ABSTRACT

Title of Thesis: BEHAVIORAL ECOLOGY OF JUVENILE PALILA (*Loxioides bailleui*): FORAGING DEVELOPMENT, SOCIAL DYNAMICS, AND HELPING BEHAVIOR

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The purpose of this study was to systematically document helping behavior and investigate consequences for social dynamics and development of foraging in juvenile Palila, an endangered Hawaiian honeycreeper found only on Mauna Kea on the island of Hawaii. Though incidental observations of helpers-at-the-nest have been made, intensive nest monitoring revealed that 30 to 50% of nests had one extra after-second-year male provisioning food to the nestling(s). Helping at the fledgling stage was also confirmed. Radiotracking revealed information regarding foraging development and movement patterns of juveniles. Adult males provided one-on-one food supplementation and foraging instruction to young for three to four months after fledging. Particular benchmarks in the development of foraging skills in juveniles were identified. Juvenile survival may be a factor limiting the Palila population. This investigation constitutes the first detailed study of a juvenile Hawaiian forest bird, and thus, may serve as model for understanding the ecology of other species.

BEHAVIORAL ECOLOGY OF JUVENILE PALILA (*Loxioides bailleui*): FORAGING DEVELOPMENT, SOCIAL DYNAMICS, AND HELPING BEHAVIOR

by

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THE PALILA: A COMPREHENSIVE OVERVIEW

PRE-HISTORICAL AND HISTORICAL PERSPECTIVES

The Palila (*Loxioides bailleui*) is an endangered finch-billed Hawaiian honeycreeper (Fringillidae: Drepanidinae) currently found only in the native mamane (*Sophora chrysophylla*: Leguminosae) and mamane - naio (*Myoporum sandwicense*: Myoporaceae) forests of Mauna Kea, a dormant volcano on the island of Hawaii. The endemic subfamily Drepanidinae evolved from a single rosefinch ancestor which colonized the Hawaiian islands 3.5 million years BP (Carpodacus sp.; Tarr and Fleischer 1995). As the finch dispersed within the archipelago and populations isolated, adaptation to diverse habitats occurred, and more than 50 species and subspecies of forest birds gradually emerged (James and Olson 1991). Often considered a classic example of adaptive radiation (Olson and James 1982; Freed et al. 1987; Scott et al. 1988), the honeycreepers with their dramatic bill shapes, along with other endemic Hawaiian avifauna are experiencing widespread extinction. To date, only 18 species of honeycreepers remain.

The arrival of humankind to the Hawaiian islands disrupted ongoing natural processes. In fact, after colonization by the Polynesians ca. 400 AD, but prior to European contact in 1778, a massive extinction of at least half of the Hawaiian land birds occurred; this loss was revealed through fossil findings (Olson and James 1982). Of the 40 extinct species, known only from bone discoveries, at least 15 are Drepanidines (Olson and James 1982).

These extinctions have been attributed to destruction of lowland forests and hunting by the Polynesians as well as predation by the Pacific rat (*Rattus exulans*) that they introduced (Stone and Stone 1989). In 1778, cows (*Bos taurus*), horses (*Equus caballus*), goats (*Capra hircus*), sheep (*Ovis aries*), and pigs (*Sus scrofa*) were introduced to the islands. These ungulates destroyed native plant communities to the point of extreme habitat alteration and hence, indirectly impacted native bird populations. Further decline of native birds has been attributed to predation by the black rat (*Rattus rattus*) and introduction of non-native birds who compete with the natives for food, disperse seeds of alien plants and spread diseases (avian malaria and avipox virus) acquired through an introduced mosquito (*Culex quinquefasciatus*) vector (Warner 1968, van Riper et al. 1986). Native bird populations gradually shifted to inhabit higher elevations where mosquitoes were not a threat; however, new habitats were most likely less preferable.

Of the 71 historically known endemic Hawaiian birds, 23 are extinct, and 30 of the last 48 species and subspecies are endangered or threatened (Jacobi and Atkinson 1995). In fact, many of the endangered species have only single or small populations and at least half have not been sighted in the past 10 years (Jacobi and Atkinson 1995).

When discovered in 1876, the Palila was present only on the island of Hawaii in upland forests. However, fossils of Palila were found on Oahu, at Barber's Point, near sea level (Olson and James 1982). This discovery reveals a once-wider distribution within the archipelago and suggests that, naturally, Palila are not restricted to high elevations. In addition, there is complementary evidence that adequate dryland forests of mamane once persisted at low elevations (Scott et al. 1984).

In 1876, Palila were common in North and South Kona, Hamakua, and Hilo districts (on all slopes of Mauna Kea, on the eastern slope of Hualalai, and on the northwestern slope of Mauna Loa) (US Fish and Wildlife Service 1986). Perkins (1903) reported that Palila were "extremely numerous" in 1982 in the mamane forest of mid to North Kona from 1220 m to 1830 m, but by 1894, they were virtually eliminated. According to Scott et. al (1984), complete extirpation from Kona probably occurred around 1905, concurrent with the extinction of three other finch-billed honeycreepers, the Lesser Koa-Finch (*Rhodacanthis flaviceps*), the Greater Koa-Finch (*R. palmeri*), and the Kona Grosbeak (*Chloridops kona*). Through 1950, Richards and Baldwin (1953) describe the Palila as locally common on the western and northeastern slopes of Mauna Kea between 2360 and 2530 m; however, during the 25 years subsequent, birds were sighted only 4 times on the northern slope (van Riper et al. 1978). This somewhat rapid decline in the Palila population may have been due to a lack of immunity to avian malaria and pox (Warner 1968, van Riper 1980a). Mosquitoes, possibly carried by winter winds, have been observed at elevations as high as 1,500 m (Scott et al. 1984). Van Riper (1986) states that Palila are very susceptible to malaria, and probably to pox as well. More recently (beginning in the early 1800s), the decline in the Palila population has been attributed mainly to the significant loss of critical habitat due to overbrowsing by introduced feral ungulates (Warner 1960, Berger et al. 1977, Giffin 1976, Scott et al. 1984, Scowcroft and Giffin 1983).

Due to significant reduction in historic range, a low population size, and ongoing degradation of its habitat by ungulates, the Palila was recognized as endangered in 1966 by the Department of the Interior and received formal federal listing in 1967. The decision in the court case, Palila versus Hawaii Department of Land and Natural Resources, represents the first successful suit brought under section 9 of the Endangered Species Act (ESA) of 1973 (Nelson 1982). The ruling included acts that significantly modified or degraded environment as "harm" to endangered species; in the case of the Palila, the harmful act was maintaining populations of feral ungulates for public hunting in critical habitat. Palila recovery action began after enactment of the ESA. Efforts included extreme reduction of feral goat and sheep in 1981, and after a second lawsuit (Palila v. Hawaii Department of Land and Natural Resources), mouflon sheep (*Ovis musimon*) were included in the reduction program in 1988. Five years after removal of these animals, significant mamane seed and sprout regeneration was evidenced on the western slope of Mauna Kea; however, it was predicted that this recovery may not benefit Palila, in regard to pod production and tree size, "until well into the 21st century" (Scowcroft and Conrad 1988). Research to determine factors limiting the Palila population have been ongoing since 1987.

CURRENT STATUS AND DISTRIBUTION

The Palila's range has been fragmented and drastically reduced to less than 5% of its pre-Polynesian range (Scott et al. 1986). The species now occupies only 26% of the remaining forest; a 139-km^2 area on the western, southern, and eastern slopes of Mauna Kea between 2000 and 2850 m (Scott et al. 1984). The Palila's range has remained unchanged since 1975 (Jacobi et al. 1996). The most recent population estimate was 2056 individuals in 1995 (Jacobi et al. 1996). Within the years censused (1980-1995), relatively large fluctuations in population size were observed (range: 1,584 to 5,685); these fluctuations have been attributed mainly to annual variations in mamane pod production which is influenced by rainfall (Jacobi et al. 1996). Jacobi et al. (1996) described the population dynamics as "two 4-5 year periods of population decline ending with a doubling of the Palila population following El Nino years."

In addition to the main Palila population (92%) on the western slope near Puu Laau, a remnant population exists on the eastern slope. Although numbers are low, the Palila retains its genetic integrity. Results of DNA fingerprinting analyses indicated low inbreeding and relatively high genetic diversity within the population (Fleischer et al. 1994). Levels of genetic variability and allelic frequencies of the two populations were not significantly different, suggesting a recent separation (Fleischer et al. 1994).

HABITAT AND CLIMATE

The dry woodland habitat on the southwestern slope of Mauna Kea is one of the last native dryforest ecosystems in Hawaii (van Riper 1980b). This open-canopy forest is codominated by mamane and naio trees and has a grassy understory. Van Riper (1980b) assessed relative composition of mamane and naio at 3 elevations; at 2290 m, the forest was predominately mamane (91.5% mamane, 8.2% naio) whereas at lower elevations naio was more prevalent (2130 m: 26% mamane, 74% naio; 1980 m: 48.2% mamane, 51.5% naio). A recent assessment of tree composition by Hess et al. (personal communication) showed somewhat similar results. This study showed that higher elevation grids Puu Laau Mauka (2591-2804m) and Puu Laau Makai (2286-2591m) were almost exclusively mamane; in mid-elevation Manao (2286-2530m), mamane and naio were equally represented; and in lower-elevation Ahumoa (2073-2243) naio was over four times as prevalent as mamane. The increase in naio dominance in the lower elevations has been attributed to selective browsing of feral sheep and mouflon sheep (van Riper 1980b). The sheep prefer mamane foliage over other vegetation (Giffin 1976, 1982) and are mostly found in Manao and Ahumoa.

Scott et al. (1984) found that Palila were more common in areas with greater total tree biomass, greater crown cover, taller trees, more mamane fruit, and more native plants in the understory. In addition, higher Palila densities were correlated with greater forest width and pure mamane versus mamane-naio mixed woodland.

The climate on this leeward slope has been described as cool and dry, with monthly air temperatures averaging 11 degrees Celsius and annual rainfall approximately 500 mm. Although rainfall is very low, the interception of cloud-water and throughfall by the canopy is extremely important in maintaining moisture in this high altitude montane forest (Juvik and Nullet 1993).

PHYSICAL CHARACTERISTICS

The Palila is large in relation to other drepanidines; an adult weighs approximately 40 g and is 15.0 to 16.5 cm long (Berger et al. 1977). Adult or after-second-year (ASY) Palila have a bright yellow head and breast, black-grey lores which extend into a thin outline around the eye, grey chin, black bill and legs, white abdomen, grey back and rump, and grey wing and tail feathers with yellow margins. Palila exhibit a relatively subtle sexual dimorphism in plumage coloration; the males have a distinct napeline (yellow head meets grey back) in comparison to the females (the grey from the back rises into the yellow head). The lores of the male are distinctly black whereas those of the female are a dull black or grey. For the most part, gender is distinguishable in the field; however, there are cases in which individual variation (extremes) can impose question. Juvenile coloration is dull (mostly grey) relative to that of an adult. Hatch-year (HY) and second-year (SY) birds have complete or incomplete wingbars. An initially yellow, later white, bill tip is the best identifying characteristic of a HY bird. In somewhat unique patterns, this light bill tip colors in black, proximally to distally.

cup with lichen (*Usnea*). Usually, the nests are built in lateral tree branches or terminal forks of mamane trees and are approximately 14 cm in diameter, 8 cm high, and 4 cm deep (van Riper 1980a). A Palila egg is about 1.6 cm in width & 2.5 cm in length; it is white with light reddish-brown splotches concentrated on the larger end of the egg (van Riper 1980a). The average incubation and nestling periods are 16.6 days and 25.3 days, respectively (Pletschet and Kelly 1990). Individual Palila nest in the same areas year after year; however, they do not show preference for natal sites as young males and females select first time nest sites an average of over 700m away (T. Pratt, unpubl.). Low productivity in palila has been attributed to few breeding birds, small clutch size, and a lengthy nesting cycle (van Riper 1980a). Pletschet and Kelly's (1990) findings over the 1988 breeding season revealed that only 25% of Palila nests were successful due primarily to hatching failure (inviability or abandonment) and depredation of nestlings. A 5-year study (1989-1993) led by T. Pratt (unpubl.) determined that approximately half of Palila nests were successful and 50-60% of both eggs and chicks survived, independent of the number of nesting attempts. However, the number of nests attempted as well as the start and end of the season varied over the years (T. Pratt, unpubl.) in coincidence with mamane seed production. The breeding season coincides with maximum pod production (Scott et al. 1984) and is longer when mamane seed production is high (T. Pratt and P. Banko, unpubl.). Mamane pod production has been correlated with amount of precipitation (van Riper 1980b, P. Banko, unpubl.).

Palila have been observed to have low egg hatchability. This may be attributable to cold (nocturnal temperatures: 0 to 5 degrees), dry (relative humidity: 20-50%) conditions in their new range. Kern and Pratt (unpubl.) determined that cold temperatures, indeed, may be a factor, at least for females who take longer (8-9 vs. 3-5 min), though less frequent (29-34 vs. 44-61 times per day), recesses from incubation. However, they state that low nest humidity probably does not contribute to low hatching success, perhaps because the lichen lining of Palila nest cups traps moisture from fog.

Known predators of the Palila include feral cat (*Felis familiaris*), black rat, and pueo or short-eared owl (*Asio flammeus*). Pletschet and Kelly (1990) determined that depredation accounted for 40% of Palila nest mortality (5% at the egg stage and 35% at the nestling stage). Although in many cases, the predator species could not be determined, evidence was sufficient to reveal that feral house cats and black rats were significant culprits. Van Riper (1980a), Lindsey et al. (1995), and Jacobi et al. (1996) agree that predation may be an important factor limiting the Palila population. Amarasekare (1993) argues that predation by mammals does not seem to be a factor limiting the Palila as black rats are mainly associated with naio trees and Palila nest almost exclusively in mamane. An investigation of owl and feral cat diets (Snetsinger et al. 1994) revealed a high incidence of bird remains in cat scats (68%) and pueo pellets (36%), although no Palila were evidenced. It was suggested by Snetsinger et al. (1994) that pueo may have an unusually high proportion of birds in their diet because of the low density of small mammals, their preferred prey, on Mauna Kea (Amarasekare 1993).

Palila do not obviously or aggressively defend large territories, but they do defend their mates and nests (van Riper 1980a, T. Pratt, personal observation). Courtship behavior consists of singing, chasing, flying displays, and feeding. Typically, females are mostly responsible for nestbuilding and solely responsible for incubation and brooding; both males and females feed nestlings; and males feed females and provide most of the post-fledging care. Males exhibit delayed breeding (i.e., no evidence of SY males breeding), while it is not uncommon for SY females to breed (Fleischer et al. 1994).

A male-biased sex ratio exists in adult Palila; 36.3% females to 63.7% males (1:1.75) (Lindsey et al. 1995). The most probable reason for this gender skew is differential mortality of adult females, whose vulnerability increases while sitting on nests or collecting nesting materials on the ground (van Riper 1980a, Pletschet and Kelly 1990). A male-biased sex ratio also exists in HY birds; 17% females to 83% males (1:4.88). Therefore, additional possible reasons for the adult sex ratio skew could include higher emigration rates of HY females and higher mortality of these females who may emigrate to less-preferable areas (Lindsey et. al 1995); however, no data exist to support these hypotheses. Sex ratios of nestling and SY Palila were equal.

Mean annual survival rates of HY and after-hatch-year (AHY) birds, 36% and 63%, respectively, were comparable to those of other Hawaiian forest birds. Annual survival of AHY males and females was not significantly different. Although adults had higher survival in years when mamane pods were abundant, survival of HY Palila was not correlated with mamane pod production (Lindsey et al. 1995).

FORAGING ECOLOGY

Palila primarily eat the immature seeds from the pods of the mamane tree; however, their diet also includes food items such as mamane buds, flowers, and young leaves; naio berries, leaves, and flowers; and occasionally, native mint (*Stenogyne microphylla*) flowers and leaves, orchard grass (*Dactylis glomerata*) seed, and mullein (*Verbascum thapsis*) flowers. In addition, parents feed caterpillars (mostly of the genus *Cydia*) and other insects to their young. Usually, mamane flowers onset during November-January, and seeds are most abundant during December-June (variable annual peaks); however, both flowers and pods are available throughout the entire year (Banko, unpubl.).

Observations of foraging juveniles indicate that they are inept foragers and depend on their parents for several months after fledging. Juvenile birds travel in small feeding flocks which include family and others for an extended period. They seem to follow shifts in mamane pod concentrations (van Riper 1978, Fancy et al. 1993). Radiotracking of Palila revealed that their range of movement was correlated with elevational changes in mamane pod abundance (i.e., where pods were scarce, Palila ranged farther) (Fancy et al. 1993).

CONSERVATION EFFORTS

As with any species which concentrates the majority of its entire population in one locale, the Palila's fate will remain fragile until another significant breeding population is established. The threat of a single stochastic natural event eliminating the species is especially present for the Palila. Extremely dry grass in an area close to military bombing (U.S. Army Pohakuloa Training Area) creates a serious fire threat.

Fancy et al. (1993) suggest that Palila exhibit a strong site tenacity which may prevent them from recolonizing former ranges or dispersing into areas of favorable habitat. The fact that 64 of 178 banded nestlings recaptured or resighted on 2-6 occasions were always within 2 km of their natal area suggests philopatry. Additionally, this character trait may have been evidenced during the 1993 translocation. In March of 1993, 35 adult Palila (23 males and 12 females) were translocated from Puu Laau to Kanakaleonui on the eastern slope. During the first breeding season at the new site, two pair sucessfully nested. Although 29 of the 31 birds that survived transport/manipulation remained at Kanakaleonui for two weeks or longer, at least 16 birds returned to Puu Laau within one year (Fancy et al. 1997).

Younger Palila were predicted to be better translocation candidates (Fancy et al. 1997; Lindsey et al. 1995). Thus, in January/February of 1997, 25 SY Palila from the western slope at Puu Laau were translocated to the northern slope. After 6 months, however, at least 17 birds had returned to the western slope (Banko, unpubl.). Perhaps, translocation of even younger birds, HYs who have attained adequate foraging proficiency, will result in greater success.

In 1996, researchers from the Peregrine Fund, a non-profit conservation organization, artificially incubated Palila eggs and subsequently reared 10 chicks successfully in captivity. Nestling (n=21) mortality was high (48%) due to infectious diseases. All birds remain in captivity for breeding purposes.

In addition to the translocation efforts, captive propagation, and other intensive research, some relatively simple, practical management activities to improve Palila habitat need to be accomplished now. These activities include elimination of remaining ungulates, fence repair to exclude ungulates, seedling planting, and predator control.

CHAPTER 1: FORAGING BEHAVIOR DEVELOPMENT AND SOCIAL DYNAMICS IN JUVENILE PALILA

INTRODUCTION

It has been well-established that efficient foraging is important (Morse 1980). Many studies have shown that juveniles were less successful foragers than adults (see Wunderle 1991 for review) and that their foraging ability improved over time, gradually converging on and eventually equaling adult ability (e.g., Greig et al. 1983; Sullivan 1988). These findings suggest that young birds need to learn foraging skills and practice them. Although most small passerines remain with their parents for 2 to 3 weeks after fledging (Nice 1943), juveniles with difficult foraging niches stay in adult company for a prolonged period, receiving supplemental food and foraging instruction (Morse 1980). In the tropics, some apprenticeships last for 10 to 23 weeks (Gill 1995). Slow development of foraging skills has been linked to the delay of breeding in some species. For example, a herring gull's (*Larus argentatus*) first breeding is delayed until the fourth or fifth year of life, probably not coincidentally, around the time when its foraging skill is equaling that of an adult (Greig et al. 1983). Greig et al. (1983) argue that a breeding bird needs to be an efficient forager as he or she is time-constrained by many other reproductive activities such as courtship, territory defense, incubation, brooding, and feeding mate and young. Therefore, there must be some connection between the age of first breeding and foraging efficiency. Thus, the importance of gaining foraging skills to enhance reproductive success (in addition to the basics for nutrition, growth, and physiological maintenance) is acknowledged.

Not only are well-developed foraging skills important to a breeding bird, but development of foraging skills by juveniles can have a dramatic effect on the population. Inefficient foraging of young Yellow-eyed Juncos (*Junco phaeonotus*) was a major factor limiting the population (Weathers and Sullivan 1989); there was a 42.3% juvenile mortality rate during the first two weeks of independence. Juveniles must learn to allocate their time efficiently to various activities such as foraging, predator avoidance, and social interaction (Sullivan 1988). Thus, understanding how an endangered species, such as the Palila, forages is important for population recovery goals.

There are relatively few behavioral studies on young birds during the time from fledging to independence (Sullivan 1988, McGowan and Woolfenden 1990, Wolf et al. 1988, Moreno 1984, Davies 1976, Zaias and Breitwisch 1989) because it is very difficult to follow birds at this stage. They are relatively sedentary and have camouflaging plumage. Therefore, early development in foraging behavior has not been very well documented. However, the literature on the development of foraging proficiency in juveniles independent from parental care is accumulating. Wunderle (1991) provides an extensive summary of over 50 bird species in which independent juveniles were documented as having different foraging proficiency than adults, though differences lessened with increasing age. He showed that in many species, juveniles were found to display lower capture success; have longer searching time, handling time, and interfood interval; capture smaller prey, less prey, and inappropriate or suboptimal prey. They sometimes utilized different foraging sites or different patches within sites, dropped food items more frequently than adults, or used inappropriate techniques. Seabirds seem to be the most popular subjects for studies on foraging behavior, perhaps because of their visibility on the open waters.

The majority of research on avian foraging is descriptive, resulting from field observations. Wunderle (1991) highlights the importance of color banding individuals to determine rate of foraging development and age at which an adult level of foraging proficiency is attained, cautioning that improvement observed in unbanded birds at different times of the year may be a result of differential mortality of less efficient foragers (Orians, 1969). Because juveniles experience high mortality (Lack 1954), they probably also experience much selection pressure (Arnold and Wade, 1984).

What is considered efficient foraging? The Optimal Foraging Strategy maintains that animals forage at an efficiency that maximizes their fitness (Pyke et al. 1977). Individuals select habitat patches and food items and use harvesting techniques which are energetically profitable (Gass and Sutherland 1985). Depending on the distribution and abundance of food, birds employ different foraging tactics to increase their success. In a habitat with widely-separated patches of concentrated food resource, a bird may spend much time foraging in or near rich areas and quickly pass through poor areas (Gill 1995). Furthermore, birds remember and regularly return to good foraging sites (Krebs et al. 1974, Smith and Sweatman 1974, Zach and Falls 1976).

Over time, the critical needs of a young bird change. Initially, the food provided to fledglings by adults is critical to their growth and survival. Subsequently, the ability to forage independently for self-survival becomes more important, and eventually, knowledge and skills to forage efficiently so as to rear offspring are necessary for fitness gains. Young birds probably require more food during the post-fledging stage than they did at the nestling stage (Wolf et al. 1988, McGowan and Woolfenden 1990, Moreno 1984). Wolf et al. (1988) found that dark-eyed junco (*Junco hyemalis*) young who did not receive help from the male parent (from fledging to independence) survived only half as well as those who received male help. Similar results were found in the seaside sparrow (*Ammodramus maritimus*) (Wolf et al. 1988).

In many species, birds other than the parents (helpers) appear at nests and actively feed the young of the breeders. In some species, parents do not reduce food provisioning to fledglings when helpers are present (McGowan and Woolfenden 1990); however, in others species, the parents expend less energy in rearing (du-Plessis, 1991). It is possible that if young are receiving extra food because of helper provisioning, they may have less need to forage independently. Heinsohn (1991) suggests that "juveniles must optimize between acquiring sufficient food from begging and devoting sufficient time to learning to forage." How do juveniles acquire and fine-tune foraging skills? Improvement in a juvenile's foraging skills may be due to muscular and nervous system development (neuromuscular coordination) as well as to learning (Cruze 1935). While initial improvement may be more attributable to maturation (Cruze 1935), improvement after independence is more often considered a result of learning and practicing (Wunderle 1991). Davies (1976) attributed foraging improvement to continual growth in cases where parents fed away from the young (e.g., Spotted Flycatcher). Another example of physical maturation leading to better foraging is provided by Struwe-Juhl (1995). He found that juvenile Black-tailed Godwits fed on arthropods until their bill lengths were long enough to probe the ground for earthworms, a more profitable food item.

Some behavioral mechanisms by which inexperienced juveniles may learn foraging skills include: 1) trial-and-error (Kamil and Yoerg 1982), repeated sampling of environmental cues which leads to incorporation of successful trials and avoidance of errors; 2) social facilitation (Thorpe 1963), observing the successful behaviors of a model which encourages the release of those behaviors already in an individual's repertoire; 3) copying (Gould 1982), the imitation of an experienced individual's behavior regardless of its outcome; 4) local enhancement (Hinde 1961), becoming alerted and drawn to a food source that others have discovered and are using.

Groups of white-throated magpie-jays (Calocitta formosa) with a trained model acquired a novel foraging skill better than groups without models (Langen 1996). Avery (1996) demonstrated that young house finches (*Carpodacus mexicanus*) that were raised by adults that avoided oats had a lesser preference for oats than birds that were raised by oat-eating adults. He suggests that extended association with parents may affect the food habits of young altricial birds. After basic foraging skills are learned, the practicing of these skills leads to improvement in efficiency.

Juveniles traveling in a flock may learn where food is abundant, acquire foraging skills more quickly (through social facilitation and copying), and thus may increase survival probability. This prediction assumes that the adults of the flock are serving as examples and teachers, rather than interrupters and competitors. Sullivan (1988) found that social foraging by juveniles increased survival after retraction of parental care. Additionally, the shared vigilance in flocking can benefit independent young by allowing them more time to forage (Sullivan 1988).

Food has been a dynamic factor in the Palila's evolutionary and ecological history. The evolution of the Hawaiian honeycreepers from a single finch species is dramatically illustrated by their diverse bill structures. The diverse lengths, curvatures, and shapes evolved in response to the various food niches discovered and occupied. The Palila stands a present reminder of its ancestor, with its strong finch bill designed for ripping open the fibrous mamane pod to access tender green seeds, the staple of its diet. Food also plays a role in the evolution of behavior. Sullivan (1988) refers to the evolution of behavior as "adaptation to constraints".

Possible constraints in the Palila population in regard to foraging ecology include food abundance and distribution, limited foraging range, and a difficult foraging niche. Food availability seems to affect both the recruitment of young Palila into the population as well as the survival of adult birds. In years of low mamane pod production, there were fewer nesting attempts (van Riper 1980a; BRD, unpubl.) and adult Palila suffered higher mortality; however, HY birds did not (Lindsey et al. 1995). Generally, Palila foraging has been limited by habitat degradation and fragmentation over the years. Further, Fancy et al. (1993) explains that site tenacity in Palila has accounted for their limited movements; limited movements may limit foraging possibilities. On average, Palila forage over 3km^2, and their ranges overlap with many other individuals (Fancy et al. 1993); such overlapping may increase competition for food resources. Flocks of foraging Palila seem to follow shifts in mamane pod concentrations (van Riper 1980, Fancy et al. 1993), ranging farther when food is scarce. Although the finch bill of the Palila is designed for opening mamane pods, there seems to exist an inherent complexity in the characteristic technique used to extract the seeds. Thus, juveniles may need a considerable amount of instruction and practice before attaining proficiency. Heinsohn (1991) agrees that a difficult foraging niche may cause "extra burdens on developmental time budgets".

In addition to immature seeds, Palila eat flower and leaf buds, flower parts (stamens, petals, nectar), and leaves (flush and leaflets) from the mamane tree. Although it is difficult to verify selection of insects from field observations of Palila pecking at bark, fecal analysis reveals that *Cydia* sp. (Lepidoptera: Tortricidae) caterpillar occurs in 98.7% of nestling fecal samples and 58.1% of adult samples, suggesting that it is a main component of the

Palila's diet. This native caterpillar infects mamane pods and feeds on the seeds; Palila may preferentially select pods containing *Cydia* (BRD, unpubl.). Geometrid larvae and other arthropods were also found in fecal samples (37.3% of nestling samples and 24.7% of adult samples). In addition to mamane, Palila use the native naio tree for food. They mostly select the mature, white berries, but have also been observed eating flower petals and leaves. Other native foods, include flowers and leaves of stenogyne, a mint whose vine crawls to entanglement in trees and berries, flowers, and leaves of the sandalwood tree (*Santalum ellipticum*: Santalacaeae), a species which, according to Wilson and Evans (1890-1899), occurred in "fair quantity" in the Palila's habitat in the late 1800s. Palila feed on non-native plants as well. They have been observed eating the seeds of orchard grass and on occasion, flower petals from the hardy and invasive mullein.

Based on a few observations of juvenile Palila which indicate that they are inept foragers who depend on their parents for an extended period, it is predicted that: 1) juveniles learn foraging skills from adults (parents, helpers, or flock mates), 2) the development of foraging proficiency in recently-fledged Palila is critically important to their survival, and 3) mortality is greatest around the time that young become independent of their parents.

STUDY SITE

This study took place in the native dry forest on the western slope of Mauna Kea between about 6500 and 9500 feet (2000-2800 m-ck) elevation in the area of Puu Laau, Puu Manao, and Puu Ahumoa. This open-canopy forest is codominated by mamane and naio trees and has a grassy understory. Van Riper (1980b) and Scowcroft and Giffin (1983) described the vegetation of this 34-km2 area.

Study transects that have been used by the Hawaii Field Station since 1987 were utilized. The study area is divided into four main elevational grids: Mauka ("toward the mountain"), Makai ("toward the ocean"), Manao, and Ahumoa. Each grid had a series of transects, each transect was approximately 1050m in length with a phenology station at every 150m (Figures 1 and 2).

Searching for active nests took place in the Puu Laau area, where most of the Palila population breeds, but foraging was observed in all areas.

METHODS

From April through August, 1994 and 1995, searches for active Palila nests in the Mauka and Makai grids were conducted, concentrating efforts in areas that have had the most breeding activity in the past. In 1994, the small field crew was not able to search systematically along transects so searches were concentrated in areas where nests were discovered the previous year. In 1995, a standardized nest searching method was used wherein a group of four walked along transect in a perpendicular line, inspecting every tree within a 40m swath (20m to each side of the transect).

Figure 1. The island of Hawaii.

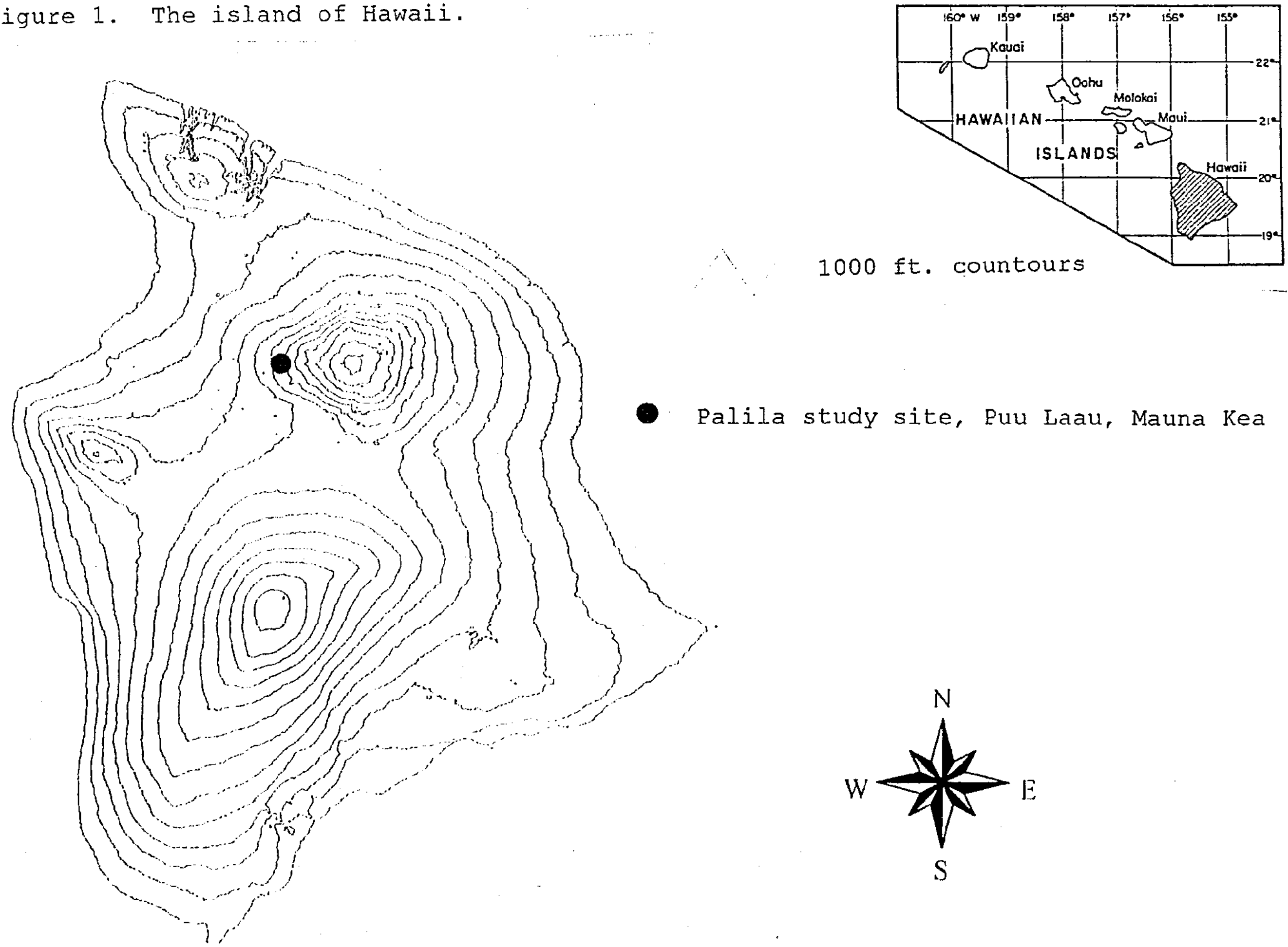
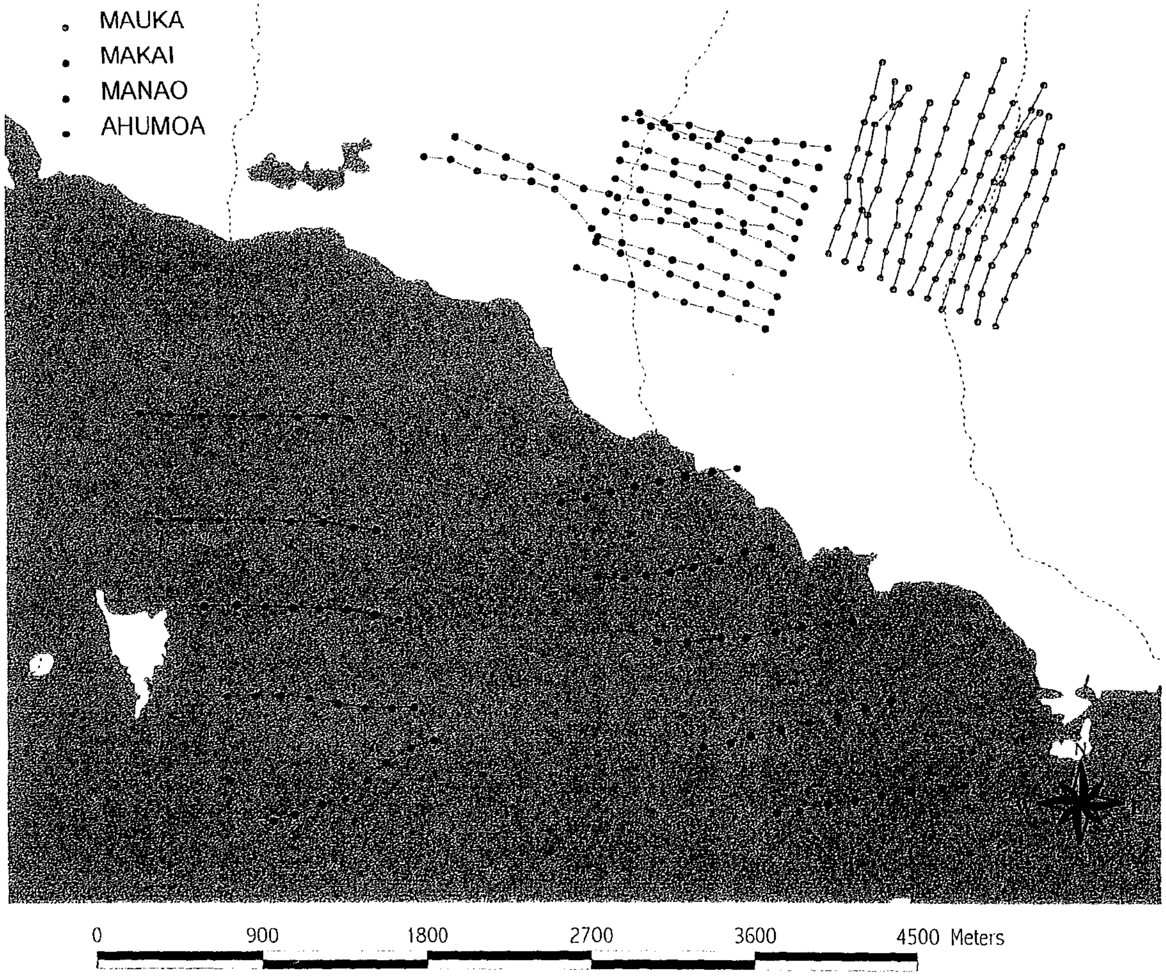


Figure 2. Study grids at Puu Laau, Mauna Kea, Hawaii



When the nestlings were at least 10 days of age and had sufficient feathering to endure an extended duration without brooding, the nest tree was surrounded with mist nests, and the attending male(s) were captured, color banded, and equipped with radio transmitters. Two bands were placed on each leg using a unique combination of 3 color bands and one numbered USFWS aluminum band. The open junction of each plastic band was welded with methyl-ethyl-ketone to prevent removal by these strong-billed birds. Previous use of super glue to secure plastic bands was not effective long-term, and accounts for the many birds with partial combinations. Color band combinations were recorded as follows: left leg top band/left leg bottom band, right leg top band/right leg bottom band (e.g., Green/Red, Blue/Aluminum). The bird was weighed and measured (tarsus, bill, tail, wing chord, and fat). Then, a 1.5g radiotransmitter (<5% of the average adult Palila's weight) was glued interscapularly using the attachment method described by Fancy et. al (1993). Radiotransmitters were procured from Holohil Systems Ltd. (3387 Stonecrest Road, Woodlawn, Ontario, Canada KOA 3MO). Preliminary studies showed that placebo transmitters attached to Palila had no adverse effects on flight, feeding, or social interactions (Fancy et. al 1993). Bird handling time was approximately 30 minutes. Newly-transmittered birds were allowed a 2-day adjustment period wherein no detailed observations were collected. During this time, the birds were checked by detecting movement (as indicated by a changing radio signal) or actually tracking them for a brief visual assessment. Thereafter, birds were tracked daily to weekly, attempting to attain independent observations of at least 100 seconds duration during the remainder of the nesting phase and postfledging. Though the life of these radios was 8 weeks, transmitters typically stayed on the adults for 4 weeks. Wet weather conditions probably accelerated the detachment. After radiotransmitter attachment, the bird's identification was recorded by its radiotransmitter frequency (e.g., 164.372) in addition to or in substitution for its color bands.

Overall, transmitters were attached to 4 males at 4 nests in 1994 (2 detached prematurely) and to 10 males at 8 nests in 1995 (3 malfunctioned). Nestlings were banded between 12 and 15 days using the same banding regime described for the adult, though measurements of wing (primary #9) and tail (rectrix #6) feather emergence from sheath were included. 7 nestlings were banded at 5 nests in 1994 and 13 nestlings at 8 nests in 1995. When the adults' transmitters were nearing expiration or expected detachment, attempts were made to capture and attach a radio to their associated fledgling. Transmitters were attached to only 5 of the juveniles that were banded as nestlings (2 in 1994 at 2 and 2.5 months postfledging and 3 in 1995, 2 at 1 month and 1 at 3 months after fledging). In addition, a radio was attached to 1 juvenile of unknown origin and age. Transmitters detached from juveniles prematurely due to the force of pin feather emergence against the underside of the transmitter.

In addition to observing males and fledglings with transmitters, incidental observations were collected on banded females that were known nesters as well as unbanded juveniles. The tendency of observations close together in time (temporal dependency) and space (spatial dependency) to be more similar than observations with large intervals or distances needs to be addressed in foraging studies (Noon and Block 1990). Thus, in order to ensure temporal and spatial independence of observations in this study, several rules were enacted: 1) Observations of the same individual were a least one hour apart, 2) No more than 3 different individuals were observed in same tree within the same hour, and 3) No more than 2 observations of the same bird within the same tree per day were used (even though the interval between observations may have been greater than one hour). Foraging observations were collected from June 1994 through December 1996, throughout the day (typically, between 8am and 5pm). Raphael and Maurer (1990) emphasize the "need to relate changes in bird behavior with changes in resource", and explain that "within-season variation in resource availability may account for much of the variation in samples of foraging behavior".

Appropriately camouflaged, the observer approached the focal bird to a distance where behavior could be observed without question, but where the bird did not appear to notice the observer. Typically, observer distance from the focal bird was between 5 and 10m. Using binoculars and a microcassette tape recorder, foraging and other behavior were recorded (Table 1). A continuous sampling method, accounting for each second of behavior, was used.

Interactions between juveniles and adults were observed. Identification of particular benchmarks in the development of foraging skills (e.g., recognition of food items, severing food items, extracting seeds from pods, grasping food, finding a suitable perch on which to eat) was attempted. Calculation of average number food item interactions, proportion of time spent foraging versus performing other active behavior, and proportion of time spent in various foraging behaviors was performed. Refer to Table 2 for a list of food items and their operational definitions.

Table 1. Operational definitions of Palila behavior.

FORAGING BEHAVIOR

PECK: a failed attempt to sever a food item
PICK: a food item is severed from the tree and held in the beak
CARRY: a food item is held in the bill while hopping or flying to a perch
GRASP: a food item is held against a branch with one or both feet in preparation for biting or eating
BITE: ripping back the wings of a mamane pod to expose the seeds
EAT: a food item is mandibulated and consumed

OTHER BEHAVIOR

HOP: movement from perch to perch without use of wings
LOOK: movement of head in vigilance
FLY: movement within or between trees by use of wings
PREEN: maintanence of plumage; includes use of bill to clean/comb feathers, ruffling of body, and/or scratching with foot.
SING: any vocalization
DEFECATE: discharge of fecal matter from vent
BILL WIPE: rubbing of each side of bill against a branch to remove food residue
FEED MATE: focal bird feeds mate
FEED CHICK: focal bird feeds chick
SOLICIT FOOD ACTIVE: focal bird makes begging sounds, shivers its wings and postures to another, following closely with its mouth wide open
SOLICIT FOOD PASSIVE: bird follows another closely with its mouth open, but does not make begging sounds or shiver its wings
COURTSHIP CHASE: focal bird chases another to pursue it
AGGRESSIVE CHASE: focal bird chases another to drive it away
WATCH: focal juvenile watches another palila feed; the two birds perch very near to one other

Table 2. Operational definitions of Palila food.

FLOWER BUD: a closed mamane flower
FLOWER: an expanded yellow mamane flower
YOUNG POD: a developing mamane pod; string bean-like; no evident expanded seeds or wings
EXPANDED GREEN POD: a fully-developed mamane pod with expanded seeds (>3mm in width) and wings
BROWN POD: an old, brown mamane pod which has no green remaining
LEAF: flush or mature leaf
NAIO BERRY: a white berry from the naio tree

Each observer transcribed his or her own observations from tape into The Observer 3.0 Program (Noldus Information Technology Inc.). Editing of the observational data files consisted of elimination of the first 10 seconds of behavior to avoid overrepresentation of conspicuous behaviors (discovery bias).

In addition to the second by second accounting of behavior, point data were recorded for each observation. At the 11th second from initial sighting of the focal bird, the following data were recorded: 1) behavior exhibited, 2) food (item indicated) or no food, 3) social or no social behavior (another Palila in the tree defined social behavior), and 4) tree species in which bird was resident. Point data allowed for use of observations that were less than 100 seconds and thus, increased sample size considerably. In addition, Noon and Block (1990) recommend gathering sequential as well as point observations of foraging behavior.

Non-parametric analysis (Mann-Whitney U test) was used to compare juvenile foraging behavior at approximately 10 days and 100 days and to compare this juvenile's foraging behavior at 100 days to a random adult bird.

Initial attempts to quantify survival by radiotracking were not successful as it was very difficult to capture target juveniles, and transmitters detached with pin feather emergence within 2 weeks. Subsequent systematic searching along transect proved to be labor-intensive and resulted in few sightings. In the end, we relied on incidental observations and simply reported minimum percent survival of the 23 juveniles that were banded (7 in 1994 and 16 in 1995).

RESULTS

Ontogenetic Patterns

Qualitative

Throughout the nestling period, degrees of food solicitation increased. Young progressed from the gaping response after hatch to the complete begging behavior which incorporates body posturing, wing flapping, and vocalization. Exploring their nest and accessing their immediate surroundings, nestlings exhibited approximations of foraging behaviors such as pecking (day 17), nibbling (day 18), and picking (day 23). One nestling, the day before fledging, left the nest and pecked at an expanded green pod which was lying against a branch. Another nestling was observed mandibulating a leaflet at 22 days. Typically, though, foraging behavior in nestlings was associated with non-food items such as twigs, grass stalk, bark, and lichen. Between days 15 and 20, nestlings began to stretch and flap wings, excercise legs, stand on the nest rim, hop, and preen. Nearing the end of the nestling phase, attending adults seemed to perch increasingly farther away from the nest upon arrival. Adults fed young who were 20 and 25 days of age at 2 and 3m from the nest, respectively.

For approximately the first week after fledging, the young were completely dependent on adults for food. They remained perched and relatively inactive for long periods of time (hours), and the adult brought food at fairly regular intervals (approximately every 15 minutes). These stationary states were interrupted with an occasional peck or nibble at a mamane flower or leaflet. Lack of balance and weak grasping and flight ability were observed at this stage. Gradually, the young became more active and coordinated, flying within and between trees. During the second week, they began more active and frequent pecking and nibbling. After pecking and repeated pulling, one juvenile (day 13) severed a leaflet. Another juvenile pecked at a brown pod. After being fed, some birds followed the adult briefly. Within the third week (day 18,20), they picked and carried food items, mostly leaflets or flush. Between 20 and 30 days post-fledging, the young birds made marked progress in regard to independent foraging. Within this interval, juveniles were observed eating mamane flowers (day 20), mamane flower buds (day 20), and naio berries and leaves (day 22); severing pods (25 days); watching adults feed from mamane pods; and actually emulating the adult's sequence of picking a pod, carrying it to a suitable perch, grasping it against the branch, and attempting to bite it open (day 29). The earliest witnessings of juveniles independently eating seeds from a pod were 29 and 31 days after fledging. Even after the juvenile seemed proficient at extracting seeds from pods, the young bird still received food from the attending adult (51 days, 89 days, 95 days). Note that this descriptive summary, unfortunately, is based upon a collection of incidental observations of known-aged juveniles. It does not represent the average development of many different individuals nor the progression of one juvenile. Nevertheless, it provides accurate information which can be used as a rudimentary framework upon which to build a timeline for Palila foraging development.

Unable to acquire numerous observations on banded juveniles at different ages, additional observations were made on random juveniles, and foraging skill and social behavior were noted in relation to bill color. Typically, the upper mandible of a HY bird became black before the lower; however, many different patterns were observed. A recent fledging usually had a bill that was more than 1/2 yellow. Random juveniles with >1/2 yellow bills pecked and nibbled at non-food (lichen, twigs) and food (flower petals, flush) items. Young Palila with 1/2 yellow bills were observed carrying, pecking, and eating food items, mainly flush and flowers. Although most juveniles were not observed foraging independently on pods until all but the tip of their bill was black, a few individuals with approximately 1/3 white bills were observed eating pods successfully, albeit with some detected difficulty (e.g., repeated regrasping of pod against branch, laborous opening of pod husk). Juveniles with white bill tips (1/4 light) were often very closely associated with an adult. The amount of interaction between the juvenile and adult seemed to be at a maximum at this point, and there was evidence of learning. Juveniles perched beside adults, watching them feed on pods or flowers, and sometimes eating the food within the adult's grasp. The juveniles at this stage were followers. They were still being fed, but engaged in successful independent foraging on pods with varying degrees of difficulty in picking pods, grasping, and finding a suitable perch. Juveniles with very slight white on their bill tips were observed still being fed by adults while others were confirmed as independent. Juveniles with no detectable white on their bills usually foraged without adult association and with apparent skill.

On several occasions, it was possible to note bill coloration and assess foraging of known-aged juveniles. At best, using bill color to estimate age or foraging skill is marginal as there seem to be marked individual differences in darkening rates or perhaps in developmental progress.

Quantitative

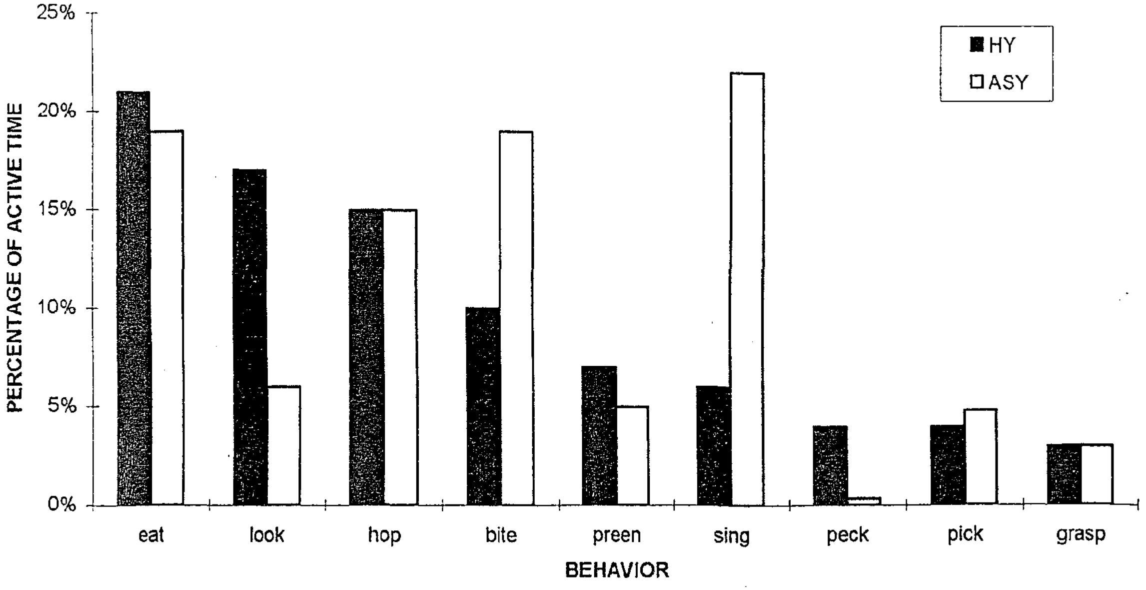
Time-Activity Budget

Across age and sex classes, Palila spent about 70% of their time perched. No difference was detected between ASY (67.3%; n=275) and HY (71.4%; n=43) birds or between males (67.3%; n=173) and females (67.3%; n=102).

Point data revealed that in 63.5% (n=301) of the observations of ASY birds (n=553), the adult was perched and in 76.7% (n=78) of all juvenile observations (n=90), the young bird was perched.

Females (n=102) spent 50.9% of their active time foraging, males (n=173) spent 42.8%, and juveniles (n=43) spent 40.1%. ASY Palila spent most of their active time singing (22%), biting (19%), eating (19%), and hopping (16%) . Active juveniles spent their time eating (21%), looking (17%), and hopping (15%). Comparing ASY and HY time budgets (Figure 3), it was found that adults spent proportionately more of their time singing than juveniles, and juveniles spent more time looking than adults. In addition, HY birds pecked more than adults.

Figure 3. A comparison of active behavior allocation in adult (ASY) (n=275) and juvenile (HY) (n=43) Palila using 100-second continuous observations



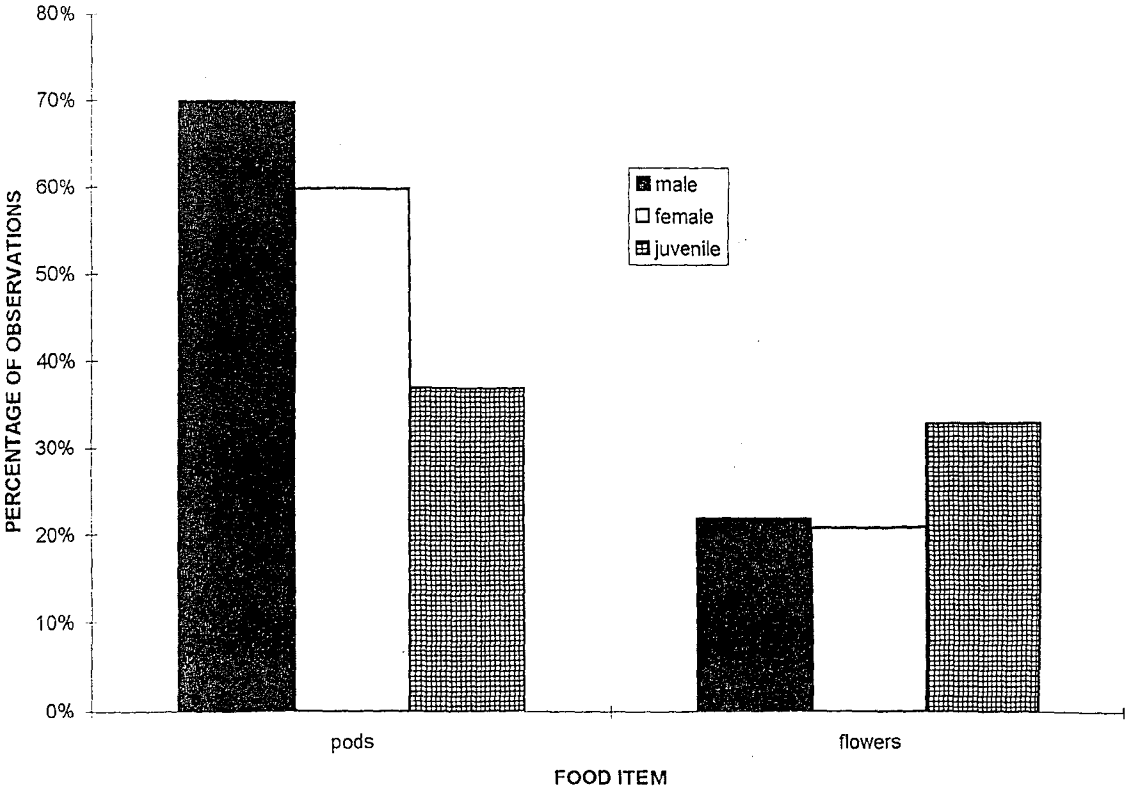
According to point data, HY birds spent the majority of their active time looking (42%) and hopping (29%) while ASY birds allocated their time to hopping (24%), biting (20%), and eating (17%) and secondarily, looking (10%) (Figure 4). Forty seven percent of the active observations of adults (n=202) were of foraging behavior whereas none of the active juvenile observations (n=21) consisted of independent foraging.

Food Selected

In 79% of 100-second continuous observations of random Palila, all age and sex classes combined (n=349), Palila interacted with food. Overall, expanded green pods were the most frequently utilized food resource (44%), followed distantly by mamane flowers (12%) and flower buds (10%). A collection of various other foods (predominantly mamane leaf, young mamane pod, and naio berry) comprised the remaining 13% of the observations. Juveniles interacted with pods less than adults, but interacted with flowers comparably. Interaction with a pod occurred in 70% of male foraging observations (n=116), 60% of female foraging observations (n=82), and 37% of juvenile foraging observations (n=30). Interaction with a flower occurred in 22% and 21% of male and female observations, respectively, and in 33% of juvenile foraging observations. (Figure 5)

Of all foraging observations, males interacted with an average of 1.09 pods (SD=1.05; n=116) in 100 seconds, females with .95 pods (SD=1.00; n=82), and juveniles with .67 pods (SD=1.12; n=30). [Average number of seeds eaten would be a better measure.] In regard to flower interactions, juveniles took 1.12 flowers per 100s; females,

Figure 5. Percentage of 100-second observations in which juvenile Palila inteacted with mamane pods and flowers (male:n=116, female:n=82, juvenile:n=30)



.78 flowers; and males, .75 flowers. Of foraging observations in mixed mamane-naio forest, females interacted with naio berries in 8% of the observations (n=36), males in 5% of the observations (n=42), and juveniles in 50% (n=6) of the observations (Figure 6).

According to point data, in 64% of all the observations in which food was being manipulated (n=17; 19.5% of all observations [n=87]), the focal juvenile was interacting with an expanded green pod, in 12% with a young pod, and in 12% with a flower. In 66% of all the observations in which food was being manipulated (n=210; 40.3% of all observations [520]), the adult was interacting with a pod and in 14.2% with a flower.

Paired t-tests of lengths of mamane pods discarded by juveniles versus their male parents revealed that males selected pods significantly longer than juveniles (BRD, unpubl.). The average number of seeds per mamane pod selected by Palila (independent, not representative, obsvns; data from observations, not pod discards) reveal that ASY birds selected pods with a mean of 2.22 expanded seeds (SD=1.31;n=18) and HY birds selected pods with a mean of 1.27 expanded seeds (SD=0.59;n=15).

Tree Species Utilized

Of all observations in mixed mamane-naio forest, juveniles (n=34) were sighted in mamane in 62% of the observations and in naio in 38% of the observations, and ASY birds (n=219) were resident in mamane in 73% of the observations and in naio in 27% (Figure 7). ASY Palila (n=71 in Ahumoa; n=69 in Manao) showed a preference for mamane

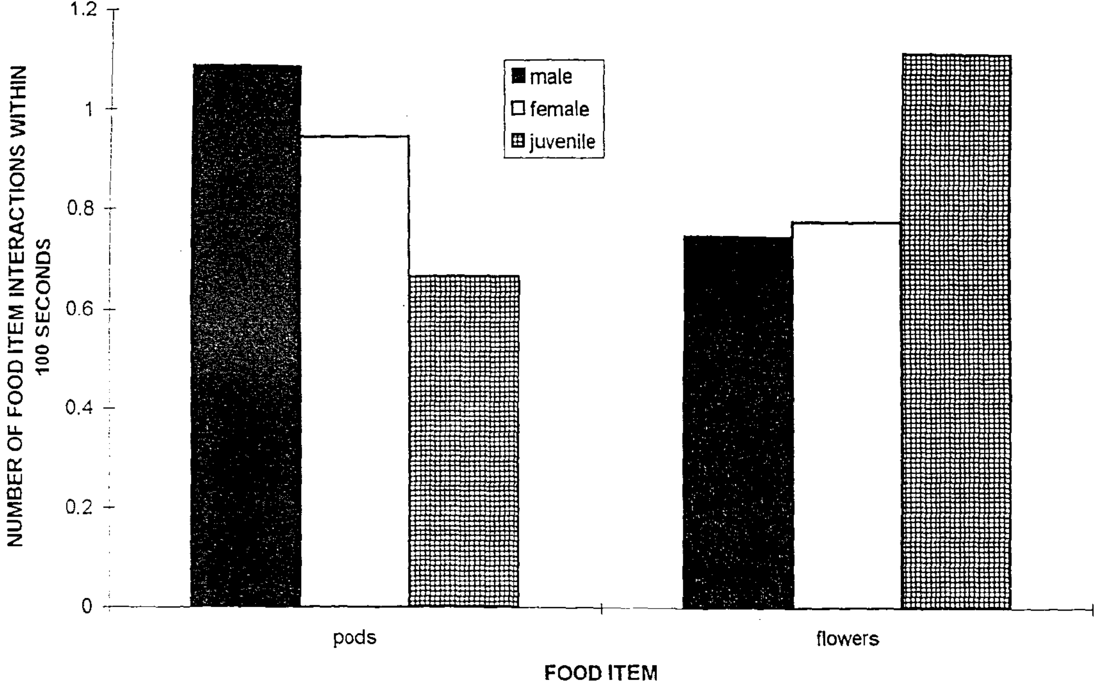
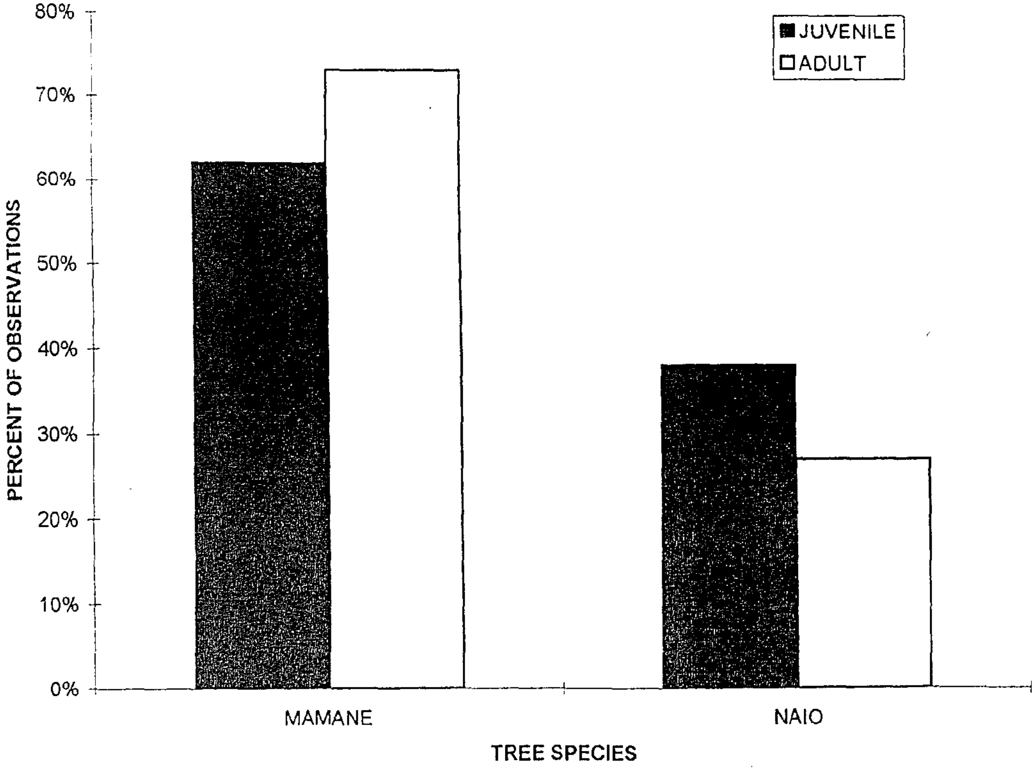


Figure 6. Average number of mamane pods and flowers handled by Palila in 100 seconds (male:n=116, female:n=82, juvenile:n=30)

Figure 7. Tree species in which Palila were resident in mixed mamane-naio forest (point data; adult: n=219, juvenile: n=34)



in Ahumoa where the ratio of mamane to naio is 4.55:1 and in Manao were the ratio is approximately 1:1. They were sighted in mamane more than expected based on these ratios (Fischer's Exact Test: Ahumoa: $p<0.0001$, C.I.: 0.03241 to 0.1632; Manao: $p=0.0003$, C.I.:0.1196 to 0.5417). In contrast, juveniles ($n=8$ in Ahumoa; $n=9$ in Manao) showed no preference for one tree species over the other (Fischer's Exact Test: Ahumoa: $p=1.0000$, C.I.: 0.1492 to 2.98; Manao: $p=0.3348$, C.I.:0.2958 to 1.397), though sample size was extremely small.

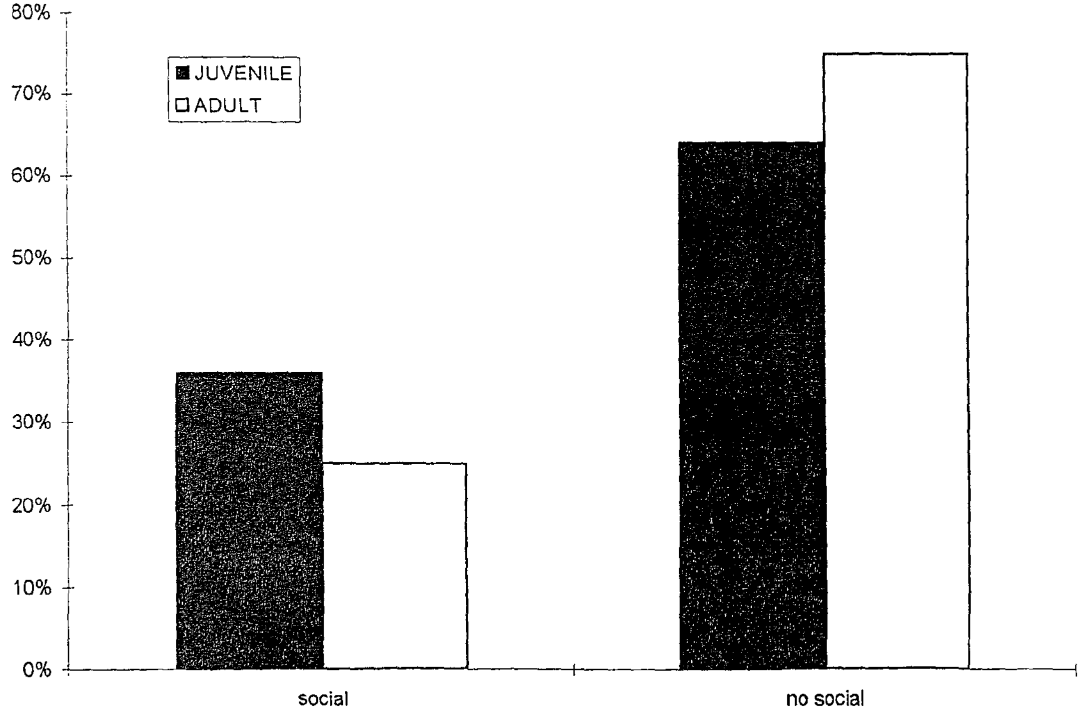
Social Behavior

Of a total of 563 observations, ASY birds were in a tree with another bird in 25% of the observations and alone in 75% of the observations. Of a total of 95 observations, the focal juvenile was in a tree with another bird in 36% of the observations and alone in 64% of the observations (Figure 8). Juveniles ($n=21$) were mostly seen in a tree with an adult male (42%) or female (38%), but were also observed with other juveniles (10%) and within groups (10%).

Length of Juvenile Dependency

Due to difficulty in capturing known fledglings and premature transmitter detachment, incidental observations were used to determine when juveniles became independent of adult care (i.e., no longer received supplemental food). The oldest dependent juveniles observed were 89 and 95 days postfledging and the youngest independent juvenile observed was possibly 102 days and definitely 124 days. Confirmation of independence of a known-aged juvenile (164.216) was determined by repeated observation through radiotracking (11 independent

Figure 8. Proportion of observations in which focal juveniles (n=95) and adults (n=563) were social (i.e., in tree with another palila (point data)



observations from 102 to 124 days). Conservatively, juvenile Palila become independent sometime between 3 and 4 months.

Relative Investment of Males and Females in Postfledging Care

Of a sample of 39 independent observations of random juveniles being fed by adults, 66.7% (26) were of males feeding and 33.3% (13) were of females feeding. Additionally, of 13 juveniles that were banded as nestlings in 1995, 7 were accompanied and supplementally fed by males post-fledging, 2 were attended by females, and 4 were not observed with an adult after they fledged. Of the six fledglings in 1994, 4 fledglings were in association with males while 2 were not observed. One of the 2, who was known to survive to independence, was probably with a male as the female was renesting even before the juvenile fledged. Note that these data are biased as only the males had radiotransmitters; however, it can be stated that, at a minimum, more than half (58%) of the HY birds were cared for by males after fledging (67% in 1994 and 54% in 1995). Of 19 observations of light-billed juveniles, 8 were fed by females, 6 by males, 2 by unknowns, 1 by both male and female, 1 by female and unknown, and 1 by male and unknown. These young birds were fed by one adult more often (16/19 observations; 84%) than by 2 adults in (3/19; 16%).

Foraging Development

Known juveniles (n=10) were grouped by days postfledging into periods 1, 2, 3, and 4; period 1 included days 0-19 (mean=9.38, sd=5.88, n=8); period 2 included days 25-43 (mean=33.67, sd=6.38, n=6); period 3 included days 81-99 (mean=92.71, sd=5.76, n=17); and period 4 included days 102-119 (mean=107.10, sd=5.04, n=10). The time periods were defined *a posteriori* by distribution of 100-second continuous observations attained.

Note that sample sizes are small and unequal and some individuals are over-represented in the age periods designated. Therefore, descriptions of general trends, rather than statistical analyses were used when evaluating the data.

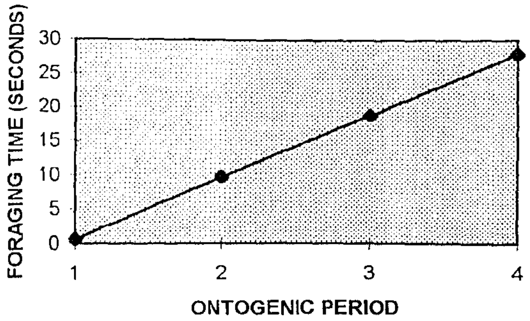
Given that all juveniles develop at basically the same rate, biologically, the data suggest a developmental progression in foraging. Progressing from period 1 through period 4, foraging time increased (Figure 9a), as did the time spent eating (Figure 9b). The mean number of total food items manipulated (Figure 9c), and specifically, the mean number of pods handled (Figure 9d) increased over time. A decrease was observed in the mean time juveniles spent actively soliciting food from adults (Figure 9e) and in the mean number of interactions with non-food items (Figure 9f). A gradual increase was detected in the time juveniles spent picking (Figure 9g), carrying (Figure 9h), and grasping (Figure 9i) food items.

Observations of Known-Aged Juveniles

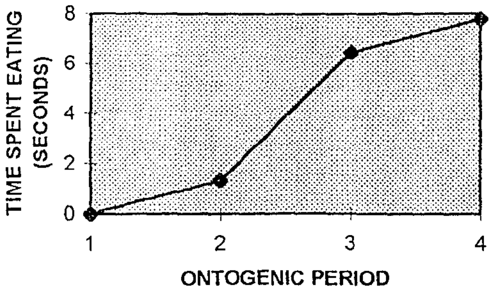
Observations of Juvenile 164.422 at an average age of 100 days post-fledging (SD=4;n=13) were made in the Mauka grid between November 29, 1994 and December 9, 1994. Within 100 seconds, this bird manipulated a mean of 3.85 food items (SD=3.75) (median=3; range=1-14), foraged for a mean of 25.15 seconds (median=21; range=6-43),

Figure 9. Development of foraging behaviors in juvenile Palila. All means are based on 100 seconds of continuous observation. Ontogenic period 1 includes days 0-19 post-fledging; period 2, days 25-43; period 3, days 81-99; period 4, days 102-119. a) mean time spent foraging, b) mean time spent eating, c) mean number of food items handled, d) mean number of pods handled, e) mean time spent actively soliciting food from adults, f) mean number of interactions with non-food items (branch tip or bark), g) mean time spent picking food items, h) mean time spent carrying food items, I) mean time spent grasping food items.

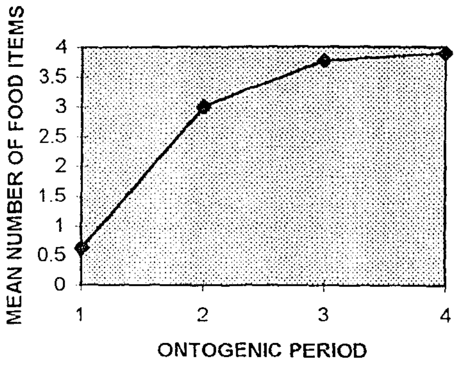
9 **a**


FORAGING TIME (SECONDS)
30
25
20
15
10
5
0
1
2
3
4
ONTOGENIC PERIOD

9 **b**


TIME SPENT EATING (SECONDS)
8
6
4
2
0
1
2
3
4
ONTOGENIC PERIOD

9 **c**


MEAN NUMBER OF FOOD ITEMS
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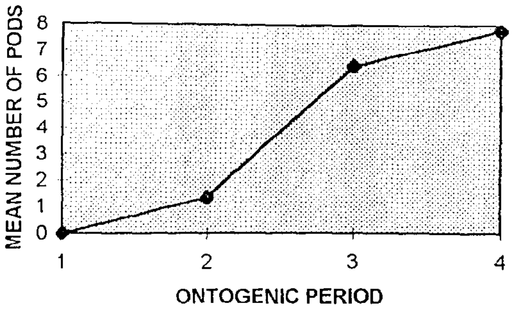
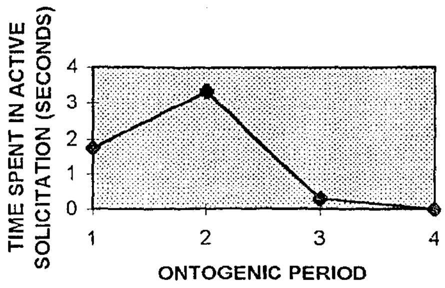
3.5
3
2.5
2
1.5
1
0.5
0
1
2
3
4
ONTOGENIC PERIOD

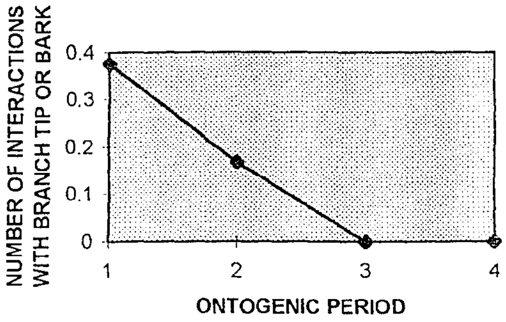
9 **d**


MEAN NUMBER OF PODS
8
7
6
5
4
3
2
1
0
1
2
3
4
ONTOGENIC PERIOD

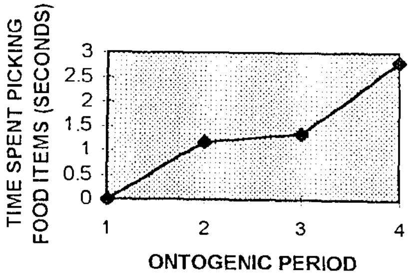
9 **e**


TIME SPENT IN ACTIVE SOLICITATION (SECONDS)
4
3
2
1
0
1
2
3
4
ONTOGENIC PERIOD

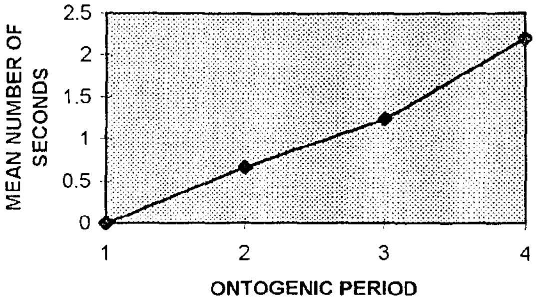
9 **f**


NUMBER OF INTERACTIONS WITH BRANCH TIP OR BARK
0.4
0.3
0.2
0.1
0
1
2
3
4
ONTOGENIC PERIOD

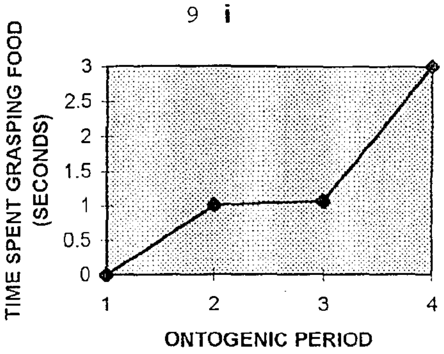
9 **g**


TIME SPENT PICKING FOOD ITEMS (SECONDS)
3
2.5
2
1.5
1
0.5
0
1
2
3
4
ONTOGENIC PERIOD

9 **h**


MEAN NUMBER OF SECONDS
2.5
2
1.5
1
0.5
0
1
2
3
4
ONTOGENIC PERIOD

9 **i**


TIME SPENT GRASPING FOOD (SECONDS)
3
2.5
2
1.5
1
0.5
0
1
2
3
4
ONTOGENIC PERIOD

manipulated an average of 1.62 (SD=1.19) pods (median=2; range=0-3), and spent an average of 6.46s (SD=4.98) eating (median=6; range=0-15). Comparison of continuous observations (n=7) of this juvenile (164.422) near independence to a random adult female (164.264) (n=7) revealed no significant differences in the following: 1) time from picking a pod to last grasp (p=0.1490), 2) time from picking a pod to first bite (p=0.5350), 3) time from first bite of a pod to first eat of a seed (p=0.3176), and 4) number of bites of a pod to first eat (p=0.0.6200).

Comparing foraging behavior of Juvenile 164.216 at Period 1 (11.25 days post-fledging, SD=6.1, n=5) and Period 4 (111.25 days post-fledging, SD=5.9, n=4), some significant differences were detected. In Period 4, the juvenile interacted with more food items (p=0.0317) and foraged for a greater amount of time (p=0.0159) (Table 3).

To identify development in independent Juvenile 164.085 (unknown age, white on bill tip), observations at the beginning and at the end of the radiotracking period (1 month apart) were compared to detect any differences in behavior (Table 4). None were identified. Note that the location was Mauka for the earlier observations and Makai/Ahumoa for the later observations.

Survival

Incidental resights through November 1996 reveal that at least 5 of the 7 Palila (71%) that were banded as nestlings in 1994 reached independence (i.e., no longer supplementally fed by an adult), and at

Table 3. Median (range) foraging times and number of food interactions of Juvenile Palila 164.216 within 100 seconds of continuous observation: a comparison between periods 1 and 4. Period 1 (11.25 days post-fledging; SD=6.1; n=5); Period 4 (111.25 days post-fledging; SD=5.9; n=4).

	Period 1	Period 4
number of food item interactions	0 (0-1)	7 (1-10)
time spent foraging (seconds)	0 (0-1)	27 (25-38)
time spent in other behavior (seconds)	13 (0-40)	6 (2-17)
time spent eating (seconds)	0 (0-0)	14.5 (4-25)

Table 4. Median (range) foraging times and number of food interactions of Juvenile Palila 164.085 within 100 seconds of continuous observation: a comparison between October and November, 1995.

	October (n=4)	November (n=4)	All observations (n=14)
number of food item interactions	4.5 (0-8)	2 (0-10)	2.5 (0-11)
time spent foraging (seconds)	17.0 (0-35)	20.5 (0-30)	20.5 (0-35)
time spent in other behavior (seconds)	13.0 (2-22)	8.0 (4-22)	7.5 (2-26)
time spent eating (seconds)	11.0 (0-20)	9.0 (0-21)	7.0 (0-24)

least 6 of 13 birds (46%) banded as nestlings in 1995 reached independence. Birds that were observed more that 4 months after fledging were considered independent. Minimum annual survival for HY birds was 28.6% (2/7) in 1994 and 43.8% (7/16) in 1995. Within a period of 3 years, 1994 juveniles were sighted incidentally an average of 2.2 times (SD=2.2). Within a 2-year period, 1995 juveniles were sighted an average of 2.0 times (SD=2.7).

DISCUSSION

Due to the small population of Palila, their elusive nature, range of movement, and foliaged foraging sites, our data are mostly descriptive, as with the majority of avian foraging studies. Therefore, as cautioned by Raphael and Maurer (1990), a concerted effort was made in this study to avoid going "too far in developing ad hoc explanations of descriptive data" and making "biological mountains out of statistical molehills".

Time-Activity Budget

Palila spent most of their time (approximately 70%) perched. Compare and contrast with literature. Perhaps an energy-reserving strategy. When recording continuous data, observers were instructed to account for each second of behavior. Being that there was not a prompt each second, it is suspected that active behavior is underrepresented and perch behavior, the default, is overrepresented. However, this should not create a problem when comparing juvenile and adult observations or when looking at the relative proportion of time spent in various active behaviors.

Continuous observations indicate that adults and juvenile spent proportionately similar amounts of time foraging; however, they also reveal that juveniles spent proportionately more of their active time looking than adults. Point data showed that juveniles spent more of their active time hopping also. Though looking and hopping were not considered as foraging behaviors in this study (foraging behavior was defined as direct action on a food item), they are, in fact, part of foraging. In retrospect, the hopping could have been associated with food searching and the looking could have represented looking for food items or a suitable perch on which to eat. Although some studies have distinguished between looking in vigilance and searching for food, the two behaviors are not always obviously different to the observer. Remsen and Robinson (1990), who present a standardized method for classifying foraging behavior, defined search as "movements leading up to sighting of food or food-concealing substrates". Time spent searching for a foraging patch has not been well-quantified, though Burger and Gochfeld (1983) recommend that adding this "habitat search time" to Schoener's (1971) concept of "search time" would lead to a more accurate assessment of total foraging effort (Wunderle 1991). Why would juvenile Palila spend proportionately more time looking? Perhaps, they have a less-developed search image than adults. Results showing that juveniles spend the majority of their active time looking (more than adults) may indicate an underdeveloped search image. Green pods, in particular, may be quite cryptic within the tree's foliage. Learning by association and trial-and-error are important in the development of searching behavior (Wunderle 1991). Perhaps, juvenile palila are limited in food item choice due to lack of foraging skill and therefore, need to bypass longer pods or thicker pods. Other possible explanations include the need to scan for predators, to keep sight of parents or other adults, or to observe other birds for learning purposes.

In addition, the young birds may have to spend more time foraging because dominant adults may be using the best feeding patches, as was observed in Crimson Rosellas (*Platycercus elegans*) at artificial feeding stations (Magrath and Lill 1985). Other examples of juveniles with longer search times than adults are Bonaparte's Gull (*Larus philadelphia*) (MacLean 1986), Northwestern Crow (*Corvus caurinus*) (Richardson and Verbeek 1987), and Yellow-eyed juncos (Sullivan 1988).

Food Items Selected

According to theory (Pyke, et al. 1977), Palila will choose foods which are energetically profitable. The finding that Palila selected pods much more frequently than any other food item, even in years (1994 and 1995) when pod production was low, suggests that pods are nutritionally important. Although nutritional analyses of Palila food have not been completed (P. Banko, unpubl.), it is predicted that mamane seeds, as other seeds are probably a significant source of protein and perhaps easier to find than insect protein. Palila preferentially chose mamane seeds even though they seem more expensive energetically to harvest. In relation to other food items (e.g., mamane flowers, naio berries, and leaves), pods are probably more difficult to sever, heavier to carry, more difficult to accommodate on a perch, and almost certainly more energy-sapping when it comes to actually accessing the food part.

After pods, Palila have a secondary preference for mamane flowers. Mamane flowers are easily accessible food. In addition, they may provide unique nutritional content (pollen), moisture content (nectar), and pigment (petals); flowers may provide something that pods do not provide, but that Palila require. These results agree with fecal analyses (Brenner et. al, unpubl.) that mamane seeds are the most utilized food resource, and mamane flowers are taken to a lesser degree. All fecal samples (n=168) contained mamane seeds and 64.0% of nestling samples and 38.7% of adult samples contained mamane flowers and other plant parts.

Very young birds which probably lack strength and skill were observed to select resources that were easily accessible such as flowers, leaves, and naio berries. Such food items were eaten directly from the tree. The finding that juveniles selected flowers more than pods, whereas adults primarily chose pods may suggest that eating seeds is more efficient (i.e., energy spent < energy gained) for adults, but not for juveniles. Juveniles may eat foods that provide less energy but also require less energy expenditure to access. Juveniles were found to select shorter pods than the adults with whom they were associated. Yoerg (1994) says of the Eurasian dipper (*Cinclus cinclus*): "The high probability of dropping larger prey and the costs of energetically expensive foraging techniques may promote the observed juvenile strategy of foraging in slow, shallow water for small prey".

Being that the Palila now occupies a realized niche, its resource use may differ from that of years past. The Palila has been considered more of a specialist than a generalist. However, it is important to keep in mind that a species may change position on the very relative continuum from specialist to generalist in response to food resource availability (Recher 1990).

Tree Species Preferred

Regardless of the ratio of mamane to naio, adult birds preferred to reside and forage in mamane. These results are consistent with the Palila's food item preference, though contrast with van Riper's (1978) finding that Palila did not show perching preference in regard to tree species. Though sample size was small, juveniles do not seem to show a preference for one tree species over the other.

Palila utilize mamane trees for their primary food, and they nest almost exclusively in mamane, perhaps due to denser foliage or branch design. Perhaps, mamane trees provide more shade, better shelter, or better refuge from predators than naio. Juveniles may simply not be as discriminating as experienced adults.

Social Behavior

Juvenile palila were found to be somewhat more social than adult birds. Perhaps, their need for others is greater due to their inexperience. Why are juvenile birds social with adults? Research indicates that, in general, adult birds tend to feed in profitable patches (Rowley 1970, Smith and Sweatman 1974, Wakeley, 1978). Although juveniles may learn of good foraging patches by observing adults, they may not forage in these areas. Juveniles may select different sites for foraging because they have different nutritional requirements, they are out-competed by dominant adults, or they simply may not have the ability to discriminate between patches yet or the skills to eat the food items in the quality patches (Wunderle 1991).

In Palila flocks, juveniles have been observed to associate with one another, and in at least one case, an inexperienced bird repeatedly followed and watched a more skilled juvenile feed. Why would juveniles socialize with other juveniles? Edwards' (1989) study of foraging development in fledgling osprey (*Pandion haliaetus*) in north-central Florida revealed that interacting juveniles may enhance one another's foraging skills. Siblings who foraged together experienced better capture success than young from single chick nests who foraged alone.

Flocking behavior may expedite learning by juveniles. Mason and Reidinger (1981) state that "foraging and observational learning of food preferences have been suggested as adaptive behaviors that support flocking." Although adult Great blue herons (*Ardea herodias*) experienced greater foraging success in flocks of more than 5 individuals, flock size did not seem to affect juvenile success (Quinney and Smith 1980).

Length of Juvenile Dependency

Van Riper (1980a) reported that young remained with parents for at least 30 days after fledging. By radiotracking birds in this study, it was determined that juvenile Palila depend on adults for 3 to 4 months after fledging. Though they seem to acquire the feeding skills considered most difficult and vital (those needed to extract seeds from a pod) as early as 1 month, continued association with and supplemental feeding by the adult reveals a need to improve efficiency. In regard to seed harvest, skills that were observed in adults were sometimes lacking in juveniles.

The length of juvenile dependency ranges from approximately 15 to 25 days in many passerines to several months in some tropical species (Davies, 1976). It "is probably determined by the development of foraging techniques of the young (Davies and Green 1976) and by the interaction between offspring and parents (Davies 1976)." (Moreno 1984). The periods of dependence for several passerines are: Northern wheatears (*Oenanthe oenanthe* L.), 2 weeks (Moreno 1984); Spotted Flycatcher (*Muscicapa striata*), 18 days (Davies 1976); Song Sparrow (*Melospiza melodia*), 20-22 days (Smith and Merkt 1980); Yellow-eyed junco, 25 days (Sullivan 1988); Prarie Warbler (*Dendroica discolor*), 24-43 days (Nolan 1978). Seabirds have especially long dependent periods as the skills they need to acquire are especially difficult (aerial attack, plunge-diving, and skimming). The length of dependency for Royal terns (*Thalasseus maximus*) is over 5 months and for the Ascension Island Frigate-bird (*Fregata aquila*), 10 months (Ashmole and Tovar 1968). Palila dependency is less than that of seabirds, greater than that of most passerines, and comparable to that of most tropical species. Brenner et al. (in review) suggest that prolonged postfledging care in Palila may compensate for a possible nutritional limitation (suspected due to slow growth rates in comparison with other tropical birds) during the nestling stage.

Davies (1976) suggests that young can "assess the profitability of their two feeding strategies and become independent of their parents when the profitability of self-feeding exceeds that of begging." Our results (Figure 9a and 9e) that as juvenile palila increase in foraging, their solicitation decreases may provide support for such profitability assessment.

Relative Investment of Males and Females in Postfledging Care

All passerines are altricial and most exhibit bi-parental care (Gill 1995). Generally, when parents are provisioning nestlings, they have to gather 2 or 3 times as much food as they would for their own energy needs (Walsberg 1983). Adult investment in fledglings may be even greater than that in nestlings due to a longer period of fledgling dependence (McGowan and Woolfenden 1990) or the greater food demands of fledglings. Moreno (1984) points out that dependent fledglings probably expend more energy than nestlings because of greater heat loss and flight costs.

Of all North American species, approximately 70% of males feed their nestlings and 88% feed their fledglings (Wolf et al. 1988, p.1601). In some species (e.g., the dark-eyed junco), males assume full care of the fledglings, and the female renests (Wolf et al.

1988). Overall, adult males were found to provide more care for Palila fledglings than females, and there is some evidence to suggest that female renesting may be a reason for this difference in investment.

Observations of Palila suggest that one adult usually assumes full responsibility for just one fledgling. Several studies of passerines have shown a division in labor in feeding fledglings, each adult feeding only certain individuals (Snow 1958, Nolan 1978, Smith 1978).

Foraging Development

Near the end of the nestling phase, attending adults appeared to perch further away from the nest upon arrival, perhaps in an attempt to encourage fledging. van Riper (1978) noted similar behavior, reporting a case of a female who "repeatedly coaxed the young off the nest with food items" during the 3 days prior to fledging. On average, a Palila fledges at 25 days (Pletschet and Kelly 1990). At this point, lack of flight experience, developed flight muscles, coordination, balance, bill strength, and foraging knowledge and skill all contribute to the fledgling's inability to forage alone.

Young Palila need to develop bill strength. It takes a certain amount of bill strength to sever a food item. The gradual gaining of bill strength may be one of the reasons why juveniles were observed selecting mamane leaflets and flowers before pods and smaller pods than adults. In addition, lack of bill strength in addition to lack of proper technique is a reasonable explanation for the finding that juveniles pecked (failed to sever a food item) more than adults. Mamane pod stems vary in diameter. Typically, an adult bird severs a pod in one swift motion which includes an almost simultaneous bite and head torque. However, adults have been observed pecking repeatedly at very thick pod stems and even using a twisting motion to detach a pod. Young birds, pulling at food items in an attempt to sever may represent an alternate technique to compensate for limited bill strength. Willson and Harmeson (1973) found that the relationship of finch bill size and strength to seed size and hardness determines husking speed. Additionally, Boag and Grant (1981) demonstrated the advantage of a large finch bill. During a drought where only large, hard seeds were available, intense natural selection occurred in favor of finches with large bills who could access food; within only a year, the population of Darwin's finches (Geospizinae) experienced an increase in bill size. Development of bill strength and foraging skill in juvenile Palila could be similarly important for survival, especially when resources are scarce or later in the season when softer pods are not as available (as pods age, the husk seems to harden).

Perhaps the first foraging skill that a young bird needs to acquire is recognition of food items. Although evidence exists for a genetic basis for development of food recognition (Smith 1983), learning through observing other foragers and independently exploring their own environment seem to be important also. A juvenile Palila that was observed leaving the nest and pecking at an expanded green pod a day prior to fledging may have been displaying recognition of an important food item. However, for the most part, recent fledglings pecked at non-food items such as branch tips and lichen. This early pecking at non-edible items has been observed in many species; the Reed Warbler (*Acrocephalus scirpaceus*) (Davies and Green 1976) and the Northern Wheatear (*Oenanthe oenanthe*) (Moreno 1984) are examples.

Young birds develop skills specific to obtaining the foods within their habitat, within the repertoire of their species. For instance, grasping ability is important for young Palila as they need to grasp mamane pods against branches to access seeds; van Riper (1978, 1980) found that nestlings began to develop grasping skills around 10 days of age. However, the first few days after fledging, juvenile Palila sometimes had difficulty remaining clasped to their perches; this may be an indication of weak grasping ability or inability to select an appropriate perching branch. Grasping food items such as mamane flowers and naio berries demonstrates ability, coordination, and skill in young birds; however, it does not necessarily translate to efficiency as adult birds toggle between eating flowers and berries from grasp and eating them directly from the tree. Before fledgling Palila had acquired skills such as picking, carrying, and grasping pods, they would sometimes perch beside and watch a feeding adult, sometimes even taking a seed from the adult's pod. Observations such as these provide evidence for observational learning in the Palila.

Overall, more time spent foraging is typically an indication of decreased skill level (e.g., Sullivan 1988). However, a developmental perspective may provide insight. Perhaps, first, there is no foraging, because there is no ability; then, there is increasing foraging because of learned skills, practicing, and inefficiency;

then, there may be a decrease in foraging time due to efficiency. This increase in foraging time was detected in young palila from 0 to approximately 120 days post-fledging (Figure 9); specifically, increases in foraging behaviors such as picking, carrying, and grasping occurred. In addition, obtaining more food items is not necessarily a sign of increased efficiency either. With the Palila, young juveniles may be dropping food items prematurely, not eating the food as completely as possible, or expending energy in picking inferior food items. In addition, the same foods may be harvested in different ways or for different parts, both of which may take different amounts of energy and time. For instance, as stated, a Palila eats a mamane flower either by directly consuming from its attached state or by picking, possibly carrying, and grasping it against a branch. The birds most often eat the petals, but sometimes only take the stamens or nectary and discard the rest. Attention is drawn to the facts that mamane pods vary in number of expanded seeds, and Palila eat varying numbers of seeds from pods. Thus, summing the number of pods selected within a certain time period to assess efficiency may not be very enlightening. However, measuring the times from pick pod to last grasp, pick pod to first bite, first bite to first eat, and number of bites to first eat may provide some insight; number of bites to first eat is probably the most reliable measure as time spent pausing and looking are not factors.

Survival

During their first year of life, small passerines have low survivorship (Lack 1954). The findings of 39% minimum annual survival for HY Palila in this study was comparable to the 36% annual survival reported by Lindsey et al. (1995) and comparable to other Hawaiian forest birds. Is our estimate of minimum annual survival likely to be a good estimate of actual annual survival? Looking at the rarity of locating a live bird (an average of only 2 incidental sightings per bird within a 2 or 3 year period), it is suspected that actual annual survival is probably greater than the minimum detected. Lindsey et. al (1995) report that survival of HY Palila was not correlated with mamane pod production; however, adult survival was greater in years when mamane pods were abundant. Why isn't HY survival correlated with pod production? Perhaps, the relevant question is not "How much food is present?", but rather "Can the food that is present be accessed?". If a HY bird has not acquired sufficient skills to forage efficiently on pods by the time the adult ceases supplemental food provisioning, then regardless of the abundance of pods, the young bird may not be able to satisfy minimum caloric requirement and may suffer mortality as a result. Although juveniles were able to open pods and extract seeds well before the adult withdrew care, the data were insufficient to determine whether juvenile efficiency neared or equaled that of an adult. However, the finding that a juvenile at the brink of independence (100 days post-fledging) was found to display similar pod manipulation as an adult bird. The finding that a greater percentage of birds reached independence (55%) than survived annually (39%) suggests that mortality may increase after adults stop providing supplemental food, as predicted.

It would seem maladaptive for the attending adult(s) to abandon the juvenile before he or she was able to forage efficiently. Four months of investment for naught in terms of fitness gains seems like a severe waste of energy. Sullivan (1988) found that the length of postfledging care was linked to the production of another clutch. She described adult aggression toward juveniles transitioning to independence as suggestive of a conflict between the costs and benefits of extended parental care. In some species, reproductive success can be enhanced by withdrawing parental care from "fledglings who are likely to survive on their own" and raising another clutch (Sullivan 1988). For Palila, however, the extensive 3-4-month period of fledgling care probably makes it difficult to raise even 2 clutches per season, even if the first clutch is produced very early in the season. From nest building to termination of fledgling care, the adult(s) have invested 5 months of time, approximately the length of the breeding season. However, Palila can successfully fledge two broods (T. Pratt, unpubl.). If 2 young were fledged by a pair, renesting would almost have to be delayed for 4 months, based upon the one-to-one care observed. However, there is evidence that some Palila pairs attempt another nest while rearing fledglings (personal observation) and have been successful (Pletschet and Kelly [1990] observed 2 cases of HY birds begging to females attending nests; 1 of the 2 nests fledged 2 young).

Ashmole and Tovar (1968) state "prolonged parental care appears to be correlated with the use of highly skilled feeding methods and the exploitation of scarce foods, and thus with low clutch size. Species showing it do not normally have second broods." Prolonged parental care in Palila may be a factor limiting the population. A 3 or 4-month period of intensive investment in the fledgling (note: no observed interaction with a female or nest during the time of fledgling care) may well limit the number of clutches per season and thus, overall productivity. It seems that having a helper, especially one who would assume full responsibility for a fledgling, would be adaptive as it could increase total reproductive success of the breeders.

CHAPTER 2: HELPING BEHAVIOR IN THE PALILA

INTRODUCTION

Social behavior was recognized as a product of natural selection in the early 1960s; this new understanding accelerated progress in the fields of sociobiology and behavioral ecology in the 1970s (Brown 1987). Areas of heated theoretical debate and basic biological interest over the past two decades include mating strategies, sexual selection, and cooperative behavior. The majority of empirical evidence on cooperative behavior has been generated from avian research.

"Chase (1980) viewed parental care as the simplest form of cooperation" (Winkler 1987). In ecological contexts where parental care results in greater survival of offspring than no parental care, it is considered an adaptive behavior. Thus, the explanation of the evolution of parental care by natural selection is non-controversial among biologists because of the direct fitness gains. The controversy arises when addressing the question of why certain species help rear young that are not their own genetic offspring. This "helping behavior" has been observed in many avian social systems. Since Alexander Skutch first formally reported that "helpers-at-the-nest" exist (Brown jays, Bushtits, Banded Cactus Wrens) in 1935, intraspecific helping has been confirmed in at least 222 of the 9,016 species of birds in the world (Morony et al. 1975). Brown (1987) notes that Emlen (1984) who reports "over 300" may have included unproven cases. Colored leg bands were used "as early as 1912" to recognize individuals, but the first extensive color-banding study on a communal species did not occur until 1965 (Rowley, 1965a) (Brown, p.93). Examples of helping behavior include nest defense, nest building, incubation, and food provisioning. Typically, cooperative breeding units are extended families; however, there are many cases of non-related helpers within these social units. Through attempts to explain cooperative breeding, a dichotomy has emerged: non-adaptationists/functionalists versus adaptationists.

Non-adaptive explanations

Brown (1987) suggests that regular intraspecific helping indicates an adaptive explanation whereas scattered cases of helping do not. An exception is helping by adults who have lost a brood or mate. This often regular, but non-adaptive behavior which results from circumstance was considered "a by-product of a flexible mating strategy" by Weatherhead and Robertson (1980). Helping is sometimes simply explained as a case of mistaken identity or misdirected parental care (e.g., Price et al. 1983). This explanation is considered most often upon initial observation of helping within a species or when helping exists in a very small percentage of a population. The "unselected hypothesis" (Jamieson and Craig 1987, Jamieson 1989) states that when helpers are presented with the stimulus of a gaping nestling, they will respond by feeding it. This non-functional, stimulus-response explanation has received much criticism by adaptationists such as Emlen et al. (1991) and Ligon and Stacey (1991).

Adaptive Explanations

According to Brown (1987), helping is considered adaptive when it is typical of a species and when benefits are measurable for the helpers and the recipients. When indirect fitness gains or direct benefits are derived from helping behavior, it is considered adaptive for the helpers. Kin selection, a process whereby individuals enhance their indirect fitness by helping relatives, is a well-supported explanation for the evolution of helping behavior (Clarke 1984, Emlen and Wrege 1989, Reyer 1984). One of the strongest supporting examples is the white-fronted bee-eater (*Merops bullockoides*) in which non-breeders are more likely to become helpers when the breeders are their close kin as opposed to distant kin or non-relatives (Emlen and Wrege 1989).

In cases where helpers are not related, reciprocity, mutual exchange of beneficial behaviors, may explain the evolution of helping behavior. Non-related helpers derive benefits such as inheritance of a territory, breeding status, a helper, experience, and increased survival. The green woodhoopoes (*Phoeniculus purpureus*) in Kenya provide support for reciprocity. Although their social units usually consist of relatives serving as helpers, there is evidence of non-related helpers providing young with more food and attention than either related helpers or parents. These non-related individuals have inherited ownership of territories, breeding status, and nest helpers (Ligon and Ligon 1978).

The most widely-accepted explanation holds that ecological factors constrain independent breeding (Stacey and Ligon 1987). Limited territory, defined either by poor territory quality or habitat saturation, has led to cooperative breeding in many avian species such as the Florida scrub jay (*Aphelocoma C. coerulescens*) (Woolfenden and Fitzpatrick 1984), the Galapagos mockingbird (*Nesomimus* spp.) (Curry 1989), and the Seychelles warbler (*Acrocephalus sechellensis*) (Komdeur 1992). A specific criterion, such as inavailability of nest sites or limited critical food resource, may be the critical determinant of habitat quality. For instance, inavailability of nest sites for the red-cockaded woodpecker (*Picoides borealis*) has led to its cooperative breeding efforts (Walters et al. 1992). Interestingly, the white-fronted bee-eater has been observed to change roles from breeder to helper and then back to breeder several times in its lifetime. The role chosen seems to correlate with environmental factors, specifically rainfall (Emlen 1981).

Kin selection, reciprocity, and environmental constraint explanations all work at the level of the individual (Lack: individual selection). However, group selection has also been used to explain helping behavior, a specific case being group defense against predators (Rabenold 1983). Upon review of all the different explanations for helping behavior, it is important to note that within a social system, there may be several processes working together to create or maintain cooperative societies. Some researchers have recognized more than one explanation for the evolution of helping behavior (e.g., Kinnaird and Grant 1982) and others have even statistically assessed the relative effects of two explanations (e.g., kinship and reciprocity) (Wilkinson 1984, 1988).

Life History Considerations

"Lack was the first to realize the potential contribution of the study of life history phenomena to understanding the nature of evolutionary adaptation" (Ricklefs, 1983). To discover why helping occurs in a particular population, Brown (1987) suggests looking at its ecology, specifically, the demographics such as survival rate, age structure, age-specific reproductive success, age at first breeding, fluctuations in population density, and dispersal. He also presents some patterns and categorizes species according to common life history traits, noting that each population is unique and not all fit neatly into the categories created. He states that cooperative breeding species are almost exclusively altricial and typically non-migratory, permanent residents; more common in low latitudes (in arid, hot climates that vary widely and have unpredictable rainfall), and present more often when there is a surplus of potential breeders. The annual survival in communally breeding birds is typically quite high (s=.8), and survival rates of breeding and non-breeding birds are "important determinants of the availability of potential helpers" (Brown 1987).

Helping in Hawaiian birds

Helping has been documented in another Hawaiian honeycreeper, the Maui Creeper (*Paroreomyza montana*), a small green and yellow bird with a short, straight bill found only on the slopes of Haleakala on Maui. There, it is common in native rain forests and exotic tree plantations above 1000m. Helping in this species is extremely common; of 85 pairs observed, approximately 90-95% had 1 or 2 helpers. The Maui Creeper follows the classic helper system neatly in that it is a territorial species with a distinct home range, and the helpers are the previous year's offspring. There is, however, no apparent skew in the sex ratio. No cases of polygamy have been observed, and only one case of cuckoldry has been documented. Blood samples reveal that nestlings were related to at least one of the adults.

There has been one observed case of helping in the Amakihi (*Hemignathus virens*) (on the island of Hawaii?), a small, greenish honeycreeper with a short, downcurved bill (Lindsey et al., unpubl.). Two SY females with brood patches and one male were present at the nest. Such a single isolated event does not prompt interest, adaptively speaking.

Review of Helping in Palila

Over the past 2 decades, there have been four verified cases of helping-at-the-nest in Palila. In a study of Palila behavioral ecology and breeding biology from 1971 to 1975, van Riper (1980) found helpers at one of the 26 nests that he monitored. In this circumstantial case of helping, two male helpers were observed provisioning food to nestlings after the female was preyed upon by a feral cat. Two chicks fledged. From 1986 through 1993, the Hawaii Field Station (HFS; initially, United States Fish and Wildlife Service

[USFWS]; later, National Biological Service [NBS]; currently, US Geological Survey, Biological Resources Division [BRD]) monitored Palila nests; however, attention was not directed upon acquiring the band combinations of each adult visiting the nest. Nevertheless, 3 incidental identifications of more than one male at nests occurred. In 1991, there were two cases. At one nest, one female and two males participated in nest defense at the egg stage. The same three birds were seen at the nest tree repeatedly; however, only one male was actually seen feeding the nestling. One of two eggs hatched, and one chick fledged. In the other 1991 case, two males were observed feeding the same nesting female, though only one was seen feeding the nestling. The male who was not observed feeding the nestling was found to be closely related to the female and was also observed with a different nesting female 30m away (T. Pratt, pers. comm.). Lastly, in 1993, two distinct males were observed feeding a nestling at a nest with a color-banded female; one male fed the female as well. One chick fledged.

In summary, all helpers were ASY males, and all nests with helpers successfully fledged young. One nest had two helpers (only one parent), whereas the others had only one helper (but both parents). One male helper helped at more than one nest and was related to the female he was feeding. Note that with the exception of van Riper's report of helpers, there was not extensive observation at the helper nests. In fact, only one instance of feeding by a helper was observed in the 1993 case and only one observation of nest defense helper was made. Thus, all of these cases seem to be either circumstantial or isolated incidents.

Reasonable Explanations for Helping Behavior in the Palila Breeding System

As described, there is not an obvious cooperative breeding society in the Palila population on Mauna Kea; however, helping is probably more prevalent than reported. Perhaps the Palila is in the primitive stages of forming a cooperative breeding society. Emlen (1982) argues that a substructuring of the population into small, stable, social units (usually extended families) is the first step in the evolution of cooperative breeding.

Palila do not exhibit several of the distinguishing characteristics that often appear among cooperatively breeding birds. For instance, Palila do not show obvious territoriality by aggressive defense or hierarchy within social units; hence, these direct benefits (territory inheritance and breeding status via hierarchical advance) are not available. However, a helper could gain experience in providing care and breeding status (through death of a breeder). Hence, reciprocity is a viable explanation, even though the range of direct gains is relatively limited. Kin selection may be involved, at least to some degree, in the formation or maintenance of a helping system in the Palila. In the one instance of helping where relatedness was assessed by blood sample, the results confirmed kinship, though further genetic analysis in this case is recommended (C. Tarr personal comm.). Brown (1987) states that association between any individuals over an extended time in the same location facilitates cooperative behavior, though kin with both relative and non-relative may prefer to associate with kin, and kin with kin encourages kin selection.

The most probable explanation for the evolution and maintenance of helping behavior in the Palila is ecological constraint. Emlen and Vehrencamp (1985) and Ford et al. (1988) argue that prolonged ecological constraints or fluctuations in resources critical for reproduction may lead to the evolution of cooperatively breeding societies. The destruction of the mamane-naio forest could be considered as a prolonged ecological constraint. In addition, there are apparent fluctuations in the Palila's critical food resource, the immature seeds of the mamane pod. In years of low rainfall, there is low pod production, and decreased nesting. Data suggest that food availability is correlated with nesting attempts (van Riper 1980b, P. Banko, unpubl.), but not nesting success (T. Pratt, unpubl.).

Palila may be limited by suitable habitat. It is more reasonable to propose a limitation by territory quality than saturation. Note that the term territory is used broadly here to describe the general breeding area around the nest as this species does not have defined defended territories. It is accurate to state that the overall range and quality of the Palila's habitat has been dramatically decreased. Although the forest is regenerating, it is difficult to assess habitat quality from the Palila's perspective. However, it is reasonable to make predictions based upon nest site selection, foraging areas, and home range. Scott et al. (1984) found that Palila were more common in areas with greater crown cover, taller trees, and more native plants in the understory. In fact, they identified availability of good habitat and staple food crop as the main factors limiting the Palila population. In addition, evidence that Palila nest in the same areas year after year (within 1 km) seems to suggest philopatry (Philopatry definition=) (T. Pratt, unpubl.). It is suspected that these nest sites are correlated with relatively high tree density or food availability; however, further study between nesting and habitat use is needed. When nesting for the first time, young males and females select sites an average of 700m away from their natal area (T. Pratt, unpubl.).

It may appear that Palila are not limited by their habitat because in many areas of seemingly suitable habitat, no Palila exist. However, Fancy et al. (1993) suggest that a strong site tenacity may prevent Palila from dispersing into these areas. In this sense, strong site tenacity may have similar effects as limited suitable habitat in encouraging the offspring's sedentary behavior. Habitat saturation as an explanation for helpers in Scrub Jays is supported by the observation that upon opening of an available space, helpers leave their parents' territory and establish their own (Woolfenden and Fitzpatrick 1984, Komdeur 1992). Although Palila do not maintain breeding territories, the fact that translocated Palila reestablished in their former area may provide some evidence that the seemingly "empty" habitat is indeed not suitable.

Other conditions which appear to encourage cooperative breeding, monogamy and a skewed male sex ratio, are present in the Palila population. More indirect fitness can be gained by helpers who help siblings that share the same parents as opposed to siblings in which paternity is different. Therefore, one would expect helping behavior to be more prevalent in monogamous species. In regard to an uneven sex ratio favoring males, Brown (1974) and Reyer (1980) suggest that it causes helper systems, whereas Woolfenden and Fitzpatrick (1984) maintain that it results from cooperative breeding. Regardless, an established population in which this sex bias exists may be a positive indication that helpers exist. Results of a six year recapture-resight study of the Palila reveal a male-biased sex ratio in adults (36.3% females to 63.7% males [1:1.75]) and HY birds (17% females to 83% males [1:4.88]), though sex ratios of nestling and SY birds were equal (Lindsey et al. 1995). This shortage of females in the Palila population may be a factor which delays breeding in the males. While it is not uncommon for females to breed in their second year, there is no evidence of males breeding in their second year (BRD, unpubl., Fleischer et al. 1994).

The Skill Hypothesis which states that "young birds have not acquired sufficient skill at foraging to enable adequate provisioning of nestlings" is another explanation for delayed breeding in birds. "It is usually considered that delayed breeding and nondispersal 'set the stage' for helping, but helping may feed back positively in this system to strengthen the causes of nonbreeding and nondispersal." (Brown 1987).

In order to discover whether helping is an adaptive feature of the Palila's breeding biology, this study attempted to characterize and determine the extent of extra-pair helping. Specifically, the objectives were to describe the type of help provided by the helpers, determine the proportion of nests with helpers, determine the average number of helpers at each nest, detect any relatedness between helpers and breeding birds. Additional objectives were to determine what proportion of the nestling feedings is provided by the helper, if nesting success is enhanced by helpers, and if helpers help fledglings (either by providing food or foraging instruction) and/or enhance their survival.

METHODS

Foraging and helping research were conducted simultaneously in the same study area; and nest searching, banding, and radio transmittering were accomplished for both studies; therefore, refer to Chapter 1 Methods section for information.

Nest activity was monitored through a spotting scope (give specs) from a blind 20m or more from the nest tree, behind camouflaged netting, or hidden within natural cover in camouflage clothing. Attempts were made to identify all color-banded birds visiting the nest. Since Palila nest in dense foliage, and typically enter and exit the nest tree elusively, it was too difficult to identify nest visitors by color bands alone. This obstacle encountered during the 1994 breeding season lead to the implementation of additional identification tools in 1995. After nestlings were 10 days of age, mist nests were placed around the nest tree to capture any nest visitors. Unbanded visitors were banded, missing color bands were replaced, unique dye was applied to the flank feathers of the females, and radiotransmitters were attached to males.

Uniquely dyeing the flank feathers of the females for individual recognition was either minimally effective or not satisfactory. Two methods were attempted: 1) applying Lady Clairol black dye after treatment with alcohol to increase absorption of dye by reducing oil and 2) applying a 10% picric acid solution directly to the feathers. The black dye was not especially distinct and faded fairly rapidly (within 1 week), perhaps because the process was accelerated to minimize bird handling time or because of preening. The picric acid was used only on one female. Although this female was readily recognizable, the bright yellow dye spread from the flanks, coloring her white belly. Although no behavioral changes were obvious after the dyeing, it was decided not to continue with this method as the yellow color of the dye was a near-match to the Palila's natural coloration. Adding more yellow, more brightness, potentially could affect behavior, specifically in regard to dominance and mate selection. Radiotransmitters were not attached to incubating or brooding females, considering the possibility that it could affect critical nest care and eventual nest success. The males were considered better candidates for radios by nature of their role during the nest phase and post-fledging. Males typically make short visits to the nest to feed, thus providing less opportunity to get a positive identification by way of color bands. Hence, receiving positive identification from a directed signal would give a needed advantage. Additionally, all past records revealed that Palila helpers were male; thus, the radio signals would provide an effective means to distinguish between different attending males. The possibility of imposing bias in regard to detecting different females is acknowledged. In regard to benefits after the nesting phase, there is a generally-held belief that, post-fledging, the males provide most of the care. If this assumption were correct, prospects of following the juveniles and learning about post-fledging care and helping would be improved.

Although banding and transmitter attachment at each nest was dealt with on a case by case basis, typically, capturing the male and the female in the same mist netting effort was attempted. After banding, the female typically returned to the nest within the hour. After attachment of a radio, the male usually did not visit the nest for a few hours (minimum: 1 hr; maximum: over 5 hours).
Attempts were made to identify all nest visitors and record the length of the nest visit or recess and the behavior performed (brooding and feeding). In 1994, 10 active nests were observed. The four that failed at the egg stage were observed for a total of 40 hours, and no helping behavior was observed. One of these four nests was a renest of a suspected helper nest. The other 6 nests were observed for a total of 155 hours, an average of 26 hours per nest. Of these 6 nests, 3 were suspected of helping and 3 were not suspected (66 hours observation for non-helper and 88 for suspected helper; more >12-day-old observations for helper than non-helper).

In 1995, each of seven nests were observed for an average of 42 hours (SD=6.87). Ninety-seven percent of the observation hours occurred at the nestling stage. In 1996, 2 nests were observed where helpers were detected by chance while conducting other research and monitoring activities.

Experimentation with supplemental feeding of nestlings was conducted at several nests that were monitored (non-helper Nests 94.001, 95.005, and 95.020 and suspected helper nest 94.004). Though supplemental feedings were few and probably did not influence nest outcome, the possibility of confounding effects is not dismissed.

The history of banded Palila in the Puu Laau population was reviewed to gain information on relatedness between birds identified or suspected as helpers and the recipient(s). Specifically examined were relatedness or association between nesters and birds described as having an "undetermined relationship" with the known nesting birds. These birds with undetermined relationship (UR birds) were observed around the nest tree or in association with the nesting birds. A Fischer's exact test was used to compare the observed ratio of male UR birds to female UR birds to that expected by the natural population sex ratio.

RESULTS

Proportion of Nests with Helpers

Of the 18 active nests found during the 1994 breeding season, 11 failed (7 at the egg stage and 4 at the chick stage). Of the seven remaining nests, 5 were found at a stage early enough for monitoring for helping. Of these 5 nests, 3 (60%) were suspected of having one ASY male helper. None of the suspected nests were verified as identification by color leg bands was difficult. All three nests with suspected helpers were successful; one nest fledged two young, and two nests fledged one. Each family appeared to be associated with a larger flock during nesting and after fledging. A radio transmitter was attached to one male from each nest; however, due to technical failures, little data were gathered. One fledgling was observed with a male other than the transmitter male in a feeding interaction, and at one nest, the female began renesting before her nestling fledged. Detailed accounts of the 3 possible helper nests follow.

1) Nest 94.004

Upon discovery, several Palila were observed around the nest, and there were most likely 2 males feeding the female (J. Jeffrey, pers. comm.). The observer recalled that on May 21, 1994) there was a male feeding the female on the nest, then another male went in. He observed a flock of as many as 10 Palila in the nest tree performing aerial fights and displacement; the flock would leave for 10-15 minutes, then return. On May, 28 1994, he observed "2 or 3 different males were flying into the nest tree" and many male Palila were flying into the tree and fighting. Subsequently, during formal nest observations, three birds (one female and two males) were seen entering and leaving nest tree, repeatedly. These birds were part of a flock of six. Positive identification of two distinct males feeding the nestling was not made. At fledging, a radio transmitter (166.911) was attached to one of the males (P/B, Y/AL). This male, as well as another male, was observed in close proximity to the fledgling (O/AL, R/G). Throughout the tracking period, the six bird group and three bird subgroup (plus the juvenile) were observed regularly.

2) Nest 94.006 and Renest 94.017

The female associated with the confirmed 1993 helper nest nested in same tree in 1994, though the males identified in 1993 were different individuals. Two males were observed entering the nest tree; however, helping behavior was not positively identified. A radiotransmitter (164.565) was attached to one of the males (G/G, OB/AL) when the nestling was 20 days old. At least 3 days prior to fledging, the female (B/P, B/AL) terminated care of her nestling (PY/AL, P/R) and at least 2 days prior to fledging was observed building another nest approximately 75 m away. The transmitter male and another male (P, Al) were traveling and socializing with the nest female. P,Al perched in active vigilance on a high snag as the female gathered sticks for nest construction. The transmitter male and up to 4 other birds were observed foraging repeatedly within the area surrounding the 2 nest trees and traveling a gulch corridor from one nest area to the other. Using habituation, a camera was mounted at this renest nest (Nest 95.017). The female was fed relatively often while on the nest, but no positive identification was made on the male or males who fed her. The female incubated for 20 days, but the eggs never hatched. The male's transmitter signal faded at approximately the same time that Juvenile PY/AL, P/R fledged, and the young bird was not found. However, over a year later, in October 1995, a radiotransmitter was attached to this bird, and he was followed for a month.

3) Nest 94.014

During nest construction, a group of Palila was observed in the area. Upon completion of the nest, but before serious incubation, a male (P*/P*,O*/AL) fed the begging female in the nest tree and was observed hopping around the nest (Note that birds with aluminum color bands, indicated by an asterisk, were participants in the 1993 translocation). Thereafter, another male (O*/O*,O*/AL) was observed feeding the female on the nest regularly. In addition, at least 2 birds were seen at the nest while the female remained sitting. NO BAND,AL ONLY was observed repeatedly in the nest tree, loitering under the nest. (O*/O*,O*/AL) chased him away with aggressive actions and vocalizations several times. In fact, many observations of unknown males involved in aggressive chases were reported. The group of birds from the nearby recently-fledged nest (94.004) were observed in the vicinity of this nest. In fact, the HY from Nest 94.004 was observed less than 5 m from the nest, in an adjacent tree with unknown male and was even captured during a netting effort to capture the adults at Nest 94.014. A transmitter was attached to O*/O*,O*/AL when the nestlings were 17/18 days old (25Aug94-9Sept94). One of the fledged young was equipped with a radio at 2 months of age (9Nov94-9Dec94).

During the 1995 breeding season, 12 active Palila nests were discovered. Of those, 3 failed (1 at the egg stage and 2 at the chick stage), and 1 was fledging a chick upon discovery. Of the 8 remaining nests, 7 were intensively monitored and one was not visible due to dense foliage immediately surrounding the nest. Four of these 8 nests (50%) had at least one observer witness a second male provisioning food to the nestling(s). At one nest, the helper also provided long-term postfledging care to one juvenile. At one nest without a helper provisioning the nestling, a bird feeding the nest female postfledging may have been helping. Herein, events considered important or interesting are highlighted at each nest, particularly in regard to cooperation.

1) Nest 95.008

Due to dense foliage, behavior at this nest was not visible from a distance. However, a few observations that revealed cooperation were secured. First, during the incubation stage, at least 3 adults visited the nest tree (C. Harada, pers. comm.). Then, one day prior to fledging, during a mistnetting effort to capture adults associated with the nest, 3 consecutive instances of 2 feedings very close together were observed. Partial identifications of the attending adults included a male with an orange or red band and a male with an unknown color band combination on the left leg and AL only on the right leg. The unbanded nest female who was distinctively small and dull in color did not visit the nest during the 8.5 hour observation period. A male a male with AL only on the right was capture, his color bands (P/O,Y/AL) were replaced, and he was equipped with a radio transmitter. This male subsequently provided all observed fledgling care. Though it is highly unlikely, he could have been the same male with the orange band who was observed feeding the nestling and within the 5 hours after the feeding and prior to capture, lost the color band. Due to the low probability of this event occurring, when comparing helper and non-helper nests, this nest is considered a helper nest.

2) Nest 95.012

In addition to the nest female, two males repeatedly and regularly fed the nestlings. Both males were 6 years of age. The male who made the most visits to the nest was considered the breeder male and the other bird was considered a helper. The female terminated care about 1 day prior to fledging. Both males were radiotracked after the young fledged and discovered that each male was caring for a different juvenile in two different locations.

3) Nest 95.015

The nest female was not observed at the nest for at least the 4 days prior to fledging, and all feedings/visits were made by the nest male with a radiotransmitter. One day after the chick fledged, the nest male and female were sighted approximately 25 m from the nest tree within a group of 5 birds. The nest female was observed being fed mamane seeds two times by a male (NO BAND, AL) other than her nest mate. The juvenile was not seen in adult company after fledging.

4) Nest 95.022

Upon initial observation of this nest at the young chick stage, 2 distinct males were observed perching near the nest. Later, NO BAND, AL ONLY fed the nestlings and an unbanded male perched near the nest being observed. After both males were color banded and transmitters were attached, repeated feeding at the nest by both birds was confirmed. The female was not observed attending during the last few days of the nesting phase or thereafter, and one male (164.498) was the sole food provisioner for the last 2 days. 164.498 was observed feeding one fledgling several times. 164.671 was untrackable due to an erratic transmitter signal. The other fledgling was not observed after leaving the nest tree, but was later found as a nesting female in 1996.

5) Nest 95.023

At the egg stage, two birds flying within the nest tree were joined by a third bird; one of the 3 birds was an unbanded male. Later, during the early chick stage, a male helper was suspected because feeding at the nest was irregular (i.e., male feedings were unusually close together). After banding and attaching a transmitter (164.072) to NO BAND, AL ONLY, a male over 6 years old, feeding by a male other than 164.072 was confirmed. Efforts to band and radiotag the second male were unsuccessful; therefore, this helper's investment in providing food to the nestling is not well-documented. Most of the time, the feeder was only identified as "NOT 164.072". An unbanded male was seen in the company of the nest female and 164.072 repeatedly, separately and together, during nestling and for 2 weeks after fledging. The fledgling was observed in close association with the nest female 19 days postfledging near the natal area. 164.072 stayed within the nest area for 2 weeks then traveled to lower elevation Manao and remained there for the month he was tracked.

Type and Quantity of Help Provided

Palila helpers have been observed to feed nestlings, defend nests, and provide food and foraging instruction to fledglings. The data were too few to accurately assess the quantity of help provided.

Description of Helpers

Of a total of 13 helpers that were observed feeding nestlings, 12 were ASY males and 1 was either an ASY female or a SY bird of unknown gender. It is suspected to be a SY as this bird, who was observed only once at the nest, begged to the nest female (without reward) after feeding the nestling. The pair at this nest had a confirmed ASY male helper. Unfortunately, most helper males were unbanded. The confirmed helper at Nest 95.012 (164.245) was 6 years old, the same age as the breeder male. At suspected helper nest 94.014, the males were at least 7 and 8 years old. Ages were determined from previous banding records. At two nests where both the breeder male and helper male were captured (95.012 and 95.022), the male deemed as the breeder (defined by more food provisioning to the nestlings) had a more yellow nape/head coloration.

Refer to Table 5 for a summary of all reported cases of helping behavior in Palila.

Birds with Undetermined Relationship to Breeders

From 1989 through 1993, data were collected on Palila that were sighted near the nest tree or associating with known nesting birds. In an attempt to gain some insight into the social behavior, group dynamics, and helping system present in the Palila population, past records of these birds with undetermined relationship (UR birds) to the breeders were reviewed. Perhaps, some UR birds were unidentified helpers. Since 92% of all confirmed helpers were ASY males (Table 5), it is reasonable to suggest that if these UR birds were, in fact, helpers, the ratio of male to female UR birds would be higher (i.e., more males) than the expected female to male ratio of the population (1:1.75). Results showed that the ratio of UR males to UR females was not different than that expected by the natural gender skew in the population (Fischer's Exact test; two-sided P value=0.4111; 95% confidence interval: 0.8817 to 1.492; relative risk=1.147). A relatively small percentage of the nests where adults were identified had UR birds (mean=13.724; SD=8.92) (Table 6). Note that the monitoring effort each year and at each nest was highly variable.

Of 65 UR birds, 60% were ASY, 15% were SY, 12% were HY. Of 57 UR birds with recorded/known age, 68.5% were ASY, 17.5% were SY, and 14% were HY.

Table 5. Summary of all reported cases of helping behavior in Palila.

Year	Nest #	Number of Helpers Observed	Age	Sex	Type of Help Provided by Helper	Clutch Size	Number of Young Fledged	Number of Independent Young	Circumstantial, Isolated Incident, or Regular Helping
1971-1975	4-74	2	ASY	M	fed nestling	2	2		Circumstantial; after female was preyed on by feral cat
1991	91.087	1	ASY	M	nest defense (egg stage)	2	1		Isolated Incident
1991		1	ASY	M	fed nesting female				
1993	93.060	1	ASY	M	fed nestling		1		
1995	95.012	1	ASY	M	fed nestlings	2	2	2	Regular
1995	95.023	1	ASY	M	fed nestling	2	1		Regular
1995	95.022	1	ASY	M	fed nestlings	2	2	Minimum of 1	Regular; helper identified as male upon capture, but not confirmed by brood patch inspection
1995	95.008	1	ASY	M	fed nestling	2	1	1	Isolated Incident
1996	96.001	2	ASY	M	fed nestling		0		
			SY or ASY	U or F	fed nestling				Isolated Incident
1996	96.008	1	ASY	M	fed nestling	2	2		Isolated Incident
1996		1	ASY	M	fed nestling				Isolated Incident

Age: ASY=after-second-year, SY= second-year
Sex: M=male, F=female, U=unknown

Table 6. Presence of Palila with undetermined relationships to the breeders (UR birds) at or near nests, 1989-1993.

	1989	1990	1991	1992	1993
Number of nests with UR birds	8	9	14	0	16
Number of nests with identified adults	85	49	68	6	79
% nests with UR birds/nests with identified birds	9.41	18.37	20.59	0	20.25

Comparison of Clutch Size and Number of Young Fledged at Helper and Non-Helper Nests

In 1995, there was no difference in clutch size nor number of young fledged at nests with and without a helper. In 1995, at least 3 of 6 young fledged from nests with a helper reached independence and at least 1 of 7 young that fledged at non-helper nests reached independence (Table 7).

DISCUSSION

Brown (1987) states that when testing theories about helping, one needs to "estimate the amount of benefit to the direct fitness of the recipients" by measuring annual reproductive success or annual survival of the recipients. The data of the study provide further qualitative evidence for helping in the Palila society, but are insufficient to reveal adaptive significance. The proportion of nests with confirmed nestling feeding by a helper male in 1995 was 4/8 (probably), 2/7 (minimally). This finding that 30 or 50% of nests have helpers is more than what one would expect from accidental happenings or circumstances such as loss of a mate. Though the extent of help provided is questionable in some cases, in the case of Nest 95.012, helping was not a result of loss of mate nor was it a brief involvement. Rather, it was repeated and extended provisioning of care to young during nesting and post-fledging.

Why would a helping system evolve in the Palila population on Mauna Kea? Perhaps, the limited range of the population, the

Table 7. Fate of helper (H), suspected helper (SH), and non-helper (NH) Palila nests, 1994-1995.

Nest Number	Helper Nest?	Clutch Size	Number of Eggs Hatched	Number of Young Fledged	Number of Independent Young	Sex of Young (as determined by resight as adult)
94.004	NH	?	?	1	?	
94.011	NH	2	1	1	?	
	Mean (SD)	2 (0)	1 (0)	1 (0)		
94.001	SH	2	2	2	at least 1	
94.006	SH	2	1	1	1	male
94.014	SH	2	2	2	?	
	Mean (SD)	2 (0)	1.7 (.58)	1.7 (.58)		
95.005	NH	2	2	2	?	
95.015	NH	?	?	1	?	
95.019	NH	2	2	2	at least 1	
95.020	NH	2	2	2	?	
	Mean (SD)	2 (0)	2 (0)	1.75 (.5)		
95.008	H	2	1	1	at least 1	
95.012	H	2	2	2	?	
95.022	H	2	2	2	1	female
95.023	H	2	1	1	1	
	Mean (SD)	2 (0)	1.5 (.58)	1.5 (.58)		

SD=standard deviation

concentration of nesting attempts in a relatively small area, philopatry, site tenacity; all would encourage relationships and may lead to cooperative behavior. The skewed male sex ratio may encourage a system with male helpers. In addition, the potential for an increase in reproductive success by way of more clutches with helper involvement is present. With a helper to provide the intensive postfledging care, the female is able to renest sooner. With limited habitat and limited females, a helper male could benefit by "getting a good reputation" and thus, be more likely to move into a breeder's place if something happened to the breeder male.

Why would helpers be ASY birds versus SY birds, as is typical of most helping systems?, and why would helpers be male versus female? Female palila have been known to successfully fledge young at age 1 (as SY birds), but perhaps their role in acquiring food is not as demanding as that of the males. Although van Riper (1978, 1980) reported that females fed nestlings more often than males, perhaps, it is postfledging care that is especially costly (energetically) for the males or that males provision females who just transfer the food to the nestlings. In addition, there is an excess of males in the population; thus, with a choice of males, the females may choose the older birds who may have more experience in rearing, may forage more efficiently (or more generally, may allocate their time better). Another possibility is greater emigration of females with males remaining to serve as helpers. This is probably not likely since helpers are not SY birds and first nestings of males and females are about the same distance from the natal site. One 1995 HY was sighted as a nesting female the following season; her nest was near to her natal site. One 1994 HY was transmittered as an ASY male; though he was occasionally tracked to his immediate natal area (Mauka), he spent most of his time in Manao.

Why are there not more male UR birds than females, as predicted? There are few helpers at each nest, and helpers visited the nest tree relatively infrequently. More than one helper helping at a nest was not observed during this study, although this could have occurred and gone undetected as identification of visitors was not always possible. Perhaps, helpers were more cautious about spending time in and around the nest tree than other birds, so as not to draw the attention of predators).

No difference was detected between helper and non-helper nests in regard to clutch size or number of young fledged. However, due to a small sample size (n=8) and the small clutch size of Palila (mode=2), it is inherently difficult to detect differences. Being that the Palila, by nature, lays a small clutch, perhaps the benefits to fitness are gained by the production of more offspring from another brood. Similar to the Palila, the Fairy Wren nests either in pairs or trios (one extra helper male) (Rowley 1965); however, in contrast with the Palila, fair wren trios produced more young than pairs. The fact that the Palila has a protracted breeding season may be supportive evidence. With a helper, the female of a nest which fledges two young is free to renest sooner as each male can care for a fledgling. van Riper pointed out that the two most important factors regulating productivity in small passerine birds are breeding season length and clutch size.

Care by the female through fledging may be necessary for non-helper nests whereas the help provided by an extra male may free the female for renesting. The finding that the females at helper or suspected helper nests typically left before fledging (though a short time before fledging), while females at non-helping nests stayed until the very end of the nestling stage may be suggestive of earlier renesting possibilities in helper groups. The only helper nest in which the female remained through fledging (95.023) was a late season nest (fledge date: August 22, 1995) and therefore, renesting was not a conflict. The only non-helper nest (95.015) in which the female left prior to fledging produced only one bird; hence, the nest male could assume full responsibility for fledgling care and she was freed to renest. The sighting that this female was fed by a male who was not her partner in the 95.015 nest may be evidence of helping. Based on previous findings supporting monogamy (Fleischer et al. 1994), it is more likely that the observed male feeding was a helper feeding and not a courtship feeding. In order to renest a female may need food supplementation (by a male), especially in years of scarce resource. If a nest mate assumes responsibility for fledgling, he may not be able to provision female adequately.

Although the data are too few to assess relative contribution of helpers to nestling feedings, the observations agree with van Riper's comment that "the feedings of the helpers were quite irregular, and when they occurred, often followed shortly after a feeding of the parent male." Van Riper (1980a) found that helpers began to help the day that a nesting female was captured by a predator. "At least two helpers made five trips to the nest with food from days 16 to 26." Helper contribution to nestling feedings was much less than the nest male who increased his feeding rate. A study of Mexican Jays in Arizona found that non-breeding helpers contributed about half of the nestling feedings and more than 1/2 of fledgling feedings. Helpers were both non-breeders and breeders (Brown 1987).

This study constitutes the first attempt to systematically document helping in Palila. The need for further research in this system is emphasized.

Recommendations for Future Research

1. It is necessary to band and transmitter all adults visiting the nest in order to maximize detection of helpers and monitor nests more frequently and for longer durations.

2. Earlier banding and transmittering is recommended to identify helpers and better quantify their relative contribution to nestling feeding. Attaching radios to females would help in identification of nest visitors and also potentially provide information on the female's role in postfledging care, information on renesting, and insight into cooperation in the Palila society. In 1996, transmitters were attached to 10 females after their eggs were collected for captive propagation. These females returned to nests to incubate wooden decoys with a safe recess time, and at least 6 birds renested (L. Johnson).

3. Use a camera and put a unique spot of dye (what kind?) on the crown of the males' heads.

4. Use lighter transmitters (1.2 g) with a longer life (12 weeks), even though 1.5 g transmitters did not seem to negatively affect even the smallest 33g juvenile. Use of harness attachment (leg loops/synsacral positioning of transmitter) may prevent detachment before radio expiration. Although this design has been used successfully for Omao, it needs to be tested with Palila. Attaching potentially long-term baggage to an endangered species needs to be considered carefully. Palila, however, could probably remove the elastic looping with their bills, especially once the elastic has endured wear.

5. Look at bill size (measure) and rate nape/brightness (take photographs) of breeders vs. helpers; may provide insight as to how the female chooses a mate; Is it based on bill size (better acquisition of food) size? brightness? In populations where the sex ratio is male-biased, females may have a choice of mates (Wolf et al. 1988).

6. Be careful when translocating individuals as there exists the potential to disturb social units/cooperative groups. It is important to be able to identify individuals in the population, track their history, and determine relationships between individuals. Rather than simply accepting the site tenacity explanation for the return of translocated Palila (Fancy et al. 1993), perhaps, a social explanation such as disruption long-term relationships or established helper groups should be considered as well.

7. Use feather pulp for genetic analysis (Marsden and May 1984) to determine relatedness between helpers, recipients, and young.

CHAPTER 3: POST-FLEDGING MOVEMENTS OF JUVENILE PALILA

INTRODUCTION

Greenwood (1980) reports that juveniles of most species are more likely to disperse than adults and that dispersal can regulate population structure, effect spatial distribution, and influence the evolution of social behavior. He distinguishes between natal dispersal (juvenile movement from natal site to first breeding site) and breeding dispersal (movement of breeders between successive sites). He also demonstrates that in most species, one sex is more philopatric while the other disperses (females are the dispersers in most avian species); the sex bias being a consequence of the type of mating system.

Prior to dispersal, juvenile Palila move around with their parents or adult helper. This period of exploration may provide the young birds with important information about good foraging patches, prime nesting areas, and social dynamics. Gathering information on the movements of juveniles and associated adults or foraging flocks may also provide insight into which individuals may be good candidates for translocation. Juveniles that have a wider range of movement may be more accepting of a new area whereas juveniles that are more sedentary and perhaps more attached to a locality might not be as resilient in or as accepting of a change in location. In addition, juveniles that naturally maintain a more restricted range may socialize with a smaller number of birds and thus, develop stronger social ties. These birds may be more apt to return to their original site due to social reasons.

Natal dispersal in Palila is approximately 700m (T. Pratt, unpubl.), and Fancy et al. (1993) have suggested that site tenacity in Palila may limit their dispersal, but very little is known of post-fledging movements. Though van Riper (1978, 1980a) observed juveniles and their parents parents approximately 100m away from their natal site 30 days after fledging, he did not gather information on movement patterns.

It is predicted that after fledging, juvenile Palila will move according to social behavior and food availability. Specifically, Palila fledgling and family will disperse to or remain in areas where energetic costs are lower (i.e., where food resources are more available).

METHODS

Refer to Chapter 1 Methods section for information on nest searching, banding, and radiotransmitter attachment. As the adults with their associated juveniles were radiotracked for foraging observations, the trees in which the birds were discovered were uniquely marked. Later, a Rockwell Global Positioning System Unit was used to acquire locations of the flagged trees. ArcView 3.0 GIS software was used to map juvenile movement patterns and measure dispersal distances from nests over time.

RESULTS

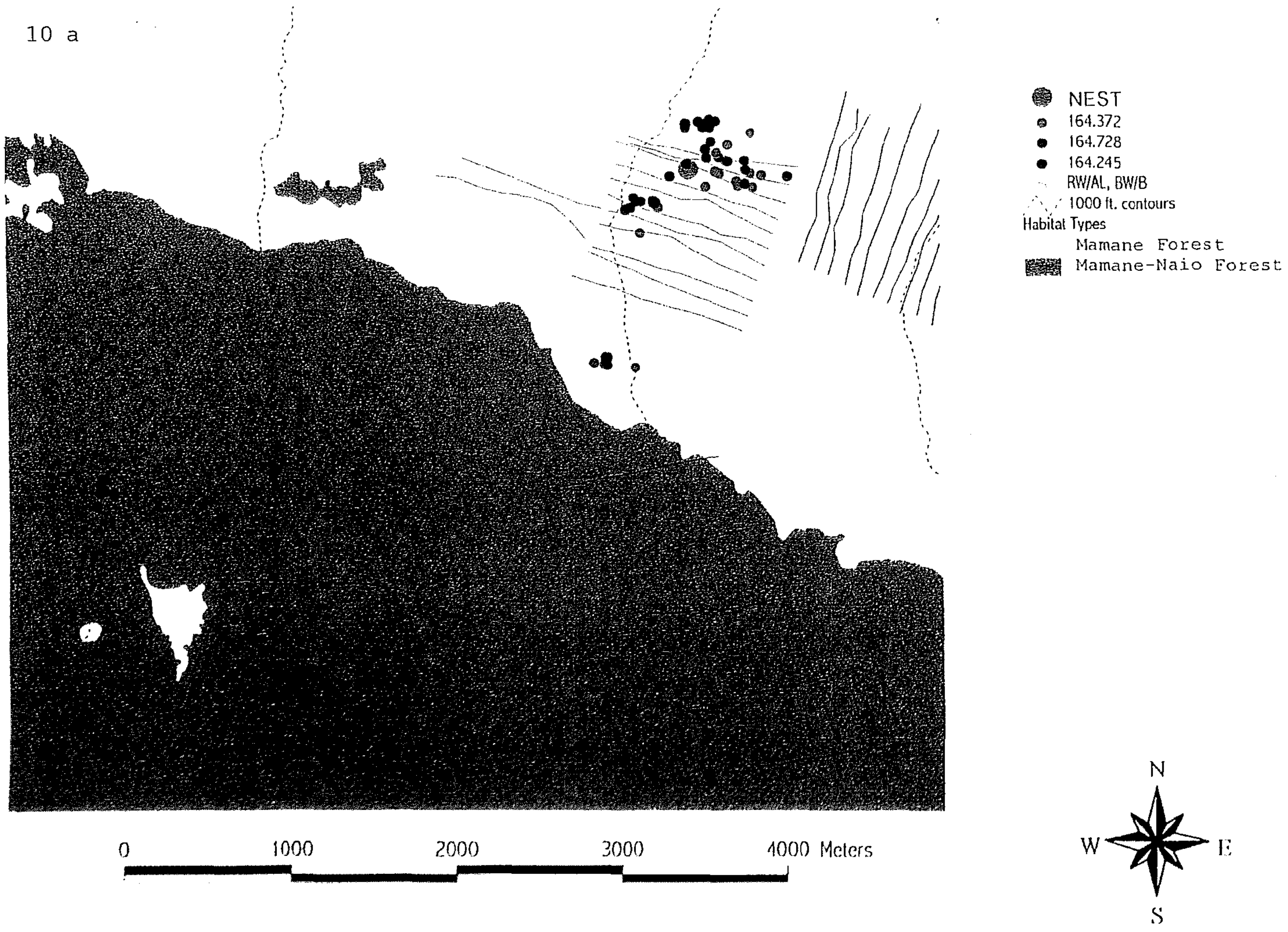
In 1994, the 2 juveniles that were tracked at 2 to 3 months postfledging were always observed in their natal grid. However, in 1995, of 8 juveniles that were resighted between 1 and 6 months after fledging, 7 traveled to a grid of lower elevation, 4 less than a month after fledging. The youngest bird known to travel the greatest distance was a juvenile 11 days postfledging who was 2250 m from the nest.

Juvenile movements are depicted by mapping of points and by line graphs of distance from the nest over time. Herein, the patterns observed are described:

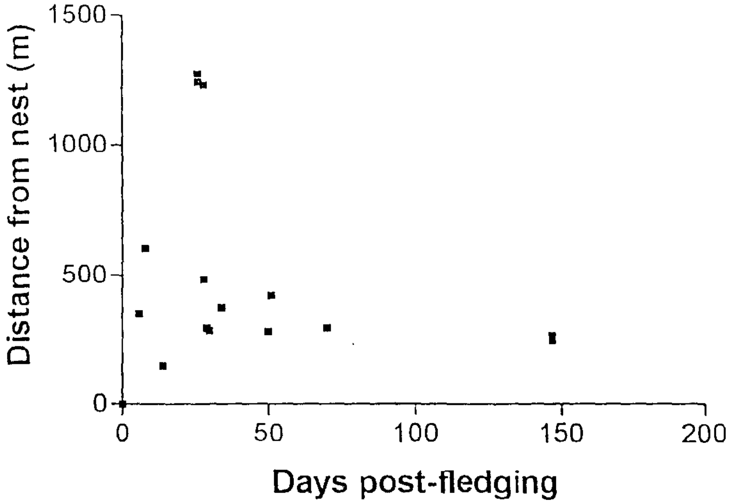
Figure 10a illustrates the movements of the fledglings and associated males from Nest 95.012. The breeder male (164.372) lead Juvenile BW/AL, RW/R to the Manao area, while the helper male (164.245) took Juvenile RW/AL, BW/B to Ahumoa for one-on-one food supplementation and foraging instruction. After traveling to Manao, Juvenile BW/AL, RW/R (164.728) and the breeder male were observed repeatedly in Mauka, less than 600m from the natal site. The juvenile was also sighted as an independent bird less than 400m from the nest. Refer to Figure 10b for the movements over time of Juvenile 164.728. The juvenile with the helper male was located at 23 days postfledging in Ahumoa, but thereafter, was not seen until the following year.

Figure 10. Post-fledging movements of individual juvenile Palila. a) movements of fledglings and associated males from nest (95.012), b) distance from nest (95.012) over time (Juvenile BW/AL,RW/R, 164.728), c) distance from nest (95.005) over time (Juvenile G/O,GW/AL), d) distance from nest (95.019) over time (Juvenile W/AL,W/G, 164.235), e) distance from nest (95.008) over time (Juvenile GW/AL,R/G, 164.216), f) movements of Juvenile 164.085 from October 5, 1995 to November 9, 1995.

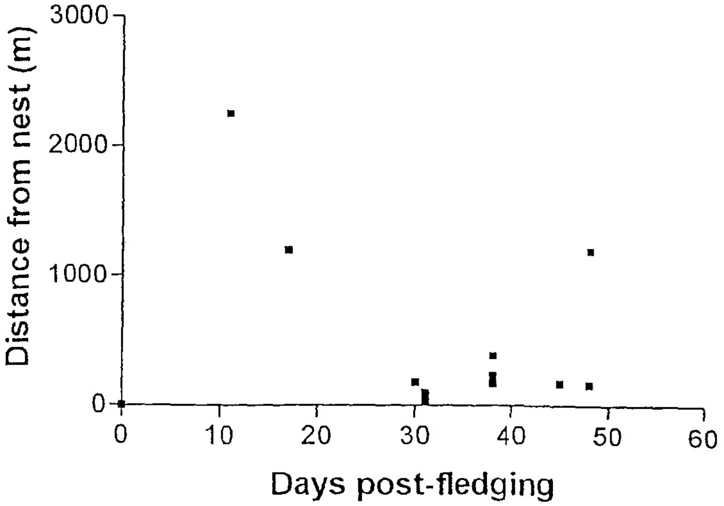
10 a


NEST
164.372
164.728
164.245
RW/AL, BW/B
1000 ft. contours
Habitat Types
Mamane Forest
Mamane-Naio Forest
0
1000
2000
3000
4000 Meters
N
W
E
S

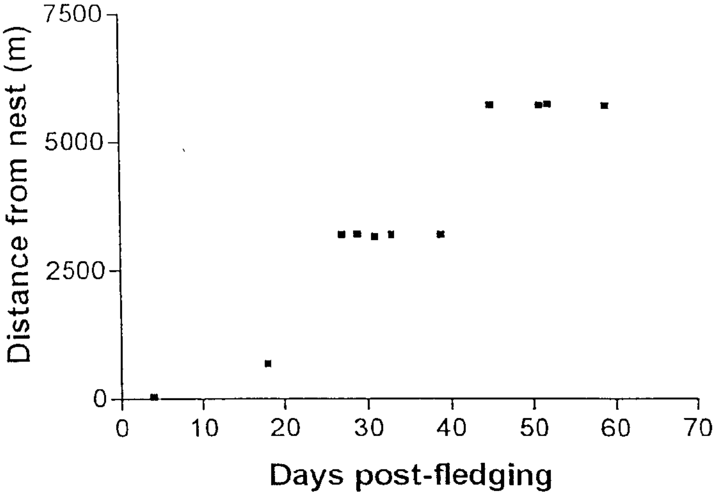
10 b


1500
1000
500
0
Distance from nest (m)
0
50
100
150
200
Days post-fledging

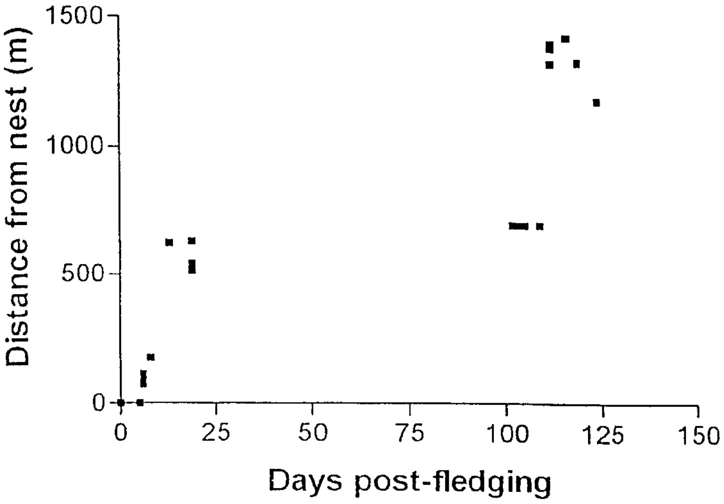
10 c


3000
2000
1000
0
Distance from nest (m)
0
10
20
30
40
50
60
Days post-fledging

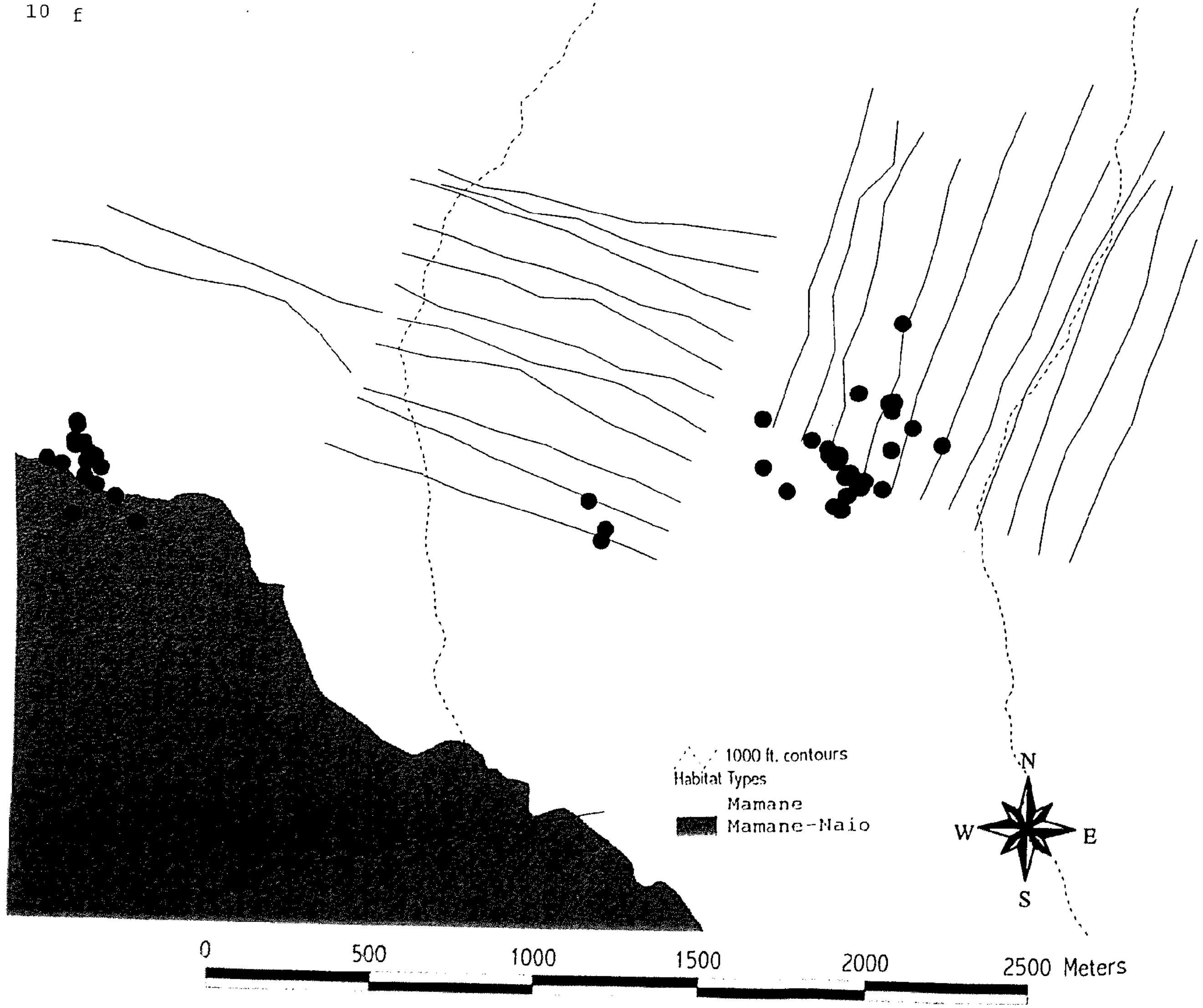
10 d


7500
5000
2500
0
Distance from nest (m)
0
10
20
30
40
50
60
70
Days post-fledging

10 e


1500
1000
500
0
Distance from nest (m)
0
25
50
75
100
125
150
Days post-fledging

10 f


1000 ft. contours
Habitat Types
Mamane
Mamane-Naio
N
W
E
S
0
500
1000
1500
2000
2500 Meters

One juvenile from Nest 95.005 (G/O, GW/AL) traveled downslope to Ahumoa at 11 days after fledging with the nest male, was sighted between Makai and Ahumoa, then back at Makai as close as 40m from the nest site. On day 48 postfledge, this HY was observed in both the Makai-Ahumoa locality and the Makai nest area within a period of less than 2 hours (Figure 10c).

Another pattern was observed in a juvenile from Nest 95.019 (W/AL, W/G; 164.235) (Figures 10d). This juvenile, with the breeder male, flew to a Makai-Ahumoa site (interestingly, very close to 95.005 juvenile's location) at least between days 27 and 38. The young bird then ventured the farthest observed distance from a nest (5700m) and was last observed on top of Puu Ahumoa (note difference in vegetation on Ahumoa).

The juvenile from 95.008 (GW/AL, R/G; 164.216) made a very gradual descent, with all observations of his dependent period less than 700m away from the nest and no observations over 1500m away (Figure 10e).

Random Juvenile O/R, Y/R (164.085), with a small amount of white on his bill tip, had reached independence upon radiotransmitter attachment. The first half of the month, the juvenile was observed within the Mauka grid and the last half of the month, in the area between Makai and Ahumoa grids. Mapping illustrates two distinct areas of concentration (approximately 2250m apart) (Figure 10f).

A linear regression was performed on the grouped data (distance traveled versus days post-fledging)of all HY birds. The slope did not deviate significantly from zero (r^2=0.005998 P=0.5179).

DISCUSSION

Fledging at approximately 25 days, some Palila chicks simply and suddenly leave their nest and nest tree while others spend a few days in the nest tree after leaving the nest (van Riper 1980a; Pletschet and Kelly 1990; T. Pratt, unpubl.); however, once they leave the nest tree they do not seem return to the nest.

Why does the adult lead the juvenile to lower elevations, from nesting grids Mauka and Makai (strictly mamane forest) to Ahumoa and Manao (mamane-naio mixed forest). van Riper (1975) reports that larger mamanes, found in greater proportion at higher elevations, produce more pods (van Riper 1978). Though there may be more pods in the upper grids early in the breeding season, there may also be more competition for food due to higher bird density. After the breeding season, the pods decline, and birds may shift to lower habitat. van Riper (1980) and Fancy et al. (1993) observed that Palila flocks follow elevational shifts in pod abundance. Though pod availability was low in both 1994 and 1995, 1995 was considerably lower. In 1994, no movement to lower elevations was observed; however in 1995, such movement occurred. With this movement, the forest composition changed from mamane to mamane-naio where independent foraging possibilities may have been greater. Naio berries are more accessible food for young birds who may lack the skills to extract seeds from pods. As Gill (1994) noted, parents move with mobile young to good feeding areas so as to reduce their workload. Juvenile palila were brought to the lower elevations within the first month of postfledging, a time when foraging skills are developing. It is also possible that Palila may eat naio berries when pods are less available (Hess et al. In press).

The linear regression analysis suggests that juvenile palila do not immediately disperse from the nest. For at least the first 150 days post-fledging, juveniles seem to either initially travel far from the nest then return to an area relatively closer to the nest (Figures 10b and c) or gradually move further from the nest (Figures 10d and e). In some instances, juveniles fly between two areas; at times, movement between the two sites is fairly rapid. This travel, perhaps between resource-rich areas, may be a strategy of optimal foraging that adults are showing to their juveniles. The precise homing ability exhibited by Palila during translocation studies (Fancy 1993) could transfer to efficient travel through resource-rich routes or revisiting good foraging sites.

Knowledge about natural patterns, behavior, and circumstances involved in natural dispersal can be used to understand how to best force dispersal (translocate). It would be interesting to discover whether independent juveniles use the same foraging areas that they did when they were associated with the adult. If so, this may be indicative of learning, in particular a transfer of knowledge from adult to juvenile in regard to good foraging areas. It might also be interesting, as well as important, to identify juvenile foraging locations and determine whether juvenile movements coincide with areas of abundant food resource. During this study, some overlap in foraging areas between different nest families was detected.

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