

DISCUSSION

MACROHABITAT

Maui Parrotbill showed strong associations with specific floristic and structural characteristics of wet forest and selected habitat non-randomly for both forest structure and plant floristics at the macrohabitat (home range) scale. Compared to unused areas, used areas contained more mature, well developed forest with a higher density of large trees, greater canopy density, subcanopy, and understory layers. Floristically, parrotbill preferred areas with higher densities of 'ōlapa, kawa'u, and 'alani. Overall species diversity also was significantly higher in used areas. Unused areas had higher densities of shrubs particularly pūkiawe and higher densities of small trees, particularly 'ōhi'a. Based on this data set, koa was not a significant indicator species of parrotbill use in either used or unused areas at the macrohabitat scale. In fact unused areas had greater densities of koa than used areas. However, this does not preclude the importance of koa at the microhabitat scale, see below.

These data suggest that at the macrohabitat scale, parrotbill are selecting habitat in well developed native forest, with high species diversity and are avoiding areas with dense small-stature trees and shrubs. Diverse forest structure and species composition may serve as proximate cues for home range use. Well developed forest may reflect a need for large mature trees for nesting, singing/song posts, protection from harsh windward showers, as well as a proxy for habitat with ample foraging opportunities.

Previous researchers have noted parrotbill utilize the canopy and subcanopy trees for nesting (Lockwood et al. 1994, Simon et al. 1997) and forage primarily in the understory and subcanopy layers (Mountainspring 1987, Simon et al. 1997), indicating the importance of all three vegetation strata for this species. Parrotbill may also assess home range areas indirectly for food and/or nesting resources by using cues such as large trees and dense vegetation as correlates of prey abundance or nesting habitat, a concept known as the structural cues hypothesis (Smith and Shugart 1987).

MICROHABITAT

At the 1-m scale, no species was a significant indicator of parrotbill foraging; suggesting birds may initially react to a suite of plant species, and not just one particular plant. This may be related to fluctuations in invertebrate abundance throughout foraging sites, as well as temporal changes associated with plant species phenology throughout the year (Swezey 1954). Selecting sites with an assortment of plant species may help to offset competition from other native and non-native insectivorous species. In montane rainforest, Maui Parrotbill are frequently sympatric with Maui 'Alauahio, the only other primarily insectivorous honeycreeper endemic to Maui. Although I did not formally survey for 'Alauahio, they were readily observed throughout the study site, as were two prolific non-native insectivores, the Japanese White-eye (*Zosterops japonicus*) and Japanese Bush-Warbler (*Cettia diphone*). These other insectivores however, primarily glean, rather than excavate during foraging so their dietary overlap may be minimal.

At the smallest scale (0-m), differences between used and unused plots were largely driven by the presence of 'ōhi'a, the most abundant species in the study site. Parrotbill avoided foraging in areas of dense 'ōhi'a. Mountainspring (1987) found similar associations.

Maui Parrotbill selectively foraged on specific plant species, tree size class and vertical height tier in Manawainui. Preferential use of these vegetation variables may reflect parrotbill morphology and behavioral ecology, foraging in areas that are energetically most profitable (MacArthur and Pianka 1966). Other researchers have found that foliar architecture of certain tree species, as well as foraging height and vegetation density can strongly influence foraging success in passerines (Robinson and Holmes 1984). Preferential use of certain plants and foraging substrates in an area may indicate greater food resource availability in that patch type (Hutto 1990). Rosenberg (1990) demonstrated that birds will allocate their foraging time between different habitat types as resource abundance levels change, selecting for the most profitable foraging areas. Thus, birds may select some plants because of the expected quantity of prey, and ignore those sites or species which are less predictable (Sipura 1999, Olsson et al. 2001).

At the microhabitat scale, I found preferential use of four plant genera in our study area, koa, 'ōlapa, 'alani, and 'ākala. This corroborates the findings of Mountainspring (1987), who studied parrotbill on windward east Maui. At this level of analysis I found preferential use of koa, not detected at the larger macrohabitat scale. This corroborates the findings of Perkins (1903), who suggested that parrotbill preferred this canopy tree as a foraging substrate. In addition, the 'Ākiapōlā'au, utilizes koa extensively (Pratt et al. 2001a, Pejchar et al. 2005). Pejchar (2004) documented preferential habitat use by 'Ākiapōlā'au in which they selectively foraged in young koa, despite its low abundance. Evidence for preferential use of koa however, does not preclude the significance of other plant species for parrotbill foraging, as preference for foraging substrates may be seasonal and/or associated with fluctuations of prey biomass (Simon et al. 1997, Berlin et al. 2001). Olsson et al. (2001) found that preferential use of tree species by Lesser Spotted Woodpeckers (*Dendrocopos minor*) within territories over the course of one year was a direct result of prey abundance in those territories. Preferential use of trees species between years however, was a direct result of the fluctuations of one particular invertebrate which was intricately tied to the phenology of several plant species.

Parrotbill foraged on 'ākala with similar intensity as koa, despite it having the lowest availability of any of the plant species the birds utilized. 'Ākala likely provides necessary specific arthropod food resources not sufficiently available in the other plant species. Dying or dead stems of akala are relatively soft and easy for parrotbill to excavate wood boring larvae. Simon et al. (1997) also noted the importance of 'ākala to parrotbill, particularly during the fall and winter months, although I noted the birds in this study utilizing 'ākala during the spring and summer as well. 'Ākala was scarcely distributed throughout Manawainui and further investigation into the relevance of this plant species is needed.

Maui Parrotbill selectively foraged on small trees in the subcanopy and canopy layers, using medium trees and the understory layer less than expected. Smaller trees may allow parrotbill to rapidly search an area for potential food resources, may harbor higher quantities of invertebrates per area than larger tree size classes, and often are composed of 'ōlapa, a favored plant species. Canopy structure can also influence availability of prey as well as affect a bird's ability to detect and capture prey and to hide from predators (North et al. 1999). Fretz (2002) found that lower canopy densities resulted in lower food availability for another endangered honeycreeper, the Hawai'i 'Akepa (*Loxops coccineus*).

Given that parrotbill appear to be relatively sedentary foragers, overall forest density could influence their choice of foraging sites and habitat. VanderWerf (1993), found that sites with higher foliage density were preferred by 'Elepaio (*Chasiempis sandwichensis*), possibly because denser vegetation structure may have facilitated prey capture, or protection of birds from predators. Other researchers have noted that foliar structure, such as multi- versus single-layered leaf patterns, also may influence a bird's ability to detect and capture prey (Robinson and Holmes 1984, Holmes 1990). They found that birds adjusted their foraging search radii according to different foliage density levels among the various vegetation strata and hypothesized that vegetation density and dispersion affected how many leaves could be searched from a given perch, influencing search patterns and time allotment. Vegetation density and stratification could similarly affect the parrotbill, a species that forages actively and deliberately, making infrequent flights among foraging patches and vertical height tier.

This study focused on attributes of foraging sites. I did not address vegetation attributes of nest site selection, an area of interest which merits further investigation. Nests for Maui Parrotbill have been primarily located in canopy 'ōhi'a trees (Lockwood et al. 1994, Simon et al. 1997, Simon et al. 2000) suggesting the importance of this species. While smaller trees such as 'ōlapa may be important for foraging, as the results of this study suggest, larger trees such as 'ōhi'a may fill other necessary roles in the ecological niche of the parrotbill.

The combined findings of macro and microhabitat suggest parrotbill respond to habitat at different spatial scales and highlight the importance of hierarchical assessments of habitat use for this species. In Hawai'i, at least two other insectivorous species have been shown to exhibit hierarchical habitat use. VanderWerf (1993) found foraging 'Elepaio preferred areas with dense foliage at all but the broadest of scales measured, possibly signaling more foraging opportunities in this vegetation type. Similarly, the Hawai'i 'Akepa has been found to prefer areas with dense canopy, likely due to higher food availability (Fretz 2002). In a study on insectivorous bark gleaning species, Adams and Morrison (1993) found that Red-breasted Nuthatch (*Sitta canadensis*) and Brown Creepers (*Certhia americana*) needed forest stands diverse in both vegetation structure and plant species composition. They found both species avoided areas dominated by dense small trees, open canopy, as well as areas lacking understory and low overall diversity of stand structure and species composition. As in this study, birds preferred mature forest with high species diversity and greater structural variation, in order to maintain habitat requirements throughout the year.

The habitat use patterns in this study mirror those documented by other researchers (Cody 1985, Rotenberry 1985, Wiens et al. 1987); parrotbill made initial broad scale decisions based on vegetation structure, and then further refined habitat use at smaller scales based on plant species composition.