

## Adaptation in the Hawaii akepa to breed and moult during a seasonal food decline

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### ABSTRACT

**Question:** How can a bird breed and moult during a seasonal food decline?

**Hypothesis:** Nestling overgrowth (weighing more than adults by storing fat) during the period of relative plenty enables parents to bank their parental care in the bodies of their nestlings for use when they are fledglings during leaner times when the parents are moulting.

**Organism:** Hawaii akepa (*Loxops coccineus coccineus*).

**Field site:** Hakalau Forest National Wildlife Refuge, Mauna Kea, Island of Hawaii, HI, USA.

**Methods:** We documented breeding, moulting seasonality, and seasonality of canopy arthropods of *Metrosideros polymorpha*. We weighed and measured nestlings and fledglings to document ontogeny. We tracked fat and mass changes of adults and offspring throughout the 4-month long fledgling period to assess condition in relation to food availability.

**Conclusion:** Nestling overgrowth is the outcome of an adaptation of offspring to consume and use more than they need at the time and of parents to provide that additional food. The newly documented role of overgrowth enables fledglings to continue to grow while parents are heavily moulting primary flight feathers during deteriorating food availability.

*Keywords:* breeding season, moult–breeding overlap, nestling overgrowth.

### INTRODUCTION

The annual cycle of an organism consists of a sequence of events that each influence survival and current or future reproductive success. For most organisms, breeding is the most energetically expensive activity of the year, and natural selection is assumed to time breeding with suitable conditions (Lack, 1954). Even for tropical organisms, for whom the environment may be much less seasonal, there can be strongly seasonal breeding (Leigh *et al.*, 1996). Following breeding, or perhaps concurrent with it, there can be expensive self-maintenance activities such as replacing integumentary structures. Among vertebrates, only birds and mammals have seasonal moulting of such structures (Ling, 1972). Only birds moult structures (feathers) that are involved in generating lift and thrust for locomotion.

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For altricial birds feeding dependent young, food is the obvious resource for determining the breeding season (Lack, 1954, 1968; Murton and Westwood, 1977; Martin, 1987). However, food may be more important while laying eggs, incubating, feeding nestlings, and feeding fledglings in different species. Food may even be most important at or after the termination of parental care, when young feed without subsidy (Perrins, 1970; Martin, 1987; Young, 1994). Natural selection is assumed to drive the peak in energy demands of the clutch to coincide with the peak availability of suitable resources (Perrins, 1970; Wyndham, 1986; Svensson, 1997). While temperate birds have breeding seasons based on a flush of food resources, many tropical birds have breeding seasonality in which the relation between breeding and food extends over a longer period (Moreau, 1950; Skutch, 1950; Stutchbury and Morton, 2001). The relation is associated with a much lower peak of energy demands from smaller clutch size, slower growth, and longer incubation, nestling, and fledgling periods (Ricklefs, 1969, 1976). Breeding seasonality in some tropical species may even be based on alternatives to food such as predation (Morton, 1971).

Since moulting in birds generally follows breeding, it is less constrained by peak availability of food resources. Nevertheless, it is an energetically expensive life-history stage for production of new feathers (Payne, 1972; Lindstrom *et al.*, 1993), and loss of aerodynamic efficiency while some wing feathers are missing or incompletely formed (Hedenstrom and Sunada, 1999). The costs of moulting may increase the cost of breeding if the two overlap (Foster, 1974), as established experimentally in temperate birds (Slagsvold and Lifjeld, 1988; Hemborg and Lundberg, 1998; Hemborg and Merila, 1999). Moulting–breeding overlap has been detected in some tropical birds and may be the basis for lower fecundity (Foster, 1974, 1975). However, moulting–breeding overlap is identified by the co-occurrence of brood patches (for incubation) with pin feathers (incomplete replacement feathers). Thus moulting–breeding overlap is limited by methodology to the nesting period. Such overlap could also occur while parents are tending fledglings, a time when the demands of the young may be greater (Martin, 1987).

Because there is no case of an organism with complex parental care that initiates breeding during a seasonal decline in food resources, the relationship between breeding and an increase in food is the most unquestioned assumption in life-history theory. A bird that nests, cares for fledglings out of the nest, and moults while caring for fledglings, during a seasonal food decline, is unexpected. There would need to be an adaptation specifically to cope with the decline in food. The adaptation would have to occur during the nestling period, since this is the stage at which food would be relatively more abundant, and nestlings can store more nutrients than eggs which are limited in size. With sufficient food, nestlings could store fat that would enable parents to use more food themselves while moulting and caring for fledglings.

Nestling overgrowth, defined as nestlings weighing more than their parents, has been documented. It is measured as the ratio of nestling growth asymptote to adult mass (Ricklefs, 1968a). In the nest, small ground-dwelling land birds tend to weigh less than adults, foliage/perch birds weigh approximately the same as adults, and aerial insectivores weigh more than adults (Ricklefs, 1968a). The most emphasized cases of nestling overgrowth are concentrated in swifts, swallows, and flycatchers. In addition, oceanic birds and even some hole-nesting birds have overgrowth (Ricklefs, 1968a; O'Connor, 1984). Aerial insectivores and oceanic birds have long nestling periods, and the young forage while flying right after fledging. Nestling overgrowth in these species is associated with recession of mass in the nest before fledging, and this recession is associated with the development of flight apparatus. Detailed analysis of the recession in an aerial insectivore demonstrated that most of the recession was water from maturing tissues (Ricklefs, 1967, 1968b). While existing cases of nestling overgrowth are

based mainly on flight requirements, there is nothing to preclude nestling overgrowth in passerines to be used adaptively for storage of fat, as documented in oceanic birds (Harris, 1966; Nelson, 1966). Adaptive periodic storage of fat is known from migratory birds, including juveniles (King, 1972; Sandberg and Moore, 1996). It could certainly evolve in non-migratory birds, given the evidence for developmental plasticity of birds (Schew and Ricklefs, 1998).

Here we document a novel adaptation in the endangered Hawaii akepa (*Loxops coccineus coccineus*), a Hawaiian honeycreeper (Drepanidinae), to deal with breeding and moulting during a seasonal decline in food. The adaptation involves nestling overgrowth for storage of fat that enables parents to care for growing fledglings and moult most of their flight feathers during the steepest portion of the food decline.

## METHODS

### Study site and organism

Breeding biology and morphometric data were obtained during a long-term study between 1987 and 1999 at Hakalau Forest National Wildlife Refuge, at an elevation of 1900 m on the windward slope of Mauna Kea, Island of Hawaii (Freed, 2001). The akepa is a specialized insectivorous bird that feeds on insects and spiders in the foliage of ohia (*Metrosideros polymorpha*) trees (Lepson and Freed, 1997), which almost form a canopy monoculture at the site (Freed, 2001). The bill can be used for gleaning exposed arthropods. In addition, the asymmetric jaws enable the bird to open tightly packed clusters of leaves or even leaf buds for extracting hidden arthropods. The bird nests obligately in cavities in trees (Freed, 2001), but is not territorial, and has a typical tropical life history: clutch size of two eggs, extended care of fledglings for 4 months, and high adult and juvenile survival (0.80 and 0.42, respectively) (Lepson and Freed, 1995). Active nests are found in March to June, mainly April to May (Lepson and Freed, 1995). During most of the fledgling period, family groups are frequently associated in interspecific flocks for protection against predation by the Hawaiian hawk, *Buteo solitarius* (Hart and Freed, 2003, 2005). Parents do not moult during the incubation and nestling periods.

### Field methods

Clutch size and measurements of nestlings were obtained from nests in artificial cavities. Because the akepa is an endangered species, nests were only visited once to minimize disturbance. Furcular fat scores were estimated as 0 (no fat), 0.10 (trace of fat on floor of furcular depression, 1 for solid floor of fat but depression not full, 2 for full depression, and 3 for surrounding fat). Mass scores were estimated to the nearest 0.1 g on a spring scale. Bill and wing length were estimated to the nearest 0.1 mm using a caliper and wing rule, respectively. The same measurements were taken on fledglings, juveniles, and adults captured in aerial mist-nets at canopy level. Individual birds were used only once per month. If multiple captures were involved, the mean of measurements was used for that individual that month. Both mass and fat are variables that can change over the short term, so the individuals with repeated measures over months and years can be considered independent samples. Sample sizes are reported in Table 1 and Fig. 2. Numbers of primary flight feathers moulting on each wing were counted during 2002–2005.

Arthropod data were collected from canopy foliage samples between 1994 and 1997, using a protocol documented in Fretz (2002). The numbers of individuals per standardized

dry foliage mass from individual trees were averaged for each month during each year. Sample sizes for the number of years in which each month was sampled are shown in Figs. 1 and 2.

### Statistical methods

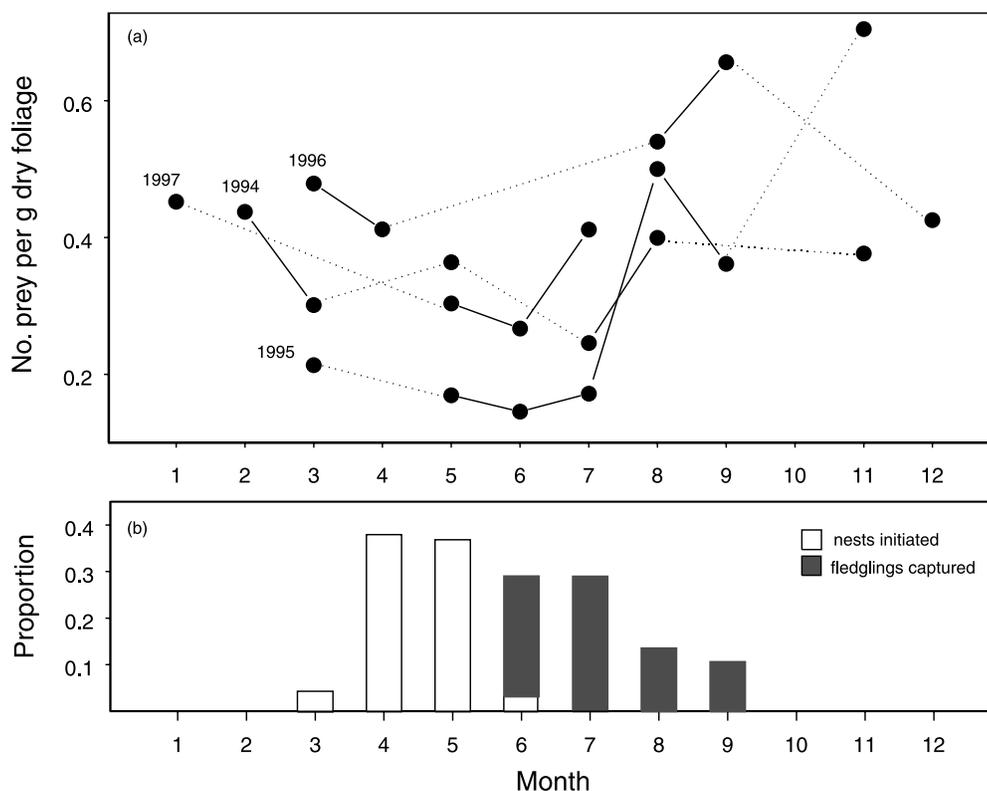
Change in arthropod data was established by linear contrast of standardized density with month from January through July. January represents the month in which at least three species of honeycreepers initiate breeding and July the month in which active nests are rarely found. Time periods (February–March, April–May, June–July, August–September, and November–December) were used for testing seasonality. Seasonality of different taxa was tested by a linear model that included time period, year, and a time period  $\times$  year interaction. Seasonality was indicated by significant time period differences but a non-significant period  $\times$  year interaction. Changes in fledgling and adult fat and mass over the 4-month fledgling period were each tested by linear contrast of the dependent variable (fat, mass) with respect to month, age as a factor, and the contrast  $\times$  age interaction.

### RESULTS

Breeding and most adult moulting occur during a decline in food resources (Figs. 1, 2). Canopy arthropods in ohia foliage decline significantly between January and July (linear contrast,  $P < 0.03$ ). Thus eggs are laid and incubated, and nestlings are reared, entirely during the decline. Fledglings are reared and parents moult most of their nine flight feathers in June and July (Fig. 2d), during the lowest portion of the food decline (Fig. 2a). The peak abundance of canopy arthropods occurs in September with a density higher than the rest of the breeding season ( $t$ -test,  $P < 0.03$ ). The termination of parental care in September coincides with this peak (Fig. 1). The availability of numerous prey would make independence easier for young juveniles.

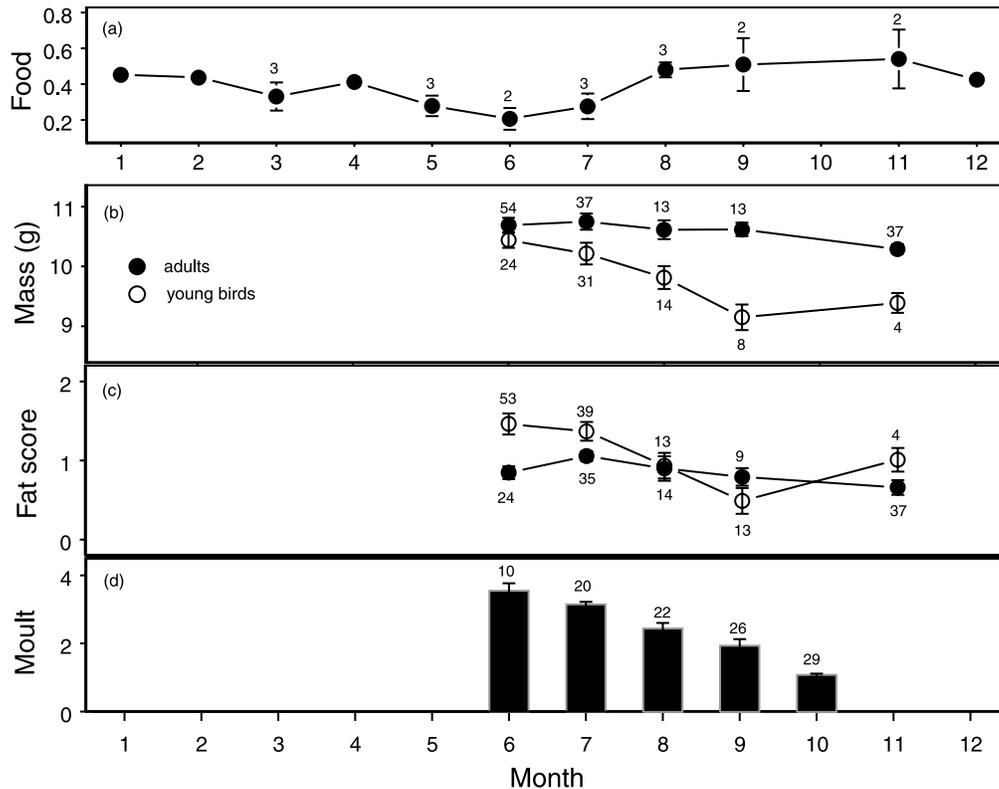
The seasonal decline in canopy arthropods known from akepa stomach samples is primarily due to numerically predominant spiders (Fretz, 2002). Caterpillars and psocids were more than two orders of magnitude less abundant than spiders, with psyllids and delphacids the rarest known prey (Fretz, 2002). Spiders were the only taxa with consistent seasonality (Fig. 1a). The peak of arthropods in August–September is based on a three-fold increase in the density of young spiders compared with March–May ( $t$ -test,  $P < 0.001$ ). There was no corresponding increase in adult spiders ( $P = 0.82$ ). Termination of parental care of akepa fledglings in September is thus associated with a flush of young spiders. The foraging specialization is assumed to be associated with much rarer bract microlepidopteran caterpillars (Fretz, 2002). Young spiders may thus subsidize the juvenile birds, in lieu of their parents, as they continue to develop specialized foraging skills.

Despite growing during a decline in food resources, nestlings that were within 6 days of fledging, with a bill length approximately 60% that of adults, were on average 1.25 times the mass of adults, with some individuals having up to 1.4 times adult mass (Table 1). Furcular fat of nestlings was uniformly high, and generally higher than other life-history stages, including breeding females. Fat could even be observed subcutaneously outside of the furcular cavity. Although nestlings were weighed only once, to minimize disturbance, mass recession could be estimated outside of the nest. June fledglings can be differentiated into



**Fig. 1.** (a) Number of canopy prey per gram dry foliage by month for each year. Points represent the mean values for trees sampled each month. Solid lines connect contiguous months; dotted lines connect months with gaps. Seasonality is based almost entirely on five groups of spiders (Thomisidae, Philodromidae, Tetragnathidae) and two species of Theridiidae (three-way interaction of subgroup, time period, and year:  $P = 0.61$ ; subgroup  $\times$  time period interaction:  $P = 0.30$ ). Four groups of caterpillars (Lepidoptera: bract-associated, foliage-associated, geometrids, and lichen-associated) showed limited seasonality (bract-associated and foliage-associated, time period  $\times$  year interaction:  $P = 0.0001$  and  $0.0032$ , respectively) or no seasonality (geometrids and lichen-associated, Kruskal-Wallis test of main effect of time period:  $P = 0.55$  and  $0.20$ , respectively). Jumping plant lice (Hemiptera, Psyllidae), psocids (Psocoptera, Psocidae), and planthoppers (Hemiptera, Dephacidae) had significant time period  $\times$  year interactions ( $P = 0.0007$ ,  $0.0001$ , and  $0.0006$ , respectively). There is a similar pattern of seasonality among years even when overall food abundance varied. For example, 1995 was an exceptionally poor year for breeding by akepa, and was the only year between 1987 and 1999 when two out of three females without brood patches were moulting body feathers before June. (b) Breeding seasonality of the akepa. Open bars represent months during which eggs were laid, as inferred by the stage at which 78 nests were detected (criteria in Lepson and Freed, 1995). Filled bars represent months during which 85 fledglings were captured in mist-nets. Nests with nestlings occurred mainly in late April through early June.

young fledglings (bill length  $< 9.0$  mm) and older fledglings (bill length  $> 9.0$  mm), based on fledging events that can occur between April and June. At minimum, 42% of mass recession occurs outside of the nest by the end of June (Table 1). Even more may occur outside of the nest since there was no correlation between mass and bill length among nestlings (range in



**Fig. 2.** Condition of young birds and adults during the fledgling period (June–September) and independence (October–November) in relation to food. (a) Food is number of canopy prey per gram dry foliage. Points represent monthly means across years from Fig. 1a, with standard error and sample size. (b) Mass trajectories with standard error and sample size. (c) Fat trajectories with standard error and sample size. For (b) and (c), June young birds are older fledglings. Sexual dimorphism does not exist for fat and mass (Table 1). June adult females with active brood patches were excluded from the analysis. At termination of parental care in September, adults weigh more than their offspring ( $t$ -test,  $t_{19} = 6.72$ ,  $P < 0.0001$ ), but fat is indistinguishable ( $t$ -test,  $t_{20} = 1.61$ ,  $P = 0.12$ ). Between September and October–November, adults lose mass ( $t$ -test,  $t_{45} = 2.31$ ,  $P = 0.03$ ), but they still weigh more than juveniles ( $t$ -test,  $t_{37} = 4.29$ ,  $P = 0.0001$ ), who do not lose mass during this interval. Juveniles and adults have comparable fat during October–November ( $t$ -test,  $t_{37} = 1.32$ ,  $P = 0.19$ ). (d) Annual cycle of moulting patterns of primary flight feathers of adults. The akepa has nine primary flight feathers. Bars show mean number of moulting primary feathers on each wing, with standard error and sample size. When moulting was asymmetric, the higher value was used. Body moult also commences in June, just before primary moult, except in 1995 (Fig. 1). Note the coincidence during June of lowest food and heaviest adult moult while fledglings are still fat and still growing (see text).

bill length 6.2–9.5 mm, range in mass 12.2–14.1 g;  $\rho = -0.30$ ,  $P = 0.70$ ). The young birds fly very little during the first 4–5 days after fledging.

Fledglings grow during June–August, the months of heaviest adult moulting (Fig. 2d). Young fledglings are intermediate in mass, wing length, bill length, and fat levels between nestlings and older fledglings approximately 1–2 months out of the nest (Table 1). Older fledglings in June have asymptotic wing lengths (59.3 mm) for hatch year birds that are

**Table 1.** Changes in morphology and condition from late nestling period to fledglings 1–2 months out of the nest, in relation to adults

Character	Age or stage			
	Nestlings	Young June fledglings	Older June fledglings	Adults
Mass (g)	12.8 (0.28, 7)	11.4 (0.38, 4)*	10.4 (0.13, 24)*	10.7 (0.12, 54)
Fat (score)	3.0 (0, 7)	1.8 (0.17, 5)*	1.5 (0.13, 24)	0.8 (0.08, 53)*
Bill (mm)	7.6 (0.56, 4)	8.3 (0.40, 5)	10.4 (0.18, 12)*	11.3 (0.07, 144)*
Wing (mm)	50.0 (0, 2)	56.0 (1.01, 5)*	60.0 (0.52, 12)*	61.6 (0.26, 81)*

*Note:* Sequential *t*-tests were performed from nestlings to adults except for bill and wing, where an ANOVA was used for older June fledglings and adults because of slight sexual dimorphism in these characters. \*Significant comparison in relation to the value in the cell to the left. Cells contain means, with standard error and sample size in parentheses.

significantly shorter than those of adults (61.6 mm, ANOVA accounting for slight sexual dimorphism,  $P = 0.0007$ ). Some older June fledglings have a discernible cross to their upper and lower bill. However, older June fledglings have significantly shorter bills than adults (Table 1). Bills grow during June and July and achieve asymptotic adult length in August.

The role of nestling overgrowth is apparent in mass and fat dynamics of fledglings and adults during the lengthy fledgling period. Parents maintain higher mass ( $P < 0.0001$ ; Fig. 2b), but fledglings maintain higher fat ( $P < 0.0001$ ; Fig. 2c). Both lose mass and fat, but the rate of each for fledglings is greater ( $P < 0.001$  for both interactions; Fig. 2b,c). The higher fat level of fledglings mainly occurs in June and July (Fig. 2c), when parents are moulting most heavily (Fig. 2d). This highlights the importance of nestling overgrowth, in which most of the loss of mass consists of fat.

The fat from nestling overgrowth is limited to June and July, the months with the lowest food. The fat levels of fledglings decline in August while parents are still moulting at least 2 primary feathers per wing. At the termination of parental care in September, adults weigh more than fledglings, but are not fatter (Fig. 2b,c). Juveniles maintain their low mass during October and November, while parents lose additional mass (Fig. 2b). The parental loss may be based on not carrying food in the crop for offspring after September. It could also be associated with colder air temperatures that include freezing temperatures at night, which increase energy requirements for thermoregulation. Fledglings recaptured as adults have generally acquired additional mass, an average of 0.8 g ( $n = 3$ , range  $-0.74$  to 1.65) for July and 0.5 g ( $n = 3$ , range  $-0.1$  to 1.3) for August fledglings. Only one September fledgling was recaptured, without change in mass.

## DISCUSSION

We have documented the first case of an organism that breeds almost entirely during a seasonal decline in food and of a bird that also moults most heavily during that decline while caring for growing fledglings. As unusual as this life history is, the akepa has very high juvenile survival of 0.42 and adult survival greater than 0.80 (Lepson and Freed, 1995). These are

high values, even for tropical birds (Stutchbury and Morton, 2001). Nestling overgrowth is part of a complex adaptation around which the rest of the life history is based. Here we discuss the many issues associated with adaptation and constraint that are illustrated by breeding and moulting during a seasonal food decline.

The nestling overgrowth is the most extreme measured in any land birds. The ratio of nestling to adult mass of 1.25 exceeds that documented for temperate and tropical swifts, swallows, and tyrant flycatchers ( $t$ -test,  $P = 0.04$ ), for which the ratio ranges from 1.03 to 1.23 (Ricklefs, 1968a, 1976; O'Connor, 1978). These species are aerial foragers, and the recession of weight, nearly complete by fledging, is mainly due to loss of water associated with maturation of tissues and development of wings used while foraging as fledglings (Ricklefs, 1968b). Lipids increase slowly during the recession (Ricklefs, 1967, 1968b). In contrast, akepa fledglings are loaded with fat, feed on stationary prey while standing on twigs, and lose a substantial amount of mass outside of the nest. In addition, the 16- to 21-day nestling period of the hole-nesting Hawaii akepa (Lepson and Freed, 1997) overlaps with the 15- to 21-day period of the open-cup nesting Hawaii amakihi (*Hemignathus v. virens*) (Lindsey *et al.*, 1998) and the 18- to 21-day period of the variably nesting Hawaii creeper (*Oreomystis mana*) (Lepson and Woodworth, 2001). Both the amakihi and creeper are insectivorous relatives of the akepa without nestling overgrowth (see below), so the obligate hole-nesting habit of the akepa does not contribute to the overgrowth. Nestling overgrowth has evolved for a different reason than in other birds.

Nestling overgrowth in the akepa enables the bird to breed and moult almost entirely during a food decline. By loading their nestlings with extra food during a time of relatively higher food resources, parents can prevent over-expenditures of energy during a time of lower resources while they are moulting heavily and fledglings are continuing to grow. High annual adult survival in birds is associated with less risk taking by parents (Ghalambor and Martin, 2001). This means that akepa parents would be expected to care for themselves over their fledglings when food becomes limiting, as would be the case in June and July from the canopy arthropod data. The nestling overgrowth is thus a clear example of a matched character between parents and offspring (Trivers, 1985). Nestlings are favoured to consume more than they need at the time. Parents are favoured to provide the extra food to nestlings. The character of nestling overgrowth is maintained by selection in both age classes.

The adaptation of nestling overgrowth involves three components: nestling use of extra food, consuming more food, and receiving more food. The overgrowth in aerial insectivores involves maturation of feathers and tissues for aerial foraging (Ricklefs, 1968a,b; Remes and Martin, 2002). Deposition of fat is involved in the akepa. Nestling overgrowth is thus more than an outcome of provision and consumption. It is also based on genes that dictate how the extra food is used. The nestling overgrowth of the akepa is more similar to that of oceanic birds, although unlike those birds, young are cared for as fledglings. The nestling overgrowth of the akepa increases the types of developmental variation known in birds (Schew and Ricklefs, 1998).

The parental contribution to nestling overgrowth in the akepa indicates prospective care. Parents are banking their care in their offspring during a time of relatively higher resources. The value of the increase in care over the requirement for normal growth and fat deposition of their offspring is apparent 1–2 months later, when food is less abundant and parents have to deal with moulting. Prospective parental care is not recognized formally as such, although parental care is recognized to contribute to offspring quality (Clutton-Brock, 1991;

Stearns, 1992). The akepa case deals with parental care for the benefit of the parental soma as well as for the benefit of offspring.

This life history is unique to the Hawaii akepa among Hawaiian birds that have been studied. Four other species of Hawaiian honeycreepers in the same environment initiate breeding during the food decline, but much earlier than the akepa. These are the nectarivorous iiwi (*Vestiaria coccinea*) and apapane (*Himatione sanguinea*) and the insectivorous Hawaii amakihi and Hawaii creeper. There is no evidence of nestling overgrowth or weight recession in the other species. For these, there is a positive slope of a regression of mass on bill length of fledglings, whereas akepa have a negative slope (*t*-test on slopes as variables,  $P = 0.009$ ). Only young akepa lose mass as they grow. The moult characteristics of all the honeycreepers in ohia/koa forests are similar (Ralph and Fancy, 1994). The nestling overgrowth adaptation of the akepa is constrained phylogenetically by moulting seasonality of adults.

An issue remains as to why the breeding season begins late enough in the year for nestling overgrowth to be a necessary adaptation. More food would be available if the birds initiated breeding earlier. However, the akepa is the smallest of the five species of honeycreepers on the study site and air temperatures are colder during January through March (Freed *et al.*, 2005), with freezing temperatures commonly occurring at night. The smaller body size means that more food intake is used for thermal maintenance, and akepa thus require warmer temperatures for females to get into breeding condition. This interpretation is supported by the fact that adult males have lower fat scores during January–March than in April (0.40 vs. 0.75; *t*-test,  $P = 0.04$ ). The initiation of breeding in March (mainly April and May) may thus be constrained by body size in relation to temperature, even though food is less abundant at that time.

Although there have been no other studies of breeding, moult, and food as detailed as that reported here, the lengths and positions of breeding cycles in relation to moult are especially relevant for understanding tropical life history. Moult–breeding overlap should be recognized even when it occurs only during the fledgling period when moulting coincides with dependent young that are still growing. Tropical species with lengthy fledgling periods may encounter predictable changes in food abundance and climate within the period. If clutch sizes of two eggs are based on factors other than food limitation, as suggested by both theoretical and empirical studies for long-lived tropical birds (Ghalambor and Martin, 2001; Stutchbury and Morton, 2001), then nestling overgrowth as observed in the akepa may be a more common dynamic link between moulting and breeding during predictable changes in food abundance. Greater parental care during a time of more resource abundance can provide a future benefit for dealing with conflicting demands during a time of lower resource abundance.

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