Evolutionary Ecology Research, 2009, **11**: 731–757

Sexual dimorphism and the evolution of seasonal variation in sex allocation in the Hawaii akepa

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ABSTRACT

Questions: Can changing sexual dimorphism of fledglings during different months reflect seasonal variation in sex allocation, given that such changes are expected? Can a major shift in the sex ratio of young birds be attributed to food limitation that affects seasonal variation in sex allocation? How is sexual dimorphism related to seasonal variation in sex allocation?

Hypotheses: Hawaii akepa females have an advantage of producing male offspring early in the breeding season, either by increasing the fitness of their sons or by minimizing their own costs of moult–breeding overlap. Sexual dimorphism in bill length is maintained by stabilizing selection on the two sexes. Dismantling of seasonal variation in sex allocation by competition with an introduced bird will be based on decline of the sex that is most exposed to the competition as a nestling or fledgling.

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

Location: Hakalau Forest National Wildlife Refuge, Island of Hawaii.

Methods: Fledglings were captured during June–September from 1987 to 2005, weighed, and measured. Sex was determined by future plumage of survivors and by CHD gene test for non-survivors. Sex was similarly determined for second-year birds captured throughout the year. Age was determined by plumage for males at all ages and for second-year and older females.

Results: The consistency over years of changing sexual dimorphism of fledglings fits the predictions of seasonal variation of sex allocation. In association with food limitation, the sex ratio of young birds became strongly biased towards males, the larger sex, with a significant change in adult sex ratio favouring males in all study sites. Stabilizing selection on male bills, particularly during sub-adult ages, indicates a fitness advantage to females that produce long-lived sons, with adequately sized bills, when food is more abundant. Females that produce sons early in the breeding season also have reduced costs of moult–breeding overlap while the bills of their sons are still growing.

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Conclusion: The Hawaii akepa has seasonal variation in sex allocation as an adaptation to produce sons with adequately sized bills when resources are highest. With food limitation, only females in the best condition early in the breeding season, with less competition with an introduced bird, reproduce successfully, and they produce mainly sons. The adaptation has become a maladaptation in the changed environment, leading to a more male-biased adult sex ratio in all study sites. The shortage of young females will lead to extinction of the bird. Sex allocation theory must be the basis for recovery of this endangered bird.

Keywords: cost of reproduction, Hawaii akepa, *Loxops coccineus coccineus*, seasonality, sex allocation, sex ratio, sexual dimorphism, stabilizing selection.

INTRODUCTION

The ability of birds and other animals to bias the number of sons and daughters through sex allocation is an important issue in evolutionary biology (Charnov, 1982; Frank, 1990; Hardy, 2002). The issue involves individual natural selection on the reproductive effort of focal females or pairs, as well as frequency-dependent selection among all females in the population (Frank, 1990). Because females are the heterogametic sex in birds, biased sex allocation should be facilitated compared with other animals (Komdeur and Pen, 2002), but meta-analysis of primarily temperate birds has revealed little evidence of this (Ewen *et al.*, 2004). Nevertheless, there are diverse circumstances in which bias occurs in birds. These include ecological and demographic conditions that favour producing males and females at different times during the season (Howe, 1977; Dijkstra *et al.*, 1990; Daan *et al.*, 1996), a bias towards more sons in relation to quality of the mate through attractive secondary sexual characters or parental quality (Ellegren *et al.*, 1996; Svensson and Nilsson, 1996; Bensch, 1999; Sheldon *et al.*, 1999; Hasselquist and Kempenaers, 2002), more sons produced by females in good condition (Nager *et al.*, 1999; Whittingham and Dunn, 2000; Whittingham *et al.*, 2002), and bias towards the sex that helps in cooperatively breeding species (Emlen *et al.*, 1986; Griffin *et al.*, 2005), when conditions permit (Komdeur *et al.*, 1997). In addition, food supplementation and diet modification can experimentally alter sex allocation (Arnold *et al.*, 2003; Clout *et al.*, 2002; Castro *et al.*, 2003; Robertson *et al.*, 2006). Both sex ratio and sex allocation in birds have been extensively reviewed (Clutton-Brock, 1986; Sheldon, 1998; Cockburn *et al.*, 2002; Komdeur and Pen, 2002).

Seasonal variation in sex allocation (SVSA) within a single breeding season is the most general condition leading to avian bias in brood sex ratio (Sheldon, 1998; Komdeur and Pen, 2002). Food conditions frequently vary between first and second broods in temperate birds with short breeding seasons (Martin, 1987), thus the ability of parents to rear the more expensive sex may vary either between first and second broods (Whittingham *et al.*, 2002) or between early and late breeders that have single broods (Howe, 1977; Cordero *et al.*, 2001).

Seasonal variation in sex allocation associated with food may be more prevalent in tropical birds. Among these birds, which represent great taxonomic diversity, many species have a single brood within a lengthy breeding season. There can be wet/dry season transitions or possibly random changes in food abundance associated with outbursts of resources (Stutchbury and Morton, 2001). In addition, most tropical birds have clutches of only two eggs (Lack, 1968). Two-egg clutches are noteworthy for sex-ratio studies because they are just as extreme as single-egg clutches (Komdeur *et al.*, 1997). Any modification from an even sex ratio means complete bias for one sex. It should thus be possible to detect biased sex allocation with higher statistical power for most tropical birds.

We here document SVSA in the endangered Hawaii akepa (*Loxops coccineus coccineus*), a Hawaiian honeycreeper (Drepanidiane) with a clutch size of two eggs. We develop a method for inferring the phenomenon in sexually dimorphic species that involves changing sexual dimorphism of fledglings in a skeletal character that grows slowly. We also deal with adaptive hypotheses for the sexual dimorphism and for the sex allocation.

HYPOTHESES AND PREDICTIONS

Inferring seasonal variation of sex allocation

The usual way to document SVSA is through the sex ratio of eggs or nestlings within broods produced at various times during a breeding season. However, most bird species have inaccessible nests, and thus the phenomenon cannot be easily documented this way. Although most studies of growth in birds deal only with nestlings, fledglings continue to grow in mass in many species of birds (O'Connor, 1984; Starck and Ricklefs, 1998). Skeletal characters also continue to grow in fledglings in species where this has been investigated (Badyaev *et al.*, 2001; Freed *et al.*, 2007; Stutchbury and Morton, 2008). For sexually dimorphic species, which include many birds (Amadon, 1959), skeletal growth during the fledgling period can be used to infer SVSA. If one sex is produced mainly during the early portion of the breeding season, it follows that in samples of fledglings containing both sexes, the earlier-produced sex will have had more time to grow that character. This differential amount of time for growth should generate sexual dimorphism in fledglings for that character, while it is still growing, that is greater than that of adults. As growing fledglings approach the asymptotic size of the character, the sexual dimorphism for that character should gradually approach the adult level. This changing dimorphism hypothesis for inferring SVSA is based on the logical consequences of biased brood sex ratio that will be manifested during the fledgling period of sexually dimorphic species. It is also based on allometric growth of males and females, which is supported by comparative growth of dimorphic species (Teather and Weatherhead, 1994). The hypothesis predicts that for dimorphic species with SVSA, sexual dimorphism of fledglings initially exceeds that of adults.

In addition, SVSA can be inferred from changes in the sex ratio of fledglings and young birds in association with an environmental change. Food supplementation experiments have resulted in a biased sex ratio of offspring (Tella, 2001; Clout *et al.*, 2002; Castro *et al.*, 2003; Arnold *et al.*, 2003). Food shortages may also play a role. Such shortages can occur naturally during poor years (Martin, 1987), or be caused by more permanent habitat degradation (Newton, 1998), including competition with introduced species and problems with introduced parasites (Freed *et al.*, 2008a, 2008b). A drastic change in the sex ratio of young birds with a permanent environmental change may reveal SVSA if the food shortage occurs unevenly over the breeding season. One sex may be reared under much worse conditions than before. Nests with that sex may fail at a higher rate or the young produced in those nests may be undernourished and not survive to their second year. The environmental change hypothesis for SVSA predicts that the sex reared during a time of most reduced food abundance will be under-represented in young birds.

Hypotheses for sexual dimorphism

There are several different hypotheses for sexual dimorphism in birds and other animals. Darwin (1874) originally proposed the mating advantage hypothesis, noting that males are usually larger and more pugnacious than females, and these characters could settle contests for access to females. This hypothesis includes both mate choice and mate sequestration (Owens and Hartley, 1998). The mating advantage hypothesis for a species predicts that larger males will have higher fitness. For a set of related species, the hypothesis predicts that the focal species will have a large positive residual in an allometric analysis, indicating that size is larger than expected. Darwin (1874) also proposed the fecundity-advantage hypothesis, noting that larger females can produce more eggs, but this hypothesis is not relevant for most birds (Szekeley *et al.*, 2007). The display-agility hypothesis (Payne, 1984) asserts that the dimorphism is based on increased manoeuvrability of one sex when displaying to the other. This hypothesis predicts that small males have more acrobatic displays that are preferred by female choice (Andersson and Norberg, 1981).

The ecological causation hypothesis for sexual size dimorphism (Shine, 1989) is based on differences in foraging behaviour of the sexes. Many species exhibit differences in niche utilization associated with sexual size dimorphism (Selander, 1966, 1972; Schoener, 1967; Clutton-Brock *et al.*, 1982), and the dimorphism may lead to ecological specialization (Futuyma and Moreno, 1988). It is a very difficult hypothesis to test directly (Shine, 1989), but should not be dismissed (Andersson, 1994; Szekely *et al.*, 2007). A new approach we use here is based on Wilson (1975), who showed for diverse taxa that the size of a trophic appendage is related to the size of food that could be efficiently handled. In comparisons of congeners, the larger species could consume all food items used by the smaller species, but the smaller species could not efficiently handle the largest food items used by the larger species. Wilson (1974) showed that this was also the case for different life stages of a single species. We deal with ecological causation by considering stabilizing selection for bill length of male and female akepa in relation to food requirements.

Hypotheses for seasonal variation of sex allocation

These are derived from more general hypotheses about sex allocation. The assumption of seasonal variation in breeding is based on the condition of females. The Trivers-Willard hypothesis, originally formulated for polygynous animals (Trivers and Willard, 1973), asserts that females in good condition are expected to rear the more expensive sex because they will achieve a marginal increase in fitness from mating success of that sex as a consequence of the marginal increase in quality derived from their care. There are extensions to this hypothesis that focus more generally on life history (Leimar, 1996). Whenever the state of a female and the environment would result in investment increasing the reproductive value of one offspring sex more than the other, females would be favoured to invest more in the sex with greater increase in reproductive value. This extension, which can be termed the reproductive value hypothesis, has been used to associate production of one sex during the season with increased likelihood of that sex reproducing the following year (Dijkstra *et al.*, 1990; Daan *et al.*, 1996). A broad alternative to the Trivers-Willard and reproductive value hypotheses is the cost of reproduction hypothesis (Cockburn *et al.*, 2002). Early-breeding females may reduce the cost of producing the larger sex if food declines seasonally. Also, producing the larger sex earlier may reduce conflicts between parental care and life-history characters such as moulting, which Freed *et al.* (2007) showed occurs during the fledgling period. The cost of reproduction hypothesis has been applied to mammals but not to birds (Cockburn *et al.*, 2002).

The following predictions will be tested in this study. The Trivers-Willard hypothesis predicts that the more expensive sex will have higher fitness from mating success when reared by females in good condition. The reproductive value hypothesis predicts that the larger sex will be more likely to survive to breed if reared by females in good condition. The cost of reproduction hypothesis predicts that most growth of the larger sex will occur before moulting by parents begins. All of these predictions are based on an assumption that early-nesting females are in good condition.

METHODS

Study animal and sites

The Hawaii akepa is a non-territorial 10.5-g insectivorous bird with an annual adult survival of 0.80, juvenile survival of 0.43, a single two-egg clutch size, and a 4-month fledgling period (Lepson and Freed, 1995, 1997). Adult males are slightly but significantly larger than females (Amadon, 1950; Lepson and Freed, 1997). Nesting occurs from March to June [mainly April to May (Lepson and Freed, 1995)], coinciding with a seasonal decline in food extending from January to July (Freed *et al.*, 2007). Fledglings beg and are fed by both parents through September (Hart and Freed, 2003). Without regard to sex, Freed *et al.* (2007) documented that fat levels decline after the nestling period, wing length reaches its asymptote by late June, and bill length reaches its asymptote in August/September after 4 or more months on post-fledging growth. Bill length is thus a suitable slow-growing character for documenting changes in sexual dimorphism of fledglings.

We conducted the study in old-growth ohia/koa (*Metrosideros polymorpha*/*Acacia koa*) forest at Hakalau Forest National Wildlife Refuge on the windward slope of Mauna Kea, Island of Hawaii (Freed, 2001). We uniquely banded akepa captured in aerial mist-nets with a numbered aluminium band and three colour-bands throughout the year from 1987 to 2006, including fledglings during June–September (Freed *et al.*, 2007). We weighed birds to the nearest 0.5 g with a spring scale, and measured bill length (exposed culmen) to the nearest 0.1 mm with callipers, wing length (length of longest flattened primary feather from bend of wing) to the nearest 0.5 mm with a wing ruler, and furcular fat as no fat (0), trace (0.1), not full (1), full (2), and overflowing (3). We sexed 41 of 92 fledglings captured during 1987–1999 by future adult plumage, reproductive characters (cloacal protuberance for males, brood patch for females), or a CHD gene test (Griffiths *et al.*, 1998) from a blood sample. Of these, 17 and 18 were captured in June and July, respectively; the remaining six were captured in August and September. We captured only 16 fledglings after 1999, when the population was non-viable (Freed *et al.*, 2008a). We documented survival of all colour-banded birds by re-sighting through 10 × 42 binoculars as well as recapture in mist-nets. We also captured and measured all species of Hawaiian honeycreepers for allometric studies of sexual dimorphism.

We used several study sites. The long-term site for studies of fledglings was at 1800–1900 m elevation. For documenting change in the adult sex ratio of akepa, we used additional sites at 1770 m and at 1710–1650 m elevations, the former during 1994–1996 and 2004–2006, and the latter during 1994–1998 and 2004–2006. The 1770 m site was located 1.5 km east (downslope) of the long-term site. The 1650 m site was located an additional 1.5 km downslope. The 1710 m site was located 3 km north-northeast of the long-term site (Hart, 2001).

We measured nestling mass, bill length, and wing length from two accessible nests 3 days before fledging at the 1800–1900 m site. These were nests where at least one nestling could be sexed by later recapture.

Baseline study between 1987 and 1999

We established age of fledglings by a positive correlation between wing length and bill length and a negative correlation between each of these variables and fat, during the first month in which fledglings were captured. The expected negative correlation is based on the fact that nestlings have more fat than fledglings, and fledglings lose fat with age (Freed *et al.*, 2007).

We tested the changing dimorphism hypothesis for SVSA by conducting an analysis of variance of bill length, wing length, and mass in models with effects of age (adults, fledglings) and sex. The sex effect indicates sexual dimorphism. The interaction between age and sex tested non-parallel sexual dimorphism between the two age groups. We conducted separate analyses for June fledglings and adults and for July fledglings and adults, only using adult masses between July and February to avoid complications from breeding and adult wing lengths between November and February to avoid complications from moulting and feather wear. Loss of significance of the interaction term between age and sex indicates parallel sexual dimorphism between adults and fledglings. Loss of significance of the age effect indicates full growth. We used a similar model to compare June and July fledglings, where the age effect was replaced by a month effect. Sample sizes were too small in August and September for formal statistical analysis, but we use the values of bill length to show the transition from July fledglings to adults.

We addressed sampling error that could influence sexual dimorphism in several ways. First, because growing fledglings were captured on different days of the month, it is possible that one sex may have been larger because more individuals of that sex were captured later in the month. It is also possible that one sex was captured more frequently during years of better or poorer growth. We thus conducted an analysis of covariance of bill length with day in month as covariate and sex and year of capture as factors, separately for the months of June and July with sufficient samples. We also used a sign test to evaluate how consistently males were larger than females in months of years when both sexes were captured. We documented considerable overlap between the distributions of adult male and female bill lengths (maximum 12.2 and 12.1 mm, minimum 10.6 and 9.0 mm, for males and females, respectively). Therefore, the absence of SVSA could be indicated by months during some years with female fledglings having longer bills than male fledglings.

We estimated sexual dimorphism as male length divided by female length. We compared estimates of sexual dimorphism between sets of years between 1987 and 1999, during which each sex was captured in June or in July, and years in which only one sex was captured in either month. This approach equally weights years for the first set and combines the second set as a single value that can be compared with the values and mean of the first set. This addresses potential uncertainty associated with sampling just one sex during a particular month of a year.

We evaluated the mating advantage hypothesis for sexual dimorphism by comparing the mass of male and female akepa, and by the size and direction of the akepa residual from major axis regression of mass and bill length of the six honeycreeper species on the study site [including the Hawaii creeper (*Oreomystis mana*), Hawaii amakihi (*Hemignathus virens virens*), akiapolaau (*Hemignathus monroi*), iiwi (*Vestiaria coccinea*), and apapane (*Himatione sanguinea*)]. This is the recommended procedure for evaluating sexual dimorphism (Ranta *et al.*, 1994). We dealt with the display/agility hypothesis by comparing the mass of akepa males and females, and the ecological causation hypothesis by documenting stabilizing selection of bill length in the two sexes (see below) in relation to energetic male activity and breeding.

We tested the reproductive value hypothesis for SVSA by documenting stabilizing selection in reproductively mature males and females. We compared survival in relation to bill length, using second-year males and females, third-year males initially captured as third-year males, second-year males and females that survived at least to their third year, and unbanded fourth-year or older males and females that were at least 3 years old. This ensured that only fully grown bill measurements were used. We determined survival by recapture or re-sighting at least one year after initial capture of the age used in the analysis, and used analysis of variance to compare bill lengths of survivors and non-survivors with respect to sex, including the interaction between sex and survival. We evaluated the Trivers-Willard hypothesis by considering the stabilizing selection in relation to opportunities for male mating success. We also compared the age and state of female akepa that paired with sub-adult males to determine if older females avoid sub-adult males.

We addressed the cost of reproduction hypothesis by assessing moult–breeding overlap during the fledgling period in relation to fledgling bill growth during June and July. Data on the moult of primary flight feathers were from Freed *et al.* (2007).

Changes in bill length and sex ratio of young birds beginning in 2000

The environmental change beginning in 2000 was food limitation associated with competition from an introduced bird, the Japanese white-eye (*Zosterops japonicus*), and an explosive increase in chewing lice (Pthiraptera) that increased food requirements (Freed *et al.*, 2008a, 2008b). No fledglings were captured during 2000–2003 (Freed *et al.*, 2008a). The sex of fledglings captured in 2004–2005 could not be determined because the US Fish and Wildlife Service prohibited us from taking blood samples for CHD gene testing and only one fledgling survived to be sexed. We thus compared the bill length of fledglings captured during 2004–2005 with those captured before 2000 without regard to sex, using an analysis of variance with month and time period as factors, together with the interaction.

We documented the sex ratio of young birds as proportion of females, using fledglings, juveniles, and unbanded second-year birds that could be sexed. We aged juveniles and second-year birds (January–June) by plumage and moult limits of greater wing coverts. Moult limits represent a point where two feather generations meet in the feather tract (Jenni and Winkler, 1994). We sexed fledglings and juveniles before 2000, and some juveniles after 2000 as described above. For second-year birds, we determined sex by reproductive characters, plumage (males have dull orange feathers in eye-ring and shoulder, females have dull yellow feathers in eye-ring), and CHD molecular sexing. We used a test of proportions to compare the proportion of females in young birds between 1987–1999 and 2000–2006.

We documented the adult sex ratio as the proportion of males, using the number of individual second-year and older birds of each sex captured. We used all adult birds, and determined sex by plumage, reproductive characters, and/or morphometrics. For the 1900 m and 1800 m study sites used within 1987–1999 and 2000–2006, we used adult birds captured between 1987 and 1999, and adult birds initially captured between 2000 and 2006, to calculate the sex ratio for each time period. The 1770 m sites were sufficiently isolated in time that all adult akepa were included within each time period. We tested differences in adult sex ratio between the two time periods in the four study areas using a paired *t*-test, which evaluated the consistency of differences.

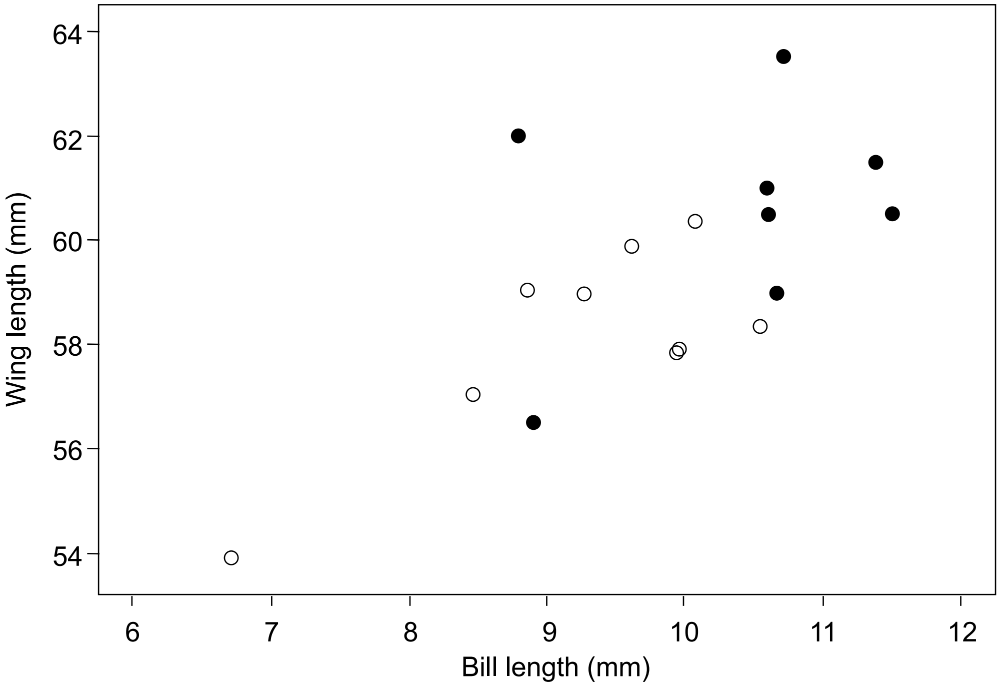

Fig. 1. Correlation between wing length and bill length of akepa fledglings captured during the month of June between 1987 and 1999. Solid circles represent males, whereas open circles represent females.

RESULTS

Seasonal variation in sex allocation

Evidence for seasonal variation in sex allocation 1987–1999

April was the earliest month when fledglings were observed, but June was the first month during which fledglings were captured in mist-nets. Fledglings captured during June would be a mixture of birds that fledged during April, May, and June. Wing length and bill length of June fledglings were correlated ($r = 0.69$, $t_{15} = 3.7$, $P = 0.002$) (Fig. 1). This correlation reflects expected diversity in age, with older birds being larger. Fat scores were not significantly correlated with either wing or bill length (wing: $r = -0.18$, $t_{15} = -0.73$, $P = 0.47$; bill: $r = -0.31$, $t_{15} = -1.28$, $P = 0.22$), but the signs of the correlations were negative, associating smaller birds with the higher fat scores of nestlings. The distribution of bill and wing lengths shows that 75% of males have longer bills than all females, and 50% of males have longer wings than all females (Fig. 1). If there was no difference in age between the sexes, and thus no seasonal variation in sex allocation, the distribution of these characters would be expected to be random with respect to sex. They are not, because there are 12,376 ways of choosing six birds with the longest bills out of the sample of 17, and 28 ways of choosing six males out of eight in the sample. The probability, by chance, of males being the six birds with longest bills is only 0.002 (28/12,376).

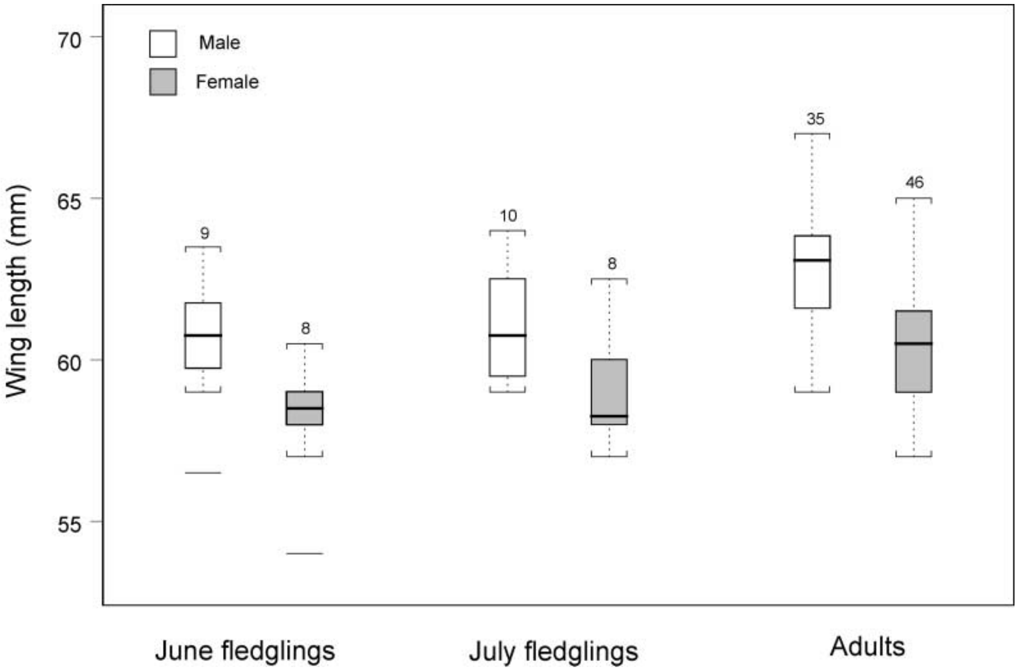

Fig. 2. Box plots of wing length of fledglings of different age and of adult birds, showing no difference in sexual dimorphism of fledglings of different age and between fledglings and adults. The difference between young and adult wing lengths is the first documentation of this for both sexes of a tropical bird. Open boxes represent males, filled boxes represent females. The horizontal line is the median, the boxes represent the inter-quartile range, the caps represent up to 1.5 times the inter-quartile range from the median, and the lines represent outliers. Sample sizes are above the caps.

June fledglings had reached their asymptotic wing length. They had shorter wings than adults, but with no difference in sexual dimorphism (ANOVA: $F_{3,94} = 24.67$; age effect, $P < 0.0001$; sex effect, $P < 0.0001$; age × sex interaction, $P = 0.97$) (Fig. 2). Fledgling wing length did not change significantly from June to July (ANOVA: $F_{3,31} = 4.05$; month effect, $P = 0.345$; sex effect, $P = 0.015$; interaction between month and sex, $P = 0.92$) (Fig. 2), indicating that asymptotic length is reached in both sexes by late June. Neither sex achieves adult size until the feathers are replaced by moult during the second year.

In contrast, both male and female June fledglings had shorter bills than comparable adults, but June fledglings had greater sexual dimorphism in bill length than do adults (ANOVA: $F_{3,157} = 32.87$; age effect, $P < 0.0001$; sex effect, $P = 0.002$; age × sex interaction, $P = 0.006$) (Fig. 3). Sexual dimorphism of fledglings, without regard to year, was 1.12, almost 10% higher than the 1.02 estimated from adults. Bill length was not related to day of capture within June or to year of capture (ANCOVA: $F_{7,9} = 2.04$; day of capture, $P = 0.78$; year, $P = 0.12$).

Fledgling bills of both sexes increased in length between June and July (ANOVA: $F_{3,31} = 7.88$; month effect, $P = 0.0003$) (Fig. 3). The extent of sexual dimorphism decreased as the difference in bill length between July fledglings and adults became marginally significant (ANOVA: $F_{3,158} = 3.02$, $P = 0.03$; age effect, $P = 0.089$), and the interaction term between age and sex lost significance ($P = 0.916$). Sexual dimorphism of July fledglings,

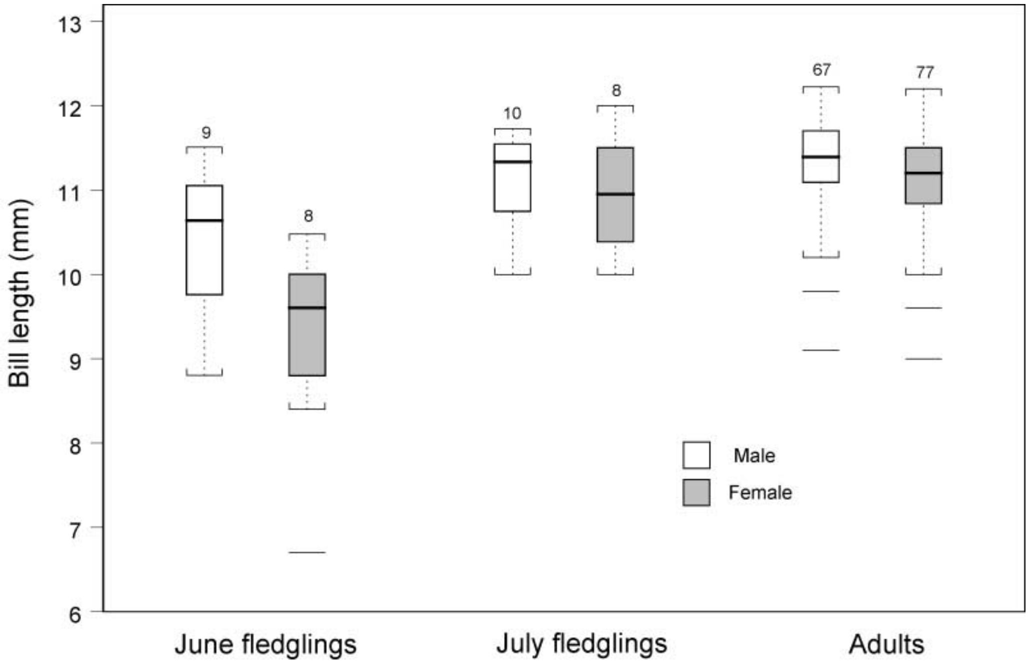

Fig. 3. Box plots of bill length of fledglings of different age and of adult birds, showing that sexual dimorphism is greater in younger fledglings and changes smoothly to adult dimorphism after July. Open boxes represent males, filled boxes represent females. See text for August and September fledglings. Box plot features as in Fig. 2. Sample sizes are above the caps.

without respect to year, was identical to that of adults (1.02). The increase in growth for both sexes between June and July, and reduction in sexual dimorphism, indicate that female bills grew faster than male bills between June and July. Bill length was not related to day of capture within July (ANCOVA: $F_{7,10} = 4.44$, $P = 0.02$; day of capture, $P = 0.27$), but there was a significant effect of year for July ($P = 0.01$), elaborated below. Fledglings of both sexes had shorter bills in 1987 than in any other year, but still showed the higher dimorphism.

The estimate of sexual dimorphism in bill length of June fledglings when years were considered separately was higher than for adults but lower than the 1.12 estimated without respect to year (Table 1). All three estimates were higher than the adult dimorphism of 1.02, including years when June fledglings differed in bill length (Table 1). The same sexual dimorphism value of 1.04 was obtained by averaging years when both sexes were captured in June and by combining years with only one or the other sex captured in June.

The estimate of sexual dimorphism in bill length of July fledglings when years were considered separately was also higher than for adults. There were 5 years during which fledglings of both sexes were captured during July (Table 2), and only one year with only one sex captured. The average sexual dimorphism from equal weighting of years was 1.03, intermediate in value between the 1.04 of June fledglings and the 1.02 of adults. With June included, there were 7 years in which both sexes were captured in the same month. In each of these, male fledglings had longer bills than female fledglings. The observed pattern of sexual dimorphism is unlikely to be due to sampling error (sign test, $P = 0.001$).

Table 1. Estimates of sexual dimorphism of bill length from different groups of June fledglings[a]

	Female bill	Male bill	Sexual dimorphism
Years: both sexes			
1988	10.14 (1)	10.72 (1)	1.06
1999	8.54 (5)	8.80 (1)	1.03
mean	9.34	9.76	1.04
Years: one sex			
1987	10.00 (2)		
1989	10.48 (1)		
1991		10.74 (4)	
1994		10.60 (1)	
1996		10.60 (1)	
mean	10.24	10.65	1.04

[a] Values within years are means with sample size in parentheses.

Table 2. Estimates of sexual dimorphism of bill length from different groups of July fledglings[a]

Years: both sexes	Female bill	Male bill	Sexual dimorphism
1987	10.00 (1)	10.25 (2)	1.03
1989	11.29 (2)	11.49 (3)	1.02
1990	10.39 (1)	11.29 (1)	1.09
1991	11.50 (2)	11.73 (1)	1.02
1996	10.90 (1)	11.00 (1)	1.01
mean	10.82	11.15	1.03

[a] Values within years are means with sample size in parentheses.

Fledgling bills continued to grow after July. No known female fledglings were captured in September and no known male fledglings were captured in August. For females, the progression of bill length (mm) from July to adult was 10.82 in July, 11.29 in August ($n = 4$), and 11.14 in adults, suggesting that bill growth may stop in August. For males, the progression was 11.12 in July, 11.28 in September ($n = 2$), and 11.37 in adults, suggesting that bill growth may extend past September. The changes in bill length during these months further decrease the sexual dimorphism from the 1.03 of July towards the 1.02 of adults.

Differences in the size of wings and bills of male and female fledglings were not associated with differences in mass (Fig. 4). Comparison of June and July fledglings (ANOVA: $F_{3,29} = 0.93$, $P = 0.44$) showed no effect of month ($P = 0.191$), sex ($P = 0.682$), or the interaction ($P = 0.373$). Comparison of adult mass with fledgling mass (ANOVA: $F_{3,180} = 0.97$, $P = 0.41$) indicated no age effect ($P = 0.86$), sex effect ($P = 0.095$), or interaction ($P = 0.812$). There was also no difference between the sexes in fat scores during June and July (ANOVA: $F_{2,32} = 0.16$, $P = 0.86$; month effect, $P = 0.76$; sex effect, $P = 0.67$).

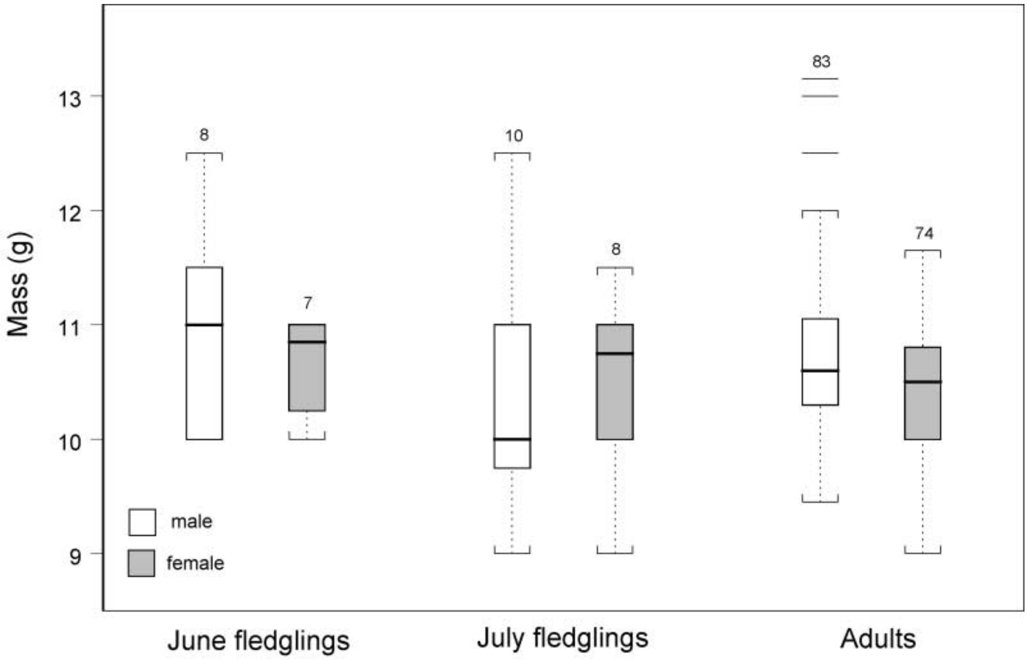

Fig. 4. Box plots of mass of fledglings of different age and of adult birds, showing no sexual dimorphism in adults or fledglings. Open boxes represent males, filled boxes represent females. Box plot features as in Fig. 2. Sample sizes are above the caps or highest outlier.

Evidence for seasonal variation of sex allocation from 2000 to 2005

As shown in Fig. 5, fledglings captured after 1999 had shorter bills than fledglings captured before 2000 (ANOVA: month, $P < 0.0001$; time period, $P = 0.0002$; interaction, $P = 0.0009$). This was associated with lower mass (Freed *et al.*, 2008a), indicating stunted growth. Based on female brood patches, the introduced white-eye breeding season extended from January to June, while the akepa breeding season extended from March to June (Freed *et al.*, 2008a). From 2000 to 2005, white-eye captures increased during the akepa nesting season, in association with increased captures of white-eye fledglings (Fig. 6). The exposure to competition from breeding white-eye would thus be greater for akepa attempting to nest during the latter half of the breeding season. Approximately 50% of nesting females would be affected (Fig. 6).

All samples used for the composite sex ratio of young birds were consistent in showing more females than males during 1987–1999, before the white-eye increase (Table 3). The majority of young birds during 2000–2006 were second-year birds that could be sexed by plumage. The sex ratio of young birds, as a proportion of females, changed drastically from 0.57 to 0.13 (test of proportions, $P = 0.0001$). Females, despite being the smaller sex, were affected more by the environmental change than males.

These changes in sex ratio of young birds were reflected in a change in sex ratio of all adult birds. The adult sex ratio became more male biased in all study sites at different elevation (one-sided paired *t*-test, $t_3 = 2.77$, $P = 0.03$) (Fig. 7). The ratios were similarly modified at all sites, indicating that the problem generating this change was uniformly widespread.

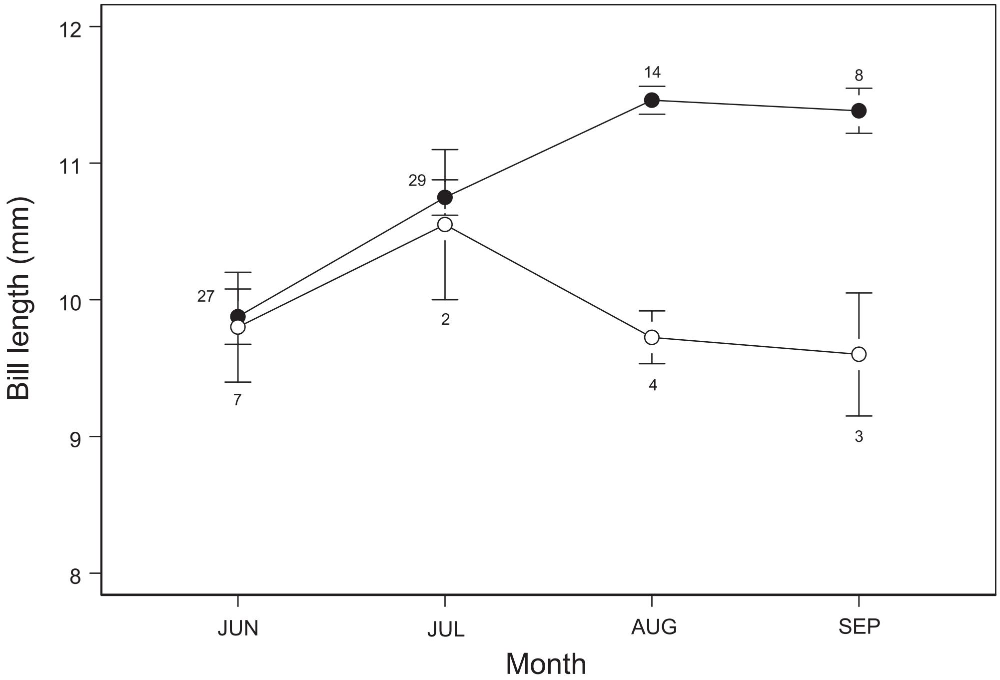

Fig. 5. Bill length of fledgling akepa throughout the fledgling period. Solid circles represent all fledglings between 1987 and 1999, including those of unknown sex. Open circles represent all fledglings between 2000 and 2005. Bill length does not decline for individual birds, so the precipitous decline during August and September in 2000–2005 represents individuals with greater stunted growth than those from June and July. Only one fledgling from 2000–2005 was known to survive.

Adaptive hypotheses for sexual dimorphism and seasonal variation of sex allocation

Sexual dimorphism

The minor sexual dimorphism of the akepa in bill and wing length does not include mass (Fig. 4). In addition, the akepa is the least sexually dimorphic of the six species of honeycreepers in bill length and mass (Figs. 8a, b), with substantial overlap between males and females in these characters, as well as wing (Figs. 2–4). While the slope of each major axis is significantly greater than 1, supporting Rensch's rule for allometry in sexual dimorphism (Rensch, 1959), there is little support for the mating advantage hypothesis because the akepa falls almost on the major axis for bill and just below it for mass (Fig. 8). Male akepa are not smaller than female akepa, and also have longer tail feathers and tarsus than females (Lepson and Freed, 1997), indicating little support for the agility-display hypothesis.

There is stabilizing selection on bill length of males and females that maintains the sexual dimorphism (Fig. 9). The analysis of variance of bill length with sex, age, survival, and all two-way interactions was significant ($F_{9,180} = 2.12$, $P = 0.03$), but only the sex effect and the sex × survival effects were significant (sex, $P = 0.006$; sex × survival, $P = 0.012$; age, $P = 0.512$; survival, $P = 0.476$; sex × age, $P = 0.603$; age × survival, $P = 0.373$). The sex × survival interaction term means that the sexes should be analysed separately. For males,

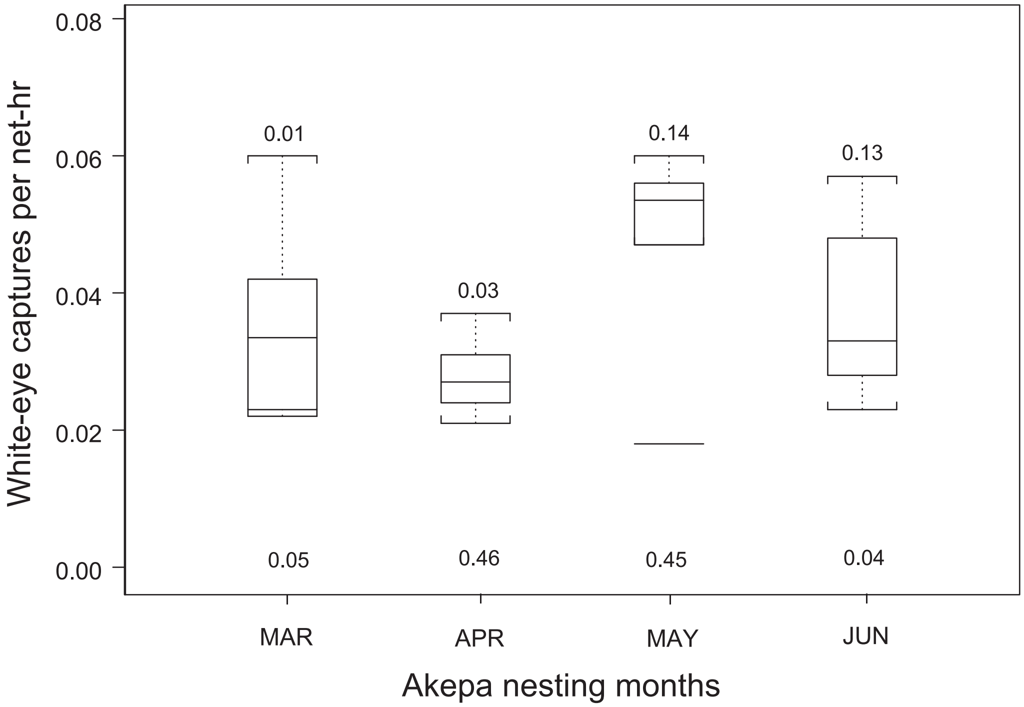

Fig. 6. Japanese white-eye captures during the akepa nesting season. Box plot features as in Fig. 2. Each plot is based on 6 years from 2000 to 2005. Numbers above the plots indicate the proportion of white-eyes that are fledglings. Numbers above the months are proportion of akepa nests initiated based on 74 nests from Lepson and Freed (1995). Akepa nesting in May and June compete with more white-eyes than those nesting earlier (Mann-Whitney test, $P = 0.042$).

Table 3. Assessment of sex ratio of young Hawaii akepa

Group of birds[a]	Sexing technique	No. females	No. males	Females/total
1987–1999				
HY birds	Survive into adults	11	11	0.50
HY birds	CHD gene	9	5	0.64
SY birds	Reproduction/plumage	8	7	0.53
SY birds	CHD gene	4	1	0.80
Overall		32	24	0.57
2000–2006				
HY birds	Survive into adults	0	1	0.00
HY birds	CHD gene	1	1	0.50
SY birds	Reproduction/plumage	3	25	0.11
Overall		4	27	0.13

[a] HY = hatch year, SY = second year.

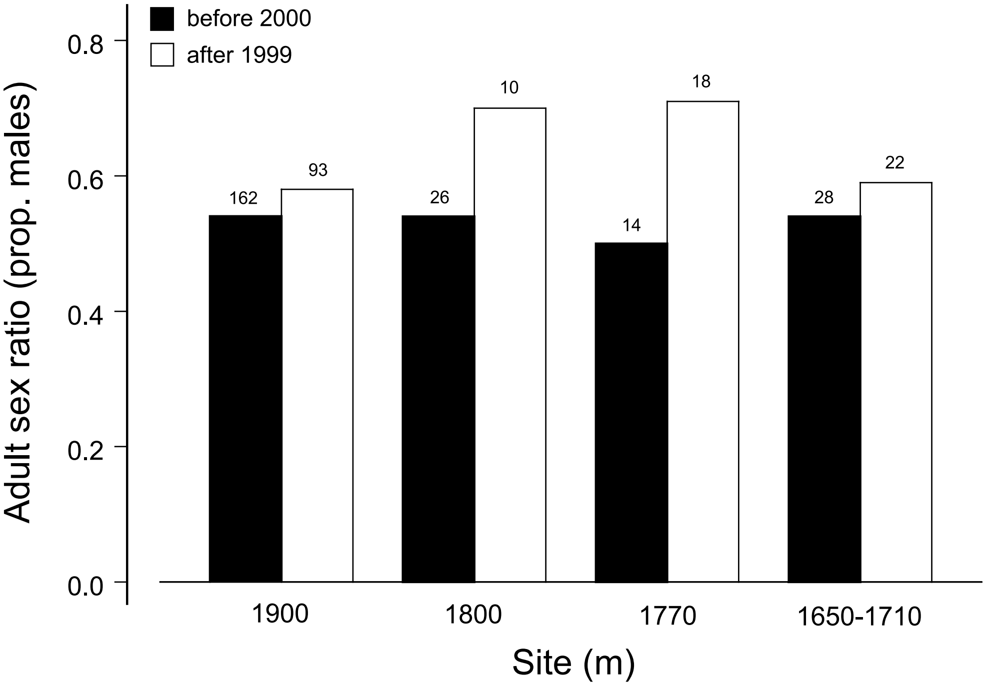

Fig. 7. Changes in adult sex ratio in four study sites at different elevations. Sample sizes indicate the total number of individual males and females, second year or older, within each time period. The 1900, 1800, and 1770 m sites were in the same or similar locations during both time periods. The matched 1710 and 1650 m sites were in different locations. The 1650 m site during 2004–2006 was considered viable because akepa fledglings, without regard to sex, had high mass as an indicator of quality (Medeiros and Freed, 2009). However, the adult sex ratio there matched the other sites used after 2000 in showing an increased biased towards males. This indicates that the fledglings were likely males and that the initial problem of food limitation from white-eyes may be dismantling the seasonal variation in sex allocation adaptation.

there was a significant survival effect ($P = 0.036$), but no age ($P = 0.336$) or age × survival ($P = 0.494$) effect, favouring males with longer bills. For females, neither the age nor survival effect or interaction were significant ($P = 0.835$, 0.162, 0.717, respectively), but in all three age classes, surviving females tended to have shorter bills. Stabilizing selection is thus focused mainly on male bill length beginning with their second year and extending over their lives. Because second-year males rarely attempt to breed, the stabilizing selection begins before breeding. This pattern is consistent with the ecological causation hypothesis for sexual dimorphism.

Seasonal variation in sex allocation

The Trivers-Willard hypothesis does not apply to male offspring during their second and third years. No second-year male, even when paired with a female, has been observed with a fledgling, so there is no mating advantage from breeding during the second year. Based on the association of over 160 colour-banded males and females over a 14-year period, these birds form life-long pair bonds. The three documented cases of mate change occurred with females paired with third-year male-like sub-adults.

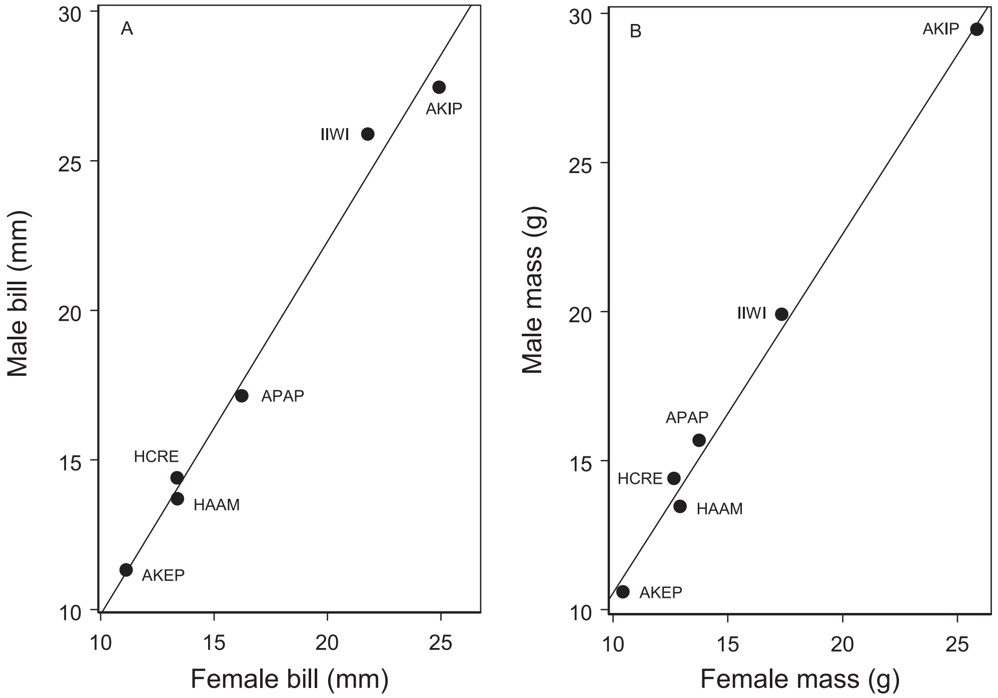

Fig. 8. Allometric analysis of sexual dimorphism (A, bill length; B, mass) of six species of Hawaiian honeycreepers in the study site. The line shown in each panel is the major axis from a Model II major axis regression, used because both female and male characters are variable. The slope of each major axis is significantly greater than one. AKEP = Hawaii akepa, HCRE = Hawaii creeper, HAAM = Hawaii amakihi, APAP = apapane, IIWI = iiwi, AKIP = akiapolaau.

Pairing patterns are consistent with female preference of adult males over sub-adults. Males in male-like sub-adult plumage have the same nesting success as adult males (Lepson and Freed, 1995), yet have been paired only with females in the two dullest of five colour classes. Females in these dull classes are mainly young females (Lepson, 1996). This is not due to chance ($P = 0.004$, based on 0.39 of females in these categories and 6 male-like sub-adults). Adult males in bright orange plumage have been paired with females in all colour classes, so the only correlation between plumage of mates is that of male-like sub-adults and dull females.

The reproductive value hypothesis is supported by the stabilizing selection on bill length of males since males must survive their sub-adult years (Fig. 9) to breed during their potentially long life with older and more colourful females. The cost of reproduction hypothesis is supported by the association of adults moulting at least six of nine primary flight feathers during June and July (Freed *et al.*, 2007), while fledgling bills are still growing (Fig. 3).

DISCUSSION

The Hawaii akepa has sexual dimorphism so slight that it is an order of magnitude lower than that of raptors (Newton, 1979; Korpimaki *et al.*, 2000) and large passerines (Howe, 1977) in which seasonal variation of sex allocation was documented. The akepa has greater sexual

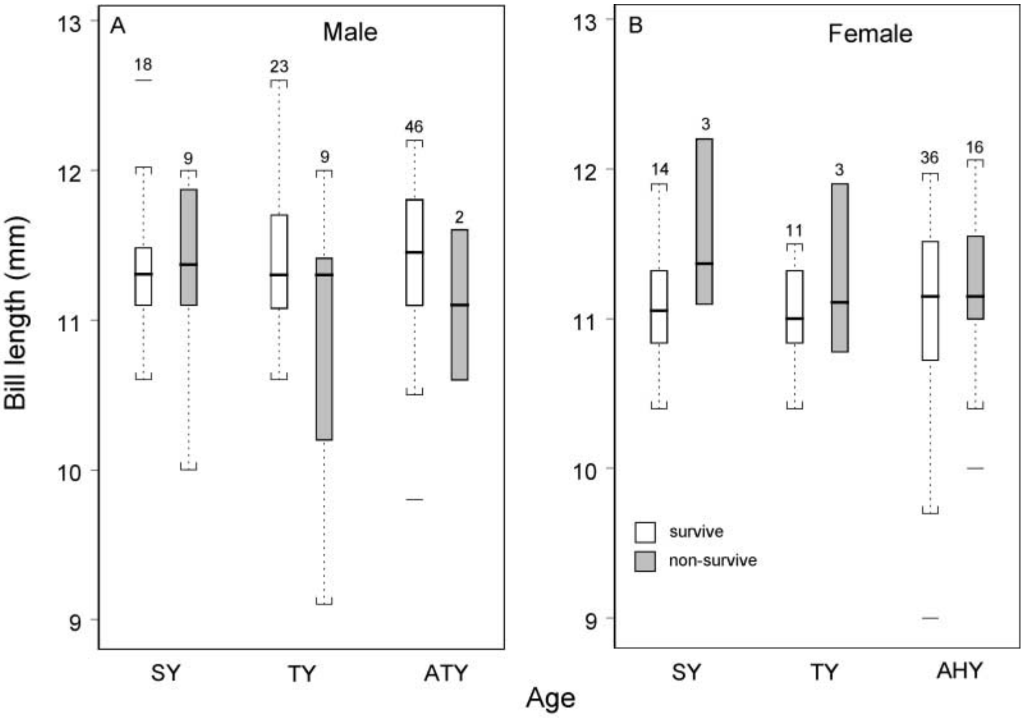

Fig. 9. Box plots showing stabilizing selection of bill length of male (A) and female (B) akepa. Open boxes represent survivors, whereas filled boxes represent non-survivors. Box plot features as in Fig. 2, with sample sizes indicated. SY = second year, TY = third year, ATY = after third year, AHY = after hatch year. ATY males are those in full adult orange plumage. AHY females might include some SY or TY birds, but the SY and TY female age classes represent pure ages. Means for survivors and non-survivors are: SY males, 11.38/11.26; TY males, 11.37/10.87; ATY males, 11.43/11.10; SY females, 11.11/11.56; TY females, 11.07/11.26; AHY females, 11.05/11.19.

dimorphism of bill length in fledglings than in adults, and the dimorphism smoothly decreases over the fledgling period to reach the adult level. The largest difference in June is a characteristic feature of bill growth during the fledgling period over a 13-year study despite annual variation in food (Freed *et al.*, 2007). This pattern is predicted by the changing dimorphism hypothesis for SVSA. Stabilizing selection maintains the sexual dimorphism that pertains to adaptive hypotheses for sexual dimorphism and SVSA. The change in sex ratio of young birds following the environmental change indicates that the smaller sex became rarer than the larger sex, and contributed to a widespread more male-biased adult sex ratio. Here we deal with the many issues raised by these results for sexual dimorphism and SVSA.

Changing dimorphism and changing environment hypotheses

The change in sex ratio of young birds strongly supports the changing environment hypothesis for SVSA. The increase in an introduced bird within a native bird community has resulted in food limitation for every native species (Freed *et al.*, 2008a). Regardless of how SVSA might be adaptive (discussed below), food conditions beginning in 2000 were different than those under which the character evolved, as indicated by the shorter bills of fledglings documented here, as well as lower nestling mass, breeding success, and fledgling mass (Freed *et al.*, 2008a). Akepa nesting during the last 2 months of the breeding season were exposed to more white-eyes than those nesting during the first 2 months. The seasonal decline in food from January to July, which formerly occurred during both good and poor food years before the increase in white-eye (Freed *et al.*, 2007), would be steeper now. Food would be lowered for all females, but more so for later nesting females.

The rarity of young female akepa, temporally associated with the white-eye increase, is consistent with SVSA and no other compelling reason. Early-nesting females are doing what they evolved to do – produce sons, even though fledglings were generally underweight and had shorter bills. Later-nesting females, evolved to produce daughters, are more food limited and are foregoing breeding, failing to fledge their young, or producing stunted young that do not survive. It is difficult to imagine any other reason why young females, with shorter bills and shorter wings than young males, have become rarer with food limitation. If the problem was simply insufficient food, then larger males would be expected to suffer as much as or more than smaller females. The timing of the change in sex ratio of young birds is precise relative to the environmental change, and precise relative to the breeding season of the white-eyes in relation to that of the akepa.

Support for the environmental change hypothesis implies that changing fledgling dimorphism reveals SVSA. The change in fledgling dimorphism between June and July must reflect different growth rates between males and females measured at the same time, but at different ages. Progression of bill growth is known in fringillid finches (Bjorklund, 1994), within which Hawaiian honeycreepers are a sub-family, and in cardueline finches (Badyaev *et al.*, 2001), within which honeycreepers are a distinct clade (James, 2004). Badyaev *et al.* (2001) determined for both sexes of house finches (*Carpodacus mexicanus*), a carduline finch without SVSA, that there is a rapid phase of bill growth followed by a prolonged slower phase. They also determined that male bills grow for a longer period of time than female bills. If male akepa come from earlier nests, they would have achieved the rapid phase of bill growth before females. Females from later nests would be in their more rapid phase of bill growth between June and July while males were progressing in their slow phase at that time. The sample of August females and September males indicates that male bills may grow for a longer period of time, as in other cardueline finches. The changes in sexual dimorphism in fledgling akepa are explained by the cardueline pattern of bill growth, where in the akepa the growth pattern of males is shifted relative to that of females simply because males are older.

Interpreting the pattern of bill growth requires incorporating the seasonal decline in food. Freed *et al.* (2007) showed that food declines throughout the akepa nesting season and during the first 2 months of the fledgling period. Nestlings of either sex from early nests should have a growth advantage. Female nestlings grow bills faster than male nestlings in the related house finch (Badyaev *et al.*, 2001). However, if females were also produced in early nests, they should have grown faster perhaps both for this reason as well as greater food availability. The faster growth of female bills relative to those of males between June and July is difficult to comprehend if females were as likely as males to come from early nests. In addition, more small male fledglings would be expected in June if males were produced throughout the season, and the growth between June and July should then have been more similar to that of females.

The changing dimorphism hypothesis for SVSA for the akepa may apply widely to tropical birds. The akepa appears to retain an ancestral pattern of bill growth, but extended almost three times as long as in a temperate relative. Female and male akepa grow bills for 90–120 days, entirely within the fledgling period while being fed by parents (Hart and Freed, 2003). With more data, it will be possible to determine if male bills continue to grow past the termination of parental care in September. In contrast, house finch females and males grow bills for 11 days during the fledgling period and another 18–33 days as juveniles [44 days for males (Badyaev *et al.*, 2001)]. This is the first comparison of complete growth of a skeletal character of a tropical and temperate bird from the same taxonomic sub-family. If this result is general (Stutchbury and Morton, 2008), then skeletal growth throughout the lengthy fledgling period of tropical birds may be an important aspect of their life history involving extended parental care. The changing sexual dimorphism hypothesis may then be especially useful for investigating SVSA in tropical birds with inaccessible nests.

Issues associated with the changing sexual dimorphism hypothesis when not supported by an environmental change include differential predation and differential mortality of fledglings by sex (see supplementary material online at: http://evolutionary-ecology.com/data/2347supplement.pdf).

Adaptive hypotheses

Sexual dimorphsim

The agility-display and fecundity hypotheses for sexual dimorphism in birds do not apply to the akepa. The akepa has a two-egg clutch typical of most tropical birds, and males are larger than females, contradicting the fecundity hypothesis. Male akepa certainly engage in displays, but these are not acrobatic. They engage in arboreal displays in which males take turns flying out from a branch while singing, and then simply turn around to return to the same branch (Lepson and Freed, 1995). They also engage in chases that can result in aerial displays where many males chase each other perhaps 100 m or higher into the air above the canopy (Lepson and Freed, 1995). Females are not part of aerial displays, but witness the arboreal displays, which can end with copulation. These non-acrobatic displays contradict the agility-display hypothesis, which usually requires males to be smaller than females.

The mating advantage hypothesis may also not apply. The akepa is strongly sexually dichromatic, is not territorial, and male competition for females involves physical and behavioural dominance for 6 months prior to breeding (Lepson and Freed, 1995). However, there is no sexual dimorphism in mass, which is generally associated with this hypothesis in birds (Szekely *et al.*, 2007). The fact that stabilizing selection is operating on second-year males who do not engage in fights, and third-year males that are less attractive to females, suggests that bill sexual dimorphism is a trophic character used for feeding rather than a character used in mate competition or choice. Mate choice is based on plumage, given the avoidance of third-year males with sub-adult plumage by older and more colourful females, and on behaviour. The low level of sexual dimorphism in bill length, with substantial overlap between the sexes, is also not consistent with female choice of males based on bill length.

There is more support for the ecological causation hypothesis for sexual dimorphism in the akepa. Previous studies of ecologically based sexual dimorphism emphasize niche differentiation between males and females (Selander, 1966, 1972; Schoener, 1967; Clutton-Brock *et al.*, 1982;

Temeles and Kress, 2003), although Shine (1989) argues that there may be more subtle differences associated with dimorphism in trophic structures that are not as obvious as foraging height or substrate. Based on Wilson (1975), male akepa with longer bills are expected to consume all prey sizes used by females as well as larger prey sizes that females cannot consume efficiently. Large prey sizes may be associated with higher metabolism. Studies in other bird species show that testosterone in dominant individuals leads to a higher basal metabolic rate (Buchanan *et al.*, 2001). Higher basal metabolism, as well as higher exercise metabolism from male competition, requires more food. Male tropical house wrens (*Troglyodytes aedon*) in Panama, where both sexes are territorial (Freed, 1987, 1991), have slightly, but not significantly, higher metabolism than females (Tieleman *et al.*, 2006). Greater food requirements of males to fuel their higher metabolism may be the general basis of ecological sexual dimorphism in species with minor dimorphism in trophic structures.

Male akepa are likely to have greater food requirements than female akepa. Together with biochemical constraints for synthesizing and sequestering carotenoid pigments, males do everything that females do except lay eggs and incubate. They are dominant over other males rather than territorial, and mate competition extends over a 6-month period from September through March (Lepson and Freed, 1995). This competition includes physical combat and strenuous arboreal and aerial group displays. This contrasts with elevated female energetic requirements for breeding that extend for one month during March–June, which males subsidize by feeding females for several months before nesting begins, during egg-laying, and during incubation (Lepson and Freed, 1997). Males also feed nestlings and fledglings. The ohia canopy where both sexes forage contains caterpillars, spiders, psochids, psychllids, and delphacids (Freed *et al.*, 2007). These are prey taxa that vary in size where slight differences in bill length may affect efficiency of handling. Further work is required to determine if males consume larger prey than females, and if the size of preferred prey is related to bill size of individual birds.

The hypothesis that minor sexual dimorphism in bill length in birds may be based on the acquisition of food to fuel the higher energy demands of males has so far not been addressed in studies of avian sexual dimorphism (Szekely *et al.*, 2007). Comparative studies have focused mainly on temperate birds and on parental care before fledging (Promislow *et al.*, 1992; Owens and Bennett, 1994). Owens and Bennett (1994) showed that the effect of dimorphism on survival was concentrated on nestlings and juveniles, and Kalmbach and Benito (2007) showed that the larger sex suffered disproportionately. Our study, using a bird with weak sexual dimorphism in body size, shows that nestling or fledgling females suffered more because of the timing of food limitation within the season, but mortality based on bill length was concentrated on sub-adult males, and continued into adult males. Longer bills may enable males to compete for mates, feed mates, and feed offspring as well as themselves more efficiently. There is nothing particularly unusual about akepa male behaviour that limits the generality of the energetics aspect of the ecological hypothesis for the significance of minor sexual dimorphism in birds.

Seasonal variation in sex allocation

All adaptive hypotheses assume that females in better condition rear the larger sex. Early nesting females are likely those in excellent condition (Price *et al.*, 1988). For akepa, these are females who get into breeding condition while the air temperature is colder (Freed *et al.*, 2005), but more food is available (Freed *et al.*, 2007). Later nesting females rear more daughters with warmer air temperature, but less available food. As a species with small body size, there is a trade-off between food and heat loss. Akepa females must be in good condition to successfully nest early while it is colder, especially because the night is longer by approximately 1.3 h in March than in June (Nullet and Sanderson, 1993). This represents a 10% reduction in time during which they can feed, even though food is more abundant, and 10% longer fasting during the colder night.

Survival to adulthood pertains to both the Trivers-Willard and reproductive value hypotheses. Juvenile survival of akepa fledglings was strongly based on mass, but not bill length (Medeiros and Freed, 2009). Surviving male fledglings are then subjected to stabilizing selection on bill length during their second and third year. During the second year, this selection occurs with virtually no breeding and with no documented breeding success. The selection occurs during the third year when breeding males are paired with only a subset of younger and less colourful females. These males have the same nesting success as older males in adult plumage (Lepson and Freed, 1995). However, stabilizing selection on bill length during the third year is stronger than that during the second year because third-year males have lower survival than second-year males (0.59 vs. 0.80) and adult males (also 0.80) (Lepson and Freed, 1995). The lower survival also means that adult males have higher reproductive value than third-year males. This implies that the reproductive value hypothesis is sufficient to account for SVSA. Sons with adequate bill length may have a long reproductive life span.

The reproductive value hypothesis deals with the marginal change in reproductive value of each sex when reared by high-quality females (Leimar, 1996; Frank, 1998). This is a within-brood comparison that does not pertain to biased sex allocation in broods with two young because both young will be the same sex. However, a relevant comparison could be made between females that bias their allocation and other females that do not bias their allocation during the early nesting months with greater food. Second-year females can breed successfully (Lepson and Freed, 1997), so it is possible that daughters produced by females in good condition are the ones that breed successfully during the second year. However, the stabilizing selection suggests that daughters with long bills may not have as long a life span, whereas sons with long bills are likely to have a long reproductive life span.

The Trivers-Willard hypothesis still might pertain to adult akepa in full orange plumage. At that time, sons in the best condition, because they have adequately sized bills, might provide higher fitness for their mothers. The brilliant orange plumage implies extra-pair copulations (Bennett and Owens, 2002), and we have observed groups of orange males displaying around females in their fertile period. While bills are not a character directly involved in female choice, males with appropriately sized bills may be more energetic and attractive to females because adult male plumage is almost invariant. Very detailed observations of male display in relation to bill size and copulatory success are necessary to determine if the Trivers-Willard hypothesis applies to adult males that survive the stabilizing selection.

Stabilizing selection on male bills during the two sub-adult years may actually select for the SVSA. Lower fitness may be concentrated on the sons produced later in the breeding season with shorter bills that have survived up to this point. If so, this would be a case of delayed manifestation of problems during early development (Lindstrom, 1999; Metcalfe and Monaghan, 2001). Male mortality, particularly in third-year males, may select against females producing males during months with lower food. It is also relevant that the stronger selection on third-year males occurs in the year that they first nest successfully and engage in displays. Their higher mortality from shorter bills may be associated with an inability to support their higher exercise metabolism associated with mating and breeding. The relevant data to link sexual dimorphism and SVSA would be the fledging date of males that survive to adulthood 3 years later. A much larger sample size of fledglings is necessary to test this link.

The cost of reproduction hypothesis also applies because by rearing the more expensive sex during the best food conditions early in the breeding season, females are minimizing the costs to themselves. This may be relevant to the akepa because it is a long-lived bird with a low reproductive rate. The savings in parental energetics of rearing males versus females of equal mass at different times may not by itself be significant. However, parents moult at least six of their nine primary flight feathers during June and July, months with the lowest food of the year (Freed *et al.*, 2007). By rearing males during the most rapid phase of growth of their bills before beginning to moult in June, females are minimizing the remaining costs of subsidizing growth of their sons' skeletal characters while they themselves are heavily moulting.

Freed *et al.* (2007) previously showed that nestling overgrowth was an adaptation that reduced the cost of moult–breeding overlap during the fledgling period. Seasonal variation of sex allocation may be a similar adaptation that further reduces the cost of caring for larger males during that period. It may actually be costlier for females, while they moult, to produce daughters with faster bill growth. In this light, such females could begin moulting later or moult primary feathers over a longer period to minimize the extra costs of greater moult–breeding overlap. Freed *et al.* (2007) documented sufficient population-wide temporal variation in moulting of primary flight feathers of adults for this phenomenon to potentially occur. It is also possible that the few males with shorter bills are produced by the few females that attempt to rear sons later in the breeding season. In principle, late-nesting parents could work harder to care for their sons, but this harder work would occur during intensive moulting of flight feathers. These rare cases may result in shorter-billed sons as parents in this long-lived bird species are preserving their own survival over that of ill-timed male offspring.

The cost of reproduction hypothesis for SVSA, based on moult–breeding overlap, may apply widely to tropical birds where adult survival is favoured (Ghalambor and Martin, 2001). Most tropical bird species have a lengthy breeding season, within which pairs may breed successfully once at widely varying times, followed by a comparatively fixed moulting season when worn plumage is replaced (Stutchbury and Morton, 2001). Tropical birds also have long fledgling periods (Martin, 1996; Freed, 1999; Stutchbury and Morton, 2001; Russell *et al.*, 2004), within which fledglings may still be growing. Freed *et al.* (2007) showed that moult–breeding overlap should include parental care during the fledgling period. Such overlap may be important for SVSA when food levels decline during a lengthy fledgling period.

Implications

The dismantling of sex allocation from an adaptation to a maladaptation after the environmental change poses significant evolutionary problems. Females would be able to produce daughters earlier in the breeding season when food is still sufficient. But for this to happen, the selection on individual females that shaped the adaptation of SVSA would need to be replaced by population-level frequency-dependent selection to produce more females. Sex allocation selection and sex ratio selection have been treated as different types of selection (Frank, 1990, 1998). The environmental change has now forced a connection between these. The adaptation of SVSA must be lost for sex ratio selection to establish greater equality of young males and females. So far, there is no indication that sex ratio selection is replacing sex allocation selection. Until this happens, the adult sex ratio will become further male biased.

The problem is deeper than the types of selection the bird is encountering. Even if SVSA is lost, there will still be fewer young produced because the latter portion of the akepa breeding season has been effectively eliminated by competition with the white-eye. Sex allocation theory has come to the aid of several endangered species to produce a more even sex ratio in the clutches of individual females (Clout *et al.*, 2002; Castro *et al.*, 2003; Robertson *et al.*, 2006). The theory must now be applied to the entire akepa population throughout the breeding season. This is to ensure that sons produced in early nests have appropriately sized bills for longevity, and that later nesting females have enough food resources to produce daughters that are in sufficient condition to recruit into the breeding population. If the current food limitation is not corrected by appropriate management, identified by Freed *et al.* (2008a), the chronic shortage of young female akepa will lead to extinction as older females are not replaced.

ACKNOWLEDGEMENTS

J. Lepson, P. Hart, E. VanderWerf, J. Rohrer, J. Bennett, M. Rowe, S. Ono, C. Hauri, and W. Kuntz assisted with data collection. We appreciate thoughtful comments on earlier drafts of the manuscript from G. Ritchison and W. Cresswell. Hakalau Forest National Wildlife Refuge provided special use permits. Financial support was provided by the MacArthur Foundation World Environment and Resources Program and National Center for Environmental Research (Science to Achieve Results, Environmental Protection Agency, R82-9093) to L.A.F. and R.L.C. Additional support was provided by the Australian Research Council Discovery-Project Grant DP451402 to L.A.F. (Partner Investigator; H. McCallum, Chief Investigator).

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