islands, many avian taxa were driven to extinction, leaving extant species confined to remnant patches of native habitat in secluded mountain regions (Olson and James 1982, Duffy 2010). Two endemic burrow-nesting seabirds, the Newell's Shearwater, or `A`o (*Puffinus newelli*; considered threatened under the Endangered Species Act and endangered on the IUCN Red List [IUCN 2012]), and the endangered Hawaiian Petrel, or `Ua`u (*Pterodroma sandwichensis*), were severely impacted by various anthropogenic disturbances (Olson and James 1982, Harrison 1990, Duffy 2010). Prior to human colonization, Newell's Shearwaters and Hawaiian Petrels likely nested from sea level to mountain slopes of the main Hawaiian Islands, though Newell's Shearwaters may have been somewhat restricted to higher elevations (Olson and James 1982). However, hunting (Kirch 1982, Olson and James 1982), modification of land for human purposes (Cuddihy and Stone 1990), and the introduction of several non-native predators (e.g., feral cats [*Felis catus*]), decimated breeding colonies of these species at low elevations (Olson and James 1982, Harrison 1990, Duffy 2010). Today, the locations of few burrows are known (especially those of

Newell's Shearwaters) and determining environmental factors associated with burrow placement is needed to improve our understanding of habitat characteristics important for these species.

The island of Kauai is thought to harbor ~90% of the entire world population of the Newell's Shearwaters. However, numbers of Newell's Shearwaters have declined during the past two decades on this island (Day et al. 2003, Griesemer and Holmes 2011) and the species appears to be experiencing a contraction in its breeding range (State of Hawaii unpublished data). Breeding birds have also been reported in recent years from Hawaii (Reynolds and Ritchotte 1997), Molokai (Harrison 1990, Reynolds et al. 1997), and Maui (Wood and Bily 2008). Breeding sites on Kauai are found in rocky volcanic soil on steep slopes covered with a thick understory of uluhe, or false staghorn fern (*Dicranopteris linearis*), and an open canopy of scattered ohia trees (*Metrosideros polymorpha*) (Ainley et al. 1997b, State of Hawaii unpublished data). Newell's Shearwaters were also recently observed consistently vocalizing in a location in Waimea Canyon on Kauai (State of Hawaii unpublished data) and the species was discovered nesting on Lehua Islet off the coast of Niihau (VanderWerf et al. 2007); both of these locations are characterized by very different habitat conditions compared to known forested sites containing active burrows.

Breeding sites for Hawaiian Petrels are far more widespread in the main Hawaiian Islands than those of the Newell's Shearwater. Hawaiian Petrels currently breed on Maui (Simons 1985, Brandt et al. 1995), Hawaii (Harrison 1990, Hu et al. 2001), Lanai (Hirai 1978, Simons and Hodges 1998), and Kauai (Day and Cooper 1995, Ainley et al. 1997a), and they may also still breed on Molokai (Simons and Hodges 1998). This species nests

in two very different habitats types: high-elevation xeric terrain on Maui (Simons 1985, Brandt et al. 1995) and Hawaii (Richardson and Woodside 1954, Hu et al. 2001) and mesic forest in the mountains of Lanai (Hirai 1978) and Kauai (Gon 1988, Ainley et al. 1997a). On Maui (Simons 1985, Brandt et al. 1995) and Hawaii (Richardson and Woodside 1954, Hu et al. 2001), breeding sites are characterized by sparsely scattered vegetation and rocky topographic features, such as boulders, rock outcrops, and lava flows. In contrast, on Lanai (Hirai 1978) and Kauai (Gon 1988, State of Hawaii unpublished data), breeding sites are characterized by a thick blanket of uluhe fern and scattered native trees.

Though these broad habitat descriptions exist for both Newell's Shearwaters and Hawaiian Petrels nesting on wet montane slopes, specific factors associated with individual burrows have not been investigated in this type of environment. In this study, I documented small-scale habitat characteristics associated with burrows of both the Newell's Shearwater and Hawaiian Petrel in mesic forest on Kauai. In addition, a recent study predicts a moderate degree of overlap in habitat predicted to be suitable for both species on a large (50 x 50 m) scale (Chapter IV), and burrows of these species are found in close proximity to one another in Upper Limahuli Preserve on Kauai. Because these species may exhibit some level of large-scale habitat overlap, I investigated possible species-specific differences in each small-scale habitat variable (i.e., in means and standard deviations) potentially associated with habitat use and partitioning.

Methods

I measured and estimated small-scale habitat characteristics associated with individual Newell's Shearwater and Hawaiian Petrel burrows within mesic montane

forest in Upper Limahuli Preserve ($n = 12$ Hawaiian Petrel burrows and $n = 9$ Newell's Shearwater burrows) and Hawaiian Petrel burrows in Hono O Na Pali Natural Area Reserve ($n = 13$) on Kauai in 2010 during the breeding seasons of both species. Burrows visited in Hono O Na Pali were >2 km from the nearest visited burrow in Upper Limahuli Preserve. In Hono O Na Pali, entrances of Hawaiian Petrel burrows were on average 313.42 m from one another (ranging from 0.89 m to 544.02 m). In Upper Limahuli Preserve, entrances of Hawaiian Petrel burrows were on average 100.06 m from one another (ranging from 0.37 m to 503.34 m) and Newell's Shearwater burrows were on average 276.52 m from one another (ranging from 4.87 m to 614.73 m). These distances were based on two-dimensional surface area and were measured in ArcGIS 9.3.1 (ESRI, Redlands, CA) using the 'Distance Between Points' tool (Beyer 2004) and a shapefile of burrow locations (provided by the Kauai Endangered Seabird Recovery Project); the locations of two Hawaiian Petrel burrows and one Newell's Shearwater burrow were not represented on this shapefile and, thus, were not included in calculation of these distances. Values of particular habitat variables were measured or estimated within a 2-m-diameter circular plot centered over the burrow entrance; variables related to vegetation were measured and estimated within an extended circular plot (4 m in diameter). Values of most variables measured within these plot sizes (see Results and Table 5.1) were comparable to those recently reported on a much larger scale (Chapter III, Chapter IV); therefore, meaningful variation was likely captured in the variables at the two chosen scales of this study (i.e., 2 and 4 m in diameter).

Plots were marked with two unfolded collapsible poles (~2 m in length), positioned perpendicular to one another radiating out from the plot center; curved plot

edges (between the ends of the poles) were estimated. Variables measured and estimated within the 2-m-diameter plot included: slope ($^{\circ}$), two linear variables related to aspect (northness and eastness [Roberts 1986, Guissan et al. 1999]), and soil hardness (MPa) at four soil depths (0, 7.62, 15.24, and 22.86 cm below the ground surface). These variables were not measured at the larger 4-m-diameter scale to prevent unnecessary trampling of vegetation surrounding burrow entrances. Variables estimated within the 4-m-diameter plot included: % vegetation volume within four height categories above ground level (i.e., 0-0.5, 0.5-1, 1-1.5, and 1.5-2 m), maximum vegetation height above plot (m), and % canopy cover above ~ 2 m above ground level. Several qualitative variables were also recorded within the 4-m-diameter plot, including: the major feature associated with the burrow (e.g., plant roots, base of a tree, fallen dead tree, clay wall, rock fragments), the most prevalent plant species occupying space 0-2 m above ground level, and the most prevalent plant species occupying space >2 m above ground level.

Slope ($^{\circ}$) was measured using the two poles (~ 2 m in length), a protractor, and string. One person was positioned at the lower boundary of the 2-m plot and another was positioned at the upper boundary of the plot (i.e., the position higher in elevation). A taut string connected the two poles from a defined mark (~ 1.5 m above ground level) as each person held a pole vertically along the plot boundary; poles were positioned vertically (determined using a bubble level attached to the pole). The person at the lower boundary of the plot measured the slope of the string using a protractor to obtain the overall degree of slope. The main axis of the plot slope was estimated and the compass direction ($^{\circ}$) that the axis was facing was recorded as the aspect of the plot. Slopes of three Hawaiian Petrel burrows appeared to be flat and were recorded as having slopes of 0° ; thus, these

burrows were not factored into summary calculations of aspect. Because aspect is a circular variable, values of aspect were converted to two linear variables (northness and eastness) (Roberts 1986, Guisan et al. 1999); northness = cosine (aspect in radians) and eastness = sine (aspect in radians).

Soil hardness was measured using a HyPen1 soil penetrometer (Pike Agri-Lab Supplies, Inc., Jay, ME). Measurements were recorded downslope from the burrow entrance (so that the burrow cavity was not penetrated) at four depths (0, 7.62, 15.24, and 22.86 cm) below the surface of the ground. If 3.45 MPa was reached before recording the measurements at all four depths (possibly indicating a root or large rock fragment blocking further penetration), a complete measurement was attempted in another nearby location within the plot and all readings were sampled from the new location. After three reattempts, if a value of 3.45 MPa was still obtained before all four readings were collected, the hardness values for the depths that were successfully collected were recorded (and values for the deeper depths were not recorded and, thus, were excluded from analyses). Holes in the soil made by the penetrometer were very small (less than ~1.2 cm in diameter); however, these holes were covered after measurements were recorded to reduce anthropogenic impact. To accompany soil hardness measurements, soil moisture deficiency of a handful of soil (obtained from within the top ~4 cm of soil) was estimated according to Table 1 in Miles and Broner (2006); moisture was not estimated for soils at greater depths to avoid unnecessary impact to the plot. Values were then placed into ordinal categories (i.e., 0-4) as follows: 0% = 0, >0-25% = 1, >25-50% = 2, etc.

Percent vegetation volume was estimated radiating out to 2 m in every direction from the burrow entrance in four categories of height above ground level (0-0.5, 0.5-1.0, 1.0-1.5, and 1.5-2.0 m). Each height layer was separated into four separate quadrants to aid in estimation. Percent vegetation volume within each layer quadrant was estimated into ordinal categories (i.e., 0-5) as follows: 0 = 0, >0-20% = 1, >20-40% = 2, etc. Some plot edges were impacted by human foot traffic and/or a recently established predator control fence; therefore, estimating vegetation cover in quadrants allowed the use of vegetation cover estimates from sections of the plot that were not previously impacted by human activity (e.g., trampling of vegetation). Maximum vegetation height (m) was estimated using both of the ~2-m-long poles to aid in estimation. To estimate % canopy cover, four photographs were initially taken at ~1.5 m in height (at ~90° angles to one another and pointed skyward with a slight downward tilt to capture a horizontal field of view of ~2 m). Though some vegetation between 1.5 and 2 m above the plot center may have overlapped with canopy cover photos in certain instances, canopy cover estimates obtained from these photos (taken from ~1.5 m in height) were considered a useful measure canopy cover above the plot not captured by the estimation of vegetation cover 1.5-2 m above the ground. These photos were then visually examined on a computer screen and % canopy cover was estimated into ordinal categories (i.e., 0-10) as follows: 0% = 0, >1-10% = 1, >10-20% = 2, etc.

Procellariids (i.e., shearwaters and petrels) and their relatives are known to be attracted to the breeding activities (e.g., vocalizations) of conspecifics. Therefore, I examined visible overlap in the 4-m-diameter plots by plotting a 4-m circular buffer surrounding each burrow entrance (represented in a shapefile) in ArcGIS (using the

'Buffer' tool). The locations of two Hawaiian Petrel burrows in Hono O Na Pali visited in this study were not represented in the shapefile of burrow entrances; however, entrances of these burrows were not located within at least 2 m of other burrow entrances visited in this study and, therefore, it is assumed that they are independent observations. The 4-m-diameter plots of some Hawaiian Petrel burrows overlapped with one another. I attempted to remove this potential lack of independence by combining overlapping 4-m-diameter plots (i.e., by calculating the mean value of each habitat variable for all overlapping plots). These combined plots were then considered new units of observation in all statistical analyses, as well as for the calculation of means, standard deviations, minimum, and maximum values (Table 5.1). This combining of certain plots reduced the initial sample size of burrows from $n = 12$ Hawaiian Petrel burrows in Upper Limahuli Preserve to $n = 7$ and from $n = 13$ Hawaiian Petrel burrows in Hono O Na Pali Natural Area Reserve to $n = 9$. Only two 4-m-diameter Newell's Shearwater plots overlapped one another; however, it was estimated that the degree of overlap was $<2\%$. Therefore, all Newell's Shearwater burrows were considered independent observations and the original number of burrows ($n = 9$) was available for analysis.

Analyses

For each habitat variable, several comparisons (in means and standard deviations) were made to test for significant differences between habitat characteristics associated with major groups of burrows; these groups included: Hawaiian Petrel burrows from Hono O Napali, Hawaiian Petrel burrows from Upper Limahuli Preserve, all Hawaiian Petrel burrows, and all Newell's Shearwater burrows (which were located only in Upper Limahuli Preserve). First, means and standard deviations of variables associated with

Hawaiian Petrel burrows from Hono O Na Pali were compared to those of Hawaiian Petrel burrows from Upper Limahuli Preserve to test for commonality among habitat characteristics and, thus, the appropriateness of combining petrel burrows from the two sites for a comparison with Newell's Shearwater burrows. All Hawaiian Petrel burrows (from both sites) were then compared to Newell's Shearwater burrows to test for significant species-specific differences potentially associated with habitat partitioning on a small scale. After the combination of overlapping Hawaiian Petrel plots, the sample size of burrows within each group was small; therefore, habitat variables were compared using a series of randomization tests to derive *P*-values.

Both the mean and standard deviation for each variable were calculated for the two groups in each comparison and the absolute value of the difference between the values for the two groups (i.e., between the means or between the standard deviations of a particular variable) was calculated as the test statistic. I used a series of randomization tests to calculate the probability that the difference in the group means of each variable and the difference in the group standard deviations of each variable could have been produced solely by randomly assigning burrows to one of the two groups. The data were organized as a matrix, and each matrix row represented an individual burrow and its observed values for each habitat variable. For each comparison, I randomly assigned (without replacement) each burrow (i.e., matrix row) to one of the two groups being compared and calculated a mean and standard deviation for each group (composed of randomly assigned burrows). Randomizing entire rows preserved any inherent correlational structure among the habitat variables.

I then calculated the absolute value of the difference in the means (as well as the difference in the standard deviations) of each pair of groups. This process was repeated 1000 times for each two-group comparison, yielding a sampling distribution of the absolute values of 1000 differences in means and 1000 differences in standard deviations (i.e., test statistic values) for each pair of groups. These randomization tests produced distributions of values that would be obtained if burrows were randomly distributed to either of the two groups in the comparison. For each two-group comparison, I compared the actual observed absolute values of differences in the means and differences in the standard deviations to their respective sampling distributions. *P*-values were calculated as the proportion of the sampling distribution greater than or equal to the absolute values of the actual observed differences. Because of the large number of individual tests conducted for each two-group comparison ($n = 14$; one for each habitat variable), the α -level was adjusted using a Bonferroni correction (Quinn and Keough 2002) to determine test significance (i.e., corrected $\alpha = 0.05/14 = 0.004$). Analyses were conducted using Program R version 2.15.1 (R Core Team 2012).

Results

Overall, plots associated with burrows of both species were found on steep slopes with a variety of northness and eastness values, and were covered in thick vegetation 0-2 m above the ground and a wide range of canopy cover values (Table 5.1). Hawaiian Petrel burrows at the two sites only differed significantly in one habitat variable (the mean of soil moisture deficiency; data not shown), suggesting that burrows from both sites could indeed be combined for a comparison with burrows of Newell's Shearwaters. Though most variables did not differ significantly between the two species ($P > 0.004$

due to the α -level adjustment), the soil associated with Newell's Shearwater burrows at 7.62 and 15.24 cm below ground level was significantly harder than that associated with Hawaiian Petrel burrows, and soil at 22.86 cm below ground level tended to be harder for Newell's Shearwater plots as well (Table 5.1). In addition, soil moisture was also more deficient in soils associated with Newell's Shearwater burrows and the maximum vegetation height above Newell's Shearwater plots was significantly greater than that above Hawaiian Petrel plots (Table 5.1).

Most burrows observed in this study were associated with a feature thought to provide support to the burrow (e.g., roots and bases of trees), including clay walls. The plant species occupying the most space (i.e., the most prevalent plant) 0-2 m above ground level within almost all Newell's Shearwater plots was uluhe (or false staghorn fern); a similar native fern, uluhe lau nui (*Diplazium pinnatum*), was the most prevalent species within one individual Newell's Shearwater plot. At 0-2 m above the ground, Hawaiian Petrel burrows contained a greater diversity of plants, including small ohia, pukiaawe (*Styphelia tameiameia*), sedges (*Carex* spp.), and mosses, as well as uluhe. Ohia comprised the most prevalent vegetation >2 m in height above most Hawaiian Petrel plots, whereas a wider variety of native trees were prevalent at this height above Newell's Shearwater plots, including ohia, ohia ha (*Syzygium sandwicensis*), lapalapa (*Cheirodendron* sp.), and trees in the genera *Melicope* and *Psychotria*.

Discussion

This study documents small-scale breeding habitat characteristics for Newell's Shearwaters and Hawaiian Petrels nesting in wet montane forest on Kauai, and my findings are largely comparable to the broad habitat descriptions from previous

observations of both birds in this type of environment. Most previous observations in mesic forest, however, did not report measurements of habitat characteristics associated with individual burrows; thus, this study provides additional information relevant to the natural history of these species. In general, plots surrounding burrows of both species were positioned on steep slopes facing a broad spectrum of compass directions and were covered in thick vegetation 0-2 m above the ground with a wide range of canopy cover values. Overall, the means and standard deviations of most habitat variables did not differ significantly between burrows of these species. However, species-specific differences in a few habitat characteristics were observed, which may be biologically meaningful (for reasons other than conspecific social attraction) and useful in future searches for nesting sites on Kauai and other islands.

Breeding pairs of shearwaters and petrels exhibit a high degree of nest-site fidelity, reusing their burrows during subsequent breeding seasons (Warham 1990). Most burrows in this study were associated with a feature other than soil (such as roots from various plants or the base of a tree) thought to provide stability (e.g., Gillham 1961, Brandt et al. 1995, Ainley et al. 1997b, Underwood and Bunce 2004, Bancroft et al. 2005, Wood and Bily 2008), and those with no visible plant-related features were usually associated with a sturdy wall of clay and/or rock fragments in the soil. These birds excavate new burrows by digging, though some may use natural crevices or abandoned burrows from previous breeding seasons if available. Therefore, soils must be soft and deep enough to support burrowing, yet sturdy enough to withstand weathering and prevent collapse (Stokes and Boersma 1991, Brandt et al. 1995, Carter 1997, Underwood and Bunce 2004). Typical soil profiles suggest that many soils in the mountains of Kauai

contain at least a moderate amount of fine soil particles, a condition linked with burrow stability (Stokes and Boersma 1991, Carter 1997, Holmes et al. 2003, Kintigh and Andersen 2005), and the soils of many known activity sites of these species are thought to contain a moderate volume of rock fragments (Chapter III, Chapter IV), which may further enhance sturdiness (Stokes and Boersma 1991). All of these elements, therefore, may comprise a set of conditions allowing burrows of these species to withstand weathering and be reused for multiple breeding seasons.

In addition to the common features and conditions associated with burrows in this study, Newell's Shearwater burrows were found within soil much greater in hardness (from 7.62 to 22.86 cm below the surface) than Hawaiian Petrel burrows. This soil was also more lacking in moisture than that of Hawaiian Petrel burrows as a whole, a condition associated with harder soils (Vomocil 1957). Soil moisture content, however, did not differ significantly between Newell's Shearwater and Hawaiian Petrel burrows only in Upper Limahuli Preserve, although soil hardness, again, did differ between the two species (data not shown). This suggests that the harder soil associated with Newell's Shearwater burrows was likely a property of soil composition and not produced solely by reduced moisture content. Though it is possible that harder soil may provide further stability to Newell's Shearwater burrows, it is unknown if it contributes to meaningful biological differences between these two species on Kauai. Additionally, though Newell's Shearwater burrows were associated with harder soils, it should be noted that Hawaiian Petrel burrows visited during this study have persisted for multiple breeding seasons, verifying at least some degree of long-term stability for their burrows on Kauai (State of Hawaii unpublished data).

Native ferns (mostly uluhe) were prevalent in the understory (0-2 m above ground level) of Newell's Shearwater plots, as previously reported for the species on Kauai (Ainley et al. 1997b) and Maui (Wood and Bily 2008), and Hawaiian Petrel burrows were associated with a much wider variety of plant species at this height level, including uluhe. Recent studies on Kauai reported that larger sites of Newell's Shearwater and Hawaiian Petrel activity were generally characterized by mean vegetation heights ranging from >0-5 to 5-10 m and by a 60-70% canopy cover of woody vegetation (Chapter III, Chapter IV), suggesting that these birds are generally found in areas of Kauai with a widespread coverage of woody vegetation and openings in the canopy above the understory. Though canopy cover and vegetation height were not limiting factors in the distribution of either of these birds when compared to random locations in previous studies, these birds may still benefit from this structural arrangement of woody plants. For example, Newell's Shearwaters (Ainley et al. 1997b) and *Pterodroma* petrels (Warham 1990) are known to climb trees, using them as launching sites for flight as in other related species (Sullivan and Wilson 2001). This behavior may be particularly beneficial when understory vegetation is thick, in that trees may be required for birds to climb above the understory to become airborne (Warham 1990). In this situation, nesting in close proximity to trees could potentially reduce the time and energy required to achieve flight, such that birds are not forced to travel long distances on foot to find appropriate conditions for launching.

Though large-scale analyses suggest that these seabirds are found in areas of Kauai with similar vegetation height values (Chapter III, Chapter IV), Newell's Shearwater plots in this study were associated with a mean maximum vegetation height of just over 6 m (ranging from 3.50 to 10.00 m), significantly higher than that observed

for Hawaiian Petrel burrows (mean = 3.35 m; range = 1.80-7.50 m). This suggests that Newell's Shearwaters nested in closer proximity to taller woody vegetation (i.e., trees and shrubs) than Hawaiian Petrels in this study. The maximum observed vegetation height value for Hawaiian Petrel plots (7.50 m), however, suggests that Hawaiian Petrels can indeed nest in locations with taller vegetation and indicates some overlap with Newell's Shearwater plots (the minimum of which was 3.50 m). On Kauai, sites of Hawaiian Petrel activity are associated with greater wind speeds than random sites on ridges at 30 m aloft (Chapter IV). Though wind speed was not measured above individual plots in this study, it is possible that a relationship between vegetation height and wind speed may exist in thickly vegetated nesting locations. For example, in sites characterized by thick vegetation and lighter wind speeds aloft, Newell's Shearwaters may use larger trees than Hawaiian Petrels as launching sites for flight, whereas Hawaiian Petrels may not require woody vegetation as tall to become airborne due to windier ambient conditions. Furthermore, when these birds are found on steep slopes in xeric environments (e.g., Newell's Shearwaters nesting in Waimea Canyon or Hawaiian Petrels in alpine habitat on Maui), becoming airborne is likely more easily achieved because of steep vertical relief and sparsely distributed vegetation. In support of this, measurements of maximum vegetation height were negatively correlated with wind speed at 30 m aloft (measured using a digital layer of average wind speed [m/s]) for all burrows ($r = -0.51$, $P = 0.008$); see the Appendix for details of this test. However, the scale of these two variables differed vastly (4-m-diameter for vegetation height and a 200 x 200 m pixel size for wind speed); thus, further speculation on this relationship will require additional study.

Finally, procellariiform seabirds are colonial breeders and sociality may play a large role in affecting the placement of burrows, as signs of breeding conspecifics (e.g., vocalizations) (Podolsky and Kress 1989, Warham 1990) are known to attract prospective breeders to investigate (and potentially nest in) locations where breeding activities are underway. Because birds are already nesting in a particular site, these signs may indicate to prospective breeders that the location is characterized by habitat conditions appropriate for nesting. Therefore, social attraction may indeed contribute to the separation of breeding sites for these species on Kauai, but burrows are still likely to be found in habitat with structural characteristics favorable for breeding. Though a moderate degree of overlap in habitat suitable for the Newell's Shearwater and Hawaiian Petrel may exist on Kauai at a scale larger than that of this study (see Chapter IV) and burrows of these species did not differ significantly in most of the habitat variables investigated herein, some of the differences observed in this study could potentially be linked to small-scale habitat requirements (though this requires further investigation). The findings of this study will be useful in future searches for these species on Kauai and other islands, especially for the Newell's Shearwater as known locations of active nests are largely lacking for this species. Documenting and monitoring additional breeding sites and active nests will provide valuable information to future conservation efforts for these two endemic seabirds in the Hawaiian Islands.

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Table 5.1. Means, standard deviations (SD), minimum, and maximum values for Newell's Shearwater and Hawaiian Petrel burrows on Kauai, Hawaii. Results of randomization tests (P -values) are shown for comparisons between group means (P mean) and standard deviations (P SD) for each of 14 habitat variables: slope ($^{\circ}$), northness, eastness, soil hardness (measured in MPa at 0, 7.62, 15.24, and 22.86 cm below ground level), soil moisture deficiency (moisture def; ordinal), % vertical vegetation volume 0-0.5, 0.5-1, 1-1.5, and 1.5-2 m above ground level (vert veg 0.5 to vert veg 2; ordinal), maximum vegetation height (max veg) in m, and % canopy cover (canopy; ordinal). See the Methods section for descriptions of ordinal classification for soil moisture deficiency, % vertical vegetation volume, and canopy cover.

Variable	Newell's Shearwater						Hawaiian Petrel							
	Mean	S D	Min	Max	Mean	S D	Min	Max	Mean	S D	Min	Max	Mean	S D
Slope	37.56	7.40	28.00	48.00	36.37	19.84	0.00	67.00	0.868	0.015	0.00	67.00	0.868	0.015
Northness	-0.12	0.72	-1.00	0.98	0.15	0.74	-0.97	0.98	0.371	0.833	-0.97	0.98	0.371	0.833
Eastness	0.17	0.74	-0.98	0.98	-0.11	0.58	-0.82	0.87	0.325	0.177	-0.82	0.87	0.325	0.177
Soil 0	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.07	0.363	0.363	0.00	0.07	0.363	0.363
Soil 7.62*	0.77	0.20	0.55	1.10	0.14	0.21	0.00	0.69	<0.001	0.879	0.00	0.69	<0.001	0.879
Soil 15.24*	0.90	0.35	0.55	1.65	0.28	0.29	0.00	0.69	0.001	0.831	0.00	0.69	0.001	0.831
Soil 22.86	1.11	0.39	0.55	1.79	0.52	0.43	0.00	1.10	0.005	0.787	0.00	1.10	0.005	0.787
Moisture def*†	4.00	0.00	4.00	4.00	1.78	1.83	0.00	4.00	<0.001	<0.001	0.00	4.00	<0.001	<0.001
Vert veg 0.5	4.64	0.91	2.25	5.00	3.77	1.10	1.50	5.00	0.062	0.599	1.50	5.00	0.062	0.599
Vert veg 1	4.42	1.21	1.25	5.00	3.20	1.11	1.50	5.00	0.014	0.712	1.50	5.00	0.014	0.712
Vert veg 1.5	2.57	0.75	1.25	3.67	2.46	1.09	0.50	4.50	0.795	0.206	0.50	4.50	0.795	0.206
Vert veg 2	1.89	0.77	0.75	2.75	1.67	0.93	0.50	3.25	0.542	0.335	0.50	3.25	0.542	0.335
Max veg*	6.19	2.46	3.50	10.00	3.35	1.40	1.80	7.50	0.003	0.190	1.80	7.50	0.003	0.190
Canopy	5.56	3.43	1.00	9.00	4.24	2.42	0.00	8.00	0.237	0.062	0.00	8.00	0.237	0.062

* Variable means differ significantly between species

† Variable standard deviations differ significantly between species

Appendix

Methods and results for comparison of maximum vegetation height and wind speed aloft

I tested if measurements of maximum vegetation height were negatively correlated with wind speed at 30 m aloft. Values of wind speed above individual Newell's Shearwater and Hawaiian Petrel burrows were measured in ArcGIS 9.3.1 using the 'Intersect Point' tool (Beyer 2004), a shapefile of burrow locations (provided by the Kauai Endangered Seabird Recovery Project), and a digital layer of average wind speed (m/s) at 30 m above ground level (obtained from AWS Truewind). The locations of three burrows were not represented in the burrow shapefile and, thus, were not used in this analysis (yielding a sample size of $n = 22$). Correlations were calculated using Pearson's correlation coefficient (r) and the P -value was determined using a randomization test. In this test, values of wind speed were randomly paired with values of maximum vegetation height and Pearson's correlation coefficient (r) was calculated for the randomized set of pairs. This process was repeated 1000 times and the P -value was calculated as the proportion of the 1000 random r -values that were less than or equal to the observed r -values (i.e., this was a one-tailed test because of the *a priori* hypothesized direction of relationship). This analysis was conducted using Program R version 2.15.1 (R Core Team 2012). Maximum vegetation height was negatively correlated with wind speed at 30 m aloft ($r = -0.51$, $P = 0.008$).

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