ECOLOGY, BEHAVIOR, AND CONSERVATION OF THE MAUI PARROTBILL[1]

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Abstract. The distribution, habitat response, sexual dimorphism, foraging, breeding, and flocking behavior of Maui Parrotbills (*Pseudonestor xanthophrys*) were studied over a five year period. The species' present range is confined to montane rainforest on eastern Maui, but dry lowland habitats on Maui and Molokai were occupied before Polynesian contact.

Birds occurred from 1,250 to 2,150 m elevation, becoming most abundant at 1,750 to 2,000 m. In Kipahulu Valley, birds moved to lower elevations in some seasons. Maui Parrotbills associated with areas where vegetation was less disturbed from feral pig activity. Activity areas had more developed understories and more open canopies than nonactivity areas.

Birds tended to forage in the subcanopy and understory, with 66% of the prey captured 1 to 5 m above ground. Plant species use deviated from expectations based on availability. The most frequent means of prey capture was excavation for timber-boring insects in dead branches on live plants. Foraging accounted for 39% of the diurnal time budget; an average prey item appeared to account for 1% of the daily energy intake. Male birds had longer, more deeply hooked bills than females, and tended to excavate to greater depths. Sexes differed in tree species use and foraging maneuvers, but not in substrate use or foraging height.

The principal limiting factors appeared to be habitat loss, avian disease, habitat degradation, predation, and competition from exotic species. Control of pig populations is a needed management action.

Key words: Activity budget; endangered species; flocking behavior; foraging behavior; habitat selection; Hawaiian Islands; Maui Parrotbill.

INTRODUCTION

The Hawaiian honeycreepers (Drepanidinae) offer striking examples of adaptive radiation in bill morphology from a single colonizing ancestor. Specialized morphological and behavioral adaptations for feeding on seeds, nectar, insects, fruit, bird eggs, and molluscs span the range of passerine variation. The Maui Parrotbill (*Pseudonestor xanthophrys*), a fascinating but poorly known honeycreeper, is a fairly small (length 140 mm) bird distinguished by a disproportionately large parrot-like bill used to excavate borers from timber. The sexes exhibit an extreme example of bill dimorphism among the honeycreepers (Amadon 1950).

The Maui Parrotbill has apparently retreated from over 95% of its original range (Scott et al. 1986). Despite its striking appearance and approachability, the species was not recognized by 19th century Hawaiians (Munro 1944). Early natural history accounts (Perkins 1895, 1903; Henshaw 1902) were followed by a half-century of neglect, and the species was feared extinct until rediscovered in 1950 (Richards and Baldwin 1953). Other sightings have since been made in the remote montane rainforests of East Maui (Banko 1968; Casey and Jacobi 1974; Shallenberger 1974, 1981; Scott and Sincock 1977; Conant 1981; Carothers et al. 1983; Scott et al. 1986), but little more has been learned of its natural history. A major survey conducted in 1980 on the distribution and abundance of forest birds on Maui, the Hawaii Forest Bird Survey (HFBS), estimated the population of the Maui Parrotbill to be 500 birds (95% confidence interval, 270 to 730), with a geographic range of 50 km[2] (Scott et al. 1986). The species has federal status as an endangered species (U.S.F.W.S. 1983), and studies of its natural history are essential in determining appropriate management actions and priorities to ensure its survival (Kepler et al. 1984).

The objectives of this report are to quantitatively describe aspects of the natural history of

the Maui Parrotbill, particularly its niche, habitat, and behavior, and to discuss its limiting factors, and management needs. This study combines intensive field work during 1980 to 1985 with analyses of museum specimens, literature reports, and unpublished HFBS data.

STUDY AREAS

THE HFBS STUDY AREA

Native bird populations and general habitat structure were surveyed in all areas of native upland forest on Maui during the HFBS. Four major habitat types occurred within the range of the Maui Parrotbill. A mesic to wet forest type, dominated by koa (*Acacia koa*) and ohia (*Metrosideros polymorpha*), occurred along the lateral margins of the main ohia rainforest of northeast Haleakala. This wet ohia forest had an upper strip adjacent to the treeline of mesic ohia forest that was shorter in stature, somewhat drier, and poorer in tree species than areas below. Above the treeline a mesic subalpine scrub community marked the lower boundary of a thermal inversion layer.

For this paper, the range of the species was divided into four contiguous units (Fig. 1). Elevational boundaries of each unit were determined by the highest and lowest Maui Parrotbill records in the area. The Waikamoi unit extended from the pasture-forest boundary north of Hosmer Grove to the east edge of Koolau Gap on the north slopes of Haleakala, and contained mesic subalpine scrub and mesic ohia, wet ohia, and koa-ohia forest. The Wailua unit which extended east from Koolau Gap to the west fork of Hanawi Stream, and the Hana unit which extended from Hanawi Stream to the north headwall of Kipahulu Valley contained subalpine scrub and mesic and wet ohia forest. The Kipahulu unit was defined by the headwalls of Kipahulu Valley and contained mesic ohia, wet ohia, and at lower elevations koa-ohia forest. Additional areas outside the Maui Parrotbill range were surveyed on windward East Maui at elevations below the known range, and over a wide variety of habitats at Waihoi Valley, Kaumakani, Manawainui Planeze, Haleakala Crater, Kaupo Gap, Kahikinui, Auwahi, Kula, and the West Maui Mountains.

THE HANAWI STUDY AREA

Studies were conducted intermittently from 1980 to 1985 on the 50-ha Hanawi study area (Fig. 1),

extending from 1,825 to 2,175 m elevation between the forks of Hanawi Stream in the Koolau Forest Reserve, and located in an area of high Maui Parrotbill density. Topography in the area is rugged and steep, with an average slope of 40% on ridges. During May 1981, the daily mean temperature at dawn was 7°C, the mean afternoon high was 18°C, and the overall 24 hr mean was 11.2°C. Temperatures of −4°C occurred in January 1985. Annual rainfall at 2,000 m elevation in the area averages 500 cm, well distributed throughout the year, except for irregular 6 to 10 week periods of low rainfall (Blumenstock and Price 1967).

At the upper limit of the study area, small patches of alpine grassland dominated by *Deschampsia australis* and *Holcus lanatus* lie imbedded in mesic subalpine scrub composed of *Vaccinium reticulatum*, *V. berberifolium*, pukiawe (*Styphelia tameiameiae*), kukae-nene (*Coprosma ernodeoides* var. *mauiensis*), pilo (*C. montana*), and the fern *Sadleria cyatheoides*. The subalpine scrub gradually gives way to mesic ohia forest at 2,070 m elevation, which grades into wet ohia forest at 2,000 m elevation. The forest canopy is dominated by ohia; the major subcanopy trees are olapa (*Cheirodendron trigynum*), kolea (*Myrsine lessertiana*), pilo (*Coprosma ochracea*), alani (*Pelea clusiaefolia* and *Pelea* undescribed species), kawau (*Ilex anomala*), oheohe (*Tetraplasandra kavaiensis*) at lower elevations, and hoawa (*Pittosporum confertiflorum*) near the treeline. The major shrubs in the forest are ohelo (*Vaccinium calycinum*), naenae (*Dubautia plantaginea* and *Dubautia* undescribed species), akala (*Rubus hawaiiensis*), kanawao (*Broussaisia arguta*), and pukiawe. Henrickson (1971) described the flora of the area in detail. Feral pigs (*Sus scrofa*) have caused moderate to severe damage to the dense understory.

METHODS

LARGE-SCALE SURVEY

The sampling design, field methodology, statistical analysis, and general results of the HFBS were described in Scott et al. (1986). Transects were systematically positioned at 1.6 to 3.2 km intervals on Maui in native forest bird habitat. Stations were placed 135 m apart along the transects and sampled once in May to August 1980. At each station observers conducted 8-min counts, recording distances to all birds detected,
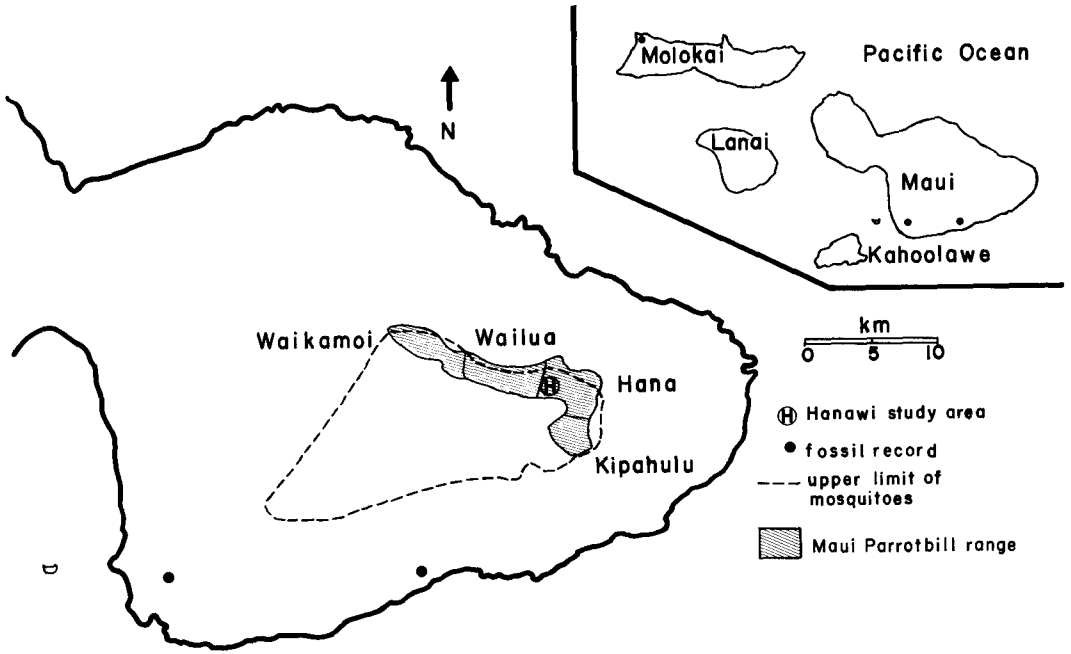
FIGURE 1. Location of Hanawi study area, four range units used in analysis, fossil records, and upper elevational limits of mosquitoes (from Scott et al. 1986).

and botanists recorded habitat structure and pig damage to the vegetation. Incidental observations of Maui Parrotbills and other endangered species along the transects, outside the systematic sampling periods, were also noted. Pig damage was classified into five general categories based on a variety of native and exotic indicator plants that differed in sensitivity and response to pig damage. The categories constituted a monotonic scale in the order: none, slight, moderate, heavy, and severe. A general vegetation map showing the habitat types in the survey area was constructed using field notes and aerial photographs.

In this report, the elevation and contour range limits for the geographic distribution of the Maui Parrotbill were inferred from HFBS records and the vegetation map. The census stations lying within the range were used to characterize the expected distribution of the Maui Parrotbill with respect to elevation, geographic area, habitat type, and pig damage. The data for characterizing the observed distributions for these variables were the appropriate subsets of records for station counts and incidental observations: all records were used to characterize geographic distribu-

tion, but for the elevation, habitat type, and pig damage distributions, the records used were those where the birds were within 50 m of the station or where the habitat of the bird was unequivocal. Records of distant calling birds were excluded from the habitat analysis because they may have occupied different habitats than at the station. This method of analysis differs from that in Scott et al. (1986) which included distant birds in the habitat analysis and density estimate for each station; consequently, results in this report are presented as birds per station rather than per unit area.

HABITAT DESCRIPTION

I sampled habitat characters in the Hanawi study area at 28 randomly placed points. The points were located in the field by using a 1:24,000 U.S. Geological Survey topographic map, an infrared aerial photograph, and landmark features. I recorded crown cover, canopy height, areal coverage, and average height for individual plant species, and the foliage height profile (vertical profile of foliage distribution) in a 50-m radius around each sample point. The foliage height

profile was obtained by optically estimating the percent areal foliage coverage in 1-m height intervals. Sample points were classified as "activity areas" and "nonactivity areas." A particular sample point was interpreted as being an activity area if Maui Parrotbills were observed making at least five prey captures within 50 m of the point within a two-day period; other points where feeding was not observed to this extent were interpreted as nonactivity areas. In addition to activity areas found among the 28 points, I also characterized the habitat at nine other sites in the Hanawi study area where Maui Parrotbills were observed foraging extensively.

The habitats of activity and nonactivity areas were compared through a stepwise discriminant function analysis of crown cover, canopy height, and plant species coverages (see Martinka 1972), using a multiple regression algorithm with zero assigned to nonactivity areas and one to activity areas.

FORAGING BEHAVIOR

Most foraging observations were made in the Hanawi area, but 20% of the observations came from other sites. Data on foraging were gathered for as long as a bird was in view, with 1 to 15 maneuvers recorded per bird. Concealing habitats such as the upper canopy, dense brush, and ravines were carefully searched to reduce bias toward conspicuous birds. Associated birds were noted. Time intervals between perch changes for Maui Parrotbills and associated Maui Creepers (*Paroreomyza montana*) were recorded on randomly selected focal individuals (Altmann 1974) using a watch with a sweep second hand. Each maneuver that appeared to result in a prey capture (or food intake in the case of frugivory) was characterized by the height of the bird above ground, plant species, prey substrate, living/dead condition of both plant and substrate, and maneuver type. Maneuver types were classified as excavating (stripping bark and digging into woody substrates), twig-splitting (cracking open a twig by forcibly closing the mandibles on it), gleaning (picking from a surface), probing (inserting bill into a floret or leaf cluster), or plucking (picking and eating a fruit). Fruits cut or crushed open to obtain insects were classified as excavated. Where possible, the foraging site was examined, and depth of the excavation measured with a dull probe. I attempted to determine the identity of

prey items by extracting additional material at these sites and from identical burrows on the same plant, and by matching prey burrow characteristics with published accounts. Insects extracted from boring sites were referenced to a monograph on the insect faunas of Hawaiian tree species (Swezey 1954).

The sex of foraging birds was determined when light conditions were adequate. Males were identified by their large bill, bright yellow superciliary line, olive back, warm yellow underparts, and larger size. Females were identified by their smaller bill, dull yellow superciliary line, grayish back, olive-washed underparts, and smaller size. In specimen series these differences were fairly obvious. Data from immature birds were not included in male/female comparisons. Immatures usually resembled small drab females and were poorly represented in collections. Although immatures were readily identifiable in family groups, I may have incorrectly identified a few lone immatures as adult females because of their somewhat similar appearance, and because the timing and sequence of postjuvenal molt is unknown.

General foraging patterns and sexual differences were characterized from data collected throughout the range, but only data collected in the Hanawi study area were used in comparing foraging substrates with available habitat. The relative availability of different plant species as foraging sites was calculated as follows: (1) an index of the biomass and foliage volume of each tree species at each sample point was constructed by multiplying the areal coverage by the average height for that species; (2) the biomass indices at each sample point were proportioned to add to 100%; and (3) the mean relative availability was calculated across all points classified as activity areas.

TIME BUDGETS AND ENERGETICS

Diurnal time budgets were estimated using watches with a sweep second hand or a digital second readout to record the duration of each activity of continuously observed birds on the Hanawi study area. Activities were classified into these mutually exclusive categories: quiet perching, pedal locomotion (hopping, climbing), flight, foraging, self-maintenance (bill wiping, scratching, defecating), and vocalization. I attempted to differentiate foraging activity into active visual
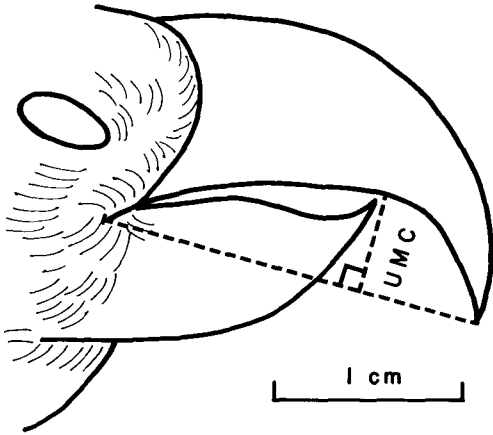
FIGURE 2. Measurement of upper mandible curvature (UMC).

searching, actual prey excavation (including twig-splitting and gleaning), and processing after capture.

Energy expenditure in kcal/day was estimated by using the regression equation of Kendeigh (1970) for body mass (24-g male, 17-g female) and mean ambient temperature (11.2°C). The net energy intake for prey items captured by excavation was calculated from borers extracted from feeding sites and nearby sites of similar appearance.

MORPHOLOGY

Morphological dimensions were measured on specimens in the Bernice Pauahi Bishop Museum, Honolulu, the American Museum of Natural History, New York, and the Academy of Natural Sciences, Philadelphia, following the procedures of Baldwin et al. (1931). Measurements were made of the culmen (length to feather bases), length of the lower mandible along the midline, width and depth of the upper mandible at the nares, upper mandible curvature (maximum perpendicular distance from the cutting edge to a plane positioned across the gape and intersecting the bill tip; see Fig. 2), wing length along the chord, length of middle tail feathers, tarsal length, length of middle toe without claw, and length of hind toe claw. I estimated the body mass of Maui Parrotbills by regression. The equation, Body Mass (g) = $-53.9 + 1.026$ Wing (mm), $r = 0.95$, was calculated from the live masses of five species on the island of Hawaii in

the tribes Psittirostrini and Hemignathini that ranged from 10 to 40 g, and from the wing arc lengths given in Amadon (1950). Regressions to other body dimensions (culmen, tarsus, tail) and nonlinear effects gave equivalent or poorer fits. Wing length was used because of its high reproducibility. This procedure gave a predicted mean body mass of 24 g for male birds and 17 g for females, with a standard error of estimate of 1 g. The mass of a male bird mist-netted in March 1984 in Kipahulu Valley was 20 g (M. A. Stemmermann Kjargaard, pers. comm.).

RESULTS

DISTRIBUTION

In the present study, Maui Parrotbills were found to be restricted to montane rainforest on the northeast slopes of Haleakala, with the distributional range centered on the eastern Wailua and Hana units (Fig. 3). The HFBS sampled 203 stations in range and recorded 30 systematic and 11 incidental detections of individual birds. The distribution of records in each unit will be discussed below.

In the Waikamoi unit, eight sightings were made during the 1980 to 1984 period in mesic ohia, wet ohia, and koa-ohia forest. The 1980 HFBS recorded only two birds on the 43 stations surveyed in this portion of the range, suggesting that densities in this unit were lower than in areas east of Koolau Gap. On 3 May 1984 at 1,585 m elevation I observed a female bird in koa-ohia forest only 400 m from the open range boundary to the west. No family groups have been recently observed in the Waikamoi unit, suggesting that breeding may be sporadic west of Koolau Gap. Around 1900, Maui Parrotbills were observed primarily in koa-ohia forest in the Waikamoi unit (H. Palmer in Rothschild 1893–1900; Perkins 1895, 1903; Henshaw 1902), probably including areas that have since been deforested. These early observers considered the species to be rare and local, and were apparently unaware that the species also occurred in ohia forests to the east (Banko 1968).

Owing to its remoteness, the Wailua unit has seldom been visited by ornithologists. Maui Parrotbills occurred in mesic and wet ohia forest in this area. The HFBS recorded 16 birds on the 47 stations in range, with densities in the eastern portion of the unit (13 birds on 30 stations) apparently being the highest in the range of the
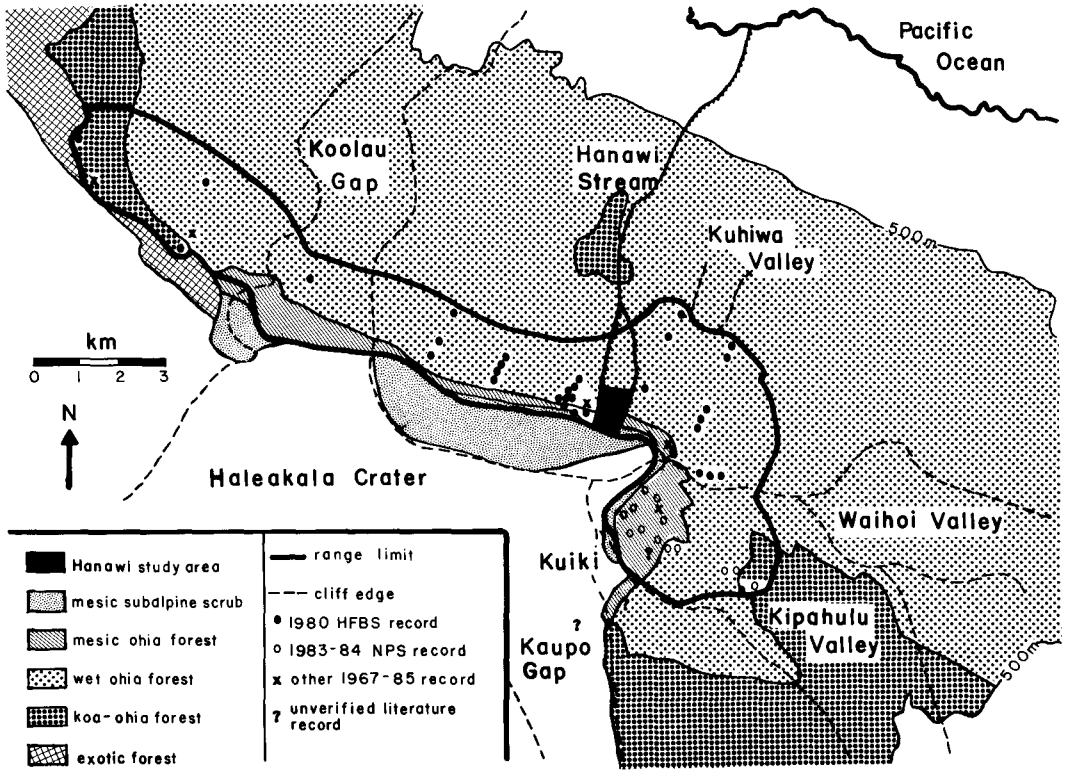
FIGURE 3.   Range of the Maui Parrotbill, showing recent records and habitat types.

species. The only previous published record from this area was by Richards and Baldwin (1953). Family groups were found 0.8 to 1.0 km north and northeast of Puu Alaea in April 1979 (T. A. Burr, pers. comm.) and June to July 1980.

In the Hana unit, the HFBS recorded 11 birds on the 57 stations in range, and in the Hanawi study area I recorded 6 birds on 28 stations in May 1981. Frequent visits by trained observers to the Hanawi and Wai Anapanapa areas have resulted in numerous sightings (Casey and Jacobi 1974, Shallenberger 1974, Scott and Sincock 1977, Conant 1981, Carothers et al. 1983, Conant and Stemmermann Kjargaard 1984, Scott et al. 1986). Family groups were found above Kuhiwa Valley in May 1980 and in the upper Hanawi area in June 1974 (T.L.C. Casey, pers. comm.), June to July 1983, July 1984, May 1985, and November 1985. Maui Parrotbills appeared to have their greatest elevational range in the Hana unit, occurring from 1,300 to 2,150 m, in

mesic subalpine scrub, mesic ohia forest, and wet ohia forest.

Maui Parrotbills were first noted in the Kipahulu unit by Palmer in 1892, presumably around 1,000 to 1,300 m elevation in koa-ohia forest (Rothschild 1893–1900). Only one bird was sighted during the 1967 Kipahulu Valley expedition, at 2,000 m elevation in mesic ohia forest (Banko 1968), and the HFBS recorded one bird on 56 stations in range, at 1,825 m elevation in mesic ohia forest. Conant (1981) failed to find the species below 1,980 m elevation in the valley, except for an unverified aural detection of a bird at 1,700 m elevation near the south wall (Conant and Stemmermann 1980). Despite this apparent rarity and restriction to higher elevations in Kipahulu Valley, however, expeditions in March 1983, July 1983, and March 1984 by the National Park Service reported 13 sightings of individual birds and family groups, from 1,250 to 2,070 m elevation in mesic ohia, wet ohia, and
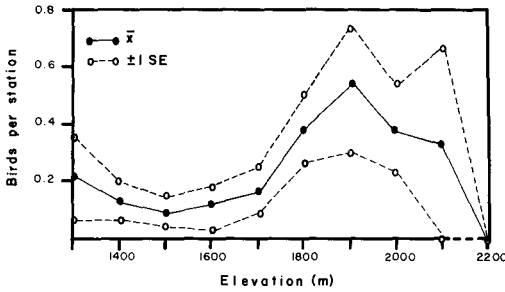
FIGURE 4.   Elevational distribution of the Maui Parrotbill (1980 HFBS data).

TABLE 1.   Distribution of Maui Parrotbill records with respect to pig damage categories.

Damage category	Stations in range	Maui Parrotbill records
None	22	3
Slight	48	12
Moderate	61	6
Heavy	58	4
Severe	14	0

koa-ohia forest (C. P. Stone and P. C. Banko, unpubl. data). These sightings indicate that birds move down into Kipahulu Valley in some years, probably from the Hana unit. A similar movement into the area in 1978 to 1979 was noted for Crested Honeycreepers (*Palmeria dolei*) (Conant 1981).

The only historical records of Maui Parrotbills outside the range described above were a secondhand report of a single bird in Kaupo Gap in 1928 (Munro 1944), and an unverified aural detection at 2,000 m elevation near Kuiki Peak (Conant and Stemmermann 1980). Maui Parrotbills probably occur at least occasionally in the ohia and koa-ohia forests between Kaupo Gap and Kipahulu Valley on the Manawainui Planeze and Kuiki Peak, although recent surveys failed to find them there (Stemmermann 1976, Scott et al. 1986).

Based on vegetation remnants and historical accounts (Rock 1913:21–22), the leeward southern and northwestern slopes of Haleakala (Kahikinui, Auwahi, and Kula areas) formerly supported a variety of dry to mesic forests that were probably inhabited by Maui Parrotbills before human contact in ca. 400 A.D. Subfossil remains have been found at 200 m elevation in the Kahikinui area and at 300 m elevation in Puu Naio (H. F. James, pers. comm., Fig. 1). Even more significant were a fossil quadrate and mandibular ramus with articulation dated about 3,000 B.C. found in dune deposits near Ilio Point on west Molokai (Olson and James 1982b). Drier low elevation forests originally supported a rich flora and avifauna, but Hawaiians burned and cleared extensive areas of these forests, causing large-scale extinctions and range truncations among the native biota (Zimmerman 1948:172, Kirch 1982, Olson and James 1982a). The original range

of the Maui Parrotbill probably included extensive areas of dry forest on Maui, Molokai, and possibly Lanai and Kahoolawe. Pleistocene connection of these islands (Stearns 1966) would have facilitated such a distribution.

LARGE-SCALE HABITAT RESPONSE

Recent records of Maui Parrotbills were distributed from 1,250 to 2,150 m elevation. The HFBS data showed that the birds were three times as abundant at 1,750 to 2,000 m elevation as at 1,400 to 1,750 m (Fig. 4). In Kipahulu Valley and perhaps elsewhere, substantial year-to-year differences occurred in elevational distribution that may have represented some seasonal movement.

About 80% of the range was wet ohia forest, 14% mesic ohia forest, 5% mesic koa-ohia forest, and 1% mesic subalpine scrub. Habitat type was determined for 35 Maui Parrotbill records made during the HFBS. The habitat types of these records were compared with the habitat of all stations in the geographic range; no significant difference (Kruskal-Wallis test, $P > 0.75$) was found in the frequency of occurrence in the three principal habitat types that constitute 99% of the range. Maui Parrotbills occurred infrequently in the fourth habitat type, the subalpine scrub immediately above the treeline. Throughout the range, both overstory and understory were dominated by native plant species. Maui Parrotbills were absent from areas adjacent to the range in the Waikamoi unit that were dominated by exotic trees.

Pig damage to the vegetation structure in the range of the Maui Parrotbill varied from virtually none to severe, with 82% of the HFBS stations falling in the three intermediate categories (Table 1). Comparing this spectrum with actual occurrences of Maui Parrotbills in the vicinity of rated stations showed that the species
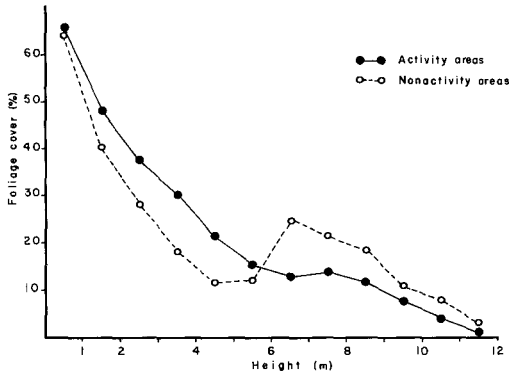
FIGURE 5. Mean foliage height profiles in activity areas and nonactivity areas in the Hanawi study area.

tended to occur more frequently in areas with less pig damage (Mann-Whitney U-test, $P < 0.05$), with 84% of the records falling in the three lightest categories of pig damage. Occasionally birds did occur in areas of heavy to severe damage.

SMALL-SCALE HABITAT RESPONSE

In the Hanawi study area, 15 activity areas and 22 nonactivity areas were identified from systematic surveys and incidental observations of foraging birds. In both types of areas, ohia dominated the canopy; pilo, olapa, ohelo, and pukiawe the understory; and graminoids and ferns

the ground cover (Table 2). Activity areas tended to have greater ohelo cover, less ohia, pukiawe, and akala cover, and greater canopy height than nonactivity areas, as shown in a stepwise discriminant function analysis ($F = 6.04$; df = 5, 31; $P < 0.001$). Two a posteriori divisions of plant coverage were significant: no activity area had <10% ohelo cover, but 10 nonactivity areas did ($\chi^2 = 9.3$, df = 1, $P < 0.01$); no activity area had >65% ohia cover, but 10 nonactivity areas did ($P < 0.01$).

The vertical distribution of foliage in activity areas had greater understory and less canopy foliage than in nonactivity areas (Fig. 5). For 1-m height increments, foliage volume in the 0- to 6-m height interval averaged 41% greater in activity areas compared to nonactivity areas ($\chi^2 = -2 \ln P = 33.4$, df = 12, $P < 0.001$), and in the 6- to 12-m interval 41% less ($\chi^2 = 24.9$, df = 12, $P < 0.02$). Maui Parrotbills thus tended to utilize areas with more developed understories and more open canopies.

Incidental observations suggested that Maui Parrotbills were relatively sedentary in their daily movements. In the Hanawi study area, I tracked individual birds and family groups during breeding and nonbreeding periods for as long as 2 hr and found that birds tended to stay within areas 200 to 300 m in diameter. On subsequent days, what appeared to be the same birds or family groups were found in the vicinity of the last sight-

TABLE 2. Cover and height characteristics of activity and nonactivity areas.

| | Height (m) | | Plant cover (%) | | | | Discriminant function (t-statistic) |
| | | | Activity areas | | Nonactivity areas | | |
Habitat component	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	
Canopy height (m)	—	—	9	2	10	3	2.49
Crown cover	—	—	57	17	57	29	—
Woody plants							
Akala	1.6	0.4	9	8	16	19	−2.98
Alani	3.3	1.6	2	3	2	3	—
Kanawao	1.6	0.4	1	2	3	7	—
Kawau	4.3	1.7	1	2	1	2	—
Kolea	3.3	1.5	2	3	2	4	—
Naenae	2.0	1.0	1	2	2	4	—
Ohelo	3.1	0.9	17	8	10	6	2.01
Ohia	8.7	2.3	40	18	52	30	−3.54
Olapa	3.1	0.9	12	15	10	7	—
Pilo	2.9	1.1	20	16	18	15	—
Pukiawe	2.6	0.8	11	14	17	18	−3.50
Ground cover							
Ferns	0.6	0.4	36	17	34	18	—
Graminoids	0.2	0.1	22	17	25	15	—

TABLE 3. Prey captures of the Maui Parrotbill by substrate and maneuver.

Category	Live					Dead-on-live		Dead	Total
	Branch	Twig	Leaf	Flower	Fruit	Branch	Twig	Branch	
Plant species									
Ohia	28	5	5	3	—	43	3	7	94
Olapa	4	9	4	—	—	22	15	2	56
Ohelo	5	24	8	—	9	4	—	—	50
Pilo	4	15	8	—	3	16	—	—	46
Kanawao	—	—	—	—	25	—	1	—	26
Alani	3	—	—	—	—	18	2	—	23
Kolea	3	4	—	—	—	8	1	—	16
Koa	2	1	8	—	—	—	—	—	11
Oheohe	4	2	2	3	—	—	—	—	11
Akala	—	2	—	—	—	—	2	—	4
Kawau	2	—	—	—	—	—	2	—	4
Naenae	1	1	1	—	—	1	—	—	4
Hoawa	—	—	—	—	—	2	—	—	2
Manono	—	—	—	—	—	—	2	—	2
Pukiawe	—	—	—	—	—	1	—	—	1
Maneuvers									
Excavating	30	—	—	—	28	106	—	9	173
Gleaning	26	44	28	3	—	9	—	—	110
Twig-splitting	—	19	—	—	—	—	28	—	47
Probing	—	—	8	3	—	—	—	—	11
Plucking	—	—	—	—	9	—	—	—	9
Total	56	63	36	6	37	115	28	9	350

ing. Perkins (1895) too noted that the birds did not make long-distance flights. If the interpretation of relative sedentariness is accurate, then it seems reasonable to conclude that Maui Parrotbills actively select the most suitable habitat sites in an area to concentrate their foraging efforts. They may thus be more sensitive to adverse local habitat modification than species that regularly move several kilometers on a daily basis, such as the Iiwi (*Vestiaria coccinea*), Crested Honeycreeper, or Apapane (*Himatione sanguinea*).

FORAGING SUBSTRATES

Maui Parrotbills foraged mostly in the subcanopy and understory at a mean height of 3.7 ± 2.4 SD m ($n = 289$) above ground; 4% of the prey captures were at 0 to 1 m height, 54% at 1 to 3 m, 16% at 3 to 5 m, 22% at 5 to 8 m, and 3% above 8 m. For heights > 1 m in the Hanawi study area, the height distribution of foraging did not differ significantly from the height distribution of foliage in activity areas (Kolmogorov-Smirnov test, $P > 0.05$), suggesting that foraging was random with respect to available foliage volume at different heights.

Maui Parrotbills captured prey on virtually all

major woody species present (Table 3). The most frequently visited species was the dominant tree, ohia (27%), but 70% of the prey captures were made on subcanopy trees and understory shrubs, especially olapa, ohelo, pilo, alani, and kanawao. In addition to the species in Table 3, Maui Parrotbills have also been reported to feed on olomea (*Perrottetia sandwicensis*) (Berger 1981). Henshaw (1902) and Perkins (1903) found that birds fed extensively on koa trees, probably reflecting the many borers associated with koa (Swezey 1954) and the location of their observations in koa-ohia forest in the Waikamoi unit.

Compared to available plant biomass in the Hanawi study area, Maui Parrotbills fed on ohia 50% and on pukiawe 93% less often than expected, but they fed on olapa 89%, ohelo 44%, and pilo 36% more often than expected (Chisquare tests, $P < 0.05$, Table 4). The most striking preferences were for the relatively uncommon alani and kolea, where feeding was 10 and 5 times more frequent than expected, respectively. Perkins (1903) also noted frequent use of alani. The apparent feeding preferences probably reflected the abundance of timber-boring insects. For example, several timber-borers that infested pilo left characteristic holes in dead branches of

TABLE 4. Distribution of prey captures by plant species on the Hanawi study area compared to biomass indices in activity areas; * indicates $P < 0.05$ ** $P < 10^{-5}$.

Plant species	Prey captures (%)	Biomass (%)	x^2 difference[a]
Ohia	27	54	34.1**
Olapa	19	8	20.1*
Pilo	18	13	4.3*
Ohelo	16	11	5.6*
Alani	7	1	139.1**
Kolea	5	1	34.4*
Pukiawe	0.4	5	12.6*
All others	8	4	7.5*

[a] Calculated from a sample of 253 prey captures.

live trees, and borer sites were found on 29 of 50 mature pilo plants located within 10 m of a randomly placed transect at 2,100 m elevation. Similar high infestation levels appeared on alani trees. On the other hand, ohia trees have been reported to have relatively low densities of timber-boring insects (Gressitt and Samuelson 1981), and I seldom noted infestations on ohia in the Hanawi study area.

About 57% of the observed prey captures were made on live substrates, and 41% were made on dead substrates on live plants (Table 3). Excavating and twig-splitting presumably took more energy than other maneuvers, and 61% of these were on dead-on-live substrates. Maui Parrotbills made 51% of their prey captures on branches, 26% on twigs, and 10% on leaves. A similar reliance on branches and twigs was noted by Perkins (1903). About 54% of the prey captures on branches were made at sites with a lichen or moss cover. The prey captures made by excavating larvae from fruit (8%) were mostly observed in November 1985, when birds were exploiting infestations in kanawao fruit—on seven randomly-chosen plants at 1,650 m elevation, 50% (±27% SD) of the ripe berries had been excavated (C. B. Kepler, pers. comm.). Infrequently (2% of all observations) birds probed ohia flowers or gleaned in oheohe flowers for nectar or insects. Ripe and green fruits of ohelo and pilo were occasionally eaten (3% of observations).

FORAGING MANEUVERS

Excavating constituted 49% of all prey captures (Table 3) and was also noted by Perkins (1903) as being a common maneuver. Typically, excavating birds began by inserting their hooked upper mandible into a bark deformity, such as a small crack, crevice, or exposed borer tunnel. They quickly dug in the hook to enlarge the opening, grasped bark laterally with both mandibles, pried on the bark, and chipped or peeled off pieces of bark and wood 1 to 3 (rarely to 5) cm long. When birds uncovered a burrow, they tracked it by peeling up the bark until coming to a frass deposit, dug in with their upper mandible, and extracted the larva or pupa using their mandibles and tongue. The upper mandible was often used to plough up and scrape out old wood or to peck like a small woodpecker. The lower mandible was used mainly in conjunction with the upper to grasp bark. Branches were often stripped of their moss or lichen cover in the search for prey. On one occasion a bird fully opened its bill and then hammered with the lower mandible, followed by probing with the upper; this pattern is virtually identical to the distinctive common feeding behavior of the Akiapolaau (*Hemignathus munroi*) (Perkins 1903). Occasionally a bird dug into a site without peeling away the bark, as on dead trees with little bark, and other times peeling alone uncovered the prey. Birds sometimes assumed inverted postures while peeling or digging on the side of branches, probably for a better attack angle or foothold. Usually 30 to 60 sec was spent at an excavation site. One specimen in the Bishop Museum (#4095) has wear marks on the upper mandible that appear to have resulted from excavating or twig-splitting.

In twig-splitting (14% of observations), birds typically alit on a small branch and after 1- to 5-sec inspection grasped the twig perpendicular to the bill symmetry plane and rather quickly split it open by clamping the bill shut. Sometimes they quickly picked at the twig stub with their upper mandible or cracked the twig again farther toward the base. When splitting stubborn twigs, they frequently used strong back-and-forth movements of the head ("wrenching") for additional shearing force. Twigs were also grasped parallel to the mandibular edge and split longitudinally. Twig-splitting and wrenching struck Henshaw (1902) and Perkins (1903) as the most impressive behavior of the Maui Parrotbill.

Gleaning (32% of all maneuvers) appeared to be an opportunistic maneuver. Perkins (1903) reported that Maui Parrotbills fed caterpillars to their young during the breeding season, suggesting that gleaning may be important then. Gleaning constituted 63% of all maneuvers in July 1983

when most birds were in family groups, but only 18% in May 1981 when no signs of breeding were noted.

Probing (3% of all maneuvers) was used to explore ohia flowers and deformed, rust-infested koa leaf clusters. Plucking (3%) was used to describe fruit taking, but otherwise resembled gleaning.

Recurring patterns in search behavior suggested that Maui Parrotbills cued in on recently dead branches with loose bark and on bark deformities that indicated probable borer activity. Perkins (1903) noted that both this species and the Nukupuu (*Hemignathus lucidus*) had systematic, methodical patterns of searching for prey, suggesting the use of some sort of search image.

TIME, RESOURCES, AND ENERGETICS

The largest expenditure in the diurnal time budget (Table 5) was the time spent capturing prey by excavation and twig-splitting (39%). Pedal locomotive activity was often associated with active feeding. During active foraging Maui Parrotbills averaged 20 ± 12 SD sec between prey captures ($n = 110$), but between foraging bouts they often rested for 3 to 10 min, and quiet perching accounted for 27% of the diurnal time budget.

Maui Parrotbills often fed from dead substrates on live plants where borers were frequent. Prey items included the larvae and pupae of beetles and moths: *Plagithmysus* sp. (Cerambycidae) on ohia and alani, *Clytarlus* spp. (Cerambycidae) on koa, *Proterhinus* sp. (Aglycyderidae) on ohia, *Nesotocus newelli* (Curculionidae) on olapa, and microlepidopterans, probably *Hyposmocoma* sp. (Hyponomeutidae), on pilo, and *Heterocrossa* sp. (Carposinidae) on kanawao. The insects extracted were moderately large, generally 8 to 20 mm long. A sample of 20 borer larvae and pupae had an average mass of 0.2 g (±0.1 SD) per borer. Assuming that borers averaged 1.2 kcal/g wet weight of metabolizable energy like other insects, and that Maui Parrotbills averaged 66% assimilation efficiency like other passerines (Ricklefs 1974), an average prey item contributed approximately 0.15 kcal (±0.10 SD) to the energy budget.

Based on regression predictions, the energetic expenditure of male birds was about 18 kcal/day and females 15 kcal/day, and hence 100 to 120 average-size prey items would be needed per day, or an average of one prey excavation every 5 to 8 min, for a balanced energy budget. Although

TABLE 5.   Time budget of the Maui Parrotbill.

Behavior	Seconds	%
Quiet perching	1,642	27.3
Pedal locomotion	742	12.3
Flight	110	1.8
Foraging		
Visual searching	587	9.7
Excavating[a]	2,357	39.1
Processing	106	1.8
Self-maintenance[b]	32	0.5
Vocalization	449	7.5
Total	6,025	100.0

[a] Includes a small proportion of twig-splitting and gleaning.
[b] Bill wiping, defecating, preening, scratching.

substantial individual and seasonal variation doubtless occurs, one general basis of the slow foraging rate and long rest periods is that an average prey capture appears to yield about 1% of the daily energy requirements. The metabolic rate (and hence energy requirements) may moreover be lower than expected from the regression equation, similar to the physiological adaptation found among other Hawaiian honeycreepers to cold wet environments (MacMillen 1981).

MORPHOLOGY AND SEXUAL DIMORPHISM

Morphological adaptations that probably facilitate excavating and twig-splitting included the extremely stout, sharply decurved bill (Fig. 2) and relatively strong and well-developed legs compared to other honeycreepers (S. Mountainspring, unpubl. data). Each mandible ends in a sharp point that was frequently inserted into borer tunnels. The slight downward flaring of the cutting edge at the middle of the lower mandible appeared to bring greater shearing force to bear during twig-splitting and to improve the grasp during bark-peeling (S. Mountainspring, pers. observ.). The internal morphology is poorly known, and a few intact fluid, skeletal, and frozen tissue specimens should be collected, examined, and preserved for further study. S. L. Olson and H. F. James (pers. comm.) found that the cranial morphology of this species "is unique among passerines in being highly convergent with that of parrots and that examination of the dried jaw musculature remaining on the skull indicates that it too is peculiar."

Amadon (1950) reported that Maui Parrotbills had the most extreme sexual dimorphism in bill length of the Hawaiian honeycreepers. Males were

TABLE 6. Morphological dimensions of the Maui Parrotbill; * indicates significant different between sexes, Mann-Whitney U-test, P < 0.05.

Dimension (mm)	Male (n = 11)	Female (n = 5)	Male/ female ratio
Upper mandible length	21.5	17.4	1.24*
Upper mandible width	6.4	5.7	1.11*
Upper mandible depth	8.8	7.4	1.12*
Upper mandible curvature	4.6	3.6	1.30*
Lower mandible length	14.6	12.1	1.20*
Wing chord length	73.1	66.5	1.10*
Tail length	42.6	37.6	1.13*
Tarsus length	22.2	20.9	1.07
Middle toe length	12.8	12.0	1.07
Middle toe claw length	6.1	5.5	1.11*
Hind toe claw length	7.3	6.6	1.12*

TABLE 7. Sexual differences in the foraging behavior of the Maui Parrotbill; * indicates $P < 0.05$, ** $P < 0.001$.

Category	Percent of prey captures		Chi-square test
	Male (n = 131)	Female (n = 102)	
Plant species			45.0**
Ohia	23	23	0.0
Ohelo	22	7	8.7*
Pilo	22	5	11.7**
Olap	8	22	7.0*
Kanawao	3	22	17.6**
All others	21	23	0.0
Substrate condition			5.8
Live	73	60	1.4
Dead-on-live	23	37	4.0*
Dead	5	3	0.4
Substrate type			7.2
Branch	39	39	0.0
Twig	28	29	0.0
Leaf	18	8	4.6*
Flower	2	3	0.1
Fruit	12	21	2.5
Maneuver			20.4**
Excavating	45	49	0.2
Gleaning	31	31	0.0
Twig-splitting	9	20	4.6*
Plucking	8	0	8.6*
Probing	8	0	7.0*
Foraging height (m)			
Mean	4.2	3.5	
SD	2.5	2.1	

larger in bill, wing, tail, and pedal morphology than females (Table 6). Assuming that the male/female ratio is proportional to functional differentiation, bill length and curvature are particularly important, with males having longer, more deeply hooked bills.

Sexes differed in foraging behavior (Table 7) as to tree species ($\chi^2 = 45.0$, df = 5, $P < 0.001$) and maneuvers ($\chi^2 = 20.4$, df = 4, $P < 0.01$), but not in substrate condition (e.g., live, dead) ($\chi^2 = 5.4$, df = 2, $P > 0.05$), substrate structure (branch, twig, etc.) ($\chi^2 = 17.2$, df = 4, $P < 0.01$), or foraging height ($t = 0.9$, $P > 0.3$). Compared to females, males tended to use pilo and ohelo more, and olapa and kanawao less; females split twigs more but were not observed probing or plucking (Table 7). The depth of excavation sites also differed, with 24 male sites ranging 5 to 13 mm and 22 female sites 3 to 10 mm (Mann-Whitney U-test, $P < 0.05$). Foraging differences that were probably correlated with the larger bills of males included greater excavation depth and more frequent probing and plucking. As noted in other avian taxa, sexual dimorphism in foraging and morphology results in exploitation of a greater variety of resources and presumably reduces intraspecific competition (Selander 1966).

ANNUAL CYCLE AND BREEDING BEHAVIOR

Few observations exist of Maui Parrotbill breeding biology. On 19 May 1985 during the breeding season, I observed two males engage in aggressive behavior suggesting territorial defense. Following a spirited bout of advertising song by both birds, bird 1 dived at bird 2 and initiated a chase sequence during which both birds continued singing. Bird 2 landed, sang, and was chased again by bird 1 who tried to hit bird 2 on the nape with his upper mandible. Seconds after the chase broke up, bird 2 landed and sang. Bird 1 flew into the air 3 m above bird 2 and both sang; then, a spectacular aerial chase ensued with bird 1 singing, wielding his bill 5 to 40 cm from the head of bird 2, and repeatedly diving at and attempting to strike and grasp the head of bird 2. This episode ended as bird 2 flew off, but if a bird were to actually grasp the head of another bird death would be a likely result because of the crushing ability of the mandibles. The pronounced sexual dimorphism of bill size may partly be a response to selective pressure arising from this sort of aggressive behavior.

On 13 January 1985, T. W. Sutterfield found the first positively identified Maui Parrotbill nest. The nest was located at 1,800 m elevation in the Hanawi study area, and was placed 11 m high in a fork formed by the branches and branchlets of the upper crown of an ohia tree on a gulch

edge. The nest was a substantial structure about 18 cm in diameter, of cup-like shape, with lichens and leaves hanging on the outside, and generally constructed from small twigs and other woody material. The contents could not be determined because the nest was inaccessible. Whether this was a cock or true nest is unknown, because the next day a storm with winds in excess of 30 m/sec struck and field work was terminated.

Sutterfield (pers. observ.) also observed nest building behavior at this nest site. While the pair was in the crown of an ohia tree, the male bird picked up a piece of sedge growing on the tree, hopped around in the canopy displaying it to the female for 10 to 15 sec, and took 10 sec to place it in the nest. Then for 30 sec the two birds chipped almost incessantly while hopping around within 15 cm of one another. The male then pulled up a small clump of *Usnea* lichen, hopped around with it for 30 sec, displaying it to the female (who frequently chipped), and deposited it in the nest. The pair hopped about in close proximity, chipping to each other, for 3 to 4 min near the nest site, before flying out of the tree as two Apapanes arrived. On 9 January 1985, A. M. Ecton and P. A. Stine noted a male bird carrying *Usnea* in its bill elsewhere in the study area. This behavior may indicate nest building activity.

The only other report of a Maui Parrotbill nest was a possible record by R.C.L. Perkins for April or May 1894 (Greenway 1958). Perkins (1903: 432) reported that the nest was built in a koa tree, "in the fork formed by a branch and the main trunk about [8 m] from the ground. The tree was covered with grey lichens and the nest was well-concealed, being itself covered with the same. It was of simple cup-like form, resembling in this respect the usual Drepanid nest. For several days two old and two young birds, just able to fly, were constantly seen in this tree, and I feel sure that they must have been the former occupants of the evidently newly deserted nest." This possible nest was similar to the 1985 nest in its fork location, cup-like form, and placement of gray lichens on the exterior.

Records of immature birds in family groups soliciting food from adult birds occurred from March to September, with 3 to 7 records per field trip from May through August, and one or two records/trip for March, April, September, and November. This suggests a protracted breeding period, with nesting occurring perhaps from January to June in various years. Nesting records over a prolonged season are typical of lower latitudes (Baker 1938), but in a given year pairs may tend to be synchronized by climatic events such as the start of the wet season (Fogden 1972).

Family groups usually comprised two immature birds being cared for by two adults; however, as many as four young occurred in a single family, and occasionally one or two immatures were cared for by only one adult, male or female.

The discoverer of a nest should note approximate age of nestlings and nest soiling, as this would help in determining the systematic position of the Maui Parrotbill. In nest sanitation, the Psittirostrini do not removing fecal sacs during the first 10 days after hatching, whereas the Hemignathini do (van Riper 1980).

VOCALIZATIONS

Maui Parrotbills have three distinct, fairly stereotyped vocalizations: a chip, a call, and a song. The chip was a sharp atonal "chick" that was virtually inseparable from the chip of the Maui Creeper. The chip note was usually given when Maui Parrotbills were in loose flocks with Maui Creepers, and probably promoted flock cohesion. The call was a somewhat thin, upslurred whistle clearer than the similar notes given by the Common Amakihi (*Hemignathus virens*), Iiwi, and Crested Honeycreeper. This vocalization was often given by two birds at some distance apart, and probably served as contact notes. It was given by apparently paired birds and by adults and young in apparent family groups.

The song consisted of 4 to 10 short upslurred whistled notes given consecutively without break and tending to descend in pitch. Only male birds have been observed singing. During this study, songs were uttered singly or continually with 5 to 60 sec breaks for as long as 5 min. Little variation over the course of the day was observed in the frequency of any vocalization, except that birds appeared to be somewhat quieter at dawn, dusk, and during rainy periods and warm sunny afternoons. Other vocalizations occasionally heard were solicitation notes by young birds and various short burry call notes rarely given.

MIXED-SPECIES FLOCKING

Maui Parrotbills frequently formed loosely associated flocks with Maui Creepers. On 20 of 39 encounters (51%), one or two (rarely as many as four) Maui Parrotbills were accompanied by two

or three (up to six) Maui Creepers. Flocking appeared to be facilitated by the nearly identical chip notes of the two species. On seven occasions the Maui Creepers left the Maui Parrotbills behind. When foraging, Maui Parrotbills changed perches every 5 ± 3 SD sec ($n = 79$), whereas Maui Creepers changed perches more rapidly, every 1 ± 1 SD sec ($n = 49$; Mann-Whitney U-test, $P < 0.001$). The faster movement rate of Maui Creepers seemed to be compensated by longer flights of Maui Parrotbills when the two species foraged together. On rare occasions a Nukupuu or Poo-uli (*Melamprosops phaeosoma*) flocked with Maui Parrotbills (Perkins 1903; Shallenberger 1981; S. Mountainspring, unpubl. data). The selective force for flocking may be predator detection, because Maui Parrotbills often direct most of their attention to excavating. Several times when Short-eared Owls (*Asio flammeus*) quartered over the rainforest, all passerines including Maui Parrotbills became very quiet and ducked into the vegetation. Before Polynesian contact, predation from now-extinct accipitrine hawks and an undescribed fossil genus of long-legged owl were probably important causes of mortality of small land birds in the Hawaiian Islands (Olson and James 1982b).

DISCUSSION

LIMITING FACTORS AND MANAGEMENT

The primary limiting factors of the Maui Parrotbill appear to be: (1) habitat loss; (2) avian disease; (3) habitat degradation; (4) predation; and (5) competition from exotic species. The first two factors act mainly to limit the range; the last three tend to act within the range by depressing densities (Mountainspring 1986).

Prior to Polynesian contact around 400 A.D., widespread dryland forests supported a rich biota that included the Maui Parrotbill (Olson and James 1982b). Burning, clearing, lumbering, ranching, and feral ungulate activity caused large-scale extinctions and retreats among this biota. Most of the original range of the Maui Parrotbill has been converted to exotic vegetation, which the species does not inhabit. Although birds formerly occurred on the Kahikinui Tract, that area is now too severely degraded to support them. Protection of the remnant koa forests in this area by feral goat (*Capra hircus*) control would enhance the potential for transplanting birds and foster possibly spontaneous recolonization from the main population. Virtually all of the present range lies on private, state, and federal preserves with some degree of legal protection.

At lower elevations, the range limits of the Maui Parrotbill have a striking coincidence with the upper elevation limits of mosquito distribution (Fig. 3). The Nukupuu, Maui Creeper, Akepa (*Loxops coccineus*), Iiwi, Crested Honeycreeper, and Poo-uli have similarly restricted distributions (Scott et al. 1986). The role of mosquitoes in serving as vectors of avian malaria (*Plasmodium relictum capistranoae*) and most likely avian pox (*Poxvirus avium*) probably restricts the ranges of species that have little resistance to these diseases to areas with zero to very low mosquito densities (Warner 1968, van Riper et al. 1982, Scott et al. 1986).

Habitat degradation by feral pigs is the most insidious and threatening factor that limits Maui Parrotbill numbers. Maui Parrotbills tend to occur on sites with significantly lower pig damage than the landscape norm, and the foliage profile they prefer to forage in is typical of areas undamaged by pigs. Moreover, the relative sedentariness of the birds would tend to make them more sensitive to localized adverse habitat modification. Rooting by feral pigs destroys understory and ground cover, most significantly the seedlings of the shrub and subcanopy trees (Giffin 1978, Baker 1979, Tisdell 1982), where most prey are captured. Other rare bird species adversely impacted in the Hanawi area by pigs are the Poo-uli and Nukupuu, whose distributions correspond to areas of lower pig damage (Mountainspring 1986), and Bishop's Oo (*Moho bishopi*), which prefers to feed on the nectar of fragile understory lobeliads (Perkins 1903, Sabo 1982). On steep slopes in the montane rainforest, pig damage leads to excessive soil erosion; on more level sites, habitat degradation gradually converts mature forest to mire. The urgently needed management action is to control pig populations in substantial areas of montane rainforest by improving public hunting access, and in remote key areas by fencing, driving, intensive hunting, and possibly poisoning (Kepler et al. 1984). It is unknown to what extent predation limits Maui Parrotbill numbers. In the high elevation rainforest where bird densities are greatest, mongoose (*Herpestes auropunctatus*) and feral cats (*Felis catus*) are relatively uncommon, but Polynesian rats (*Rattus exulans*) and black rats (*R. rattus*) occur at moderate levels of abundance (R. T. Sugihara, pers. comm.). Stomachs of both rat species have contained bird feathers in Waikamoi Preserve

(R. T. Sugihara, pers. comm.) and Kipahulu Valley (C. P. Stone, pers. comm.).

Indirect competition for food resources may occur from introduced insect species that prey on timber-boring insects. Yellow jackets (*Vespula pennsylvanica*) are common in some years in the Hanawi study area; *Ischiogonus* wasps that parasitize cerambycid beetles (Zimmerman 1948) may also affect the resource base. A quantitative study of resource availability and probable exotic impacts would be helpful in assessing the role of food limitation and competition.

ACKNOWLEDGMENTS

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