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REPRODUCTIVE ECOLOGY OF THE MAUI PARROTBILL

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ABSTRACT.—The endangered Maui Parrotbill (*Pseudonestor xanthophrys*) is an excavating, insectivorous Hawaiian honeycreeper endemic to the high elevation rain forests of east Maui, Hawaii. From March 1994 to June 1997, we studied various aspects of their breeding ecology. We color-banded 18 individuals, located and monitored 9 active nests, and took behavioral data during 440 hrs of nest observation. Both members of a pair maintained a year-round, all-purpose territory that included nest sites and food resources. Maui Parrotbill were monogamous within and between years; we found no evidence of polyandry, polygyny, or helpers at the nest. Nests were cup-shaped, composed mainly of lichen interlaced with small twigs, and positioned in the outer canopy forks of mature ohia (*Metrosideros polymorpha*) trees. Modal clutch size was one. Females performed most nest construction and all incubation and brooding; males provisioned females and assisted in feeding nestlings after their fourth day. Fledglings depended on parental care for 5–8 months, during which their bill strength increased and foraging skills improved. We calculated the overall nest success rate by the Mayfield Method as 0.42 for the 1995/1996 and 1996/1997 breeding seasons combined. Nest failure and fledgling disappearance coincided with events of high rainfall. Their breeding ecology most closely resembled the Akiapolaau (*Hemignathus munroi*), another excavating, insectivorous Hawaiian honeycreeper found on Hawaii Island. As with the Akiapolaau, the threat of extinction is persistent and results from both the constraints of inherent life history traits and artificial ecological changes. We advocate the protection and expansion of habitable forest areas and an ongoing program to monitor and mitigate the effects of invasive species. *Received 3 Feb. 2000, accepted 23 June 2000.*

The Maui Parrotbill (*Pseudonestor xanthophrys*) is an endangered Hawaiian honeycreeper (Fringillidae: Drepanidinae) and the sole member of its genus. Its range is now limited to the high elevation (>1200 m) forests on the northern and eastern slopes of Haleakala, a dormant volcano which constitutes east Maui Island. Maui Parrotbills are primarily insectivorous, biting open fruit, soft stems, and decaying wood to extract hidden invertebrates (Perkins 1903).

Prior to the arrival of the first Polynesian colonists around 400 AD, the Maui Parrotbill probably occurred throughout much of Maui, Molokai, and Lanai islands and inhabited a diverse assemblage of forest environments from sea level to treeline, as inferred from subfossil evidence and its historic distribution (Olson and James 1982a). During the period of human settlement, expanding agriculture and harvesting of wood products destroyed most of the habitat of the Maui Parrotbill (Olson and James 1982b, Scott et al. 1986). Human colonization also brought alien plants and animals, most notably two mammalian predators of birds, the feral cat (*Felis catus*) and rats (*Rattus* spp.). The introduction of mosquitoes, and, later, alien birds, put in place the building blocks of an avian malaria (*Plasmodium relictum*) epidemic, to which the endemic species had little or no resistance (Atkinson et al. 1995). By the mid- to late 1800s, the Maui Parrotbill was considered rare and highly localized (Perkins 1903). In 1980, the comprehensive Hawaii Forest Bird Survey mapped the species' geographic range at approximately 50 km^2 (Fig. 1; Mountainspring 1987) and estimated the population at 500 ± 230 individuals (95% C. I.; Scott et al. 1986). Early behavioral studies of the Maui Parrotbill focused primarily on foraging ecology (Carothers et al. 1983, Mountainspring 1987). The first two active nests were discovered by Lockwood and coworkers (1994), who described many important aspects of parrotbill breeding biology.

Our study focused on documenting the life history and nesting success of Maui Parrotbills with the aim of assessing factors limiting the population of this endangered species. In

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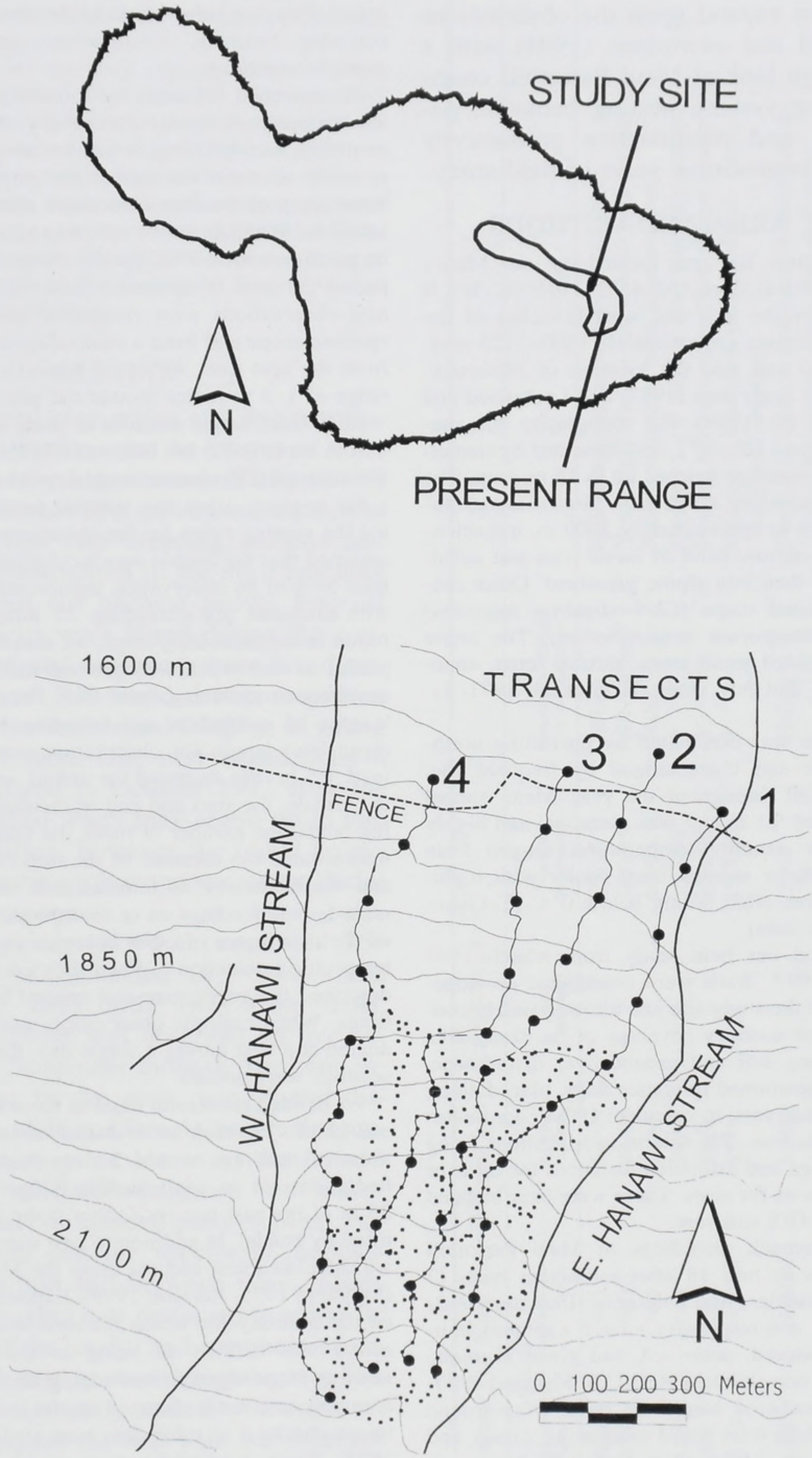

FIG. 1. Study site and location on the island of Maui, Hawaii. Reference flags (small dots) above 1850 m follow trails of main study area. Contour interval = 50 m.

this paper, we expand upon the observations of Lockwood and coworkers (1994) with a more thorough look at Maui Parrotbill courtship, breeding system, nesting behavior, parental roles, and reproductive productivity during three consecutive years of field study.

STUDY AREA AND METHODS

Our 35-ha study site was located on east Maui's northern (windward) slope (20° 45′ N, 156° 08′ W). It was bounded by the east and west branches of the upper Hanawi Stream, approximately 1800–2125 m elevation (Fig. 1) and was the location of Mountainspring's Hanawi study area (1987) and Lockwood and coworkers' site #2 (1994). The topography was rugged, steeply sloped (20–30°), and dissected by numerous ridges and drainage gulches up to 15 m deep. The area was dominated by a wet ohia (*Metrosideros polymorpha*) forest to approximately 2000 m, transitioning above to a narrow band of mesic ohia and subalpine scrub and then into alpine grassland. Other canopy trees included olapa (*Cheirodendron trigynum*) and hoawa (*Pittosporum confertiflorum*). The dense understory included small trees, shrubs, ferns, abundant epiphytes, and few vines (Henrickson 1971, Jacobi 1989).

Local climate was dominated by prevailing northeast tradewinds and characterized by frequent fog, mist, and rainfall throughout the year. Mean annual rainfall exceeded 5.1 m and was aseasonal and highly variable. Mean monthly temperatures ranged from 9.9–13.4° C. Winter months were cooler with nighttime temperatures often falling below 0° C (T. Giambelluca, unpubl. data).

We conducted our field study from March 1994 through June 1997. Trails were established on ridgetops throughout the study site and allowed nearly continuous visual or auditory coverage of the study area while minimizing soil and groundcover disturbance. We used GPS positioned reference flags, placed along trails at 25 m intervals, to calculate UTM coordinates for all other locations. We determined locations using compass bearings and estimated distances for birds or measured distances for nests. These were later mapped using ArcView GIS software.

We used playback recordings of Maui Parrotbill songs and calls to lure 18 after-hatch-year birds (7 males and 11 females) into mist-nets. (Immature birds were generally non-responsive.) Each captured individual was measured, described, and given a unique combination of one stainless steel U.S. Fish and Wildlife Service numbered band and three wrap-around color bands. Adults were sexed using wing, tarsus, and bill measurements. Males were larger (Simon et al. 1997; Berlin et al., in press). We gathered behavioral data as we encountered both banded and unbanded birds throughout the study area. Once a band combination (or unbanded status) was determined, observers waited approximately 10 seconds (to minimize observer effect) before recording observations including location, foraging behavior and substrate, pursuit flights, courtship behavior, vocalizations, group size, and group interactions.

We searched for nests by following individuals as we encountered them, particularly those exhibiting courtship, nest-building, or provisioning. We attempted to cover all trails throughout the study area equally; however, poor weather sometimes affected our search schedule. When an active nest was located, we marked its position with a PVC spotter (Simon 1998) and departed the area to minimize disturbance. Subsequent nest observations were conducted with the aid of a spotting scope and from a camouflaged blind 10–50 m from the nest tree. We could typically see a viewing range of 1–3 m radius around the nest.

Most observation sessions at nests lasted 2–4 hr ($\bar{x}$ = 3.0, max. = 8.6 hr) between 07:00 and 17:00 HST. We attempted to observe each active nest at least once a day or every other day, weather permitting, and varied the starting times for the sessions at each nest. We assumed that the female was incubating if she spent at least 50% of an observation session sitting on the nest with absences not exceeding 25 minutes. For nests found in the incubation stage, we assumed the nestling period to start when we observed the female feeding nestlings or removing fecal sacs. For analyses of the lengths of incubation and brooding bouts, we used mean bout length for observation sessions lasting at least 1.5 hr. We recorded the arrival and departure of the female, the start and end of incubation and brooding bouts, the number of times the female checked or manipulated the contents of the nest (when possible), and the frequency of female-chick, male-chick, and male-female feedings on or near the nest. We also noted the occurrence of other behavior and intra- and interspecific interactions. When they could be seen, we described the appearance and general behavior of nestlings. When multiple observation sessions were conducted at a nest during a single day, the data for those sessions were pooled.

We defined successful nests as those fledging at least one chick. We took as evidence of success observations of nestlings within 2 days from the expected fledge date or an adult feeding fledged young within 25 m of the nest tree (or farther if the adult was identified by bands). In addition to nest summary statistics, we calculated nest success using the Mayfield Method (Mayfield 1975, Johnson 1979). Exposure days included the first day for which the nest was active, where active was defined as being in the incubation or nestling stage, through to fledging or nest failure. We assumed nest status changed on the midpoint date between checks if no other data were available (Mayfield 1975). Because we could not see newly hatched chicks below the nest rim, we did not attempt to differentiate between success rates for incubation and nestling stages. We determined nest fate by direct observation and/or subsequent collection of the nest. Excluded from the analyses was the only active nest found in the 1996/1997 breeding season; only cursory observations were made in order to facilitate collection of the egg for captive rearing.

Post-active nests and their contents were collected by climbing to them when possible. For collected nests, we measured the nest height above ground with a weighted line; we measured nest height for nests not collected, and tree height with a clinometer. Dimensions of the nests were measured while they were fresh. Collected eggs and nests were deposited at Bishop Museum, Honolulu. We also collected one live egg in 1997 for rearing at the Zoological Society of San Diego's Keauhou facility.

RESULTS

We monitored nine active and five inactive Maui Parrotbill nests over the course of three winter/spring breeding seasons (Table 1). We found an additional nest under construction in each of the first two breeding seasons and three under construction in the third breeding season that did not become active. Four of nine active nests were found during the construction stage, and four more were found early in incubation. We found nest construction as early as 1 November and fledging of young as late as 28 June. One nest attended by a female was found in October 1997 after the field study ended. Pairs may renest up to two times after failure; however, we found no evidence of renesting following successful fledging within a season.

Breeding system.—We accumulated 766 observations of unbanded (n = 497) and banded (n = 269) birds away from nests. Courtship behavior was observed on five occasions from November through April and included singing by the male, wing-flutter displays by both male and female, and males presenting small twigs or leaves to the female. Females also solicited regurgitate from males. Evidence from two banded pairs of Maui Parrotbill suggests that the species is monogamous both within and between years. Members of one banded pair remained together for three years of the study, and members of another banded pair remained together for two years before the study ended. Although we found no nests for the first pair, we observed them attending fledglings in two years. We observed no evidence of helpers at any nest (n = 9; Table 1).

Based on resighting locations for banded birds, we observed that each breeding pair with at least one member banded (n = 6)

TABLE 1. Summary of Maui Parrotbill nest activity, 1995–1997.

Breeding pair	Banded? Female	Banded? Male	Breeding season	Nest attempt	Start of incubation	Successful?/Stage at termination	Notes
1	WWWA	NO	94/95	1	2/8/95	N/Egg	Failure associated with poor weather.
1	WWWA	NO	94/95	2	3/20/95	N/Nestling	Nest empty; failure assoc. with poor weather.
2	NO	NO	94/95	1	4/8/95	N/Egg	Failure associated with poor weather.
3	(BABR)	NO	94/95	1	5/23/95	Y	Fledged 1. (♀ banded after breeding season.)
3	BABR	NO	95/96	2	4/24/96	Y	Fledged 1. First nest in 1996 season not active.
4	GAGB	ABGR	95/96	1	12/23/95	Y	Fledged 1. Fledgling presumed lost; assoc. with poor weather.
4	GAGB	ABGR	95/96	2	2/96	N/Egg	Start of incubation unknown. Abandoned in incubation stage; associated with poor weather. Seen later in season with 1 Fledgling.
4	GAGB	ABGR	96/97	1	1/97	Egg	Egg collected for rearing
5	GAGG	NO	95/96	1	1/15/96	Y	Fledged 1. Young possibly lost within 1 week of fledging; not seen after extended rainfall.

maintained a relatively stationary, year-round home range. Because adjacent home ranges had minimal overlap and males exhibited both counter-singing and agonistic chase behavior throughout much of their home range, we suggest that a defended territory overlies most of the home range area.

Nest construction.—All nests were a basic cup design and located in canopy forks just below the outer canopy of mature ohia trees. Nest heights above ground level, measured for eight active nests and one inactive nest, averaged 11.6 m [±3.0 (SD), range 8.7–18.3], and the height of the nest trees averaged 13.4 m (±3.1, range 9.5–18.8). Nest construction was performed primarily by the female. The two males we observed carrying nesting material to nests did so early in construction, suggesting that males might play a role in nest site selection. All nests were composed primarily of lichen (*Usnea* sp.) with small (<2 mm diameter) defoliate pukiawe (*Styphelia tameiameiae*) twigs interspersed throughout. We did not observe the initial attachment stage of nest building. Middle to late construction consisted mainly of adding material to the inside of the nest cup and using legs, belly, and breast to integrate it into the overall nest structure. Four nests contained fine strips of fern root fibers as cup lining; one contained thread-like strips of inner bark material, probably olapa. We estimated nest construction to be 7–18 days. Light rainfall did not appear to impede work on the nest, but heavy rains or high winds slowed or delayed building activity.

Eggs.—Maui Parrotbill eggs were ovate with an off-white to tan base color and lavender brown mottling concentrated on the rounded half, decreasing near the apex. Six eggs averaged 21.7 mm long (range 20.6–22.9) and 15.4 mm wide (range 14.6–16.5; our data plus unpubl. data from the Zoological Society of San Diego from eggs collected after our study and from within 5 km of our study site). We found clutches of one egg only. All successful nests fledged single young and nests that we collected containing eggs held a single egg.

Nest attendance.—At seven of nine active nests with at least one adult banded, incubation and brooding was performed exclusively by the female. We estimated the incubation period to be 16 days from a single nest we followed from construction to the nestling stage. We accumulated a total of 126.5 hours of nest observation at six nests during incubation and found that females spent an average of 75.3% of daylight hours on the nest. The balance of their time was typically spent foraging away from the nest tree or soliciting feedings from the male with soft *chew* calls and wing-flutter begging displays. Males provisioned the females almost exclusively by regurgitation and averaged 0.31 feedings/hr. Because many feedings took place off the nest and out of our observation area, actual provisioning rates were likely higher.

We followed one nest from late incubation to fledging and found the nestling stage to last approximately 20 days. Observations on four nests with nestlings totaled 214.2 hours. During the first 3–4 days, the female's brooding times were comparable to those at incubation, and the male provisioned the female exclusively, with the female periodically regurgitating smaller boluses to the hatchling. Feedings during this stage were not clearly visible to observers; therefore rates could not be accurately determined. The adults removed the fecal sacs of young nestlings (1–9 days old); afterwards, nestlings defecated over the nest rim and occasionally on it.

Older nestlings were fed by both adults at a rate of 1.8 feedings/hr. As the chick grew, the female spent more time away from the nest area, typically brooding during the day only during periods of rain or cold. Nestlings remained alert throughout the day and spent much of their time preening.

Fledglings.—Fledglings left the nest quickly, typically spending less than 1 day in the vicinity of the nest before permanently departing the nest tree. Newly fledged young were moderately strong flyers but usually stayed quiet and immobile in mid- to upper canopy foliage. Adults, most often the male during the first 7–10 days, sought out fledglings for feedings. Young Maui Parrotbill remained with their parents 5–8 months after fledging (n = 2). During this period, young were frequently observed following foraging adults and soliciting feedings (79% of all juvenile-adult sightings; n = 75). These juveniles persistently emitted a *chew* begging call at 1–2 sec intervals.

Young left the nest with bills not fully developed in size or rigidity. General observations of fledgling and immature Maui Parrotbills suggested that foraging behavior developed gradually. Initially, they showed no signs of feeding themselves. Foraging began first as leaf and twig gleaning and then over the course of several months transitioned to lifting epiphytes, probing decaying wood and soft fruits, and, finally, to splitting stems and other harder vegetative matter. Only when the next nesting season began did adults chase young from the breeding territories.

We obtained little information on the dispersal patterns of Maui Parrotbill young. One subadult female parrotbill banded 2.5 km east of our study site appeared at our site 44 days later in association with a banded resident male who had not bred that year. The occasional association of immature individuals with nesting pairs suggests that young may stay at the periphery of their parents' territory until the end of their first year.

Nest success.—Nest success rates (successful nests divided by active nests with known fate) for the 1994/1995 and 1995/1996 breeding seasons were 25% and 75%, respectively for all four nests in each breeding season. Mayfield estimates of the overall success rate averaged 0.42 (166 exposure days). With the exception of one nest that failed because the egg was probably infertile, unsuccessful nests and the disappearance of a single fledgling banded in the nest occurred during the heaviest rainfalls in the nesting season. We found no evidence of nest depredation. However, two active nests that failed contained no eggs or nestlings when collected and possibly were depredated.

It was difficult to find all nests for each pair because few home ranges lay entirely within the boundaries of our study area. One banded pair, whose home range was only partially within the study area and for whom we did not find nests, was observed with young in both the 1994/1995 and 1995/1996 breeding seasons. An empty nest without fecal material on the rim was found in this pair's territory late in the 1996/1997 breeding season, suggesting that they bred unsuccessfully that year. In 1995/1996, the only other banded pair lost one fledgling during an extended period of heavy rain, abandoned a second nest in heavy rain during incubation, but was seen later in the season with a fledgling. Other pairs, too, may have had a nest fail in our study area and have had a later, successful nest outside it.

DISCUSSION

Our research confirmed that Maui Parrotbill have an extended breeding season, November through June, as surmised by Mountainspring (1987). As a result of this long breeding season and the extended period of juvenile dependency, parents with young can be found throughout the year. The nesting period overlaps that of sympatric, nectarivorous honeycreepers (Berlin and VanGelder 1999). However, it is longer and begins earlier than that of the insectivorous Maui Alauahio (*Paroreomyza montana*; H. Baker and P. Baker, pers. comm.). Because heavy rainfalls that disrupt nesting are seasonally unpredictable, parrotbills cannot avoid them by seasonal breeding. Instead, nesting phenology may correspond to an annual increase in prey biomass and/or a decrease in the cost of capturing them.

In the Hanawi study area, Maui Parrotbill showed a uniform pattern of nest construction and placement. In other parts of their range, Maui Parrotbill have been known to utilize other nesting materials. To the east of our study site, where *Usnea* lichen is less abundant or absent, nests may be constructed with epiphytic mosses including *Thuidium plicatum, Macromitrium microstomum,* and *Floribundaria floribunda* ($n = 2$; P. Baker, H. Baker, and W. Hoe, pers. comm.). Nest placement may vary with habitat. Maui Parrotbill formerly showed a close association with koa (*Acacia koa*) forests; Perkins (1903) found a nest typical of the Maui Parrotbill in a koa. Whatever the substrate, the placement of nests in the outermost layer of the canopy may limit nest depredation by introduced mammalian predators, particularly rats. The only confirmed nest depredation by rats during our larger study was that of an Akohekohe (*Palmeria dolei*) female and eggs in a nest that was atypically low in a tree and close to the main stem (Pacific Island Ecosystems Research Center, unpubl. data).

Weather had a substantial effect on nest success and the survival of dependent young. Exposure might kill eggs, nestlings, or fledglings and might drive females from their nests or limit foraging. Although our observations were curtailed during inclement conditions, we noted that Maui Parrotbill appeared to spend less time foraging during periods of moderate or heavy rainfall. Rain and wind might significantly reduce the visual and auditory cues used to detect large, energy-rich borer larvae and might reduce foraging success.

Nesting pairs in our study never raised more than a single young in any given season. The Maui Parrotbill has been known to successfully hatch 2 egg clutches, based on observations of adult pairs with two dependent young; however, such sightings have been rare (less than 5 cases out of at least 40 parent/juvenile groups; this study, P. Baker and H. Baker, pers. comm.). No data are available on the percentage of young that reach independence from 1 or 2 young clutches or broods. Information on the recruitment rate for this species was, and will continue to be, difficult to acquire.

Some of our findings have implications for Maui Parrotbill systematics. We found marked differences between the breeding biology of Maui Parrotbill and sympatric nectarivores, such as the Hawaii Amakihi (*Hemignathus virens*), and the only sympatric insectivore, the Maui Alauahio (Table 2). Parrotbills also differed from the finch-billed honeycreepers with which they have traditionally been classified (Table 2; Berger 1981, Pyle 1997). On the other hand, the maintenance of large territories, one-egg clutches, and exceptionally long juvenile dependency period show that Maui Parrotbill share more features of their life history with the Akiapolaau (*Hemignathus munroi*) an insect excavator found on Hawaii Island. Perkins (1903) allied the two species, and recent DNA evidence indicates that they are sister taxa among the living Hawaiian honeycreepers (R. Fleischer, pers. comm.).

The future of the Maui Parrotbill remains very much in question. This honeycreeper is now confined to the wettest and highest portion of its original range. This habitat may be marginal, as indicated by the loss of eggs, nestlings, and fledglings to heavy, but not atypical, rainfall. Koa trees, strongly favored by the Maui Parrotbill as a foraging substrate (Perkins 1903), are rare and patchy above 1200 m elevation, and efforts to re-establish koa forests have so far been minimal. Trans-

TABLE 2. Comparison of select life history traits. See footnotes for scientific names and source references.

Common name	Palila[a]	Laysan Finch[b]	Maui Parrotbill[c]	Akiapolaau[d]	Maui Alauahio[e]	Hawaii Amakihi[f]
Primary food types	Green seeds/ Insects	Omnivorous	Insects (Excavator)	Insects (Excavator)	Insects (Gleaner)	Nectar/ Insects
Year-round, all purpose territory/Breeding territory	N/N	N/N	Y/Y	Y/Y	Y/Y	N/Y
Typical clutch size	2	3	1	1	2	2–3
Mean incubation/Nestling period (days)	17/26	16/24	16/20	?/21	16/18	14/17
Juvenile (dependence) period	<1 mo.	~1 mo.	5+ mo.	4–5+ mo.	18–20	<1 mo.
Maximum number of broods/year	2	2	1	1	1	2

[a] *Loxioides bailleui*; Pletschet and Kelly (1990), Pratt et al. (1997).
[b] *Telespiza cantans*; Morin 1992.
[c] *Pseudonestor xanthrophrys*; this study, Simon et al. (1997).
[d] *Hemignathus munroi*; Ralph and Fancy (1996), Pacific Island Ecosystems Research Center, unpubl. data.
[e] *Paroreomyza montana*; H. Baker and P. Baker, pers. comm.
[f] *Hemignathus virens* (Hawaii Is. ssp.); van Riper (1987).

location of individuals into lower elevation areas within their former range would not be expected to be successful because of the high probability of mortality from avian malaria.

Inherent life history traits, such as large home range, apparent high site fidelity, extended juvenile dependency, and low productivity presumably slow population growth for the Maui Parrotbill. Coupled with a restricted geographic range and low abundance, these traits may also limit the species' ability to recover from severe weather events or from the advent of new threats. If this fascinating species is to survive beyond the immediate future, every effort must be taken to protect, restore, and expand upper elevation ohia/koa forests, and to consistently assess and respond to potential threats posed by non-endemic flora and fauna.

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