Wilson Bull., 102(1), 1990, pp. 109–122

ECOLOGY, BEHAVIOR, AND CONSERVATION OF THE POO-ULI (*MELAMPROSOPS PHAEOSOMA*)

STEPHEN MOUNTAINSPRING,[1] TONNIE L. C. CASEY,[2]
CAMERON B. KEPLER,[2] AND
J. MICHAEL SCOTT[2]

ABSTRACT.—Studies of the population density, habitat structure, foraging behavior, and activity budgets of the Poo-uli (*Melamprosops phaeosoma*) were conducted intermittently between 1973 and 1985 in a 50-ha study area in the upper Hanawi watershed, island of Maui, Hawaii. Poo-uli have apparently declined in density on this site by 80% from 1975 to 1981 and by 90% from 1975 to 1985. During this period, pig activity, as indexed by ground cover disturbance, increased 473%. Compared to values in the range of the Poo-uli, pig activity was 9–24 times greater in two adjacent out-of-range areas. Poo-uli most frequently foraged from 4–7 m height on ohia (*Metrosideros polymorpha*), olapa (*Cheirodendron trigynum*), ohelo (*Vaccinium calycinum*), and kanawao (*Broussaisia arguta*) in decreasing frequency; feeding on kanawao was significantly more frequent than random expectation. Chief food items were land snails and insects. Most prey were captured on branches from under moss, lichen, and bark by gleaning, probing, and pecking. Birds spent 48% of their daylight hours foraging and 30% quietly perching. Poo-uli frequently formed small mixed-species flocks, usually with Maui Creepers (*Paroreomyza montana*), that probably facilitated predator avoidance and foraging efficiency. The major limiting factors at present appear to be habitat modification from feral pigs (*Sus scrofa*), predation, avian disease, interspecific competition from the introduced garlic snail (*Oxychilus alliarius*), and possibly gene pool impoverishment. Control of pigs is recommended. *Received 9 Oct. 1986, accepted 20 May 1989.*

The Poo-uli (*Melamprosops phaeosoma*) is a drab, black-faced, short-tailed Hawaiian honeycreeper (Drepanidinae) that was discovered in 1973 on Maui, Hawaii (Casey and Jacobi 1974). It has proved difficult to find and elusive to study. Stomach analyses of two specimens suggest that the Poo-uli is one of the few passerines to feed extensively on molluscs (Baldwin and Casey 1983). Due to limited anatomical material and few life history reports, systematic relationships are uncertain, with the monotypic genus *Melamprosops* generally considered *incertae sedis* among the honeycreepers (Pratt 1979, AOU 1983). Because of this species' poorly known natural history, we report here on its abundance, range, habitat relation-

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[1] The Conservation Agency, 6 Swinburne Street, Conanicut Island, Rhode Island 02835.

[2] U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708.

Present address: SM Chambers of Judge Malcolm F. Marsh, U.S. Courthouse, 620 S.W. Main St., Portland Oregon 97205; CBK U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Southeast Research Group, School of Forest Resources, University of Georgia, Athens, Georgia 30602; JMS U.S. Fish and Wildlife Service, Idaho Cooperative Fish and Wildlife Research Unit, College of Forestry, Wildlife and Range Science, University of Idaho, Moscow, Idaho 83843. Address reprint requests to CBK.

ships, foraging behavior, social behavior, and factors that may limit its abundance and range.

STUDY AREA AND METHODS

Intensive studies on bird density, habitat structure, foraging behavior, and activity budgets were conducted in 1973–75, 1980–81, and 1984–85 on the Hanawi study area, a steeply sloping 50-ha site located at 1800–2100-m elevation between the branches of Hanawi Stream on the island of Maui, Hawaii (Fig. 1). The area supports a rainforest averaging 13 m in height and 60% crown cover, dominated by ohia (*Metrosideros polymorpha*) and olapa (*Cheirodendron trigynum*). The understory is composed of native subcanopy trees, shrubs, and ferns.

We laid a transect in the study area perpendicular to the contour from 1800- to 2100-m elevation with stations at 30.5 m elevational increments. At these stations we estimated the cover of all major plant species in 5 height strata delimited at 0.3, 1.5, 4.6, and 9.1 m and the percent of ground cover showing recent disturbance by the rooting and wallowing activities of feral pigs (*Sus scrofa*). In addition, we recorded foliage cover in 1 m height increments at 28 stations randomly located within the study area. Expected height use was computed from the foliage height profiles at the 28 random sample points using a goodness-of-fit analysis. The 0–1 m height interval was excluded from this analysis because the very dense vegetation in that interval obscured bird behavior and therefore probably biased observations.

Population densities were estimated in the study area using the variable circular-plot method (Reynolds et al. 1980). Estimates were based upon eight-minute counts and a Bayesian estimator (Johnson 1981) for the variance. Bird counts were made in 1975 at the 30.5 m elevational stations, in 1981 at the 28 random points, and in 1985 at 15 systematically placed points that were censused 2–4 times. We used an effective detection distance of 28 m for this species (Scott et al. 1986).

Data recorded on foraging behavior for each food item we observed or believed to be captured included: elevation, height above ground, plant species item was taken from, substrate (leaf, twig, branch), maneuver (peck, probe, glean, hover), and food item identity when determinable. To determine expected plant species use, we computed the relative abundance of each plant from the relative cover in the five height strata sampled at 30.5 m elevational increments; these covers were weighted by the amount of time birds were observed in each stratum at each elevational band. For sample size in statistical tests, we used the number of independent behavioral sequences observed (i.e., substantial difference in place or time between observations).

Activity budget data were gathered on birds observed during June 1974–August 1975 and May 1980–January 1985. For each observation of a focal bird, we recorded the elevation, height above ground, plant species of perch, activity type (sedentary activities: stationary perching, vocalizing, preening, defecating; locomotive activities: hopping, climbing, hanging, flying; foraging activities: active peering, gleaning, probing, pecking), duration of the activity, and associated bird species for as long as the bird was in sight. To reflect the relative amount of energy required for different activities, we estimated the metabolic cost of each activity as a multiple of the standard metabolic rate, using the values in Holmes et al. (1979) as guides. The standard metabolic rate multiples used for each activity were: perching 1.5, vocalizing 2, preening 2, defecating 2, hopping 5, climbing 5, hanging 5, flying 10, peering 2, gleaning 2, probing 2, and pecking 2. These values were multiplied by the amount of time birds devoted to each activity, the resulting values totaled, and percentages calculated to show the relative amount of energy expended in each activity.

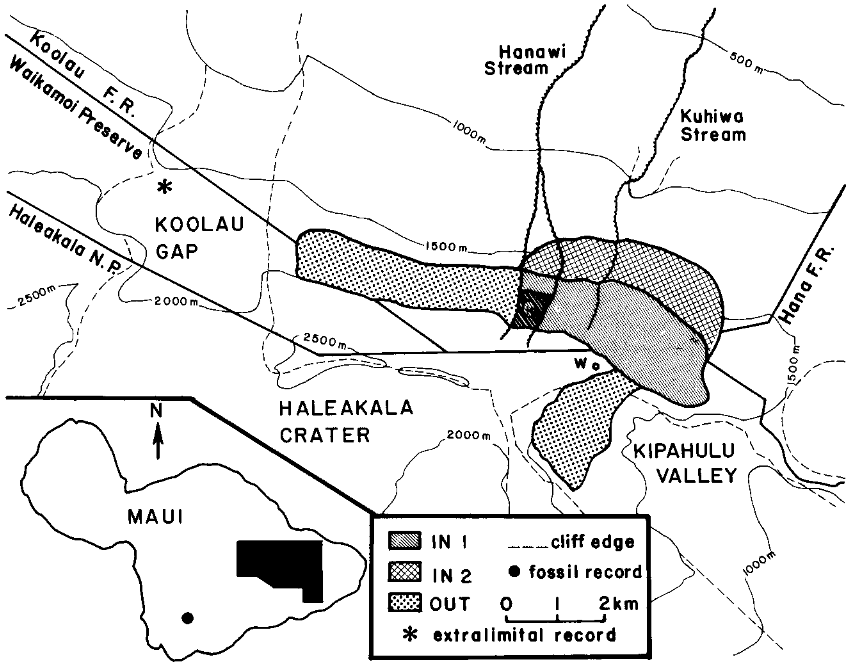

FIG. 1. Geographical distribution of the Poo-uli. H = Hanawi study area; IN-1 = area within range used in analysis of habitat features; IN-2 = remaining area within range not used in analysis; OUT = areas outside range used in analysis; W = Lake Wai Anapanapa.

Habitat features within the present range of the Poo-uli were compared with features in two adjacent areas outside the range, one west of the range, lying in the Koolau Forest Reserve between Hanawi watershed and Koolau Gap ("West Koolau"), and the other south in Kipahulu Valley (Fig. 1). These areas contained the same general habitat type, partly closed ohia forest. The lower elevational limit was 1675 m; the upper was determined by the upper limit of forest cover and varied from 2000 to 2100 m. The area within the range comprised the known range above 1675 m elevation. This elevation was chosen because these areas were well above the lower elevational limits of the Poo-uli, where range delineation was difficult, and above the upper elevational distribution of mosquitoes, to avoid the potentially confounding factor of avian disease (van Riper et al. 1986). Areas north or east of the range were not compared with the area within range because we suspect avian diseases borne by mosquitoes limit the distribution in those directions, based on the absence of other presumed disease-sensitive species (e.g., Maui Creeper). Data for comparing habitat features were collected in 1980 during the Hawaii Forest Bird Survey (HFBS). The HFBS used stations 134 m apart on parallel transects 1.6–3.2 km apart that were aligned perpendicularly to elevational contours (see Scott et al. 1986 for further details). At each station, canopy height, pig activity, and the areal cover of tree crowns, shrubs, herbs, and ground ferns were optically estimated by trained botanists following the methods described in Scott et al. (1986).

ECOLOGY

Range and habitat.—The Poo-uli is confined to an area of about 13 km^2 on the outer northeast slopes of Haleakala Volcano on the island of Maui in Hawaii (Scott et al. 1986). Given the extreme rarity and inconspicuousness of the species and the sampling intensity of the HFBS (15 counts/km^2), the range defined by Scott et al. (1986) may be conservative. Our records show that the range (Fig. 1) is bounded on the west by the west branch of Hanawi Stream, where understory modification by feral pigs increases substantially (HFBS data). Numerous scattered sightings east of the Hanawi study area indicate that the range continues eastward across the upper Kuhiwa watershed, ending somewhere in an unexplored region northeast of Lake Wai Anapanapa. The range of all sightings is 1400–2100 m elevation, with 80% of the sightings at 1800–2050 m. All sightings have been in ohia rainforest; most birds were seen in areas of relatively dense, moss-draped understories, frequently along gulches and other areas less disturbed by pig activity. The HFBS made three Poo-uli sightings, located over a 7.1 km distance along transect 9 in upper Kuhiwa and Hanawi watersheds, in a habitat mosaic of relatively pristine areas and others heavily impacted by pigs.

Poo-uli have not been reported from Kipahulu Valley, a comparatively well-studied area. One record made on The Nature Conservancy's Waikamoi Preserve in April 1983 (G. L. Holroyd, Canadian Wildlife Service, pers. comm.) lies 7.8 km west of the next nearest record and may represent a scattered low density relict population in and west of Koolau Gap. Several subfossils found at 500 m elevation on the dry leeward side of East Maui near Ulupalakua (H. F. James pers. comm.) suggest that mature dry mesophytic forests were also originally occupied and may have been the optimal habitat. This habitat has been almost totally altered to scrub vegetation and introduced plant communities through human and introduced ungulate activity.

Comparison of areas within and outside the range.—We compared an area within the present range of the Poo-uli to adjacent areas lying to the west and south, West Koolau and Kipahulu Valleys (Fig. 1). All three areas were above 1675 m elevation, had the same general habitat type, partly closed ohia-olapa forest, and harbored relatively high populations of Maui Creepers and endangered passerines (Scott et al. 1986).

At the level of resolution we used to describe the vegetation, only minor differences appeared in vegetation structure among the sites (Table 1). Significant differences in herb and fern cover appeared between the area within range and the West Koolau area, but Poo-uli were rarely observed using these substrates, and no difference in these habitat components appeared between the area within range and Kipahulu Valley. The con-

TABLE 1
HABITAT COMPARISONS OF AREAS WITHIN AND OUTSIDE OF THE CURRENT RANGE OF THE POO-ULI[a]

		Outside of range			
		Week Koolau		Kipahulu Valley	
Feature	Within range		P^c		P^c
N (sample size)	20	22		22	
Canopy height (m)	12 ± 3[b]	13 ± 3	0.52	12 ± 3	0.88
Percent					
Crown cover	58 ± 18	52 ± 11	0.22	60 ± 15	0.75
Shrub cover	57 ± 27	52 ± 15	0.41	64 ± 24	0.44
Herb cover	10 ± 8	5 ± 5	0.006	10 ± 11	0.90
Fern cover	66 ± 7	59 ± 5	10^{-4}	65 ± 23	0.78
Pig digging	1 ± 2	24 ± 21	10^{-7}	9 ± 12	0.002

[a] Out-of-range areas lie adjacent to areas within range.
[b] x ± SD.
[c] Two-tailed probabilities from t-test comparing values for areas within and areas outside of the range.

sistent difference between areas within and outside the range was pig damage; the range of the Poo-uli on the whole was restricted to areas of low or apparently recent pig damage. Pig damage averaged 9–24 times greater in areas outside the range. The areas within and outside the range have similar coverages of the major understory species that Poo-uli forage upon (species list in Table 2; $P > 0.05$ based on HFBS data).

Population estimates.—Poo-uli densities in the Hanawi study area declined from 1975 to 1985. In 1975 we estimated a density of 76 ± 8 [SE] birds/km^2 (N = 22 bird counts); in 1981, 15 ± 7 birds/km^2 (N = 28); and in 1985, 8 ± 4 birds/km^2 (N = 45). Density values declined 80% from 1975 to 1981 ($t = 5.7$, $P < 0.0001$) and 90% from 1975 to 1985 ($t = 7.6$, $P < 0.0001$). Opportunistic observations by Casey during 1973–83 and by Kepler, Mountainspring, and Scott during 1980–86 corroborated the decline, suggesting that it was not merely random variation. Although the high density in 1975 may have been a population peak attributable to favorable environmental conditions in the preceding years, the low values to which the density fell by 1981 indicates cause for concern. The 1980 HFBS reported a mean value of 11 birds/km^2 across the range (Scott et al. 1986), indicating that the values in the Hanawi area were relatively typical in 1981 for other areas in range.

BEHAVIOR

Foraging behavior.—Heights of Poo-uli perching and foraging sites had a slightly skewed distribution (Fig. 2) averaging 4.9 ± 1.9 [SD] m, indi-

TABLE 2

PERCENT PLANT SPECIES USE BY THE POO-ULI COMPARED WITH VEGETATION COMPOSITION

Plant species	Frequency of use		χ^2
	Observed	Expected[a]	
Ohia (*Metrosideros polymorpha*)	43.9	38.5	0.6
Olapa (*Cheirodendron trigynum*)	18.3	11.5	3.3
Ohelo (*Vaccinium calycinum*)	11.0	15.4	1.0
Kanawao (*Broussaisia arguta*)	6.1	0.9	24.2[b]
Kolea (*Myrsine lessertiana*)	6.1	8.5	0.5
Kawau (*Ilex anomala*)	4.9	1.7	4.9[c]
Pilo (*Coprosma ochracea*)	3.7	8.2	2.0
Other plants[d]	6.1	15.3	4.5[c]
Total	100	100	41.2[b]

[a] Based on vegetation composition at the foraging sites.

[b] $P < 0.001$, goodness-of-fit test based on a sample size of 82 independent behavioral sequences weighted by the number of feeding observations in each sequence (N = 171 observations).

[c] $P < 0.05$.

[d] Akala (*Rubus hawaiiensis*), alani (*Pelea* spp.), pukiawe (*Styphelia tameiameiae*), and naenae (*Dubautia* spp.).

cating extensive use of the understory and subcanopy. Compared to the foliage height profile above 1 m (Fig. 2), foraging sites were more often selected at 4–7 m height than expected by chance $\chi^2 = 51.0$, df = 1, $P < 0.0001$). On three occasions, we noted birds foraging in the ground layer. Because of the concealing nature of the foraging column at heights below 1 m, we may have missed some birds foraging there.

Plants most frequently used as foraging sites were ohia, olapa, ohelo (*Vaccinium calycinum*), kolea (*Myrsine lessertiana*), and kanawao (*Broussaisia arguta*) (Table 2). Use of these plants was not random based on the relative foliage composition at the elevations and heights that the behavior was observed ($\chi^2 = 41.2$, df = 7, $P < 0.001$). For example, Poo-uli used kanawao, a 1–2 m high shrub, six times as often as expected based on availability. This was probably related to food levels, as kanawao foliage had higher densities of native snails than other understory species. Kanawao foliage comprised 12% of the total foliage volume in the 0.3–1.5 m height class, but 37% of the native snails found (N = 24) were on kanawao ($\chi^2 = 14.0$, df = 1, $P < 0.001$). Infrequent visits to pukiawe (*Styphelia tameiameiae*), akala (*Rubus hawaiiensis*), and ground ferns (mostly *Dryopteris wallichiana*) may reflect the relatively few snails we noted on these plants (33% of the total foliage volume v. 8% of the snails found; $\chi^2 = 6.8$, df = 1, $P < 0.01$).

Poo-uli fed primarily by gleaning, probing, and pecking prey items from branch and leaf substrates (Table 3). The most frequently used substrates

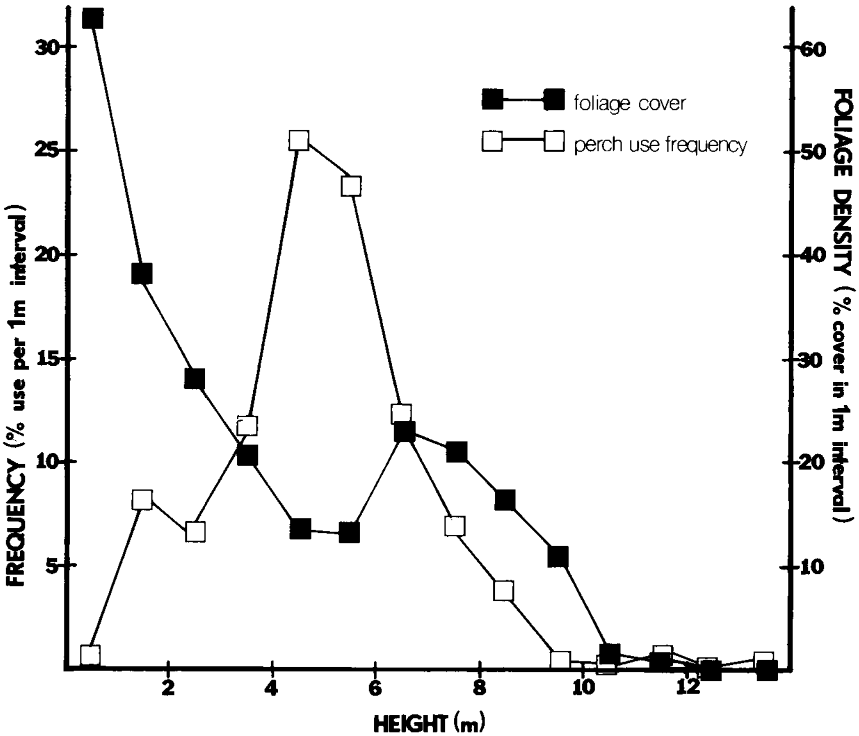

FIG. 2. Frequency of perching compared to foliage coverage in 1-m height intervals.

(85% of all prey captures observed) were branches where small invertebrates were captured by gleaning, prying into cracks, tearing up bits of lichen and moss, and more rarely by flaking off bits of bark. Birds often pulled up lichen and moss mats in search of prey.

Poo-uli were observed feeding on small tree snails (N = 7), insect larvae (6), insect adults and spiders (5), and olapa fruits (2). These observations corroborated an analysis of two stomachs (Baldwin and Casey 1983) that contained small snails (63% of 465 items), arthropod adults (28%), insect larvae (5%), and olapa fruits (4%). The lower proportion of insect larvae in the stomachs analyzed may represent sampling error or the faster digestive rate for soft-bodied prey. The presence of seven ground beetles (Carabidae) in each stomach indicates occasional ground foraging, which is also suggested by the bird's drab color and stout pedal morphology. Similar color patterns of brown and black occur among many antbirds (Formicariidae) that feed on the forest floor (Meyer de Schauensee and

TABLE 3
FORAGING BEHAVIOR OF THE POO-ULI BY SUBSTRATE AND MANEUVER

	Maneuver type				
Substrate type	Peck	Probe	Glean	Hover	Total
Leaf	0	11	9	1	21
Twig	0	3	1	0	4
Branch	20	42	84	0	146
Total prey captures	20	56	94	1	171

Phelps 1978). The snails and insects taken by Poo-uli were usually partly concealed among lichen, moss, and bark. Twice, Poo-uli were seen handling larger snails (>5 mm length) for 10–30 sec after capture to remove part of the shell.

The morphology of the Poo-uli appears to be adaptive for several aspects of its feeding behavior. The large, stout toes may be adapted for foraging for tree snails by prying up moss and bark. The stout bill may reflect the force needed to manipulate snails. Bock (1978) noted that the species has a distinctive spoon-shaped tongue with strong associated musculature; this would appear to be adaptive for prying prey from substrate refugia and for extracting larger snails from their shells.

Activity budget.—Poo-uli spent 48% of their day and 40% of their energy foraging (Table 4), although they were most frequently seen quietly perching, and less frequently peering or gleaning. Locomotive activities represented 15% of the diurnal time budget and about 36% of the energy budget. Our data on the activity budget of the Poo-uli are in conformance with that of typical passerine birds (King 1974).

Flocking behavior.—In 46% of 28 sightings, Poo-uli were in loose flocks with Maui Creepers; two of these flocks also included a Maui Parrotbill (*Pseudonestor xanthophrys*). Typically, one or two Poo-uli associated with two to five Maui Creepers. Interspecific aggression was noted once, when a Poo-uli chased a Maui Creeper that had approached to within 1.5 m. Flocking may be facilitated by Poo-uli and Maui Creeper chip notes, which are very similar to each other.

Several times, one or more birds in a mixed-species flock examined the foraging site where another bird had just captured prey, and then examined other similar sites in the vicinity. On several occasions Short-eared Owls (*Asio flammeus*) were observed quartering low over the forest canopy. At these times, the birds in the mixed flock gave alarm notes and retreated quietly into denser cover.

TABLE 4
DIURNAL ACTIVITY BUDGET OF THE POO-ULI

Activity	Percent of time[a]	Percent of energy
All sedentary activities	36.4	23.9
Stationary perching	29.5	18.2
Vocalizing	3.9	3.2
Preening	2.9	2.4
Defecating	0.1	0.1
All locomotive activities	15.3	36.4
Hopping	7.1	15.0
Climbing	3.7	7.6
Hanging	2.3	4.7
Flying	2.2	9.1
All foraging activities	48.2	39.7
Active peering	18.3	15.1
Gleaning	18.0	14.8
Probing	10.2	8.4
Pecking	1.7	1.4

[a] N = 5003 seconds.

The flocks we observed seemed typical of mixed flocks in continental areas, although our heuristic observations indicated that flock cohesion was lower and on the order of several minutes rather than hours. Flocking of Poo-uli with Maui Creepers was noted in Berger (1981) and Shallenberger (1981) and dispels the concept advanced by Willis (1972) that mixed-species flocks are absent in the Hawaiian avifauna. Mixed-species flocks are known from Fiji, which also has diurnal avian predators, but not from Samoa or Micronesia which lack such predators, suggesting predator avoidance as a selective force (H. D. Pratt, in litt.). Recent fossil finds in the Hawaiian Islands indicates that extinct hawks and owls morphologically adapted to catching small land birds may have been numerous prior to Polynesian contact (Olson and James 1982).

Vocalizations. —Poo-uli are relatively quiet, vocalizing about four percent of the day (Table 4). A developed song similar to that of other Hawaiian honeycreepers has never been observed. Most frequent vocalizations are single chip notes. Single chip notes are difficult to distinguish from those of the Maui Creeper. Also frequently given is a series of 3–4 chip notes, the first often emphatic and followed by a short pause (ca 0.5–1 sec), with the remaining notes given in quick succession at a slightly lower pitch and volume. This series has a characteristic "burry" quality and is a distinctive vocalization. Short *tschew* notes and a fast *chi-chi-chi* series have been noted when immatures were in the area and may be alarm notes.

CONSERVATION

Limiting factors.—Several factors may presently limit the range and numbers of the Poo-uli: (1) habitat modification, (2) predation, (3) avian disease, (4) interspecific competition, and (5) gene pool impoverishment.

In the Hanawi study area and most montane rainforests in Hawaii, the principal agent of habitat modification is the feral pig. As documented for similar forests on the island of Hawaii (Giffin 1978, Baker 1979, Ralph and Maxwell 1984) and elsewhere (Tisdell 1982), rooting and wallowing activities of feral pigs cause extensive damage to native ecosystems by radically altering the understory composition, hindering forest regeneration, facilitating invasion of introduced pest plants (Mueller-Dombois 1981), and leading to severe soil erosion on steep slopes (USFWS data). In addition, pig activity generates mosquito breeding sites, which may assist mosquitoes in establishing populations at higher elevations (Scott et al. 1986, Van Riper et al. 1986). Although pigs were introduced by Polynesian colonists, substantial populations were not thought to have been established in montane forests until after European pigs were introduced (Tomich 1969, Warshauer 1980).

The analysis of areas within and outside the Poo-uli range (Table 1) suggests that pigs are a significant limiting factor. Quantitative surveys of pig activity in the Hanawi study area showed a significant increase from 1975 to 1983 (Fig. 3; $P < 0.002$, sign test). The percent ground cover disturbed by digging increased an average of 431% (range = 33–1500%). Present levels of pig activity now approximate values for adjacent areas lying outside the range (Table 1). Circumstantial evidence thus suggests that the decline in Poo-uli abundance on the Hanawi study area during 1975–85 was related to the rise in pig activity during this period.

Disruption of the ground cover by pig activity may reduce native snail populations, because many snail species graze extensively on terrestrial foliose lichens, and some species depend on the ground layer for their life cycle or during drought periods. Pig activity may promote dispersal of the introduced garlic snail (*Oxychilus alliarius*), which is predatory on other land snails, occurs in numbers on Maui at high elevations, and appears to be well adapted to disturbed habitats (Severns 1984).

The garlic snail is probably a very effective competitor for food resources with the Poo-uli. Severns (1984) has suggested that predation by the garlic snail has decimated populations of native land snails, particularly ground species. Garlic snails were probably introduced during World War II (Cooke and Baker 1947) and are abundant in montane rainforests on

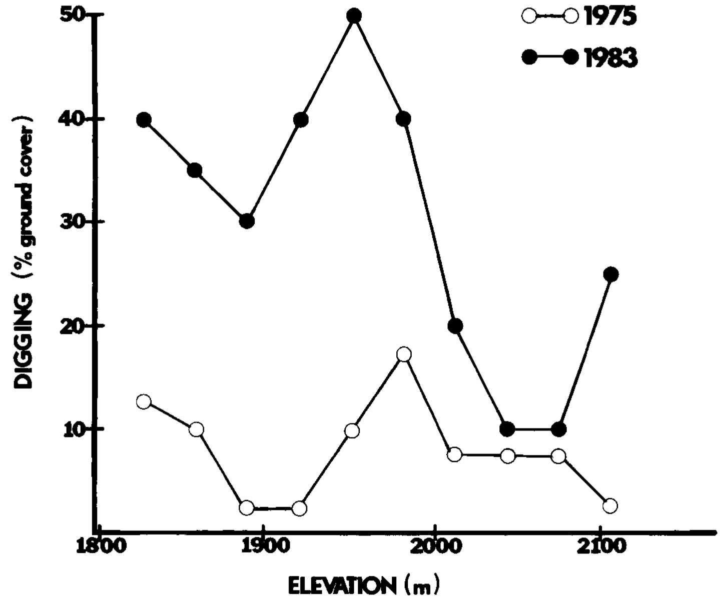

FIG. 3. Percent surface area disturbance by pig digging along an elevational transect in the Hanawi study area, 1975–83.

Maui. In two plots in the Hanawi study area, we found 133 ± 33 [SE] live snails/m^2 on localized mossy substrates, and nearby we saw thousands more empty shells of the same species. Garlic snails may substantially deplete the Poo-uli food base; their edibility to Poo-uli is unknown, and they are infrequent in the understory. Since their introduction, garlic snails may have had a major, hitherto unsuspected impact on the Poo-uli.

Interspecific competition for food resources from other birds is probably minor for the Poo-uli because of its distinctive foraging niche. Mountainspring and Scott (1985) found that competition between native and exotic birds in Hawaii was relatively minor for species whose foraging niches did not extensively overlap.

The low foraging height and frequent use of understory substrates may make Poo-uli vulnerable to mammalian predators. Substantial populations of the black rat (*Rattus rattus*) and the Polynesian rat (*R. exulans*) occur as high as 2000 m elevation in the study area, and unidentified feathers have been found in the stomachs of both species (R. T. Sugihara pers. comm.). Atkinson (1977) hypothesized that because of its arboreal habits, the black rat in particular had a significant negative impact on native birds (Perkins 1903). Cats (*Felis catus*) have been observed ten times in the study area. The small Indian mongoose (*Herpestes auropunctatus*) may also be an occasional predator of Poo-uli because of its ground feeding habits (Baldwin et al. 1952).

The endemic Hawaiian avifauna evolved in the absence of many disease factors prevalent in continental areas. Many species show marked susceptibility to, and occasionally demonstrate mortality from, introduced mosquito-borne avian diseases, particularly avian malaria and pox (Warner 1968, van Riper and van Riper 1985, van Riper et al. 1986). On Maui, the lower elevational range limits for the Poo-uli, Maui Creeper, Iiwi (*Vestiaria coccinea*), and other endangered passerines lie near the upper limit for mosquito vectors. These lower elevational limits are probably at least, in part, determined by disease (Scott et al. 1986). Based on circumstantial evidence, Mountainspring (1986) estimated that 80% of the presently available suitable habitat is unoccupied by Poo-uli because of the presence of disease vectors.

The fossil records from areas that were formerly dry mesophytic forest suggest that the Poo-uli originally had a wider distribution and higher numbers before Polynesian contact (ca 400 A.D.). Scott et al. (1986) hypothesized that the present range comprises only about 1% of the original range. Quite possibly the present range is suboptimal or marginal habitat. The population, estimated at 140 birds in 1980 (Scott et al. 1986), has probably lost some genetic variability originally present, based on calculations of minimal population sizes needed to ensure long-term maintenance of rare alleles (Franklin 1980, Soulé 1980, Schonewald-Cox et al. 1983). Reduction in genetic variability could lead to reduced ability to adapt to novel environmental perturbations such as pig activity, introduced competitors, or climatic changes.

Management recommendations.—Because our data indicate that increased pig activity was highly correlated with the 1975–85 decline of the Poo-uli, and a likely contributor to its decline, the most pressing management action needed is reduction and control of pigs within the Poo-uli range. We recommend that pig-proof fences be constructed and pigs removed from the upper Hanawi and Kuhiwa watersheds (see Kepler et al. 1984). Control of pigs in montane rainforests should lower disease vector levels, improve watershed quality, and possibly reduce garlic snail populations as the ground cover regenerates.

ACKNOWLEDGMENTS

Our research on the Poo-uli has been supported by the U.S. Fish and Wildlife Service, The Conservation Agency, the Frank M. Chapman Memorial Fund of the American Museum of Natural History, the Student Originated Studies Program of the National Science Foundation, the Hawaii Natural History Association, and the University of Hawaii Foundation.

We would like to thank J. H. Carothers, S. J. Doyle, A. M. Ecton, R. B. Hansen, J. D. Jacobi, J. J. Jeffrey, P. Pyle, F. L. Ramsey, T. W. Sutterfield, P. W. Sykes, Jr., D. M. Taylor, F. R. Warshauer, R. Western, and J. E. Williams for sharing their field observations; T. A. Burr, S. Conant, S. J. Doyle, P. A. Stine, P. W. Sykes, Jr., C. van Riper III, and J. W. Wiley for reviewing and commenting on drafts of the manuscript; C. C. Christiansen for identifying mollusc specimens; and the curators of the B. P. Bishop Museum and American Museum of Natural History for access to their collections. We thank officials of the Hawaii Department of Land and Natural Resources and the U.S. National Park Service for access to the study areas and permission to conduct our research.

The Idaho Cooperative Fish and Wildlife Research Unit is funded and supported by the Idaho Department of Fish and Game, University of Idaho, U.S. Fish and Wildlife Service, and Wildlife Management Institute. This is contribution number 426 from the University of Idaho, Forestry and Wildlife Resources Experiment Station.

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