INTRODUCTION

BACKGROUND

Reintroduction of captive-reared birds to augment existing bird populations in the wild is a major emphasis of current avian recovery efforts in Hawai‘i (Banko et al. 2001, Tweed et al. 2003). Conservation and restoration of habitat for the benefit of avian species is specified as a major recovery objective in the current Recovery Plan for Hawaiian Forest Birds (USFWS 2006). Understanding which aspects of habitat are most critical in determining site occupancy for forest bird species is imperative if restoration efforts are to be effective in guarding against further extinctions. In the past, recovery efforts in Hawai‘i for many birds of rarity, such as the Po‘ouli (*Melamprosops phaesoma*), were initiated when population levels were already too low to accurately assess and identify limiting factors (Groombridge et al. 2003). Therefore, it is essential to initiate studies on aspects of habitat that may be limiting for endangered birds before they become too rare. Understanding habitat factors and determining the suitability of potential release areas is an important step in the development of effective conservation strategies, particularly for endangered species (Conway and Martin 1993, Pasinelli 2000).

The Maui Parrotbill (*Pseudonestor xanthophrys*) (population 500 ± 230, 95% CI individuals) is among the most threatened of the remaining Hawaiian honeycreepers (Scott et al. 1986), reproducing at a rate of only one young/year (Simon et al. 2000). It is now restricted to the island of Maui, where it occupies approximately 5% of its original range (Scott et al. 1986). Parrotbill maintain year-round all-purpose territories, a characteristic common to many insectivorous Hawaiian honeycreepers (Pratt et al. 2001b). Recently, this medium-sized (20-25 g) olive-green honeycreeper has become a target for conservation efforts on the island of Maui because it is the only endangered insectivore that may still benefit from recovery measures. Two other endangered, insectivorous honeycreepers on Maui that historically had similar habitat requirements, the Po‘ouli and the Nukupu‘u (*Hemignathus lucidus*), may be extinct. Both species foraged on invertebrates from woody trees, shrubs, and/or epiphytic material in similar habitat types as the Maui Parrotbill (Perkins 1903, Scott et al. 1986, Baker 2001). Their decline suggests that parrotbill may be subject to the same threats. The Maui ‘Alauahio (*Pareomyza montana*) the only other native insectivore on Maui, is not endangered and is frequently sympatric with Maui Parrotbill (Baker and Baker 2000). ‘Alauahio however, occupy a slightly different foraging niche which may account for their more extensive range.

Since the early 1900s, the Maui Parrotbill has continued to persist in low numbers in the upper elevation montane rainforests of the dormant Haleakalā volcano (Scott et al. 1986, Simon et al. 1997). However, fossil evidence suggests that parrotbill existed in the dry lowland and mesic leeward forests of Maui prior to human contact (Olson and James 1982a, Scott et al. 1986, Mountainspring 1987) (Figure 1). A variety of dry and mesic forests once occurred from tree-line to sea level on the leeward side of the island of Maui. By the late 1890s most of these forests, some composed of the dominant canopy tree koa (*Acacia koa*), had been destroyed (Scott et al. 1986). Perkins (1903) and Henshaw (1902) noted that parrotbill frequently foraged in koa; currently this canopy tree is now greatly diminished. It is widely believed that logging of this valuable wood decreased much of the habitat available for parrotbill (Olson and James 1982b, Scott et al. 1986, Simon et al. 2000). This habitat loss, as well as the introduction of avian disease to which native birds lacked resistance (Atkinson et al. 1995, van Riper and Scott 2001),

may have contributed to the contraction of the parrotbill's historical range. Parrotbill currently persist in upper-elevation ʻōhiʻa (*Metrosideros polymorpha*) rainforests at densities of 10 birds/km^2 (USFWS 2006). Research in the 1990s indicated this species was at carrying capacity in its current range and further suggested that this habitat was only marginally suitable for the species (Simon et al. 2000, Pratt et al. 2001b). No recent studies have validated this. Ongoing research occurs in Hanawī, a core activity area for Maui Parrotbill, but the forests of Waikamoi and Manawainui at the edge of this species' range have been little explored.

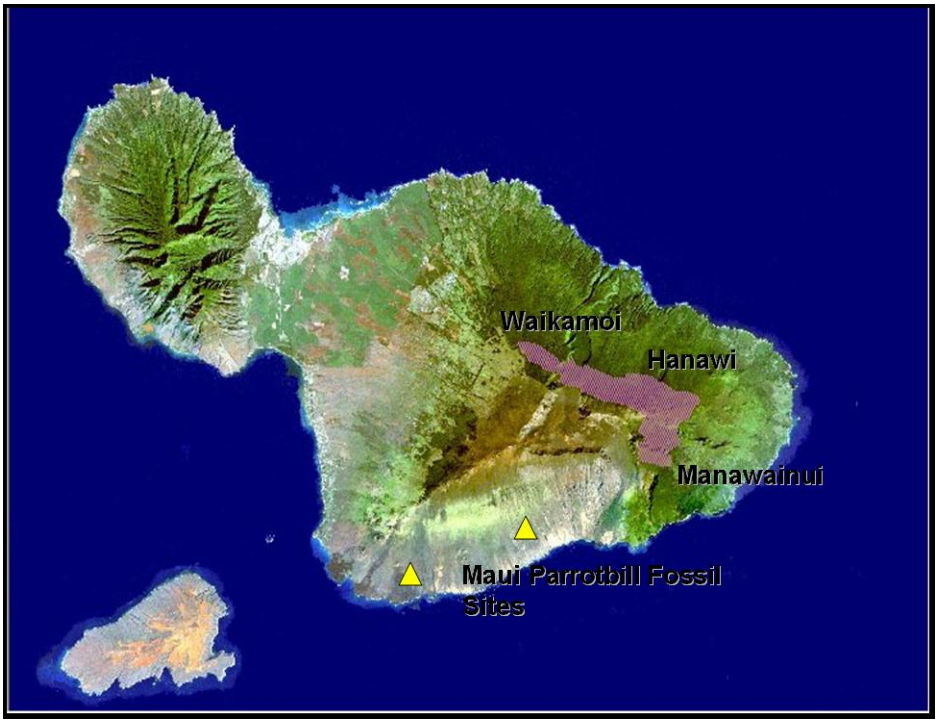


Figure 1. Current and historical range of Maui Parrotbill on Maui (adapted from the USGS-Pacific Basin Information Node website).

Mountainspring (1987) identified lack of suitable habitat as the primary threat for Maui Parrotbill. The protection, acquisition, and restoration of parrotbill habitat in areas of its historic range are high priorities in the Revised Recovery Plan for Hawaiian Forest Birds. The State of Hawaiʻi's Division of Forestry and Wildlife is currently committed to the long-term restoration of remnant koa forests that exist in portions of historic parrotbill range, with the ultimate goal of reintroducing captive-reared birds to the leeward side of Maui (Scott Fretz, pers. comm.). However, reintroductions and the acquisition and subsequent restoration of critical habitat are costly and time consuming ventures. Before new areas can be made usable for parrotbill, it is important to determine which attributes of its habitat in occupied areas are most important. Previous researchers have provided insight into parrotbill breeding biology, morphology, and territoriality (Lockwood et al. 1994, Simon et al. 1997, Simon et al. 2000, Pratt et al. 2001b). However, research on Maui Parrotbill habitat use has been limited. General assessments of Maui

Parrotbill distribution and habitat use were documented in the 1980s and suggested a preference for upper montane ʻōhiʻa and ʻōhiʻa-koa forest (Scott et al. 1986). Mountainspring (1987) found parrotbill foraged extensively in the forest understory and subcanopy and made a majority of prey captures on ʻōlapa, ʻōhelo, pilo, ʻalani, and kanawao. Perkins (1903) also noted heavy use of koa and ʻalani, suggesting the importance of these plants. These early investigations of habitat use occurred prior to intensive management for feral ungulates. Recent quantitative assessments of Maui Parrotbill habitat requirements are lacking. A quantitative approach, may identify limiting factors in habitat that may qualitatively appear suitable (Fretz 2002).

The evaluation of habitat is a crucial first step toward implementing a sound wildlife management or monitoring program (Wiens and Rotenberry 1981a) and rigorous quantification of habitat should precede any reintroduction program (Armstrong and McLean 1995). The reintroduction guidelines set forth by the International Union for the Conservation of Nature and Natural Resources stress the importance of evaluating the suitability of potential habitat (IUCN 1998) for reintroductions and translocations. Successful reintroduction and translocation projects should carefully consider factors such as habitat quality and quantity at the release site, numbers of individuals released, and the relationship of the release site to the animal's historic range (Wolf et al. 1998). Reintroductions frequently fail because of immature or inadequate habitat, or because key factors responsible for a species' initial extirpation have not been adequately identified and remedied (Armstrong and Ewen 2002). Incorporating a scientific approach with hypothesis testing can greatly enhance the outcome of potential reintroduction projects by more accurately identifying limiting factors (Armstrong and McLean 1995, Seddon et al. 2007). This study highlights the merit of using this method to quantitatively assess habitat as a precursor to the potential reintroduction of an endangered bird.

Research Objectives

The Manawainui forests of Haleakalā National Park were previously identified by the Maui Parrotbill Working Group as one of three potential release sites for future Maui Parrotbill reintroductions (Figure 2). Subsequently, this project was initiated to assist the National Park Service in determining the suitability of Manawainui as a release site for captive-bred parrotbill. Initial bird surveys by Stemmerman (1976) and the Hawai'i Forest Bird Survey (Scott et al. 1986) failed to confirm the presence of parrotbill in this area. However, in the early 1990s following ungulate management efforts of Haleakalā National Park, biologists started to detect parrotbill locally in low numbers (Reynolds and Snetsinger 2001, Haleakalā National Park unpubl. data). It is uncertain if these detections were a direct result of management efforts, better census data, or both. Park biologists, continue to conduct yearly forest bird surveys on U. S. Fish and Wildlife Service transect 18 which is oriented north to south through the Manawainui area. Until recently, parrotbill distribution from east to west in this area was not known. To better understand the relationship between parrotbill and its habitat use, the main objectives were to (1) determine the distribution of parrotbill in Manawainui, (2) determine which proximate vegetative factors make habitat suitable for Maui Parrotbill, and (3) determine the effect of scale on habitat selection by this species.

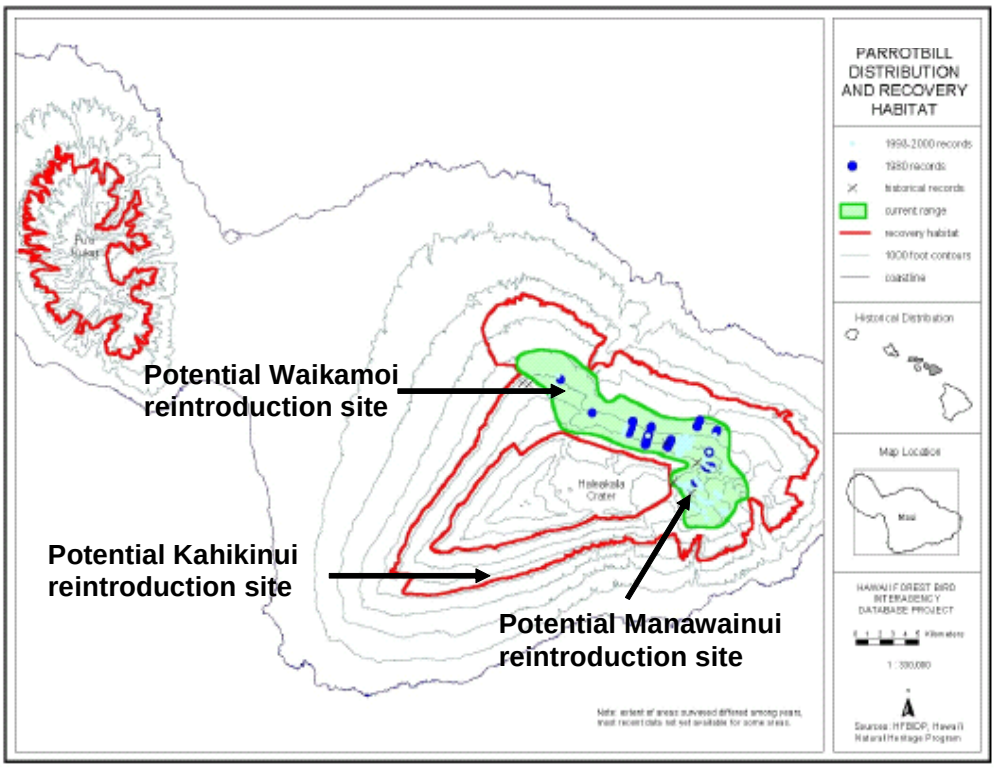


Figure 2. Potential reintroduction sites for Maui Parrotbill on East Maui. Current habitat is in green; proposed recovery habitat is denoted by red boundary (adapted from USFWS 2006).

The identification of habitat variables important to Maui Parrotbill could guide the selection of future release sites and the restoration needs of these areas. Understanding resource use is necessary to determine the relationship between an organism and its habitat (Heglund 2002). Vegetation structure and composition are the primary proximate factors that determine where and how a species uses its resources (Block and Brennan 1993) and quantifying the relationships between parrotbill and vegetation are critical to its recovery. Vegetation attributes influence the distribution and abundance of birds either directly, such as for nesting sites, or indirectly through the provision of food resources (Wiens and Rotenberry 1981a, Rotenberry 1985, Luck 2002). Thus, understanding how a species uses certain habitat features such as vegetation is useful for communicating the physical significance of these attributes to resource managers and scientists by facilitating more effective design of natural area reserves and appropriate vegetation components.

Because key habitat variables will be most accurately identified when studied at the appropriate scale (Orians and Wittenberger 1991), hierarchical assessments of habitat variables at different scales have become essential to understanding avian habitat use and needs (Kristan and Scott 2006). Single-species assessments of habitat use at several increasing scales of resolution can be especially useful because they may provide more direct insight as to why a species is selecting for a particular habitat type (Cody 1985, Orians and Wittenberger 1991, Bergin 1992, Luck

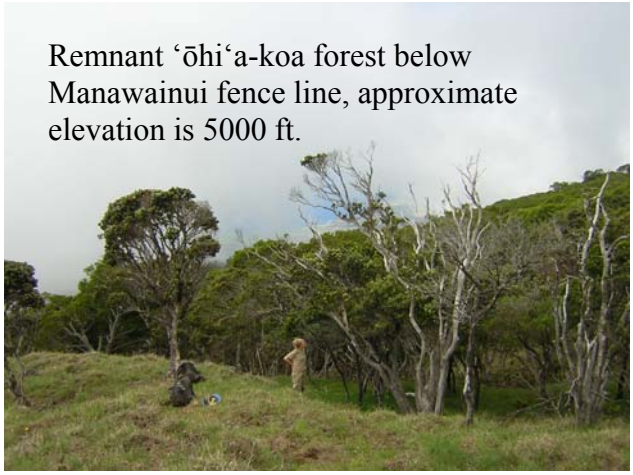
2002, Hobbs 2003). Wiens and Rotenberry (1981b) found that the initial occupation of habitat in shrubsteppe birds was driven by vegetation structure and that within site distribution patterns were further refined by their association with plant species composition. The simultaneous assessment of the relative importance of gross or "coarse" habitat features, in an area as well as those obtained by watching specific behavior such as singing or foraging has predictive significance because it allows us to determine which habitat variables are most important and at what scale (Bibby et al. 2000). For example, Luck (2002) studied habitat use by Rufous Treecreepers (*Climacteris rufa*) in Australia at four spatial scales and found birds prefentially selected habitat based on different vegetation variables at each scale. At the broadest or landscape scale, birds preferred to settle in particular forest-type. They then selected territories and foraging sites based on the presence of scale-specific habitat variables.

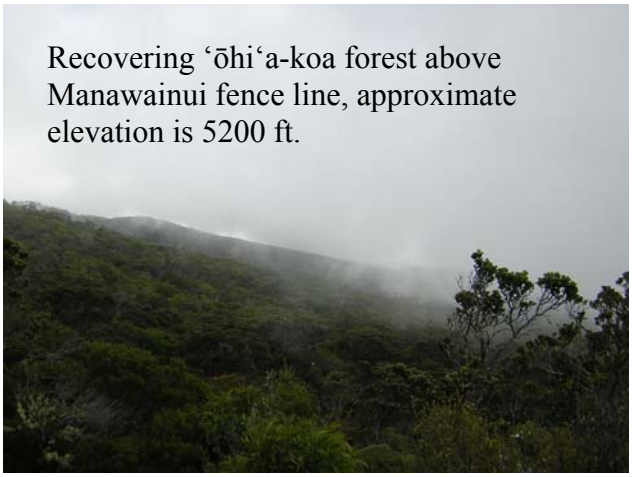
To explore the relationship between vegetation structure and composition and Maui Parrotbill habitat use, I asked the following questions at three spatial scales of increasing resolution (home range, foraging site, and plant species; see Johnson 1980) in used and unused sites within the same general habitat type: (1) do differences in vegetation structure and/or composition across the forest influence patterns of home range use by parrotbill? (2) do parrotbill preferentially select foraging sites based on certain structural or compositional aspects of the vegetation? and (3) is use of certain plant species, vegetation strata and tree size class by parrotbill proportional to availability throughout the study site?

METHODS

STUDY SITE

This study was conducted in Manawainui (20°41'43" N, 156°7'59" W), a 526-hectare (1300-acre) parcel of Haleakalā National Park at the southeastern-most edge of the East Maui rain forest (Figure 3). Manawainui has been recovering from feral ungulate damage for approximately 24 years; longer than most other sites on Maui. As a result of this recovery and its proximity to historic parrotbill range, it is an area of forest being considered for future reintroductions of captive reared Maui Parrotbill. It is an ecotone between wet and dry forest, dominated by wet ʻōhiʻa forest, mesic koa and mixed ʻōhiʻa-koa forest.


Remnant ʻōhiʻa-koa forest below Manawainui fence line, approximate elevation is 5000 ft.


Recovering ʻōhiʻa-koa forest above Manawainui fence line, approximate elevation is 5200 ft.

Gross vegetation cover classes have been previously documented by Jacobi (1989). The topography in the area is extreme, divided by gulches and streams with an average slope of > 30%. Environmental and anthropogenic disturbance in the area has included degradation by feral goats (*Capra hircus*) and pigs (*Sus scrofa*), and invasion by weeds (Peterson 1976, Loope et al. 1992). Interestingly, this forest was initially isolated by lava flows which inundated nearby Kaupō Gap and Kīpahulu Valley and may be much older than the surrounding environs due to this isolation (Peterson 1976). Climactically the area is dynamic, with high precipitation (i.e., orographic rains and mist) in excess of 5,000 mm per year. Rainfall tapers off from east to west, marking the transition from the windward to leeward sides of the island. Manawainui is intensively managed to control feral ungulates, and marks the edge of current parrotbill range on southwest Haleakalā.

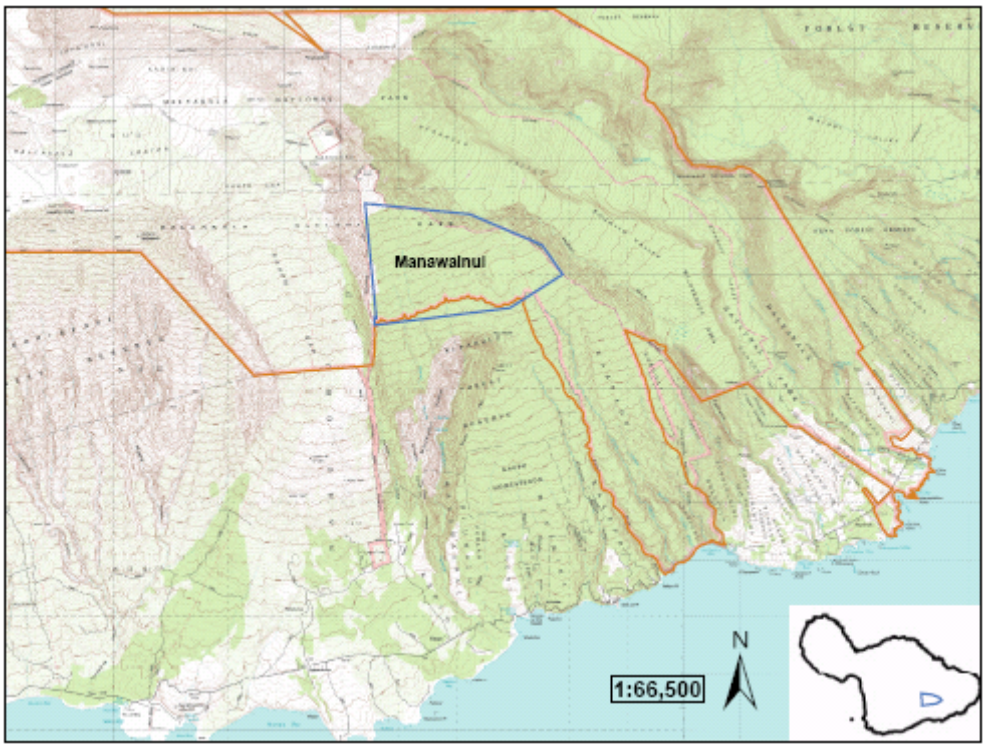


Figure 3. Overview of Haleakalā National Park with inset of Manawainui area.

All work was conducted above 1585m elevation (5200 ft). Therefore, the effect of disease as a confounding factor on parrotbill distributions was minimized. Conducting work at this elevation also reduced the spread of invasive weeds that occur at lower elevations in Manawainui because elevation limits natural recolonization of some weeds in this recovering forest. To assess whether changes in vegetation across the habitat gradient in Manawainui were affecting parrotbill distribution and use, simultaneous surveys of vegetation, birds, and bird foraging behavior were conducted over the course of two field seasons from February 2005 to August of 2006. This spans most of the known breeding season for parrotbill (Simon et al. 1997) and should have

reflected the time of year when resources would be most critical for the reproduction and survival of young.

I selected 10-hectare areas as my study unit in which to conduct vegetation sampling and foraging observations as a conservative estimate of home range size for the parrotbill. Home ranges for Maui Parrotbill average 2.3 hectares (5.7 acres) in size (Simon et al. 2000, Pratt et al. 2001b). As the birds in this study were not banded, each 10–hectare home range (used) or "pseudo home range" (unused) helped to maintain a level of independence throughout the course of the study. Using Geographical Information Systems technology, I superimposed a grid partitioned into 10-hectare units across the area, and assigned each 10-hectare survey area a unique letter identifier (Appendix 1). The initial survey grid included 27 ten-hectare study areas. Subsequent vegetation sampling was conducted in 22 of these 10 hectare areas in accessible areas where parrotbill occurred and in areas where they were absent (Figure 4).

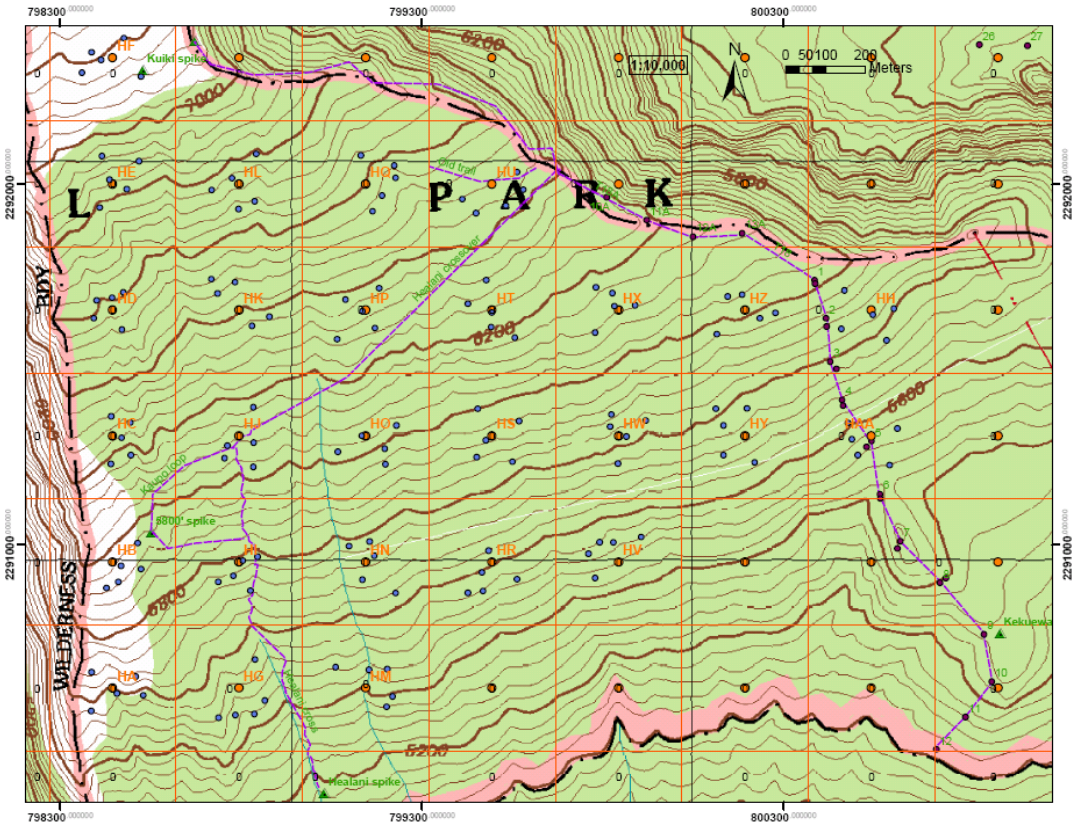


Figure 4. Detailed overview of Manawainui study site with lat-long references. Blue dots indicate (0.04 ha) vegetation plots and orange gridlines with letters denote each 10 ha area surveyed for Maui Parrotbill.

BIRD SURVEYS

Spot-mapping techniques (Bibby et al. 2000) were used to assess the density and distribution of parrotbill across the study site. I searched 27 10-hectare areas from February 2005-August 2005,

and January 2006-August 2006. Full vegetation and bird surveys were conducted only in 22 of the 27 survey areas because treacherous topography made surveying all areas difficult. To maximize the potential of encountering parrotbill, I attempted to survey each 10-hectare area for at least four hours each month; however, this was not always possible due to poor weather conditions. Selection of survey areas was arbitrary, but without preconceived bias. Survey times were alternated (morning vs. afternoon surveys) to increase encounter rates with individuals active at only certain times of the day. Observers were rotated among home ranges to prevent bias. Audio playback equipment was used to increase the chance of detecting birds in new areas. Observers moved around each 10-hectare area during each 4-hour survey period, as is done in standard spot mapping surveys (Bibby et al. 2000). If a parrotbill was observed foraging during a survey, the observer stopped to conduct foraging observations and microhabitat analysis. Individual birds were assigned ID numbers which associated them to the nearest survey area in which they were found. In addition to location, individuals were further identified by unique coloration and/or vocalizations. Parrotbill are sexually dimorphic and singing is unique to males (Simon et al. 1997), thus birds were sexed based on vocalization and obvious dimorphisms such as bill size and plumage coloration. I was unable to search many of the areas below 1646m elevation due to treacherous terrain and the possibility of spreading incipient weeds. I did not consider these to be priority areas however, due to the prevalence of avian malaria at lower elevations (Atkinson et al. 1995).

VEGETATION SAMPLING-MACROHABITAT

I selected a random sample, of 0.04-hectare (11.3 m radius) circular plots stratified by each 10-hectare survey area across the Manawainui study site, $n = 107$ (Figure 4). These plots spanned the east to west habitat reflecting the structural and compositional heterogeneity of the area as suggested by Noon (1981). Due to habitat heterogeneity, I randomly selected five replicates in each home range using the random sampling extension in ArcGIS. UTM coordinates of sampling areas were uploaded into Garmin GPS units to locate plots in the field. I used the methods of James and Shugart (1970) as modified by Noon (1981) to sample habitat data at each plot. These variables were comprised of slope, elevation, percent canopy and ground cover, canopy height, shrub and tree densities (in 3 different size classes); canopy, subcanopy, and understory density, and plant species (Table 1).

I identified all woody and herbaceous plants within each 0.04-hectare plot concurrent with stem counts to ascertain relative abundance of plants throughout the study area. Most woody plants were identified to species. Unidentified specimens were brought back to Haleakalā National Park (HALE) headquarters for identification by National Park Service botanists. Specimens were deposited in the HALE herbarium. I attempted to identify all plants to species; however some plants could be identified only to genus due to morphological heterogeneity and hybridization (P. Welton, pers. comm.).

Table 1. Description of habitat variables measured for each 0.04 hectare plot in used and unused areas.

Habitat Variable	Abbreviation	Description
Percent canopy closure	CanCo	Estimated as the presence or absence of leaves sighted through densitometer along two 22m transects in each plot
Percent ground closure	GrnCo	Same as above but for ground cover
Canopy height	CanHgt	Estimated as the mean canopy height for each plot using a clinometer
Density of small trees	DBHsmall	Number of trees per home range (3-15 cm dbh) measured using a forester's diameter tape.
Density of medium trees	DBHmed	Number of trees per home range (16-53 cm dbh)
Density of large trees	DBHlarge	Number of trees per home range (≥ 54 cm dbh)
Density of shrubs	Shrubtls	Total woody shrub stem count at breast height < 3 cm dbh, estimated for two 22m transects in each plot
Canopy density	Cantot	Index of species abundance ≥ 12-m tall according to Braun-Blanquet cover abundances
Subcanopy density	Subcan	Index of species abundance 5-12-m tall according to Braun-Blanquet cover abundances
Understory density	Under	Index of species abundance 0-5m tall according to Braun-Blanquet
Plant Species		Counted and identified to genus and species
Slope		Estimated using a clinometer
Elevation		Estimated using an altimeter

DATA ANALYSES-MACROHABITAT

All data were input into Microsoft Access 2000 and proofed for errors. Tree height data were computed from field-based clinometer readings and all heights converted into meters. Plant species stem counts were converted to stems per hectare. Due to the large amount of data collected, it was necessary to reduce many of the original variables into smaller subsets of manageable data for further analysis. For example tree size class data were originally collected in nine different dbh size categories but was later condensed into three size classes (small, medium, large) for easier interpretation. The data collected from the original 107 vegetation plots were expressed as mean values for the variables in each of the 22 10-hectare areas sampled. Due to incomplete data, survey area HA (n = 3) was dropped from further analyses, leaving a final sample of 104 plots in 21 10-hectare areas. A complete list of vegetation plots sampled with UTM coordinates and mean values for the variables measured can be found in Appendices 2 and 4. Data were assessed for strong outliers (cut off of > 3 SD) and normality using frequency distributions, normal probability plots and the Shapiro-Wilkes test. I did not detect any strong outliers, for structure or floristics, however the data were non-normal and heteroscedastic. I assumed those variables that were univariate normal approximated multivariate normality (McGarigal et al. 2000). All descriptive and statistical analyses were performed in Systat 11 and PC-Ord version 5.

I used multi-response permutation procedure (MRPP), a non-parametric multivariate method, to test for significant differences between used and unused areas; $n = 21$ (used = 10 vs. unused = 11). MRPP is a distribution free test similar to discriminant analysis (DA) and multivariate analysis of variance (MANOVA) that tests for differences between groups but with relaxed assumptions. The MRPP *T*-test statistic is based on numerous permutations of the data itself, instead of a predetermined distribution (Mielke 1984, Mielke and Berry 2001). I used the Sorensen (Bray-Curtis) distance measure with the recommended weighting of n/sum (n), as it is sensitive to heterogeneous data (McCune and Grace 2002). The data matrices were rank-transformed to account for heterogeneity of the data set. I followed this procedure for both structure and floristics and ran separate MRPP tests for each.

I used Nonmetric Multidimensional Scaling (NMS), a robust, iterative ordination technique to graphically represent the degree of dissimilarity between the used and unused areas. NMS avoids the assumptions of linearity used in other ordination methods (Kruskal 1964, Mather 1976). In addition, NMS differs from other ordination procedures in that the assignment of axes is arbitrary. I used autopilot mode in PC-Ord with the Sorensen (Bray-Curtis) distance measure, and ran 250 runs of real data and 250 runs of random data. Dimensionality of the data set was assessed graphically by a scree plot, by seeking a low stress solution and by assessing Monte Carlo *p*-values ($p < 0.05$) for significance. I followed this procedure for broad patterns in both vegetation structure and floristics and used the methods below for more detailed analysis of specific variables in each group.

Vegetation structure

The final group of ten habitat variables retained for further analyses of vegetation structure was based on biological relevance and included: percent ground cover, percent canopy cover, mean canopy height, small, medium, and large tree totals, sub-canopy, canopy, and understory foliage density indices and shrub stem totals. Since the variables were expressed using different units, variables were standardized by column totals.

Because MRPP does not distinguish between those variables contributing most to group separation, Discriminant Analysis was used in a descriptive mode to identify what variables might be affecting group membership of used and unused areas. Values were screened for normality separately for each group of used ($n = 10$) and unused ($n = 11$) areas. Medium trees (DBHMED) and canopy densities (CANTOT) were log transformed to meet assumptions of normality and homogeneity of variance. Multicollinearity was assessed using scatter plot matrices and tested for significance using the Pearson correlation coefficient with an $r \geq 0.7$ as criterion for deleting a variable (Tabachnick and Fidell 1996). The final seven variables included density of the understory, subcanopy, and canopy layers, and the number of small, medium, and large trees and shrubs.

Floristics

Relative abundance of all woody species was calculated separately for trees and shrubs because I wanted to assess whether or not certain shrubs or tree species might be particularly influential. I considered as shrubs all woody species with a diameter at breast height (dbh) less than 3 cm and trees anything over 3 cm. I also estimated the relative abundance of ferns and forbs; however these data were omitted from further analysis because of its unlikely contribution to parrotbill

habitat use. Those other woody species that occurred in < 5% of the sample units were also omitted from further analyses. I retained a total of 10 plants for my final analyses which included: ʻalani (*Melicope* spp.), kanawao (*Broussaisia arguta)*, kawaʻu (*Ilex anomala*), koa, kōlea (*Myrsine* spp.*)*, ʻōhelo (*Vaccinium calycinum)*, ʻōhiʻa, ʻōlapa (*Cheirodendron trigynum),* pūkiawe (*Leptecophylla tameiameiae)*, and standing dead trees.

Data were non-normal and heteroscedastic, therefore non-parametric analyses were used. I ran an indicator species analysis to identify those species that were most useful in separating used from unused areas (Dufrene and Legendre 1997). This procedure calculates the proportional abundance of a species in one group versus its abundance in all groups. An indicator value is obtained for each species, ranging from 0 (no indication) to 100 (perfect indication). Statistical significance is evaluated by a Monte Carlo randomization test for each species ($p < 0.05$).

Diversity

I assessed diversity between all used and unused areas for trees, shrubs, and trees and shrubs combined. Shannon Wiener (H) and Simpson's (D´) diversity indices were calculated for all areas using PC-Ord and tested for significance using separate Mann-Whitney U tests for those species used in the MRPP analyses. Finally I tested for differences in overall species diversity including those species that occurred in < 5% of the survey areas.

VEGETATION SAMPLING-MICROHABITAT

Within each used 10-hectare survey area, detailed foraging observations on individual parrotbill were collected following the standard behavior classification scheme of Remsen and Robinson (1990). I also noted bird age and sex when possible. Since parrotbill are rare and encounters infrequent, I spent as much time watching a foraging bird as possible, recording the total observation time for each individual. Only initial observations were included in the analyses however, to minimize the effects of autocorrelation. In addition to collecting behavioral data, vegetation data was collected on foraging microsites or "patches". Upon encountering a parrotbill, bird-centered vegetation plots were selected by marking the first location it was seen foraging (Larson and Bock 1986). The first foraging observation point was identified as the point at which the first foraging maneuver was observed, after waiting ten seconds to remove any observer imposed bias.

Data on vegetation parameters were collected at several scales of increasing resolution using the first foraging location as the center reference point from which to collect additional data. In addition to collecting data at this point, I also collected data at two other scales of 1-m and 2-m radii. The 1-m radius might influence parrotbill foraging at the inner portion of a patch while the 2-m radius might represent the maximum extent of the foraging patch that the bird might spend time in before moving somewhere else in its home range.

I collected information on a series of vegetation variables that may be important to parrotbill foraging behavior, based on a review of pertinent literature (Table 2). At the point of initial contact, I identified the plant species and determined its height, as well as the bird height above ground (using the same height tier classes as for macrohabitat), substrate type (foliage, wood, and berries), tree size class, and branch size (small, medium, large).

In the 1-m radius, I collected data on foliage density and bark surface area, using one of six categories (Remsen 1985), and the number of branches approximating the number of perches parrotbill could have used.

At the broadest scale (i.e., the 2-m radius), I recorded data on species and the foliage density of each vertical vegetation class (i.e., canopy, subcanopy, understory) according to the Braun-Blanquet cover abundance scale (Braun-Blanquet 1932) and percent canopy and ground cover, using a densitometer.

I then measured these same variables (with the exception of bird height and substrate type) at the same scales at randomly located plots 20 m away (following methods of Moser et al. 1990, VanderWerf 1993). Habitat variables were measured in 36 used and 36 random plots at these three different scales of resolution in nine of the home ranges parrotbill were actively using.

Table 2. Summary of habitat variables measured for microhabitat at foraging sites and random sites.

Habitat Variable	Scale	Description
Plant Species	0,1,2m	counted as presence/absence
Plant Height	0m	estimated in meters
Canopy Height	0m	estimated in meters
Branch Size (cm)	0m	circumference estimated in cm using Maui Parrotbill as a "ruler"
Tree dbh (cm)	0m	estimated using a forester's diameter tape
Branch Count	1m	counted all branches in the same plane as first foraging maneuver
Foliage density index	1m	estimated in the same plane as the first foraging maneuver
Bark surface area index	1m	estimated in the same plane as the first foraging maneuver
Vertical Ht tier index	2m	estimated for understory, subcanopy, and canopy
Canopy Cover (%)	2m	estimated using a densitometer
Ground Cover (%)	2m	estimate using a densitometer

0m is the point at which the bird's first foraging maneuver was observed

1m is a 1-m radius extending out from the first point of observation

2m is a 2-m radius extending out from the first point of observation

DATA ANALYSES-MICROHABITAT

Data were screened for normality, outliers, and homogeneity of variance using the same criterion as for macrohabitat, for each of the three microhabitat scales (0-m, 1-m, and 2-m). The data for structure and floristics at all three scales were highly non-normal and heteroscedastic. Monotonic transformation of individual variables had little effect on normality; therefore I utilized non-parametric multivariate methods to test for significant differences in forest structure and floristics between plots. Structural data measured on different scales or units was standardized by column totals. Species data was represented as presence/absence and standardization was unnecessary. To test the hypothesis of no difference between used and random foraging plots, I used PerManova, a “distribution free” significance test for balanced study designs (Anderson 2001). The unit of analysis was the foraging site and not the individual. PerManova calculates an *F* test

statistic similar to MANOVA; however, the test statistic is evaluated for significance by running a series of randomized permutations of the data. I followed the suggestions of Anderson (2001) and ran 1000 permutations of the data, with $\alpha = 0.05$.

I assessed differences in diversity between all used and unused foraging plots at the 1-m and 2-m scales. Shannon Wiener and Simpson's diversity indices were calculated for all plots using PC-Ord and tested for significance using a Mann-Whitney test.

To assess in more detail how parrotbill were selectively using foraging habitat, I calculated proportional use of foraging habitat in used areas (Dodge et al. 1990). I summed the total observation time for each individual on each plant species, tree size class, and vegetation stratum in each home range and divided by the total observation time for each variable observed to get relative use. Relative availability of each variable was calculated in a similar manner by summing the availability of each variable in each home range and dividing it by the overall total. Tree size classes were converted to basal area so that comparisons between plant species would be weighted appropriately. I calculated overall availability of woody species only, since parrotbill do not forage on herbaceous vegetation. Percent cover was estimated for each vegetation strata (canopy, subcanopy, and understory) according to the Braun-Blanquet cover abundance scale (Braun-Blanquet 1932) and I used the midpoints for each cover class in the analyses. Data were initially collected in six different height tiers, but were analyzed due to statistical considerations based on three layers-canopy, subcanopy, and understory.

Once relative proportions were calculated for each parameter of use and availability, direct comparisons were made for each individual ($n = 14$) using a series of simple linear regressions. Calculating use and availability in this manner is an appropriate method for territorial species such as parrotbill because comparisons for each individual are made only across the territory or home range that each individual has access too. Each separate regression analysis was then assessed for statistical significance ($p < 0.05$). If a regression was significant, proportional use for each vegetation variable was derived by examining the slope of each regression line. Slopes greater than 1 signified use greater than availability while slopes less than one signified availability greater than use. Finally, I averaged values for use and availability across individuals to estimate percent use and availability for each plant species, height class, and tree size class (VanderWerf 1993, Pejchar 2004).

RESULTS

BIRD SURVEYS

Surveys suggest parrotbill occupy a greater portion of Manawainui than was previously documented. I estimated that 16 individuals occupied approximately 100 of the 270 ha of the forest comprising the study site (Figure 5). Maui Parrotbill occurred at densities of 0.06 birds/ha over the entire 270 hectare study site or 0.08 birds/ha over the 210 ha of forest intensively surveyed for birds and vegetation. I did not detect any juvenile parrotbill or nesting attempts in the study area. With the exception of the ʻĀkiapōlāʻau (*Hemignathus munroi*), parrotbill fledglings have a longer juvenile dependency period than many other honeycreepers and elicit frequent, loud begging calls while following foraging adults (Simon et al. 1997, Simon et al. 2000, Pejchar 2004). It is therefore unlikely that juvenile birds went undetected.

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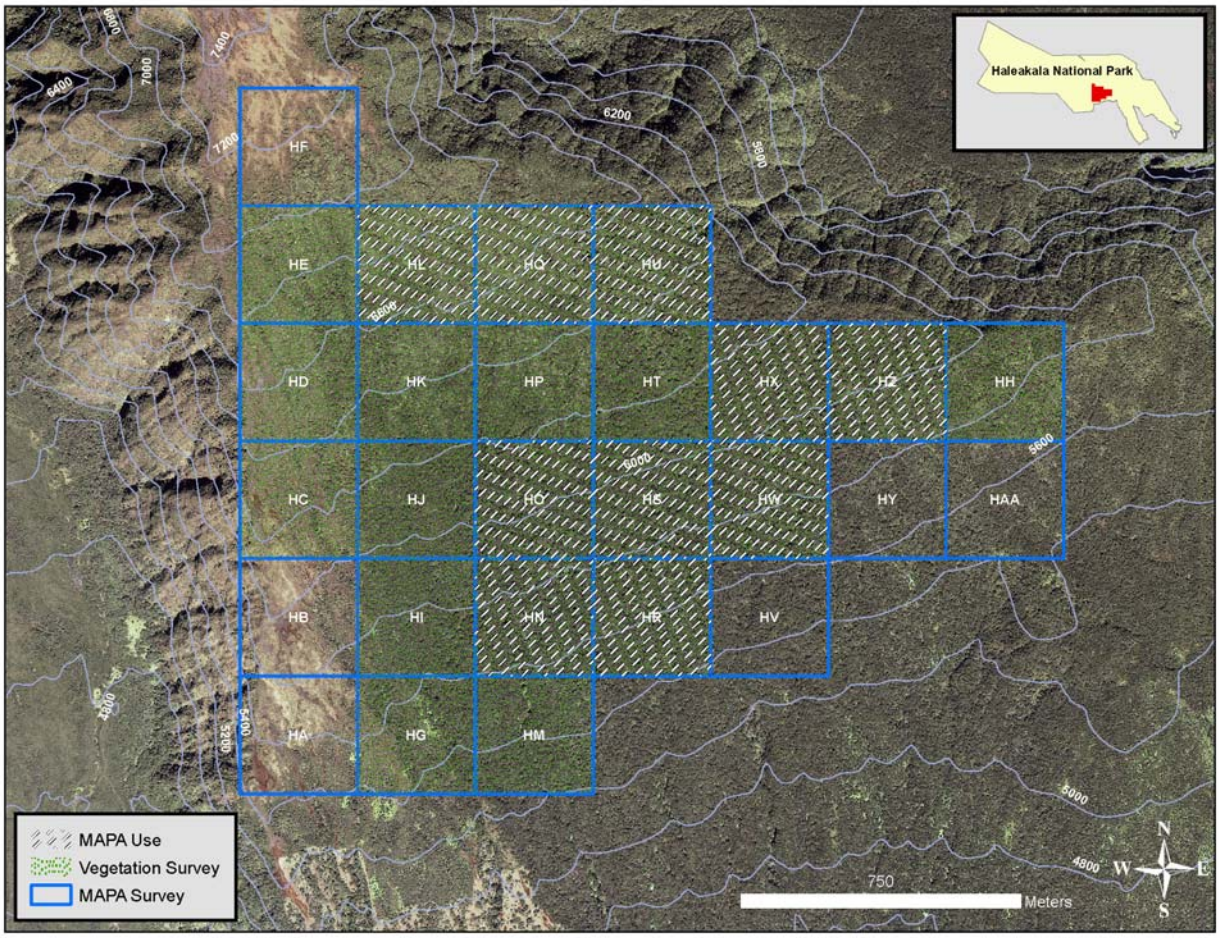


Figure 5. Distribution of Maui Parrotbill across the study site. All 10-hectare areas surveyed for birds are indicated by letters.

MACROHABITAT

Vegetation structure

I found significant differences between used and unused areas (p = 0.004, A = 0.116), based on vegetation structure (Table 3). NMS autopilot in PC-ORD selected a 2-dimensional ordination based on a low stress solution ($p < 0.05$). Most of the difference between used and unused areas was captured by axis 1 (59 %) while axis 2 captured another 30% of the variation between used and unused areas. This result was achieved after 135 iterations and had a final stress of 12.3. Plotting survey areas against axes 1 and 2 clearly segregated used and unused areas, although used areas appeared more similar to each other than unused areas (Figure 6). The number of large trees and density of subcanopy were strongly associated with the first axis, while the number of small trees and shrubs were most strongly associated with the second axis. The follow up discriminant analysis expressed these results in more detail. The standardized discriminant function coefficients associated with each variable suggest that unused areas had higher densities

of small (dbh ≥ 3-15) sized trees and shrubs. Used areas had more large trees (dbh ≥ 54cm) and denser canopy, subcanopy, and understory layers (Table 4).

Table 3. Summary statistics for vegetation structure and floristics.

Scale	Statistic	Vegetation Structure	Floristics
Macrohabitat			
10 ha	T	-3.92	-2.45
	p	**0. 004**	**0. 025**
	A	0.116	0.072
Microhabitat			
2m	F	1.39	0.78
	p	0.239	0.587
	DF	1,35	1,35
1m	F	1.56	3.97
	p	0.186	**0. 001**
	DF	1,35	1,35
0m	F	2.99	2.31
	p	0.065	**0. 026**
	DF	1,35	1,35

Macrohabitat results are for the MRPP analysis.

Microhabitat results are for the PerManova.

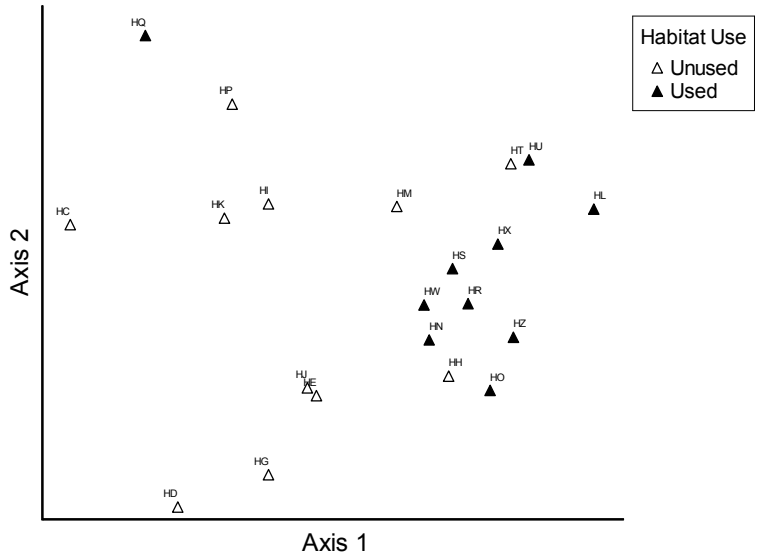


Figure 6. Final NMS ordination of 21 home ranges and habitat variables grouped by use. Each point represents a 10-hectare survey area. The degree of similarity (based on forest structure) between points is represented by the distance between each point. Significant differences between used and unused areas were evaluated using a MRPP test, see Table 3.

Table 4. Canonical discriminant functions of vegetation variables standardized by within group variances following a complete discriminant analysis.

		Group Means	
Variable	1st axis	Unused	Used
DBHLARGE	-0.671	0.84	2.48
CANTOT	0.313	0.619	0.736
UNDER	-0.532	13.18	15.34
SHRUBTLS	0.614	252.15	226.42
DBHMED	0.153	1.35	1.132
DBHSMALL	0.355	145.805	110.06
SUBCAN	-0.369	5.52	6.22

CANTOT and DBHMED values are log transformed

Floristics

A total of 55 herbaceous and woody plant species was recorded in the understory, subcanopy, and canopy in used and unused areas. A complete list of all species found in the Manawainui area with common names and taxonomic abbreviations can be found in Appendix 3. ʻŌhiʻa, was the dominant tree comprising nearly half of all tree species (48 %), followed by pūkiawe at 15%. ʻŌhiʻa, ʻōhelo, and pūkiawe were similarly dense in the shrub category, and cumulatively accounted for roughly 71% of the species. Koa accounted for less than 1% of the species surveyed in either the shrub or tree categories but was included in the analyses because the

parrotbill were known to use koa in historic times (Perkins 1903). In addition, koa is used extensively by the closest extant relative to the parrotbill, the ʻĀkiapōlāʻau.

I found significant differences between used and unused areas based on floristics ($p = 0.025$, $A = 0.072$) (Table 3). Areas without parrotbill had higher densities of ʻōhiʻa trees ($p < 0.024$), while those areas with parrotbill had higher densities of both ʻōlapa trees ($p = 0.027$), and kawaʻu trees ($p = 0.031$). Higher densities of pūkiawe shrubs ($p = 0.005$) occurred in unused areas and higher densities of ʻalani shrubs ($p = 0.012$) occurred in used areas (Table 5).

The corresponding NMS ordination selected by PC-Ord had a 2-dimensional solution with a final stress $p = 0.004$ after 78 iterations of the data. The first axis described 45 % of the variation between used and unused areas, while the second axis described 43%. The ordination graphs showed some clustering between used and unused areas although the graphs were more difficult to interpret than that for structure (Figure 7). Axis 1 was strongly correlated with the density of ʻōhiʻa, ʻōlapa, and kōlea trees and kanawao and ʻalani shrubs. Axis 2 was strongly correlated with the density of ʻōhiʻa trees and pūkiawe shrubs.

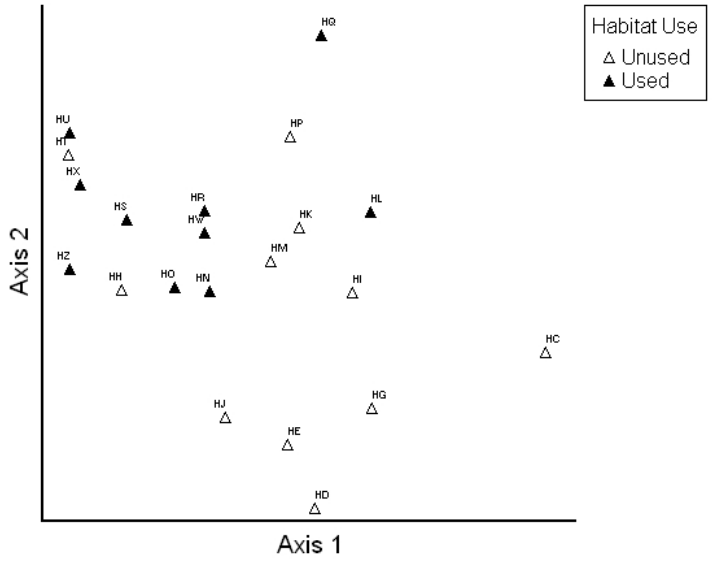


Figure 7. Final NMS ordination of 21 home ranges grouped by use. Each point represents a 10-hectare survey area. The degree of similarity (based on floristics) between points is represented by the distance between each point. Significant differences between used and unused areas were evaluated using a MRPP test, see Table 3.

Table 5. Summary of indicator species analysis results for shrubs and trees in unused (0) and used (1) 10-hectare areas.

Species	Use	Indicator value	Mean	S.Dev	*p*
Shrubs					
Metrosideros polymorpha	1	50.9	56.3	4.74	0.912
Vaccinium calycinum	0	54	56.3	4.67	0.626
Leptecophylla tameiameiae	0	77.5	59.4	6.61	**0.005**
Broussaisia arguta	1	57.5	39.5	9.17	0.052
Melicope spp.	1	73.6	48.6	8.54	**0.012**
Trees					
Metrosideros polymorpha	0	65.5	56	4.36	**0.024**
Leptecophylla tameiameiae	0	64.1	58.3	5.63	0.165
Dead	0	50.3	54.5	3.55	0.961
Cheirodendron trigynum	1	63.8	55.2	3.86	**0.027**
Vaccinium calycinum	1	50.7	57.1	7.04	0.8
Ilex anomala	1	66.7	48.1	8	**0.031**
Acacia koa	0	41.2	35.9	9.92	0.255
Myrsine spp.	1	61.9	49.1	8.82	0.096

P-values in bold indicate significance at $\alpha = 0.05$.

Diversity

Diversity of tree species was significantly higher in used areas than in unused areas for the Simpson's index only ($F = 7.75$, $p = 0.005$, df = 10, 9). There was no significant difference in species diversity between used and unused areas for trees and shrubs combined as well as for shrubs alone ($p > 0.05$) for those plants used in the MRPP tests. However, overall species diversity was higher in used areas than unused areas for both the Shannon-Wiener ($p = 0.035$) and Simpson's diversity indices ($p = 0.041$) when including all species, not just those used in the MRPP (Table 6).

Table 6. Summary statistics for diversity following a Mann-Whitney test at the macrohabitat and microhabitat scales.

	Scale					
	Macrohabitat		Microhabitat			
	10 ha		2m		1m	
	p	U	*p*	U	*p*	U
Diversity (H)	**0.035**	25	0.323	562	0.933	641
Diversity (D′)	**0.041**	26	0.323	562	0.933	641

H is Shannon Wiener index

D′ is Simpson diversity index

MICROHABITAT

A total of 22 woody plant species was recorded in the understory, subcanopy and canopy strata in 9 different home ranges. Maui Parrotbill primarily foraged on 9 different plants which included ʻākala (*Rubus hawaiensis*), ʻalani, koa, kawaʻu, kōlea, ʻōhelo, ʻōlapa, pilo (*Coprosma* spp.), and pūkiawe.

Maui Parrotbill exhibited non-random selection of foraging habitat at the two finest scales I measured (0-m and 1-m) based on floristics. Structure was not a significant factor at either scale, and overall species diversity did not differ between used and unused plots, (Table 3, Table 6).

At the 2-m scale, results of the PerManova for structure ($F = 1.39$, $p = 0.239$, df = 1, 35) and floristics ($F = 0.777$, $p = 0.587$, df = 1, 35) were non-significant ($p > 0.05$). At the 1-m scale, significant differences were detected between used and random plots based on plant species only ($F = 3.97$, $p = 0.001$, df = 1, 35). The complementary indicator species analysis however did not detect any one significant indicator species which contributed to group separation (Table 7). No significant differences for structure were observed at the 1-meter scale ($F = 1.56$, $p = 0.186$, df = 1, 35). At the finest scale, (0-m), I found significant differences between foraging sites and random sites for floristics only ($F = 2.31$, $p = 0.026$, df = 1, 35). The results of the corresponding indicator species analysis were significant for only one species; ʻōhiʻa ($p = 0.005$) which was more abundant in random than used foraging plots. No significant differences were found for forest structure at the 0-m scale ($F=2.99$, $p = 0.065$, df = 1, 35). No significant differences were detected in diversity between used and random plots at either the 1-m or 2-m scale for either diversity index using a significance level of $\alpha = 0.05$.

Table 7. Summary of indicator species analysis results for trees at the 1-m scale.

Species	Maxgrp Value	Indicator value	Mean	SD	*p*
Acacia koa	1	13.9	6.6	2.45	0.052
Alyxia oliviformis	0	2.8	2.8	0.04	1
Broussaisia arguta	0	2.8	5.4	2.58	1
Cheirodendron trigynum	1	32.1	24.4	4.18	0.088
Clermontia grandiflora	0	2.8	2.8	0.04	1
Coprosma spp.	0	16	19.4	3.76	1
Dead	0	8.7	9.1	3.2	0.713
Ilex anomala	1	11.6	7.3	2.88	0.197
Labordia venosa	1	2.8	2.8	0.04	1
Leptecophylla tameiameiae	0	6.9	10.7	3.34	1
Melicope spp.	0	16.2	11.7	3.22	0.185
Metrosideros polymorpha	0	27.2	18.6	3.99	0.066
Myrsine lessertiana	1	7.4	7.4	2.93	0.683
Rubus hawaiensis	1	11.1	10.1	3.08	0.472
Tetraplasandra oahuensis	1	2.8	2.8	0.04	1

Significance was evaluated at $\alpha = 0.05$.

I collected 32 foraging observations for an estimated 14 individuals in 8 different home ranges with a mean observation time of 380.63 seconds ± 301 SD for each observation. Parrotbill utilized koa, ʻōlapa, ʻalani and ʻākala in greater proportion than their availability throughout the home ranges ($p < 0.05$) (Table 8). Parrotbill foraged on ʻōlapa 23% of the time, koa and ʻākala 10% of the time each, and ʻalani 1% of the time (Figure 8). Plants used in proportion to their relative abundance were kawaʻu, pilo, pūkiawe, kōlea, and ʻōhelo. Standing dead trees were not utilized at all, despite their availability (11%) throughout the birds' home ranges. Parrotbill frequently excavated and gleaned invertebrates from dead wood and bark (Appendix 5).

The regression results for use versus availability of the three main height tier classes (canopy: 5-12m, subcanopy: 2-5m, and understory: 0-2m) were all significant ($p < 0.05$) with the subcanopy and canopy used more than expected, and the understory used less than expected based on availability. Parrotbill foraged at a mean height of 4.6m ± 2.24 SD and selectively foraged in the subcanopy and canopy vegetation layers, spending 41% of the time in the subcanopy and 39% of the time in the canopy (Figure 8). Birds foraged less than expected in the understory layer (Table 8).

The regression results for the analyses of use and availability for tree size class were significant ($p < 0.05$) for both small (3-15 dbh) and medium (16-53 dbh) tree size classes. Parrotbill used small trees greater than expected based on availability, foraging on them 41% of the time and used medium trees less than expected based on availability foraging on them 43% of the time (Figure 8). Parrotbill used shrubs (0-2.9 dbh) and large trees (≥ 54 dbh) in proportion to their availability. When foraging in the canopy, parrotbill foraged on ʻōlapa, koa and kawaʻu, and foraged on ʻalani, kōlea, and pilo in the subcanopy.

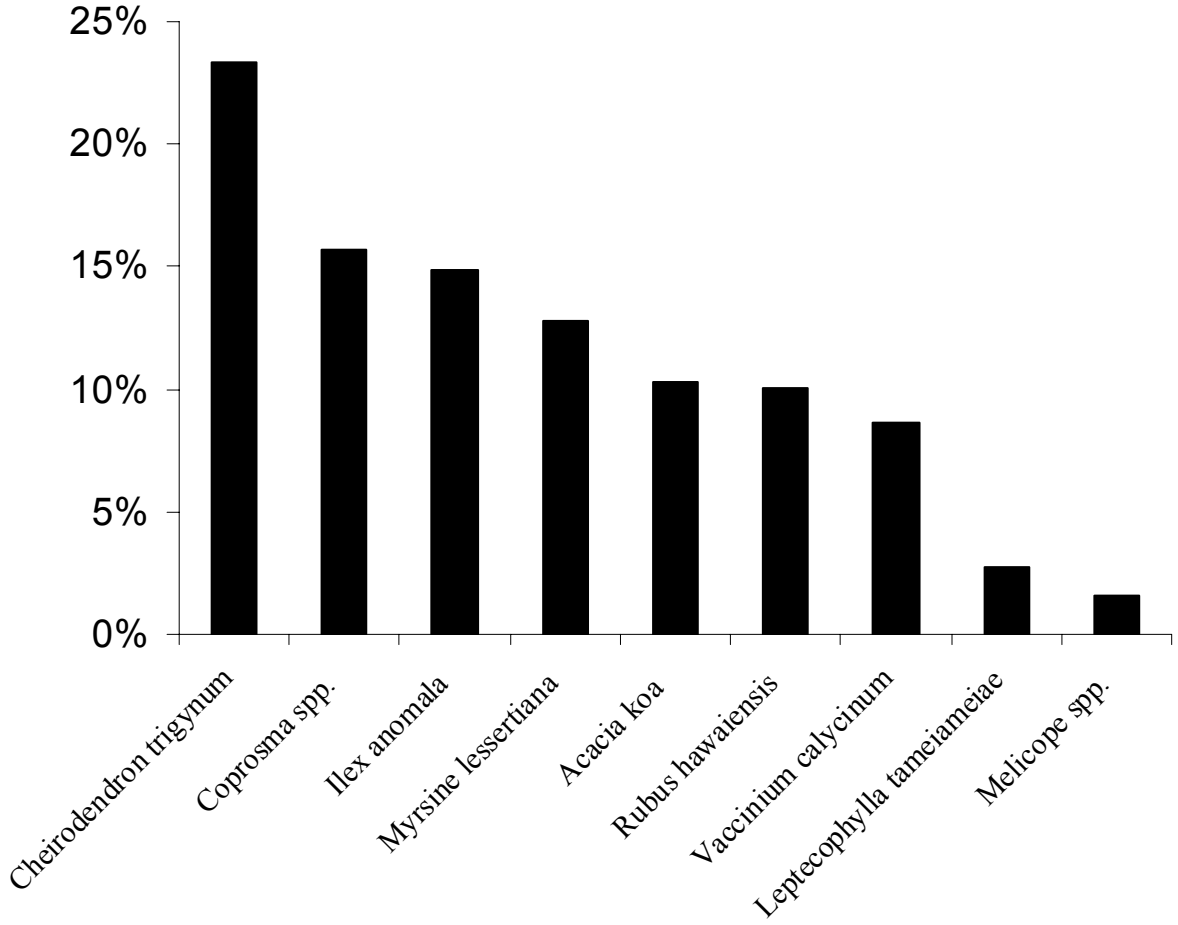
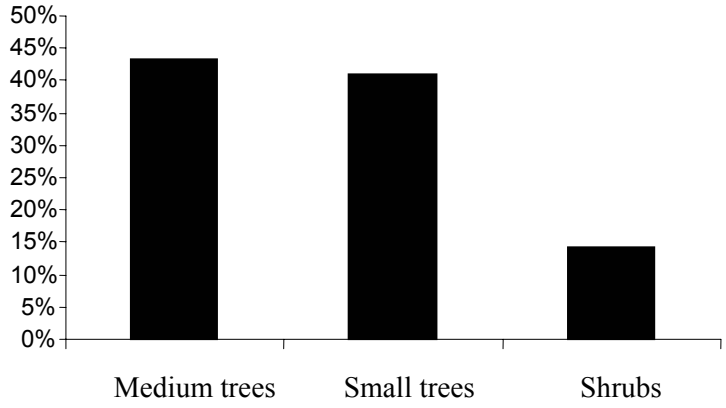


Figure 8. Mean percent time parrotbill (n = 14) spent foraging on different plant species, height tier and trees size class in 8 different home ranges in Manawainui.

Figure 8. (Continued).



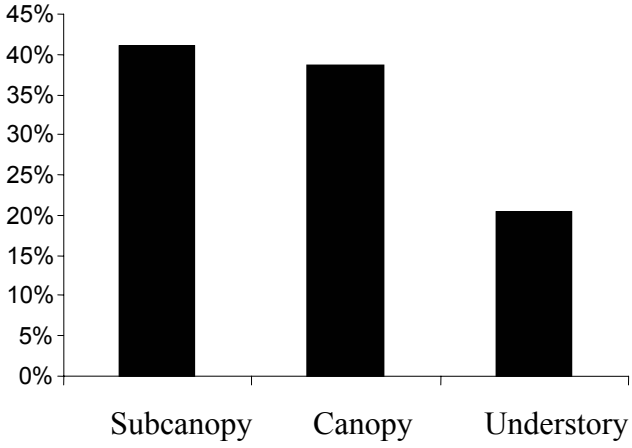


Table 8. Results of the separate regression analyses of Maui Parrotbill use vs. availability of plant species, vertical height tier, and tree size used for foraging, $n = 14$ birds.

Plant Species	**Use**	**Availability**	**Slope**	**SE**	***t***	***p***	**Conclusion**
Cheirodendron trigynum	0.234	0.039	6.51	2.10	3.09	**0.01**	U>A
Coprosma spp.	0.157	0.010	15	6.79	2.21	0.05	U=A
Ilex anomala	0.149	0.015	3.48	4.75	0.73	0.48	U=A
Myrsine lessertiana	0.128	0.013	6.98	5.42	1.29	0.22	U=A
Acacia koa	0.103	0.013	8.27	1.90	4.16	**0.00**	U>A
Rubus hawaiensis	0.100	0.001	146	52.39	2.78	**0.02**	U>A
Vaccinium calycinum	0.086	0.010	7.05	3.88	1.82	0.09	U=A
Leptecophylla tameiameiae	0.027	0.023	0.35	1.07	0.33	0.75	U=A
Melicope spp.	0.016	0.015	1.65	0.74	2.23	**0.04**	U>A
Metrosideros polymorpha	0.000	0.749	-	-	-	-	-
Dead	0.000	0.107	-	-	-	-	-
Vertical Height Tier*							
Subcanopy	0.410	0.209	1.84	0.53	3.46	**0.00**	U > A
Canopy	0.385	0.134	2.72	0.57	4.74	**0.00**	U > A
Understory	0.205	0.595	0.329	0.14	2.29	**0.04**	U < A
Upper Canopy	0.000	0.062	-	-	-	-	-
Tree Size Class**							
Medium trees	0.434	0.425	0.967	0.21	4.55	**0.00**	U < A
Small trees	0.411	0.157	2.65	0.68	3.88	**0.00**	U > A
Shrubs	0.143	0.013	6.72	4.94	1.36	0.20	U = A
Large trees	0.011	0.405	-	-	-	-	-

* Understory = 0-2m, Subcanopy 2-5m, Canopy 5-12m, Upper Canopy 12-25m

** Shrubs 0-2.9 dbh, small trees 3-15 dbh, medium tress 16-53 dbh, large trees, ≥ 54 dbh.

Use (U) and availability (A) are relative proportions, availability is the mean value for basal area of each species, and use is the mean value of foraging time. Significant regressions with slopes greater than one signify use greater than availability. Slopes less than one signify use less than expected.