A FLEDGLING-MASS THRESHOLD GREATLY AFFECTS JUVENILE SURVIVAL IN THE HAWAII AKEPA (*LOXOPS COCCINEUS COCCINEUS*)

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ABSTRACT.—Offspring quality is an important issue in avian life-history theory, particularly with regard to birds that have low reproductive rates and extended parental care. Offspring mass has been identified as an indicator of quality in several bird species. These studies have shown that nestling mass is predictive of offspring survival outside the nest, but few studies have considered the role of fledgling mass. Mass during the fledgling period may change and influence juvenile survival. Fledgling mass may be especially relevant for tropical birds that have very long fledgling periods during which food conditions randomly or seasonally change. Here, we show that fledgling mass predicts juvenile survival in the Hawaii Akepa (*Loxops coccineus coccineus*), an endangered Hawaiian Honeycreeper with high annual adult survival and a two-egg clutch. Juvenile survival of Hawaii Akepa approximated a trimodal pattern of no survival, low survival, and high survival that corresponded to ascending mass classes. Fledglings in the highest mass class had an apparent juvenile survival probability that was more than double that of fledglings of the lower mass classes and that was statistically indistinguishable from survival rates of adults. This mass-dependent juvenile survival has important implications for understanding the life-history evolution and population biology of the Hawaii Akepa and perhaps of other tropical birds. *Received 16 January 2008, accepted 31 October 2008.*

Key words: fledgling quality, Hawaii Akepa, juvenile survival, life history, *Loxops coccineus*, recruitment.

Un Umbral en la Masa de los Volantones Afecta Fuertemente la Supervivencia de los Individuos Jóvenes en *Loxops coccineus coccineus*

RESUMEN.—La calidad de las crías es un aspecto importante de la teoría sobre las historias de vida de las aves, particularmente para las que presentan tasas reproductivas bajas y cuidado parental extendido. La masa de las crías ha sido identificada como un indicador de la calidad en varias especies de aves. Esos estudios han mostrado que la masa de los pichones predice la supervivencia de las crías fuera del nido, pero pocos estudios han considerado el papel de la masa de los volantones al momento de abandonar el nido. La masa durante el período de emplumamiento puede cambiar e influenciar la supervivencia de las aves jóvenes. La masa de los volantones podría ser especialmente relevante para las aves tropicales que tienen períodos de emplumamiento muy largos, durante los cuales las condiciones cambian aleatoria o estacionalmente. En este estudio demostramos que la masa de emplumamiento predice la supervivencia de las aves jóvenes en *Loxops coccineus coccineus*, una especie de mielero hawaiano amenazada que presenta una supervivencia anual de los adultos alta y una nidada de dos huevos. La supervivencia de los jóvenes se aproximó a un patrón trimodal de no supervivencia, supervivencia baja y supervivencia alta, que correspondió a una escala creciente de clases de masa. Los volantones en la clase de masa más alta presentaron una probabilidad de supervivencia aparente de más del doble en comparación con la de los volantones de las clases de masa menores, y su tasa de supervivencia fue estadísticamente indistinguible de la de las aves adultas. Esta supervivencia dependiente de la masa en las aves jóvenes tiene implicaciones importantes para entender la evolución de la historia de vida y la biología poblacional de *L. c. coccineus* y quizás de otras aves tropicales.

A UNIVERSAL PATTERN in life-history theory is that juvenile survival is lower than adult survival in iteroparous organisms (Roff 1992, Stearns 1992). Hypotheses for this pattern are (1) that smaller juveniles are subject to greater predation pressure than adults and (2) that survival in the absence of predation depends on sufficient nutrition (Lack 1954, Williams 1966, Weathers and Sullivan 1991).

There are several contexts in which nutritional limitation applies. Juveniles may need to be of sufficient size to be successful competitors for food (Smith and Fretwell 1974, Brockelman 1975). Juveniles may also need stores of reserve nutrients to use as they hone foraging skills or when food becomes limiting because of weather or seasonal changes (Lack 1954, 1968). The tradeoff between quality and

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quantity of offspring, a major issue in life-history theory (Smith and Fretwell 1974, Stearns 1992), is based on the allocation of food. Higher offspring quality leads to increased survival, as documented for diverse taxa (Sinervo et al. 1992, Kirk 1997), including birds (reviewed by Perrins and McCleery 2001). Tropical birds, with small clutch sizes (Moreau 1944, Skutch 1985) and extended fledgling periods (Russell 2000, Russell et al. 2004), are thought to occupy the quality end of the quality–quantity continuum. Offspring quality is emphasized in tropical avian life-history strategies because the high adult survival and stable populations in such regions are associated with a limited number of annual recruitment opportunities (Greenberg and Gradwohl 1986, Ghalampor and Martin 2001, Stutchbury and Morton 2001). The few recruitment opportunities are expected to be available mainly to young birds in the best condition (Cody 1966).

There are many opportunities during the breeding cycle for quality to make a difference in the survival of young birds. Egg quality, mainly size, has been related to nestling growth and survival up to fledging in many species (reviewed in Martin 1987, Williams 1994). In addition, there are numerous cases in temperate birds of stunted growth of nestlings and mortality in the nest associated with food shortages (Martin 1987). Freed (1987) also documented the phenomenon during an El Niño event in the House Wren (*Troglodytes aedon*) in lowland central Panama. Mortality during the fledgling period is more difficult to document, because fledglings have rarely been followed. When they have, mortality has been detected before the termination of parental care in both temperate passerines (Yellow-eyed Junco [*Junco phaeonotus*], Weathers and Sullivan 1989; Brown Thornbill [*Acanthiza pusilla*], Green and Cockburn 2001; Great Tit [*Parus major*]; Coal Tit [*P. alter*], Naef-Deanzer et al. 2001) and tropical passerines (House Wren, Freed 1988; Spotted Antbird [*Hylophylax naevioides*], Styrsky et al. 2005). Weathers and Sullivan (1989) even documented higher mortality in Yellow-eyed Juncos during the week following termination of parental care. This was associated with fledglings capturing smaller insects than adults, leading to an increase in foraging time and energy budget deficit (Weathers and Sullivan 1989, 1991).

Juvenile survival is the demographic parameter most influenced by quality, because recruitment depends on this survival. Fledgling condition may be more relevant than nestling condition for juvenile survival because fledglings have survived the exigencies of the nestling period and are still under parental care. Because of the difficulty of capturing and measuring fledglings, prefledging mass has been used as a surrogate of fledgling quality (Davies 1986, Weathers and Sullivan 1989, Tinbergen and Boerlijst 1990, Magrath 1991, Both et al. 1999, Green and Cockburn 2001, Naef-Daenzer et al. 2001, Perrins and McCleery 2001, Monrós et al. 2002). Prefledging mass has successfully predicted juvenile survival in all the studies cited above except that of Weathers and Sullivan (1989). Parents caring for fledglings may have limited ability to compensate for earlier deficiencies, because fledglings require more food than nestlings as they continue to grow, fly, and thermoregulate without insulation from nest mates and the nest (Royama 1966, Martin 1987). Nevertheless, when growth, mass, and fat changes occur during the fledgling period, as has been identified in the tropical Hawaii Akepa (*Loxops coccineus coccineus*; hereafter "akepa"; Freed et al. 2007), fledgling quality

may be evident in these changes and be especially useful for predicting juvenile survival.

We determined whether condition during the fledgling period is related to juvenile survival in the akepa, a federally listed endangered Hawaiian honeycreeper (Drepanidinae). This subspecies, endemic to Hawaii Island, has a typical tropical life history with small clutch size (2 eggs), a long incubation and nestling period (14–16 and 16–20 days, respectively), a four-month fledgling period, and high annual adult survival of 0.80 (Lepson and Freed 1995, 1997). The subspecies has high juvenile survival (0.43; Lepson and Freed 1995), despite nesting during a seasonal decline in food that reaches its minimum while fledglings are still growing their bills (Freed et al. 2007). This estimate of juvenile survival, which emphasizes average survival, may be misleading if it ignores profound differences in survival of fledglings with different mass.

Methods

Field methods.—The 600 × 400 m study site was located at an elevation of 1,900 m in the Pua Akala Tract of Hakalau Forest National Wildlife Refuge, on the windward slope of Mauna Kea, Hawaii Island. The site consists of old growth Ohia–Koa (*Mestrosideros polymorpha–Acacia koa*) forest, which supports the densest population of the akepa (Freed 2001). The birds are year-round residents in the study site and are frequently found during the fledgling period in mixed-species flocks consisting mainly of native species (Hart and Freed 2003).

Fledgling akepa were captured in aerial mist nets during 1987–1999, from June until the termination of parental care in September (Freed et al. 2007). Each bird was banded with a federal aluminum band and a unique set of three color bands. Survival to the following year (minimum 330 days after capture) was based on recapture in mist nets or identification of unique color-band combinations through binoculars. Recapture–resighting efforts continued through July 2006. Rulers and calipers accurate to the nearest 0.1 mm were used to measure wing length (as the longest flattened primary feather) and bill length (as culmen length). Mass was measured to the nearest 0.5 g with a spring scale. Subcutaneous fat deposits within the furcula were scored as 0 (no fat), 0.1 (trace), 1 (partially full), 2 (full), and 3 (bulging). Fledglings captured as adults were remeasured.

Seventy-one fledglings were captured. Young fledglings were excluded from analysis because of morphometrics (high fat, short bills) associated more with the nestling stage (Freed et al. 2007). Twenty-seven recruits were documented by capture or resighting. Eleven fledglings were captured more than once. To maintain independence of observations in the analyses, for the six fledglings that were recaptured in the same month, measurements were averaged for that month. For the six birds recaptured during different months, including one bird also recaptured within the same month, only one month was used. Analyses were repeated with alternative months to determine whether the outcome changed with the selection. More importantly, the recaptures were used to determine whether differences in mass were sufficient to move individuals between the trajectories of survivors and nonsurvivors.

Nestling mass was obtained from seven nestlings in four broods in accessible cavities. The birds were weighed within four to six days of fledging.

Statistical analysis.—We used several methods to identify size variables of fledglings relevant to juvenile survival. Principal component analysis was used to score fledglings on the basis of correlations between wing, bill, and mass. Logistic regression was used to test the effects of principal components on survival. The effects of wing, bill, and mass on survival were also analyzed separately. These logistic regression models included month and year of capture, because size varies with month and food abundance varies among years (Freed et al. 2007). Analysis of variance (ANOVA) of mass, with juvenile survival status and linear contrast of month as categorical factors, along with the interaction, was used to test differences in population mass trajectories over the fledgling period of eventual survivors and nonsurvivors based on independent samples.

An ANOVA was used to test the relationship between mass and fat. A linear contrast of sequentially higher fat classes was tested. An *F*-test of variance, based on natural logarithms of both nestling and fledgling mass, was used to compare relative variability between the two life-history stages (Lewontin 1966).

We used the program MARK (White and Burnham 1999) to estimate juvenile survival. Because logistic regression showed a significant relation between mass and survival, independent of month and year, the candidate models did not include specific effects of month or year. The fully parameterized model included annually varying survival and probability of capture. Candidate models were based on an age effect (juvenile and adult, from surviving juveniles) and mass group effect. Fledglings were assigned to four groups based on unit of measurement and mean adult mass of 10.5 g (Freed et al. 2007). The high-mass group (≥11 g) had higher than mean adult mass. The average-mass group (10–11 g) had essentially mean adult mass. The low-mass group (9–10 g) had lower than mean adult mass. The very-low-mass group (8–9 g) had mass levels rarely detected in adults. All supported candidate models had annually varying probability of capture. The models included (1) annually varying juvenile survival without groups, (2) constant juvenile survival without groups, (3) constant juvenile survival with a four-group effect, (4) constant juvenile survival with two groups (high mass plus other groups combined), and (5) constant juvenile survival with three groups (high-mass, very-low-mass, and combined average-mass and low-mass). Goodness-of-fit was tested using Test 2 and Test 3 in the program RELEASE (Pollack et al. 1990) on the most parameterized model. These respectively test the assumptions that every marked animal present in the population at time *i* has the same probability of recapture at time *i* and has the same probability of surviving to time *i* + 1. All five models, with parameters of adult survival and juvenile survival indexed by mass class, were evaluated using corrected Aikake's information criterion (AIC$_c$) and associated Akaike weights because of the low ratio of sample size to number of parameters (Burnham and Anderson 2002).

Because none of the very low-mass fledglings survived, these birds were excluded from a model that included more than one adult survival parameter. A model with two adult survival parameters was compared with a model with one adult parameter to test whether survival based on fledgling mass carried over into adult survival. One adult parameter was associated with the high-mass group. The second adult parameter was associated with the average- and low-mass groups. The same goodness-of-fit tests described above were used with this model.
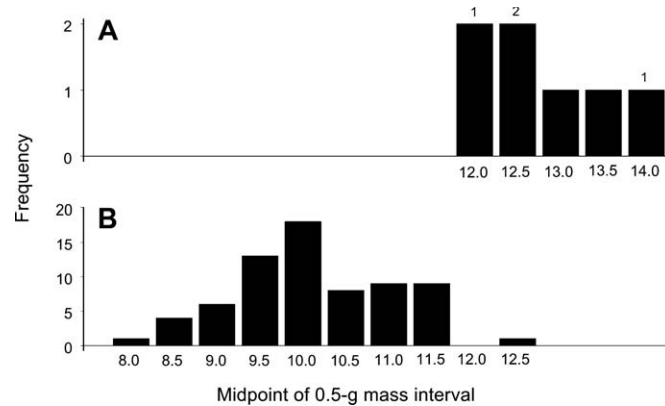

FIG. 1. Histograms of nestling (A) prefledging mass (*n* = 7) and (B) fledgling mass (*n* = 71) of Hawaii Akepa. Numbers above nestling bars indicate the number that survived to adulthood.

Surviving fledglings from the different mass classes, measured as adults, were compared for mass and bill length with *t*-tests.

RESULTS

Fledglings varied more in mass than nestlings (*F* = 2.45, df = 6 and 77, *P* = 0.032; Fig. 1) and also in fat, because nestlings invariably had a fat score of 3. Fledgling mass was correlated with fat (Spearman ρ = 0.55, *P* < 0.0001).

The first principal component (PC1) of fledgling size had positive loadings of mass and wing length without any contribution from bill length (Table 1). PC1 did not vary significantly with month (*F* = 1.02, df = 3 and 64, *P* = 0.39), and the variance among years was marginally significant (*F* = 1.98, df = 9 and 64, *P* = 0.06). PC2 distinguished mass from size and varied among months (*F* = 7.02, df = 3 and 64, *P* = 0.004) and years (*F* = 2.41, df = 9 and 34, *P* < 0.0001). PC3 distinguished mass and bill length from wing length and varied marginally among months (*F* = 2.41, df = 3 and 64, *P* < 0.08) and significantly among years (*F* = 2.39, df = 9 and 64, *P* = 0.03).

Scores of birds on the principal components are shown in Table 1. Only PC1 had a significant effect on survival (logistic regression: χ² = 7.34, df = 1, *P* = 0.007; χ² = 0.52, df = 1, *P* = 0.47

TABLE 1. Principal component (PC) analysis of Hawaii Akepa fledgling measurements, and comparison of scores (± SE) of survivors and nonsurvivors.

	Principal component		
	PC1	PC2	PC3
Loadings			
Mass	0.70	0.32	0.64
Bill length	0.00	−0.91	0.41
Wing length	0.72	−0.25	−0.65
Variance explained	0.44	0.36	0.20
Scores			
Survivors (*n* = 28)	0.50 ± 0.23	−0.04 ± 0.19	0.22 ± 0.15
Nonsurvivors (*n* = 43)	−0.23 ± 0.15	0.14 ± 0.16	−0.15 ± 0.12

Table 2. Survival of Hawaii Akepa fledglings with respect to morphometrics and conditioned on year and month of capture.

Variable	Survivor [a]	Nonsurvivor [a]	P (without year, month) [b]	P (with year, month) [b,c]
Mass	10.5 ± 0.2	9.9 ± 0.1	0.005	0.04 (0.16, 0.27)
Bill length	11.0 ± 0.1	10.6 ± 0.1	0.15	0.10 (0.16, 0.27)
Wing length	59.8 ± 0.4	59.2 ± 0.3	0.23	0.47 (0.16, 0.27)

[a] Values shown are means ± SE.
[b] P values are from analysis of deviance of logistic regressions with wing, bill, and mass entered, in that order, after year and month.
[c] Numbers in parentheses are P values for year and month, respectively.

and $\chi^2 = 3.67$, df $= 1$, $P = 0.06$ for PC2 and PC3, respectively). PC1 became marginally significant ($\chi^2 = 3.5\ 9$, df $= 1$, $P = 0.06$) when month and year were added to the model ($\chi^2 = 5.22$, df $= 3$, $P = 0.16$ for month; $\chi^2 = 11.15$, df $= 9$, $P = 0.27$).

For the subset of fledglings of known sex, 18 male and 16 female fledglings differed in PC1 and PC3 (PC1: male, 0.83; female, -0.05; $t = 2.36$, df $= 32$, $P = 0.02$; PC2: male, -0.31; female, 0.22; $t = 1.56$, df $= 32$, $P = 0.13$; PC3: male, -0.16; female, 0.44; $t = 2.50$, df $= 32$, $P = 0.02$). However, there was no difference between the sexes in mass (for both sexes, mean $= 10.4 \pm 0.2$ [SE] g).

To isolate the effect of mass on survival of all fledglings, a logistic regression model included wing length, bill length, and mass, added in respective order. Only mass had a significant effect on the probability of surviving, though surviving fledglings were larger in all measurements (Table 2). When month and year were added to the model before the other variables, mass remained significant, and bill and wing remained nonsignificant (Table 2).

Both surviving and nonsurviving fledglings lost mass over the fledgling period ($F = 8.15$, df $= 3$ and 67, $P = 0.0001$; linear contrast of month, $F = 17.83$, df $= 1$ and 67, $P < 0.0001$; Fig. 2). Nonsurviving fledglings lost more mass (survival group, $F = 8.10$,

df $= 1$ and 67, $P = 0.006$). The interaction between linear contrast of month and survival group was not significant ($F = 0.39$, df $= 1$ and 67, $P = 0.54$), which suggests that the changes were essentially parallel. There were six fledglings that were captured during more than one month. Similar results were obtained for all effects when only data from their initial month of capture were used. Only one of these fledglings increased mass by >1 g between months. The remainder did not change. There were six individuals that were captured more than once within a month. Two of these changed mass by 0.5 g, one with an increase and one with a decrease. The remainder did not change. This sample indicates that only 25% of fledglings may have been able to move between the population-level mass profiles of survivors and nonsurvivors within and between months.

For estimating apparent juvenile survival, there were several years in which insufficient data were available to test goodness-of-fit. However, for both overall Test 2 and overall Test 3, the data fit the most parameterized model in MARK ($\chi^2 = 1.85$, df $= 9$, $P = 0.99$; $\chi^2 = 3.07$, df $= 18$, $P = 1.0$). AIC_c rather than quasi-AIC_c was used to evaluate the different models, because the data were underdispersed ($\hat{c} < 1$; White et al. 2001).

Two models contributed >85% of AIC_c weight (Table 3). These included models with constant adult survival and with juvenile survival grouped by mass classes. The model with the most support distinguished the high-mass class, combined average- and low-mass classes, and very-low-mass class. The next-most-supported model distinguished the high-mass class from all the others. The rest of the models received low to negligible support (Table 3). The apparent juvenile survival by mass class is shown in Figure 3.
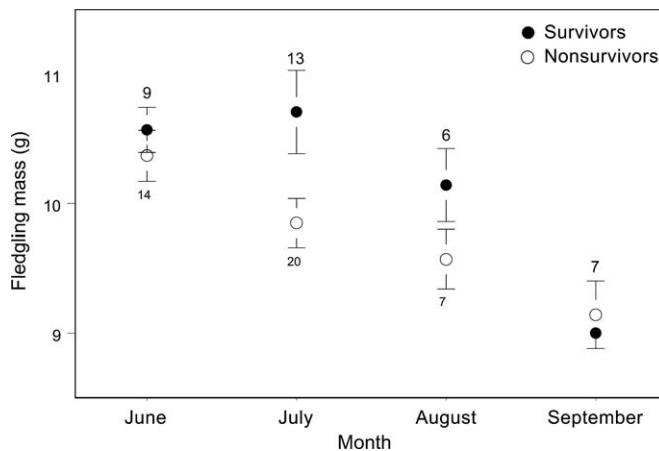

Fig. 2. Mass profiles of Hawaii Akepa fledglings during the entire fledgling period in relation to future survival. Solid circles represent survivors and open circles nonsurvivors, each with ± SE and sample size. The error bar and sample size for September are for the nonsurvivors; only one fledgling captured in September survived. The six birds with mass measured during more than one month are included in the figure to show the profile by month. The analyses were the same when only the first month of capture or only the last month of capture was used (details in text).

Table 3. Results of analyses in the program MARK to determine mass-related patterns of juvenile survival in Hawaii Akepa.

Model[a]	Number of parameters	AIC_c	AIC_c weight
Survival: J (A-BC-D), A con	23	339.0	0.52
Survival: J (A-BCD), A con	22	340.0	0.35
Survival: J (A-B-C-D), A con	24	341.9	0.12
Survival: J (AB-CD), A con	22	348.1	0.01
Survival: J con, A con	21	348.8	0.00
Survival: J var, A var	92	732.7	0.00
Recapture: J var, A var			

[a] Model specification. J = juvenile, A = adult, var = annually varying parameters, and con = constant parameter over the study. A = high mass, B = average mass, C = low mass, and D = very low mass, as defined in the text. The mass classes that are contiguous were specified by a single parameter. All models except the "J var, A var" had constant parameter for survival and annually varying parameters for probability of recapture for each age.
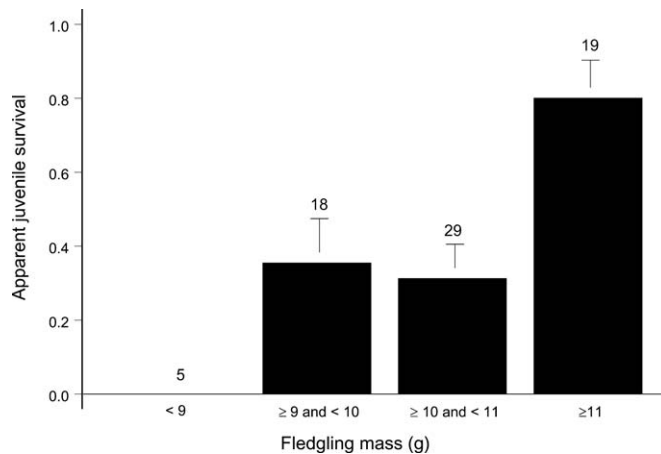
Fig. 3. Apparent juvenile survival of Hawaii Akepa fledglings, by fledgling mass class, from the program MARK, with ± SE and sample size, indicating a threshold effect of high mass (≥11 g) on survival. Mass class for birds captured during more than one month was based on mass during recapture. The most-supported model combines the two middle-mass classes and distinguishes the lowest- and highest-mass classes from the middle-mass class (Table 3).

It appears that 9 g may be a lower threshold for fledgling survival, because none of the birds that weighed <9 g survived. Apparent juvenile survival of the average-mass and low-mass classes are indistinguishable, which is consistent with the most-supported model. An upper threshold is indicated for the high-mass class. The apparent juvenile survival of this mass class (0.80 ± 0.10) is indistinguishable from the apparent adult survival (0.78 ± 0.04) obtained from both models.

High-mass fledglings were disproportionately represented among recruits. Although high-mass fledglings constituted only 27% of all fledglings (19 of 71), 46% of surviving fledglings (13 of 28) were high-mass (one-sided test of proportions, $P = 0.049$).

High-mass fledglings achieved larger size as adults. Only surviving females were captured in both the high-mass class and the average- to low-mass classes ($n = 4$ and 5, respectively). High-mass surviving females had both longer bills (mean = 11.4 ± 0.2 mm) and greater mass (mean = 11.3 ± 0.3 g) than average- to low-mass surviving females (mean bill = 10.9 ± 0.1 mm, mean mass = 10.3 ± 0.3 g; t-test, bill: $t = 2.72$, df = 7, $P = 0.03$; t-test, mass: $t = 2.55$, df = 7, $P = 0.04$). In MARK, there was little support for the possibility that high fledgling mass influenced adult survival from those fledglings (AIC$_c$ weight = 0.12 for two-parameter adult survival vs. 0.45 for single-parameter).

Discussion

Several studies have shown that fledgling survival increases with mass (Both et al. 1999, Green and Cockburn 2001, Naef-Danzer et al. 2001, Monrós et al. 2002), but the Hawaii Akepa is the first example in tropical birds of mass-related juvenile survival and, in any birds, of juvenile survival that can be equivalent to adult survival. The highest-mass class of fledglings indicates fledgling quality through a threshold effect with more than double the apparent juvenile survival of lower-mass classes, independent of month and year of initial capture. Fledgling mass was positively correlated

with fat, which suggests that young with greater mass had more lipid reserves. Below, we discuss the possible mechanism that produces the effect of mass on survival, consider the role of fledgling condition in akepa life history, and deal with the importance of juvenile survival (considered survival from nestling or fledgling to recruitment) in the population biology of birds.

Mass can influence survival in two ways. First, mass may be associated with competitive advantage in dominance situations that contribute to survival, as inferred for the Great Tit (Sandell and Smith 1991, Both et al. 1999). However, the akepa is nonterritorial (Lepson and Freed 1995) and feeds on arthropods in abundant Ohia trees during the fledgling period (Hart and Freed 2003). Judging from thousands of observation hours, neither fledglings nor adults interact aggressively over food (Lepson and Freed 1995, Hart and Freed 2003). Second, mass may reflect general body condition (Perrins and McCleery 2001). The "body-condition" hypothesis may be especially relevant for the akepa, because fledglings lose both mass and fat while parents are molting during the seasonal food decline (Freed et al. 2007). The correlation between fledgling mass and fat throughout the fledgling period provides support for the body-condition hypothesis. Fat may serve to subsidize growing fledglings during changes in food abundance and can sustain metabolism when rainy weather impedes foraging.

The condition-dependent juvenile survival of akepa may reveal the fitness consequence of the adaptation of nestling overgrowth (Freed et al. 2007). The akepa provides another example of survival that is independent of nestling mass (Weathers and Sullivan 1989). The lower variance of nestling mass and high survival of nestlings independent of mass suggest that condition of fledglings may be influenced by poorer food conditions during the fledgling period than during the nestling period. These poorer food conditions have been documented (Freed et al. 2007). A low rate of individual mass changes between the trajectories of survivors and nonsurvivors indicates that the early fledgling period may be most critical to juvenile survival. Nestling overgrowth may get offspring into the best condition for this important time, especially if parents have a limited ability to compensate for earlier deficiencies during the fledgling period because of lower food abundance and increasing self-maintenance costs associated with molting. Maintenance of high mass and correlated fat of fledglings more than doubles their probability of surviving to recruitment. This threshold effect of mass on survival may be the selective advantage that ultimately drives the nestling overgrowth adaptation, which shapes the extra food consumption by nestlings and the conversion of this extra food into fat. Parents also benefit from providing extra food to nestlings because the fat in fledglings is available when parents are molting most of their primary flight feathers (Freed et al. 2007).

The hypothesis that the fledgling-mass threshold effect on juvenile survival shapes akepa nestling overgrowth depends on the nature of the physiological changes associated with the mass accumulation and eventual decline. The phenomenon of nestlings achieving a larger size than their parents has been documented in oceanic birds and aerial insectivores (Ricklefs 1968a, b; O'Connor 1978). In the latter taxa (swift, tyrant flycatcher, and swallow species), the pattern of development has been termed "weight recession" and is associated with the loss of water during wing feather development. For these birds, the weight recession is nearly complete by fledging and lipids tend to increase during this period, though the trend in fat is generally not significant. The phenomenon of nestling

Table 4. Tropical forest birds for which estimates of both juvenile and adult survival are available.

Species	Number of adults	Number of juveniles	Adult survival	Juvenile survival	References [a]
White-bearded Manakin (*Manacus manacus*)	182	15	0.82	0.33	1 and 2
Spotted Antbird (*Hylophylax naevioides*)	1032	92	0.81	0.36	3
Ocellated Antbird (*Phaenostictus mcleannani*)	160	30	0.70	0.53	3
Bicolored Antbird (*Gymnopithys leucaspis*)	280	36	0.71	0.42	3
Hawaii Akepa	27, 36	71, 57	0.76, 0.82	0.44, 0.43	4, 5
Hawaii Elepaio	110	11	0.87 male, 0.81 female	0.32	6

[a] References: (1) Snow 1962, (2) Snow and Lill 1974, (3) Willis 1974, (4) present study, (5) Lepson and Freed 1995, and (6) VanderWerf 2008.

overgrowth in the akepa is different (Freed et al. 2007). In this species, the recession in mass continues for one month postfledging and, within the population of fledglings, does not end until after the termination of parental care four months after fledging. Some of the loss in mass may be water loss associated with weight recession during the first month of the fledgling period. The development of wings (proportion of asymptotic length) is at least 83% complete in the nest and 93% complete in young fledglings, and is 100% complete within the first month (Freed et al. 2007). However, there is concurrent and significant loss of fat while the wings are developing (Freed et al. 2007). The adaptation of nestling overgrowth is that fledglings during the second month of the period still have surprisingly high levels of fat, given the lowest levels of food and most intensive molt of primary flight feathers by parents during this two-month period (Freed et al. 2007).

Juvenile survival is the least understood and most difficult parameter to document in avian demography. Yet it is considered essential for understanding the negative correlation between clutch size and adult survival among birds in general (Martin 1996, Styrsky et al. 2005). Table 4 shows tropical bird species for which both adult and juvenile survival have been estimated, though only the akepa and Hawaii Elepaio (*Chasiempis sandwichensis sandwichensis*) have parameters estimated by mark–recapture analysis. The overall juvenile survival and adult survival of the akepa are comparable to those of other tropical birds. However, our study shows that juvenile survival can be an overall estimate of a trimodal parameter (no survival, low survival, high survival). The estimate is potentially misleading, because it is far from any mode. It is closer to the low-survival mode than to the high-survival mode, but fledglings in the high-survival mode are disproportionately represented in the next generation. Future detailed studies of tropical birds will be necessary to determine the generality of a trimodal distribution of juvenile survival based on mass. Mass-related juvenile survival in the akepa with a two-egg clutch shows that food can be important during both the nestling and the lengthy fledgling periods, despite a low reproductive rate.

The disproportionate recruitment of high-mass fledglings into the breeding population has additional implications for avian population biology. High-survival fledglings contribute the most to the population viability of a species with a low reproductive rate. In addition, the mass and bill-length distributions of the adult population are influenced by mass-related juvenile survival. Akepa bills grow throughout the long fledgling period (Freed et al. 2007). The high-mass fledglings contribute to the high end of both the mass and bill-size distributions of the adult population.

Perrins and McCleery (2001) indicated that this may be occurring in the Great Tit as well. Juvenile survival is considered the "black box" of avian demography (Martin 1996). That box must now include another feature: that threshold effects on juvenile survival go beyond simple recruitment and may shape the distribution of characters in adult populations.

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