Evolutionary Ecology Research, 2008, **10**: 931–965

Incipient extinction of a major population of the Hawaii akepa owing to introduced species

Leonard A. Freed[1], Rebecca L. Cann[2]
and Gustav R. Bodner[1]

[1]*Department of Zoology and* [2]*Department of Cell and Molecular Biology,*
University of Hawaii at Manoa, Honolulu, Hawaii, USA

ABSTRACT

Background: The akepa population in its high-density site crashed in 2006, after being non-viable from 2000 to 2005.

Hypothesis: The crash was caused by increases in certain ectoparsites and an introduced avian competitor.

Organisms: Hawaii akepa (*Loxops coccineus coccineus*), Japanese white-eye (*Zosterops japonicus*), and Phthiraptera (chewing lice in Ischnocera and Amblycera).

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

Methods: We mist-netted birds at a high elevation site from 1987 to 2006, documenting increased numbers of introduced Japanese white-eye from 2000 to 2005, and compared Hawaii akepa nestling mass, breeding success, fledgling mass, juvenile survival, juvenile bill length, and sex ratio of young birds before and after the increase in white-eye. We inspected birds captured in mist-nets for ectoparasites. We identified colour-banded birds through binoculars to supplement the mist-netting for estimating population changes.

Results: Declines in all demographic parameters of Hawaii akepa related to recruitment coincide with the first 5 years of increased numbers of Japanese white-eye. A severe decline in adult survival was observed in 2006, following the explosive increase in chewing lice between 2003 and 2005 and continued exposure to increased white-eyes. Further decline was observed in 2008. Mass, fault bars in feathers, fat scores, and changes in begging indicated that the decline was due to strong food limitation. The white-eye overlaps foraging substrates with all species of native birds, and additional native species have declined with the akepa.

Conclusions: There has been a collapse of every demographic parameter of the akepa. The population is continuing to decline over a large area and may go extinct without management.

Keywords: demography, environmental change, food limitation, interspecific competition, introduced species, population crash.

Correspondence: L.A. Freed, Department of Zoology, University of Hawaii at Manoa, Honolulu, HI 96822, USA. e-mail: lfreed@hawaii.edu

INTRODUCTION

Adaptation and extinction shape all taxa (Futuyma, 1998). The study of extinction is more difficult since it requires detailed knowledge about the biological community of the taxon in question, and information on demographic response and potential to evolve adaptation to changing environments. Natural catastrophies and biological problems in the form of predators, competitors, parasites, pathogens, human exploitation, and habitat modification are involved in modern extinctions (Diamond, 1984). Anthropogenic environmental changes, with consequences for extinction, include elimination of habitat (Vitousek *et al.*, 1997), deliberate or accidental introduction of alien species (Mooney and Hobbs, 2000), and altered climate (Root *et al.*, 1993; Pounds *et al.*, 1999).

Introduced competitors are known to have an effect on native species (Schoenherr, 1981; Wootton, 1987; Ogutu-Ohwayo, 1990; Case and Bolger, 1991; Lydeard and Belk, 1993; Petren and Case, 1996), but no extinction event attributable to them has been documented. The role of competition from introduced species for the extinction of native species has thus been questioned (Ross, 1991; Davis, 2003; Gurevitch and Padilla, 2004). Even cases of interference competition, involving introduced cavity-nesting birds aggressively competing with native birds for tree holes, have rarely resulted in significant declines of native birds (Koenig, 2003).

Here we show that increased numbers of the Japanese white-eye (*Zosterops japonicus*), a generalized introduced bird in Hawaii (van Riper, 2000), and an explosive increase in ectoparasites (Freed *et al.*, 2008), have resulted in complete demographic collapse of the insectivorous endangered Hawaii akepa (*Loxops coccineus coccineus*), and destabilized the entire native bird community in an upper elevation forest. Introduced in 1929, the white-eye was well-established in upper elevation forests on the Island of Hawaii when the area was first surveyed during the late 1970s (Scott *et al.*, 1986). The akepa is a small bird (10.5 g) that mainly consumes arthropods and nectar from ohia (*Metrosideros polymorpha*) and koa (*Acacia koa*) trees, the dominant canopy species in montane forests of Hawaii (Freed, 2001). It has a low reproductive rate with single two-egg clutch, lengthy incubation and nestling period, lengthy 4-month fledgling period, and high annual adult survival (Lepson and Freed, 1997).

Our approach documents changes in condition and behaviour of the akepa and other native birds over a 19-year study. We model changes in demography and viability of the akepa and white-eye, and evaluate diverse mechanisms that could generate the changes. We then show that the white-eye must be controlled to prevent extinction of the akepa.

METHODS

Field methods

Hakalau Forest National Wildlife Refuge, an old-growth ohia–koa forest (Freed, 2001), is on the windward slope of Mauna Kea, Island of Hawaii. Our major study site covered 33 hectares at 1900 m elevation. From 1987 to 2006, we ran 20 aerial mist-nets for most months of the year. We banded birds with a permanent aluminium band with unique tracking numbers and for some species a unique combination of three plastic colour bands. This enabled us to identify individual birds with 10 × 42 binoculars without re-capturing them. We recorded age and sex, health (avian pox-like sores and shivering), breeding condition (brood patch or cloacal protuberance), moult, ectoparasites, broken wing and tail feathers, and the fault bars in these feathers (illustrated in Freed *et al.*, 2008) that reflect nutritional stress during moult (Slagsvold, 1982; Bonser, 1995; Bortolotti *et al.*, 2002). We weighed birds to the nearest 0.5 g (0.1 g in 2004 and later), scored furcular fat (Freed *et al.*, 2007), and measured bill length (exposed culmen from tip to feather line, nearest 0.1 mm). After 2001, we used a portable intensive care unit with bottled oxygen and chemical heat for birds that appeared stressed (Freed *et al.*, 2005).

We banded birds during 2004–2006 in additional sites at 1770, 1650, and 1580 m elevation, each approximately 0.1 km^2. The 1900 and 1700 m sites are in the highest density akepa area on the refuge (Scott *et al.*, 1986). The 1650 m site is at slightly lower density, and akepa are extremely rare at the 1580 m site. We also banded at 1830 m in the high-density area during the mid-1990s and after 2002.

We re-sighted akepa and other colour-banded birds, opportunistically before 2006. During 2006, we re-sighted systematically, resulting in an inventory of the 1900 m site, covering each portion of the site on at least 10 different days between April and July, including every nest-site tree used since 1987. Most birds counted as survivors were sighted more than once. All research was halted in July 2006, when L.A.F. was threatened with arrest by the US Fish and Wildlife Service (USFWS), which suspended his endangered species permit. We observed birds for several days during 2007–2008 with visitors and students. We conducted replicate searches for akepa and other endangered species at the 1900 m and 1770 m sites during late March and late May/early June 2008, with an additional search at the 1770 m site during April. Personnel moved slowly throughout each site listening for vocalizations and identifying each bird seen moving in the foliage.

We established breeding seasonality of bird species by capturing females with brood patches for incubating eggs. Length of breeding season was month of first to month of last brood patch. We obtained data on clutch size, proportion of eggs hatched, and nestling mass of akepa from 10 accessible nests in artificial cavities from 1992 to 2003. We weighed nestlings from accessible nests when approximately 14 days old.

We estimated akepa breeding success as number of pairs with fledglings in relation to the total number of identified pairs, an appropriate methodology for comparing different populations or one population over different time periods (Thompson *et al.*, 2001). The birds have a 4-month fledgling period during which success can be documented (Hart and Freed, 2003). We followed family groups in 2005 to determine the loss of fledglings before the termination of parental care. Sex ratio of young birds is from Freed *et al.* (in press).

To determine relative abundance of tree species, we counted all trees with a diameter at breast height of 10 cm or larger, in 100 plots 30 m in diameter, evenly spread over 1 km^2. We identified foraging substrates on these trees and foraging techniques of bird species in the *Birds of North America* species accounts (Poole, 2005), supplemented these with personal observations of researchers familiar with the birds at Hakalau, and calculated connectance as the number of species–foraging substrate combinations observed divided by number possible. During 2004–2005, we used pole-based mist-nets along with aerial mist-nets in the 1900 m study site, with a highly disturbed understory from prior cattle ranching, and in the more pristine study site at 1650 m elevation, to compare understory use by the same species in different landscapes. We estimated morphological similarity of the white-eye to native birds by comparing sequential ratios of bill lengths of species ranked by bill length. During 1989 and 2008, we counted the number of individuals of each species entering focal ohia trees during one-hour observation periods.

Ohia leaf buds, which house *Carposina* microlepidopteran larvae, are a foraging substrate used exclusively by the akepa (Lepson and Freed, 1997). We collected buds in two sites, one with and one without akepa in 1995, to estimate prevalence of larvae. We collected additional ohia leaf bud data from the site without akepa in 2001, where both prevalence of caterpillars and parasitoids in caterpillars was estimated.

We obtained weather data from a centrally located station at 1940 m elevation operated by the US Forest Service (1989–1991) and the USFWS (1993–2006). Air temperature and precipitation data were recorded every 15 min. Anomalous high or low temperature values, from 60 isolated days during 1996–1999, were discarded.

We maintained 12 oviposition buckets to document mosquito breeding from October 2001 to July 2005, when the USFWS required us to discontinue their use. These were 5-gallon plastic buckets with 1–2 gallons infusion of brewer's yeast and rabbit alfalfa pellets. After 4–6 days of infusion, we positioned buckets evenly in open, shady, and partially shady spots close to a gulch. We searched for mosquito egg rafts and larvae every third day and replenished buckets on day 12.

Statistical methods

We documented the increase in Japanese white-eye by regressing annual captures on mist-net hours, after which we regressed residuals on year, using a break point based on the longest run of residuals greater than 0. We used mean percentage increase, over what was predicted following the break point, as the estimated population increase. We documented change in white-eye residency by regressing proportion of individuals recaptured on year. Change in ectoparasites was based on Freed *et al.* (2008).

We used mist-netting data from all study sites before 2000 and after 1999 (justified below) to document increase in white-eye and decrease in akepa. First, we compared the native bird community at each site, minus the akepa, during the time periods with Morisita's Index of Similarity (Krebs, 1999). Next, we calculated proportions of akepa and white-eye in the community during the two time periods, counting individual birds once per period. Then we regressed (logistic) proportion of akepa on proportion of white-eye, with site as a factor.

We compared mass and bill length of young akepa and white-eye during 1987–1999 and 2000–2005 using *t*-tests for akepa nestling mass and for juvenile bill length (both species). For fledgling mass for akepa and juvenile mass for white-eye, we used analysis of variance that included month and time period in sequential order.

We used analysis of variance with month and time period as factors in sequential order to compare air temperature between time periods. For precipitation, we employed a *t*-test between time periods, using just years with data available each month. To determine if problems in 2006 were associated with unusually cold wet weather, we compared monthly low air temperature and precipitation by analysis of variance for the months of December through April from 2003 to 2006.

Demographic comparisons

We used Program MARK (White and Burnham, 1999) to estimate adult and juvenile survival for the akepa and white-eye from 1987 to 2006. We included birds initially captured as adults and initially captured as juveniles. Every model with annually varying probability of capture had more support than models with constant probability of capture. Candidate models included two age classes with (1) a single survival parameter over 1987–2006, (2) one survival parameter for 1987–1999 and one for 2000–2006, and (3) one survival parameter for 1987–2000 and one for 2001–2006, to account for possible lagged effects of the white-eye increase. We calculated weighted averages of supported models for estimates of juvenile and adult survival. We used the quasi Akaike information criterion (QAIC) and weights to evaluate models adjusted for overdispersion (C-hat = 1.014 for akepa, 1.216 for white-eye). In the Appendix, we contrast demographic results with survey data that showed no increase in white-eye or decline in akepa.

Program MARK could not estimate adult and juvenile survival between 2005 and 2006, because probability of capture during 2006 could not be estimated, and all applications by the authors to continue the study in 2007–2008 were rejected by the USFWS. For akepa, we used observational data from 2008 to show that a crash had occurred. For white-eye, we adjusted adult survival in 2006 for the number of birds expected to be captured after July, and by estimated probability of capture from previous years. We used mean probability of capture from 2002 to 2005, when netting was conducted each month of the year.

Comprehensive demographic data for calculating lambda were only available for the akepa. We used Guest (1973) for clutch size and number of broods for white-eye. We used a Lefkowitz-Leslie matrix with $f_x = s_y b$, where s_y = survival of young birds and b = number of female offspring produced (Ebert, 1999; Case, 2000). The parameter b is a product consisting of clutch size, hatching success, breeding success, and sex ratio of young birds, and s_y is survival of fledglings to a second year. Survival of adults is s_a. Assuming constant fecundity, juvenile survival, and adult survival, the matrix is simplified as $s_y b$ for the first row and s_a for the second row (Case, 2000).

We estimated lambda separately for three time periods for akepa based on environmental and demographic changes. The time periods, justified below, were 1987–1999, 2000–2005, and 2005–2006. We estimated adult survival for 2005–2006 based on the inventory during 2006. We used the value of b from 2000 to 2005 for 2005–2006, because insufficient data were available from 2006.

We calculated the 95% confidence interval for lambda, based on the variance of lambda being the sum of variances of $s_y B$ and s_a, weighted by the squared sensitivity of the parameters (Caswell, 2001). Variance of $s_y B$ was the variance of a product of four random variables (Goodman, 1962), assuming no covariance. We established the 95% confidence interval as 1.96 times the square root of the variance of lambda, assuming normality.

RESULTS

Changes in the condition and behaviour of the akepa by year

Beginning in year 2000. No fledglings were captured in mist-nets during June–September for four consecutive years (Fig. 1). Because no fledglings were captured in only 3 years during 1987–1999, four consecutive years during 2000–2003 is not expected (binomial test, $P = 0.03$). This was not based on lower effort (average 1100 net hours during June–September 2000–2003 vs. 129 net hours during the same months before 2000). Additional breeding changes include lower nestling mass and lower breeding success (Fig. 2a,b).

Second-year birds captured after 1999 were predominantly males (0.89, $n = 28$), compared with 0.47 ($n = 15$) before 2000. Proportion of females in all young birds changed between the two time periods from 0.53 to 0.13 [test of proportions, $P < 0.001$ (Freed *et al.*, in press)].

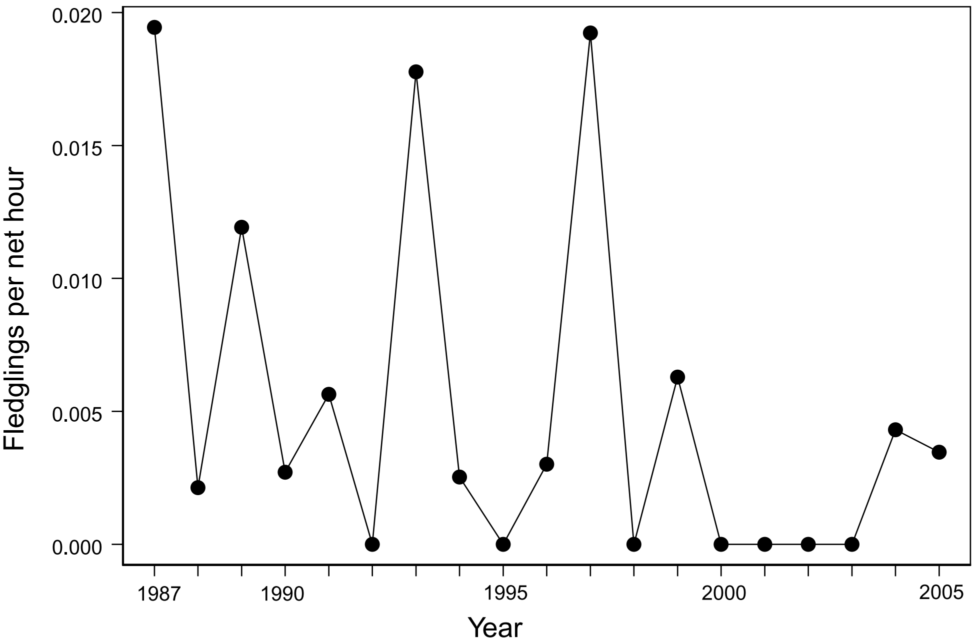

Fig. 1. Long-term pattern of captures of fledgling akepa in aerial mist-nets at 1900 m elevation. The fledgling period extends from June to September (Hart and Freed, 2003). Note the run of 4 years without fledglings beginning in 2000.

Adult male fat during the cold months of January–April was significantly lower during 2000–2006 than during 1987–1999, and all ages were more likely to have broken wing and tail feathers after 1999 (Freed *et al.*, 2008). These changes occurred in akepa and most other species. During 2003–2005, all species had a high prevalence of major fault bars in wing and tail feathers (Freed *et al.*, 2008). A male akepa captured in April 2006, in the net for less than 20 min (usual time) and easily extracted, had no fat and required oxygen to recover from stress.

Beginning in year 2001. Living parents abandoned nestlings for the first time. A nest was abandoned with one dead recently hatched nestling and a dead imminent hatchling in a second. In 2004, only the non-brooding male was observed feeding nestlings over 4 days of observation. The female was foraging in the area without entering the nest. After 4 days, the nest was abandoned, and neither parent was with fledglings. Previously, rare nesting failures occurred at the nest-building or incubation stages.

Beginning in year 2002. Family groups with fledglings during June of 2002 and 2003 lost them during July (Freed *et al.*, 2008). A formal survey of fledglings over 0.5 km^2 during July 2002 revealed only four fledglings per square kilometre. In 2005, seven of 16 pairs lost fledglings by July and August, before normal termination of parental care in September (Hart and Freed, 2003).

Beginning in year 2003. There was an explosive increase in chewing lice (Phthiraptera) in the akepa and every other species on the 1900 m site (Freed *et al.*, 2008). All bird species in all study sites had them during 2004–2005 (Freed *et al.*, 2008).

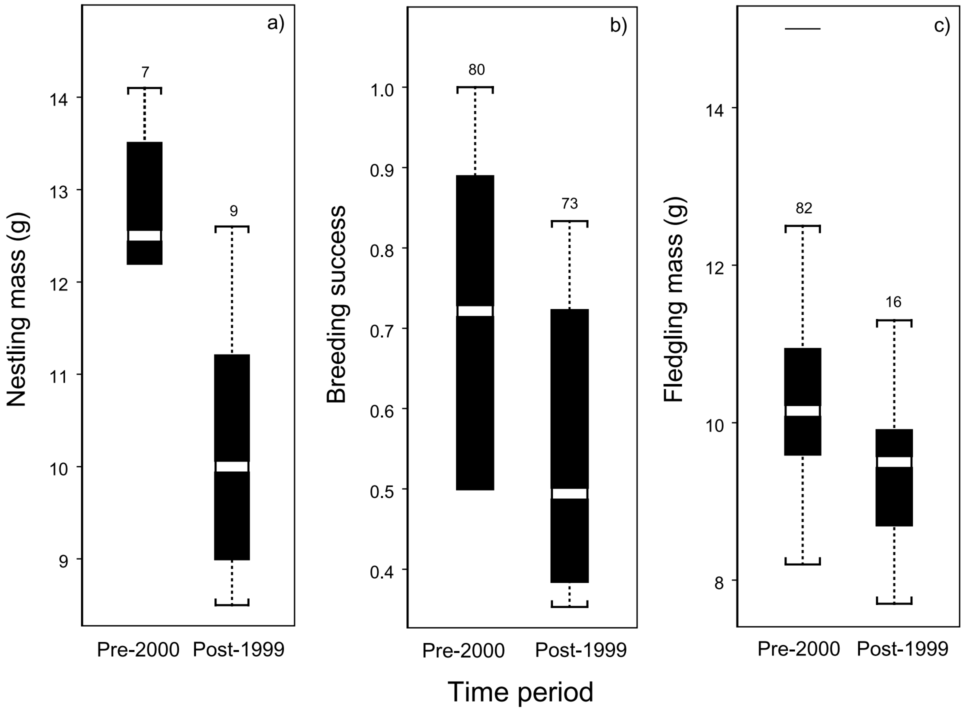

Fig. 2. Changes in reproduction between 1987–1999 and 2000–2005 as series of box-plots indicating median (white bar), inter-quartile range (black box), extreme points within 1.5 times inter-quartile range (caps), and outliers (isolated horizontal line). Sample size above caps. Nestling mass (a) was from accessible nests in artificial cavities. Nestling mass decreased after 1999 (*t*-test, $P = 0.03$). There was no difference in bill length of the nestlings measured (*t*-test, $P = 0.15$). Direct comparisons of nestlings with similar bill length during the two time periods revealed lighter nestlings after the white-eye increase. Breeding success (b) was based on documenting colour-banded adults with or without fledglings during the early months of the fledgling period (June and July). Sample size reflects total number of breeding attempts monitored within each time period, whereas the box-plot shows variation among years within each time period. The decrease in nestling mass was associated with lower breeding success, which dropped from 0.70 to 0.53 (test of proportions, $P = 0.003$). Fledgling mass (c), which is related to juvenile survival (Medeiros and Freed, in press), decreased after 1999 (ANOVA: month effect, $P = 0.0001$; period effect, $P = 0.049$).

Beginning in year 2004. Fledglings captured during 2004 and 2005 (Fig. 1) were underweight compared with fledglings captured before 2000 (Fig, 2c).

Changes in plumage coloration of adult akepa were detected. At 1900 m, a male older than 3 years was brownish-orange instead of bright orange. At 1770 m, two males, captured contemporaneously, differed in brightness. In 2008, two of 10 adult male akepa observed closely through binoculars had duller orange plumage than others. A female in 2008 had dull orange-brown feathers rather than the brighter yellow-orange feathers on her breast and neck, observed in 2006. In the past, adult males had brilliant orange with no visually detectable variation, and females either remained the same or became brighter with age.

Beginning in year 2006. Survivors from 2005, as pre-breeding pairs, moved distances exceeding 100 m. Previously, female akepa rarely travelled more than 50 m from the eventual nest. During 2006, female begging for a mate feeding persisted up to 30 min without a feeding, and in two cases the female continued begging after she was fed. In 2008, most females were silent, and some dropped one of the two syllables of their normal begging call. Begging and silence during these years were atypical of mate interactions (Lepson and Freed, 1997).

Foraging speed changed during 2006. Re-sighting colour bands of foraging akepa in the past was straightforward because of slow, deliberate movement of birds gleaning arthropods from ohia foliage (Lepson and Freed, 1997). Correct orientation of the leg was the major requirement for re-sighting. In 2006, birds were moving so rapidly through the foliage that it was impossible to identify colour bands until the birds stopped. This movement persisted in 2008.

Beginning in 2007. During November, 2007, we searched for akepa at the 1900 m site for 5 hours on each of 2 days with warm sunny weather. No akepa were detected either visually or by sound in the entire area, although common species were active. During 1988–2003, on average 2.45 accurately identified colour-banded birds were detected per day of re-sighting during November. In addition, there was usually one colour-banded bird inaccurately identified per day, and many unbanded birds that were detected (24% of akepa captured in mist-nets were unbanded during previous Novembers). We expected seven colour-banded birds and some unbanded birds during the 2-day period. In 81 days of re-sighting akepa during previous Novembers, there was never a day, with good weather, when no akepa were detected.

During February 2008, we observed birds at the 1900 m site over 2 days (4 hours per day when most species were active) with good weather. A male akepa sang briefly to his mate just outside the study site. No additional birds were detected. During 1989–2005, on average 2.74 colour-banded birds were detected per day in February, and with unbanded birds, there would be an expected eight birds during the period. There has never been a time with good weather during February when only one male was detected in 2 days.

We also surveyed birds along two separate transects, approximately 400 m apart, from the 1900 m site to the 1830 m and 1770 m elevations, distances of 0.6 and 1.5 km, respectively. The only akepa detected was the pair mentioned above, and one pair at a distance of 0.9 km along the second transect.

Beginning in 2008. Nine days were spent during late March 2008 at various sites. At 1900 m, we detected nine pairs of akepa based on male singing, and an unpaired bird. However, we heard no calling and saw no interaction among males. The number of birds was corroborated during early June. This contrasts with a study performed during late March 2001, when more than nine pairs of akepa were detected in only 3 hours, with calling, singing, and male displays. At 1707 m, 3 km north, akepa were present based on singing, but there was no calling. A mate feeding that normally involves calling and begging was observed in silence. At the 1770 m site, no native bird was seen or heard in 2 hours. During April 2008, one pair of akepa was detected in 2 hours. This was the only pair detected during a 4 hour period in May.

An akepa nest was found in March 2008 at the 1900 m site, and incubation behaviour was observed for 5 hours over 3 days. For 14 sessions on the nest, the female averaged 9.9 min (range 0.5–23 min), lower than the average 54.6 min documented before 2000 (Lepson and Freed, 1997) (t-test, $P < 0.0001$). Communication between mates was highly reduced, with no calling by the female either on or off the nest, and no calling by the male, behaviours always seen before with mate feeding and incubation (Lepson and Freed, 1997). The female begged on only two and was fed on only five of nine recesses.

Changes in demography and population viability of the akepa

We estimated parameters of the Leslie matrix and calculated lambda during 1987–1999 and 2000–2005 based on changes documented above. Clutch size was uniformly two eggs, based on inspection of 18 nests in artificial cavities spanning 1994 to 2003. Inspections of nests after fledging indicated that one egg did not hatch in seven of the 18 nests, associated with three of six different females. The average number of eggs hatched was 1.6. Because these nests spanned both time periods, the value of 1.6 was used for both. Other parameters of the birth function are displayed in Table 1.

Juvenile survival (s_y) was based on banded nestlings, fledglings, and independent juveniles captured during their first year surviving to at least March (breeding season) of their second year. Alternative models showed that juvenile survival changed with a break point at 2000, and also at 2001 (Fig. 3a). With model averaging, the change in juvenile survival began in 2000, decreased further in 2001, and then remained constant. For purposes of demographic modelling, two time periods were used, pre-2000 and an average of 2000 and greater than 2000 (weighted average). Juvenile survival thus decreased from 0.44 to 0.31 (Fig. 3b), although this estimate may be optimistic because the 2001 break model was most supported with juvenile survival of 0.19 (Fig. 3a).

The most supported model for adult survival in Program MARK was constant survival from 1987 to 2005 (0.76, standard error = 0.02). The next most supported model included change beginning in 2001, comparable to the break in juvenile survival, but with increase in adult survival to 0.78. The model average of 0.77 was used for both time periods.

Table 1 summarizes parameters used in the matrix model for testing differences in lambda. Every demographic parameter except clutch size and annual adult survival decreased significantly between 1987–1999 and 2000–2005. The calculated value of lambda for 1987–1999 was significantly greater than 1, indicating that the population was viable during that time period (Fig. 4). The calculated value of lambda for 2000–2005 was

Table 1. Summary of parameters used to calculate lambda for Hawaii akepa during different time periods (mean values with sample sizes in parentheses)

	Time period		
Parameter	1987–1999	2000–2005	2005–2006
Eggs hatched	1.61 ($n = 18$)	1.61 (*)	1.61 (*)
Breeding success	0.70 ($n = 80$)	0.53 ($n = 75$)	0.42 ($n = 11$)
Sex ratio	0.58 ($n = 55$)	0.13 ($n = 31$)	0.13 (*)
Juvenile survival	0.44 ($n = 71$)	0.31 ($n = 19$)	0.31 (*)
Adult survival	0.77 ($n = 161$)	0.77 ($n = 89$)	0.44 ($n = 66$)

* The value from the previous time period was used.

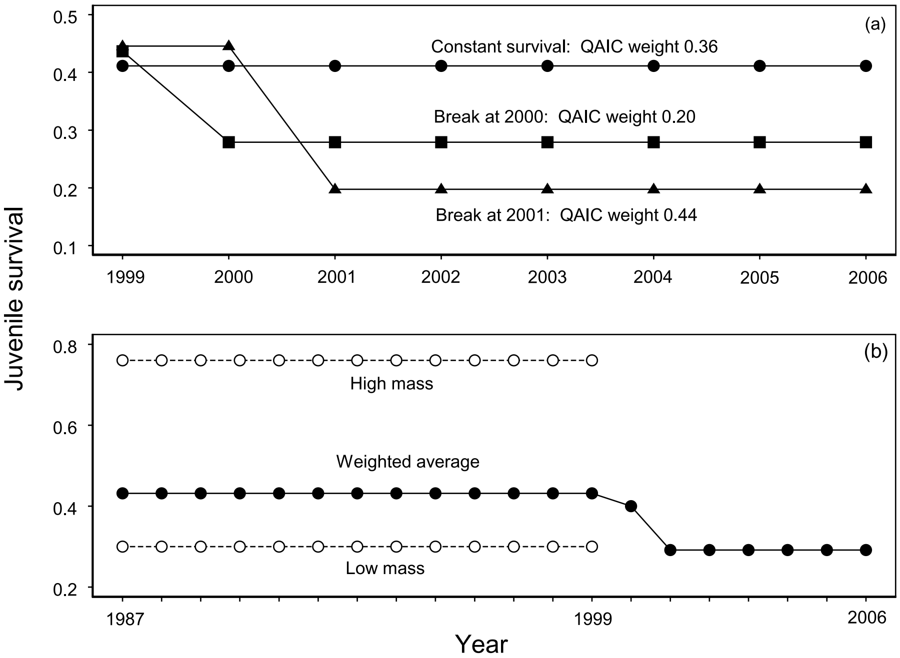

Fig. 3. Estimation of juvenile survival over different time periods. (a) Three different models for juvenile survival from 1987 to 1999 and later years showing no change, change in 2000, and change in 2001. The QAIC weights from Program MARK indicate some support for each model, with the greatest support for the change in 2001. (b) Model averaging from the three models in (a), where the estimates from each model are weighted by the QAIC weights. Also shown are the survival rates of fledglings between 1987 and 1999 by mass class, where high mass is 11 g or greater and low mass is less than 11 g (Medeiros and Freed, in press), for evaluating the change in fledgling mass shown in Fig. 2c. The estimate of juvenile survival for demographic modelling was based on additional model averaging between 2000 and later years.

significantly less than 1 (Fig. 4). There was no overlap between the 95% confidence intervals. The akepa population became non-viable. There was slow loss of breeding pairs between 2003 and 2005, averaging two pairs per year, as recruitment could not match normal adult mortality.

Between 2005 and 2006, lambda decreased further (Table 1, Fig. 4). Only 24 of 67 (0.36) colour-banded adults known to be alive in 2005 were detected in 2006, compared with the expected 52 of 67 from the constant adult survival of 0.77 estimated during 1987–2005 (test of proportions, $P < 0.0001$). The proportion of surviving males and females was similar (13/39 vs. 11/28; test of proportions, $P = 0.69$).

Non-viability continued through 2008. The number of akepa known to be alive in 2006 was 28 (24 from previous years plus three newly banded adults plus an unbanded adult known from a particular location), but only 19 birds were detected in 2008. The decline thus continued, with lambda in 2008 less than lambda during 2000–2005 but greater than lambda during 2005–2006 (see Fig. 4 for range). Using 71 birds in 2005 (67 colour-banded birds, plus four known unbanded birds), the decline between 2005 and 2008 amounted to 73% of the population on the 1900 m site. The decline at the 1770 m site was more severe,

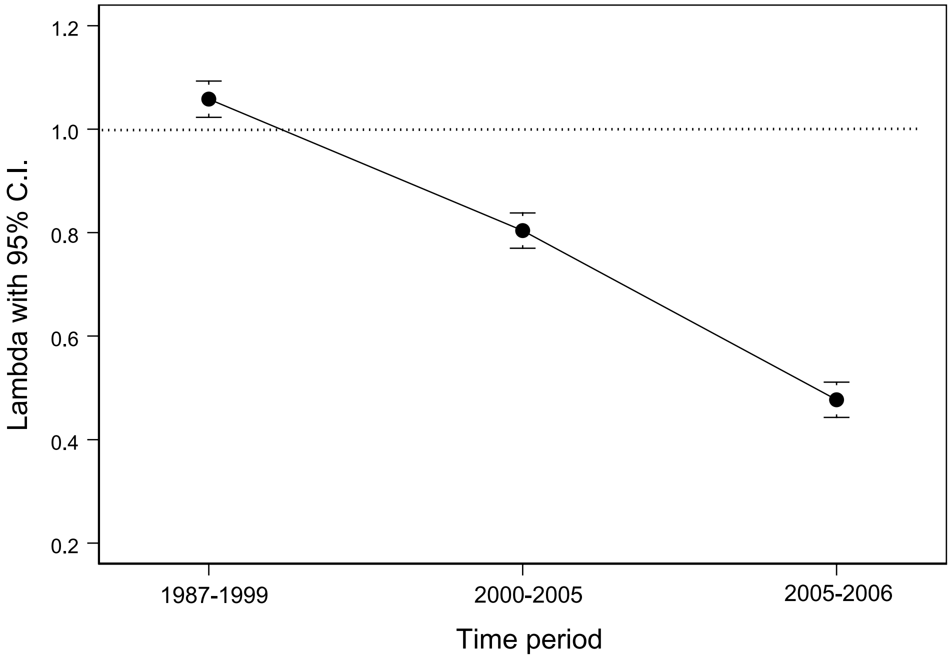

Fig. 4. Estimates of lambda, the intrinsic rate of natural increase, for Hawaii akepa during three time periods. The first period was before the increase in Japanese white-eyes. The second period was during the increase, with lower juvenile survival but retained adult akepa survival from the first time period. The third period shows the effects of lowered adult survival. The horizontal dotted line at lambda = 1 is the threshold for population viability. Values below the line indicate non-viable populations that are declining. Values above the line indicate a growing population. The vertical bars represent the 95% confidence interval for the estimates.

because the population dropped from at least 23 birds alive in 2004–2005 to only two birds (91%).

There was no evidence of selection during the akepa crash. Bill length did not differ between survivors and non-survivors (ANOVA: sex effect, $P = 0.02$; survival effect, $P = 0.25$; interaction, $P = 0.41$) (Fig. 5a). For birds weighed in 2005, body mass was not significantly lower in the non-survivors (t-test: d.f. = 36, $P = 0.42$). Both survivors and non-survivors contained birds 10 years or older; but the higher age of surviving birds was not significant (t-test: d.f. = 66, $P = 0.13$). Akepa juvenile bill lengths were significantly shorter after 2000 (t-test: d.f. = 17, $P = 0.02$) (Fig. 5b). However, consistent with smaller nestlings and smaller fledglings, this reflects stunted growth rather than adaptation to changed conditions.

Mechanisms responsible for the demographic collapse

Environmental changes associated with demographic collapse of the Hawaii akepa were also associated with declines in condition (and numbers, see Appendix) of all native birds in the study area. Changes need to be general enough to account for poorer condition of all species and specific enough to account for the collapse of the akepa.

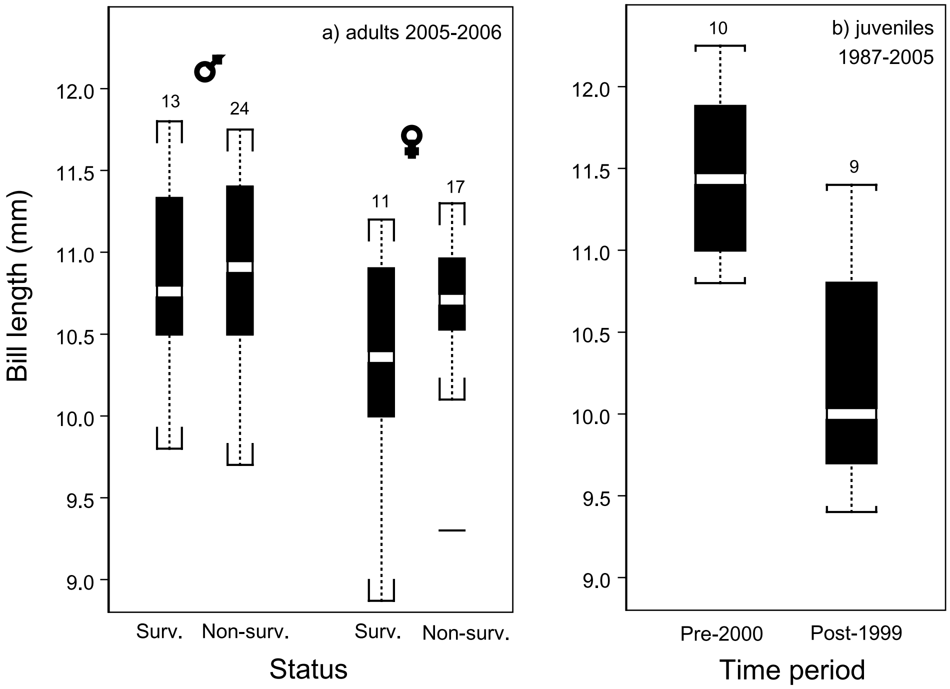

Fig. 5. (a) Box-plot comparing bill length of Hawaii akepa adult males and females known to be alive in 2005, in relation to surviving the population crash between 2005 and 2006. (b) Box-plot showing bill lengths of akepa juveniles captured during October–December, past the termination of parental care, during years of viability (pre-2000) and non-viability (post-1999). Sample sizes are above caps. The bill reaches adult length during August–September (Freed *et al.*, 2007). The juveniles could not be sexed, but the difference between time periods greatly exceeds the mean 0.13 mm difference between males and females. Because personnel measuring the birds differed between the time periods, comparison was made between individual birds measured during 1987–1999 and re-measured after 1999. There was no significant difference between such measurements. Box-plot components are the same as for Fig. 2.

Possible changes in weather

Mean air temperature and precipitation did not change significantly between time periods 1989–1999 and 2000–2005 (temperature: period effect, $P = 0.17$; precipitation: period effect, $P = 0.75$) (Fig. 6a,b). Apparent cycles in temperature are associated with the 1991, 1994, 1998, and 2004 El Niño events. Each time period had a strong El Niño event, and no years could be considered part of prolonged droughts or excessive rain. Relative humidity, which affects ectoparasites, did not change during the epizootic (Freed *et al.*, 2008).

Other weather comparisons pertain to the akepa crash during 2005–2006. There was no difference in rainfall during the winter and early spring months between 2004 and 2006 (month, $P = 0.16$; year, $P = 0.07$) (Fig. 7a). Daily low air temperature differed between months and years over 2004–2006, along with the interaction (all $P < 0.0001$) (Fig. 7b). However, the major difference in temperature was not consistent with cold weather-based mortality. The strongest deviation of 2006 monthly low air temperatures from previous years was the warmer March of 2006.

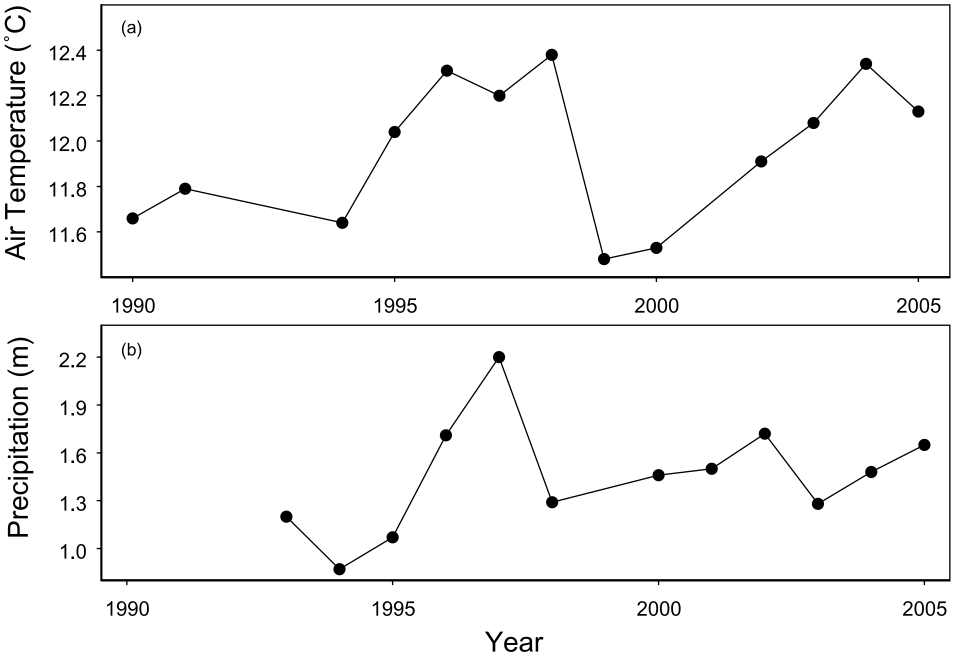

Fig. 6. Long-term pattern of air temperature (a) and precipitation (b) at 1940 m elevation near the study site. For air temperature, points shown are for years where valid measurements were taken each month. Points are the mean of monthly means. Years with incomplete data were included for statistical analysis where month was included as a factor along with time period. El Niño events occurred in Hawaii during 1991, 1994, 1998, and 2004. Precipitation data were not available until 1993. Only years with at least 10 months of data were used. The points belie the extreme rains that can occur. The record rainfall was over 0.75 m during January of 1989.

Possible changes in mosquitoes and infectious disease

Thorough surveys of mosquito breeding sites involving 1024 water sources on the refuge were conducted during November 1994, February 1995, and October 1997 with no detection of larvae (Woodworth *et al.*, 2001). We detected second instar larvae of *Culex quinquefasciatus* in one mosquito bucket in December 2001, at the 1900 m site, associated with an epizootic of malaria (Freed *et al.*, 2005). No mosquitoes were detected during 12-day duty cycles from January 2002 to July 2005.

Pox virus did not increase in prevalence in the akepa and other species, except for the omao (*Myadestes obscurus*), throughout 2000–2006, beyond baseline values of 4.5%. All individuals of all species tested for malaria in 2002 ($n = 308$) were negative except for elepaio (*Chasiempis sandwichensis ridgwayi*) (Freed *et al.*, 2005, plus unpublished data), so malaria was unlikely to be responsible for akepa non-viability in 2002, when they had normal adult survival, or for declines in condition of all species of native birds in 2002.

Changes in food supply

In 1995, the site without akepa had a significantly higher prevalence of ohia leaf buds with caterpillars than the site with akepa (0.48 vs. 0.19, $n = 286$ vs. 219; test of proportions, $P < 0.0001$). In 2001, ohia leaf buds in the site without akepa had a lower prevalence of

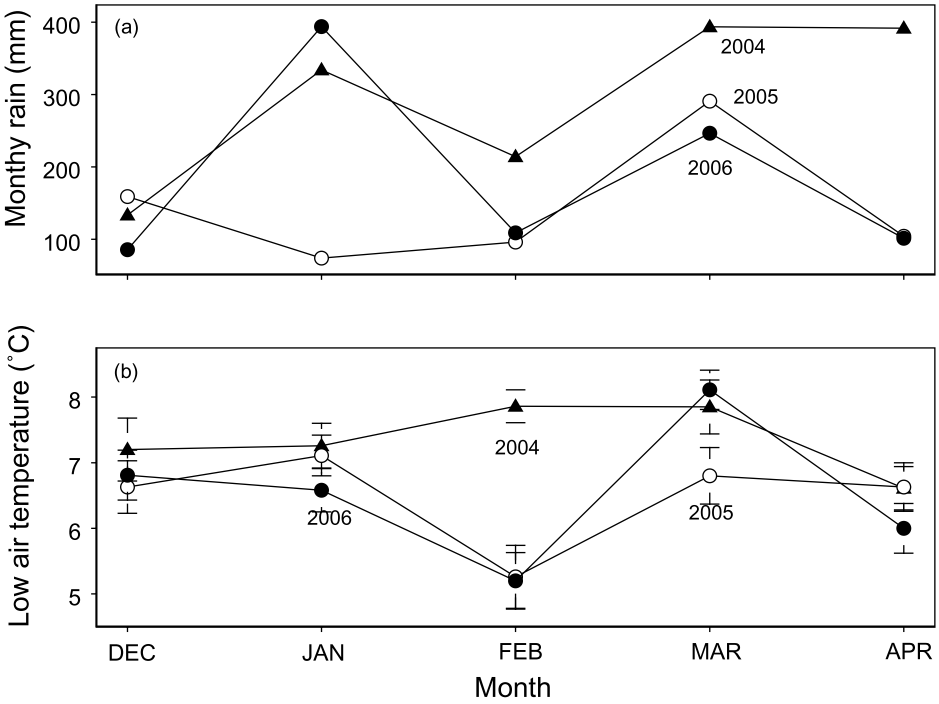

Fig. 7. Low temperature and precipitation during the winter and early spring months of 2004–2006. The akepa population crash occurred between 2005 and 2006.

buds with caterpillars than in 1995 (0.14 vs. 0.48, $n = 298$ vs. 286; $P < 0.0001$). Prevalence of a parasitoid wasp in the caterpillars was 0.45 in the 2001 sample. Parasitoids were not investigated in the 1995 samples.

In a study of arthropods conducted in 2002 on the 1900 m site, very few geometrid caterpillars were found in foliage (F. Howarth, personal communication). These caterpillars were present in high numbers in ohia foliage during 1994–1997 (Fretz, 2002).

Increase in ectoparasites

There was an explosive increase in prevalence of ectoparasites in the akepa (Fig. 8), and in all species of native and introduced birds, in all study areas (Freed *et al.*, 2008). The ectoparasites were primarily chewing lice (Phthiraptera) in the suborders Ischnocera and Amblycera, and were likely introduced lice (Freed *et al.*, 2008). The increase began in 2003 at the 1990 m site (other sites were not used by us until 2004). Therefore, ectoparasites cannot be responsible for the problems documented during the period of population non-viability during 2000–2002.

Ectoparasites may have contributed to the akepa crash between 2005 and 2006. Although there was no difference in survival between adults with and without ectoparasites (0.30 vs. 0.33; test of proportions, $P = 0.98$), intensity of parasitism influenced the survival of adults during the crash. One component of intensity, number of body areas infected, was not equal between survivors and non-survivors during 2004 and 2005. Among measured survivors, only two of 15 individuals had intensity class 3 or higher, compared with seven of

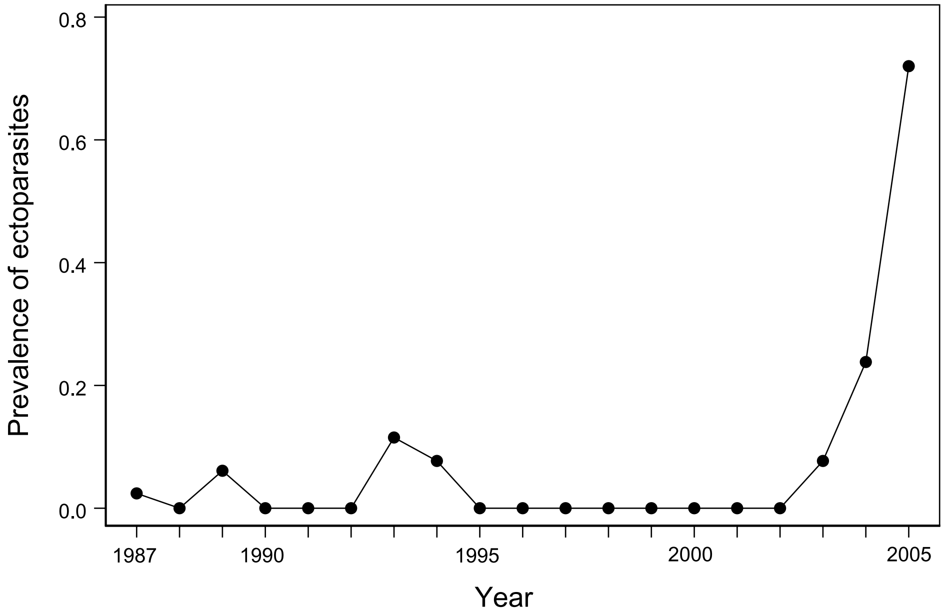

Fig. 8. Long-term pattern of prevalence of ectoparasites in Hawaii akepa, showing an explosive increase during 2003–2005. The increase, which was experienced by all other native birds and established introduced birds, was mainly due to chewing lice (Phthiraptera). Mites (Acari) were also present and had been documented before 2003.

18 non-survivors. The probability of two or fewer individuals with intensity class 3 or higher in 15 survivors, with 7/18 of non-survivors in these classes, is unlikely due to chance ($P = 0.03$). Some non-surviving birds with high-intensity infections may have survived if they had fewer parasites.

Ectoparasites could account for the decline in condition of all native species because individuals with ectoparasites were more likely to have major fault bars than individuals without ectoparasites (Freed *et al.*, 2008). For all native species except the omao, individuals with ectoparasites were less likely to be recaptured during 2004–2005 than individuals without ectoparasites (Freed *et al.*, 2008). However, changes in fat levels and broken wing and tail feathers for all native species preceded the increase in ectoparasites by several years (Freed *et al.*, 2008).

Increase in introduced Japanese white-eyes

We captured white-eye every year. Beginning in 2000, white-eye captures increased (Fig. 9). The trend from 1987 to 1999 was not significant ($P = 0.29$), but that from 1987 to 2005 was ($P = 0.023$) (Fig. 9). The longest run of positive residuals was from 2000 to 2003, the same years when no akepa fledglings were captured, and when all native species showed a decline in condition. During 2000–2005, white-eye numbers increased an average 29% over expectation from mist-netting effort.

Changes in white-eye life history. The white-eye increase included higher proportions of individuals each year that were recaptured from previous years (Fig. 10). During

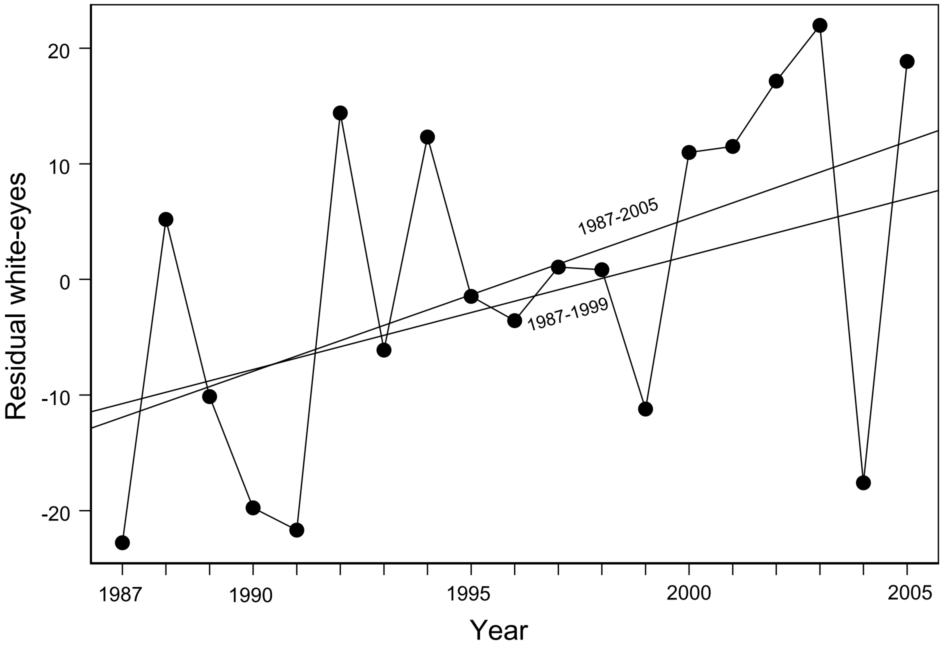

Fig. 9. Documentation of the increase in white-eye over time at the 1900 m site. White-eyes were captured each year. Residuals were calculated from the regression of captures on mist-net hours. Shown are those residuals plotted over time. The least-squares lines show slopes for the analysis of data from 1987 to 1999 (not significant) and from 1987 to 2005 (significant). Note the run of positive residuals from 2000 to 2003.

1987–1999, the proportion of recaptured white-eyes decreased (negative trend, $P = 0.02$). During 1987–2005, there was an overall increase ($P < 0.0001$). This could not be explained by banding effort. White-eye recaptures increased over 2002–2005 (trend in logistic regression, $P < 0.0001$), years in which comparable mist-netting was conducted each month. By 2005, the proportion of white-eyes recaptured became indistinguishable from that of the akepa (test of proportions, $P = 0.69$). Increase in density was thus associated with change in life-history behaviour. However, no white-eye aggressive behaviour was observed towards any native species throughout the study.

The increase resulted in major demographic change (Table 2). Both models with a break associated with the increase showed a drop in juvenile survival from 0.27 to 0. None of the 35 young white-eyes banded after 1999 were recaptured, even during the years 2002–2005 with greatest banding effort. Given the previous probability of juvenile survival of 0.27, this could not be due to chance ($P < 0.0001$). There was no change in mass of young birds before and after 2000 (10.9 vs. 10.6 g; ANOVA: time period effect, $P = 0.68$). There was also no change in bill length of juveniles (12.1 vs. 11.9 mm; *t*-test: $t = 0.075$, d.f. = 49, $P = 0.46$). Nevertheless, with no juvenile survival, lambda had to have been less than 1. White-eye numbers both increased and were maintained with no apparent juvenile survival.

Persistence of the white-eye depended on immigration every year. No nests were inspected in the study site. However, previous work at lower elevations in the State determined that a clutch size of three eggs was modal, most pairs could nest twice in a breeding

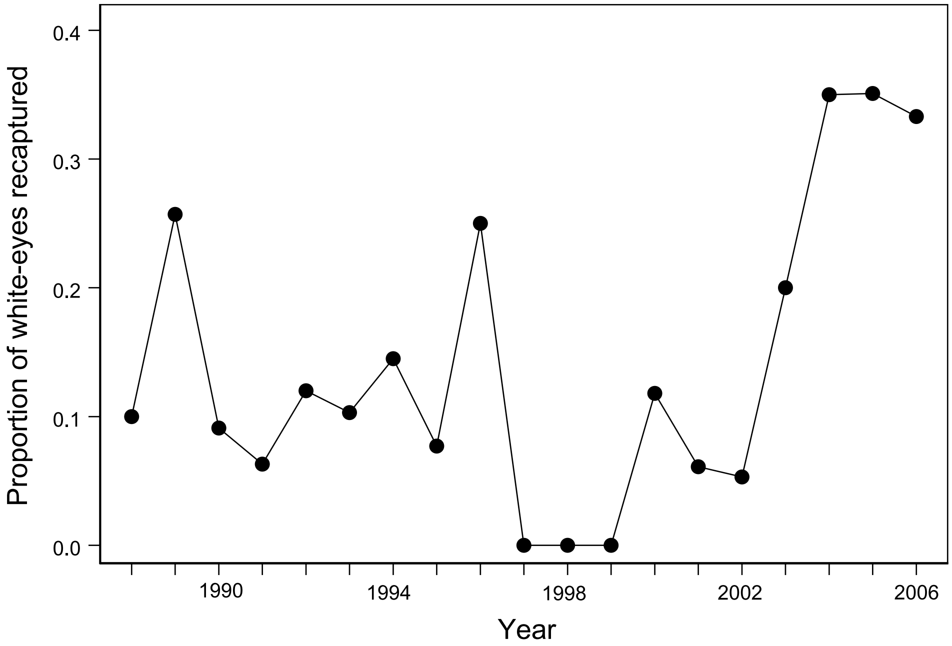

Fig. 10. Long-term pattern of recaptures of Japanese white-eye at 1900 m elevation. Points represent the proportion of individuals captured in a given year that had been banded during previous years. The trend between 1988 and 1999 was significantly negative. The trend between 1988 and 2005 was significantly positive. The pattern indicates a change in behaviour rather than a change in demography (see text).

Table 2. Results of Program MARK analyses for Japanese white-eye[a]

Model	QAIC	QAIC weights	Parameters	Adult survival	Juvenile survival
Constant survival, each age class	820.0	0.54	40	0.51	0.27
Break in survival at 2000, each age class	821.5	0.25	41	0.56/0.49	0.27/0
Break in survival at 2001, each age class	821.8	0.22	41	0.54/0.49	0.27/0
Annually varying survival	835.0	.00	41	—	—

[a] Survivals are maximum likelihood estimators from Program MARK. For models with a break point, the values are for the first time period and second time period, respectively.

season, and hatching success was 85.3% (Guest, 1973). Breeding success in the upper elevation site is probably much less than that at lower elevations because of strong rainfalls that can destroy open-cup nests (Woodworth *et al.*, 2001). Lambda was thus calculated using several different assumptions of breeding success ranging from 0.4 to 0.6. Calculation of lambda for 1987–1999 was based on juvenile survival of 0.27, an assumed even sex ratio, and adult survival of 0.56. The results range from lambda = 0.83, 0.90, and 0.97, all indicating some immigration necessary to maintain population size before the increase. Immigration had to increase substantially during 2000–2005.

Immigration continued to play a role during 2006. Adjustment of raw recapture data for 2006 increased apparent adult survival from 0.11 to 0.27. This is just under half of annual adult survival after 2000 (Table 2), so the white-eye crashed along with the akepa. The number of unbanded white-eye captured during January–July 2006 (18 vs. mean 53 during January–July of 2003–2005) was still more than expected by the number of net hours (0.025 vs. mean 0.017; *t*-test: $t = 3.57$, d.f. = 2; $P = 0.035$). The source of unbanded white-eyes was not affected by whatever caused the birds on the study site to crash.

Role of the white-eye in the forest bird community. Ohia trees provide the major food resources. Based on 3210 trees systematically tagged and identified, ohia comprised 87.7% of the community. Koa was the second most common tree (2.6%), and while much rarer than ohia, is an emergent canopy tree over 30 m in height. Based on abundance and size of these species, most foraging substrates observed for native and introduced birds are on different portions of these trees (Fig. 11). The six other woody plant species are both rarer and smaller.

All bird species have multiple foraging substrates (Fig. 11), including specialized insectivorous honeycreepers like the akepa, Hawaii creeper (*Oreomystis mana*), and akiapolaau (*Heminathus munroi*). The Hawaii amakihi (*Hemignathus virens virens*) is the native bird with greatest number of foraging substrates. Connectance between native birds and foraging substrates is 0.48. The white-eye uses as many foraging substrates as the amakihi, and connectance of the community increases to 0.50 with the white-eye included. The only foraging substrates/techniques used exclusively by single species are ohia leaf buds by the akepa, wood excavation by the akiapolaau, and flycatching by the elepaio. These species possess morphological and behavioural adaptation for exploiting these substrates. It is also possible that the creeper can better exploit arthropods from bark probing because its eyes are located closer to the base of the upper bill. The Hawaii akepa has few foraging substrates and these overlap with most other native birds and the white-eye. Except for leaf buds, the white-eye completely overlaps the foraging substrates of the akepa.

Use of the understory, based on capture in pole-based nets, varied among species ($P < 0.0001$) but not between sites with greater or lesser understory ($P = 0.67$) (Fig. 12). There was no interaction between species and site ($P = 0.24$). The generalized foraging of the white-eye extends to the understory. In contrast, the akepa rarely forages there. Most native birds, even in a location with a well-established understory, concentrate their foraging on canopy substrates.

White-eyes in 2008 were equivalent to most common native species in their temporal use of ohia trees (Fig. 13). Twelve of the 72 birds (0.17) that entered six ohia trees during one-hour observation periods were white-eyes. This represents an increase from 1989, when only two of 492 birds in 11 trees were white-eyes (0.004; test of proportions, $P < 0.0001$). There was an average of 44 birds per tree in 1989 versus 12 birds per tree in 2008, reflecting depression of all species of native birds in Fig. 13 (see Appendix).

Bill lengths of native species that feed on arthropods in ohia foliage are hyperdispersed. The amakihi/akepa bill size ratio is 1.24 and the apapane (*Himatione sanguinea*)/amakihi ratio is 1.20. For larger birds, such as the iiwi (*Vestiaria coccinea*)/apapane, the ratio is 1.58. The white-eye bill is significantly longer than the akepa bill (11.5 vs. 11.2 mm; *t*-test, $P = 0.005$), but the ratio of 1.03 suggests greater similarity between these species. The ratio of 1.21 for amakihi/white-eye is similar to ratios of native species. The white-eye is also most similar to the akepa in body mass, but heavier (11.3 vs. 10.6 g; *t*-test, $P = 0.0003$).

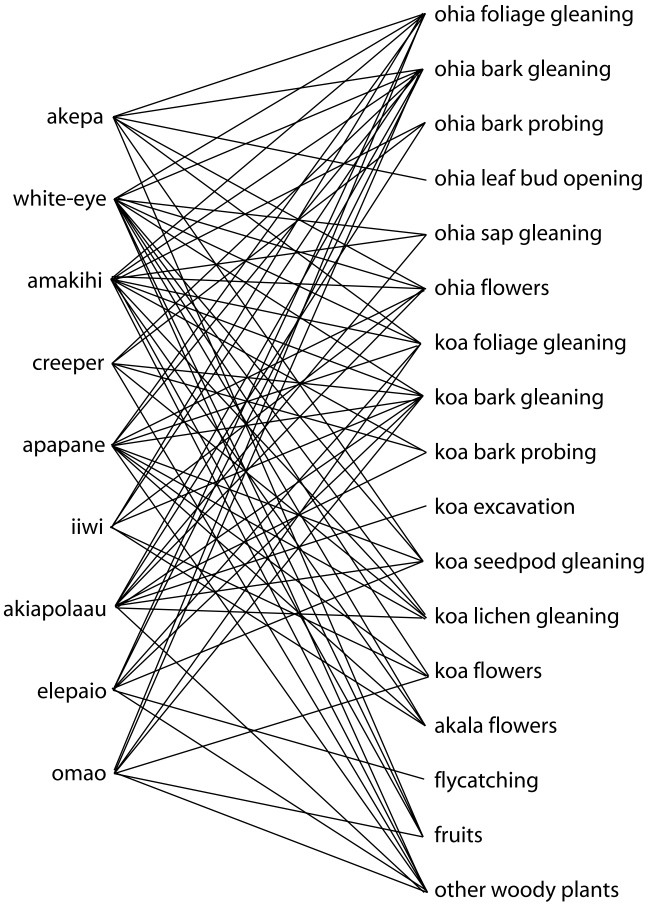

Fig. 11. Hawaiian forest birds and their foraging substrates, showing overlap between introduced Japanese white-eye and every native bird species. References include Fancy and Ralph (1997, 1998), Lepson and Freed (1997), Lepson and Woodworth (2001), Lindsey *et al.* (1998), Pratt *et al.* (2001), VanderWerf (1993, 1998), van Riper (2000), and Wakelee and Fancy (1999).

The breeding seasons of ohia foliage gleaning birds and white-eyes overlap (December–June). However, the akepa nests later in the year (March–June) (Lepson and Freed, 1995), and would be differentially affected by the increase in white-eyes. Native species with longer breeding seasons have a portion of the season with less exposure to cumulative depletion of food by breeding white-eyes. Of the five native species that glean arthropods from the foliage of ohia trees, only akepa manifested a lower young/adult ratio during breeding months in 2000–2005 versus 1987–1999 (paired t-test of differences using akepa value as hypothesized mean: $t = 16.46$, d.f. = 3, $P = 0.0005$).

Role of the white-eye in the widespread decline of the Hawaii akepa. The three sites in the former high-density area of the akepa, where mist-netting efforts were conducted during both time periods, had similar community structure (minus akepa and white-eye) (Morisita's Index of Similarity = 0.98, 0.97, 0.97). Logistic regression shows that the

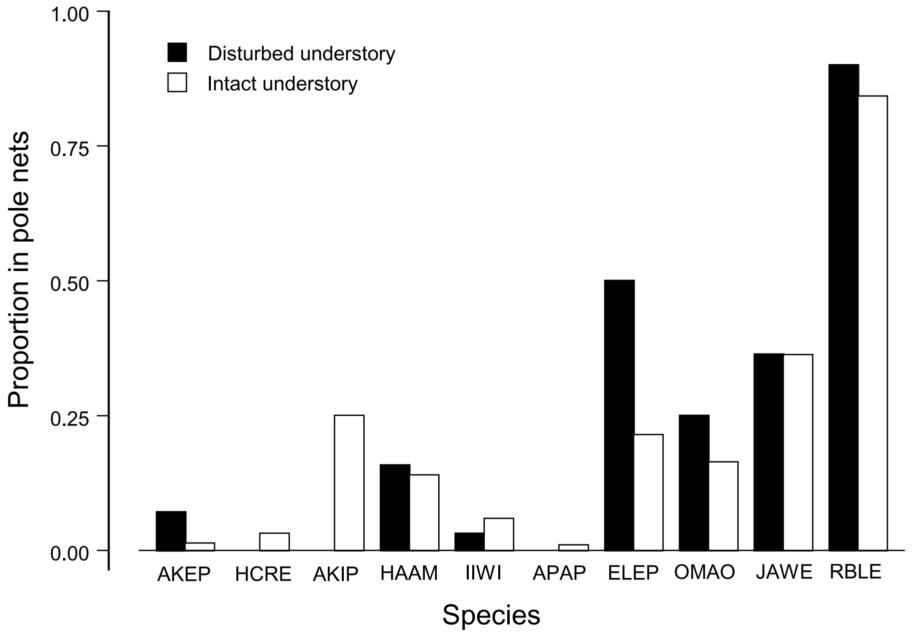

Fig. 12. Proportion of individuals captured in pole-based mist-nets in two study sites (1900 m and 1650 m). At both sites aerial and pole-based mist-nets were operated during 2004–2005. The 1900 m site has a disturbed understory associated with prior cattle ranching. The 1650 m site has a more intact understory. Understory plants are included in Fig. 12 as other woody plants and akala (*Rubus sandwichensis*). Abbreviations: AKEP = akepa, HCRE = Hawaii creeper, AKIP = akiapolaau, HAAM = Hawaii amakihi, IIWI = iiwi, APAP = apapane, ELEP = elepaio, OMAO = omao, JAWE = Japanese white-eye, RBLE = red-billed leiothrix.

white-eye is replacing the akepa in the area (proportion of white-eye, $P < 0.0001$; site, $P < 0.0001$; interaction, N.S.) (Fig. 14). The only potentially viable population was at 1650 m, which had the lowest proportion of white-eyes. The viabililty is based on mass of fledglings. Medeiros and Freed (in press) showed that fledglings that weighed 11 g or more survived as well as adults. When the akepa population at the 1900 m site was viable, 30% of fledglings were of high quality and the proportion dropped to 16% after 2000. The 1770 m site, used during 2004–2005, had only 14% high-quality fledglings. In contrast, the 1650 m site had 40% high-quality fledglings during 2004–2005. However, this was the site where the stressed male akepa without fat was captured during April 2006. The 1580 m site had the highest proportion of white-eye and lowest proportion of akepa. No fledglings were captured at this site.

Associated effects on other species of native birds. In 2006, the endangered Hawaii creeper lost fledglings, before the termination of parental care in August (Hart and Freed, 2003), in the 1900 m site. In May 2006, 12 family groups of creepers were heard throughout the study area. By early July, no more than six parents had fledglings.

In 2008, the creeper bred successfully at the 1900 m site, but fledgling begging changed. Begging was previously a distinctive three-syllable call. In 12 of 14 detections of begging fledglings, the call was only of one or two syllables. Fledglings called only when close to a

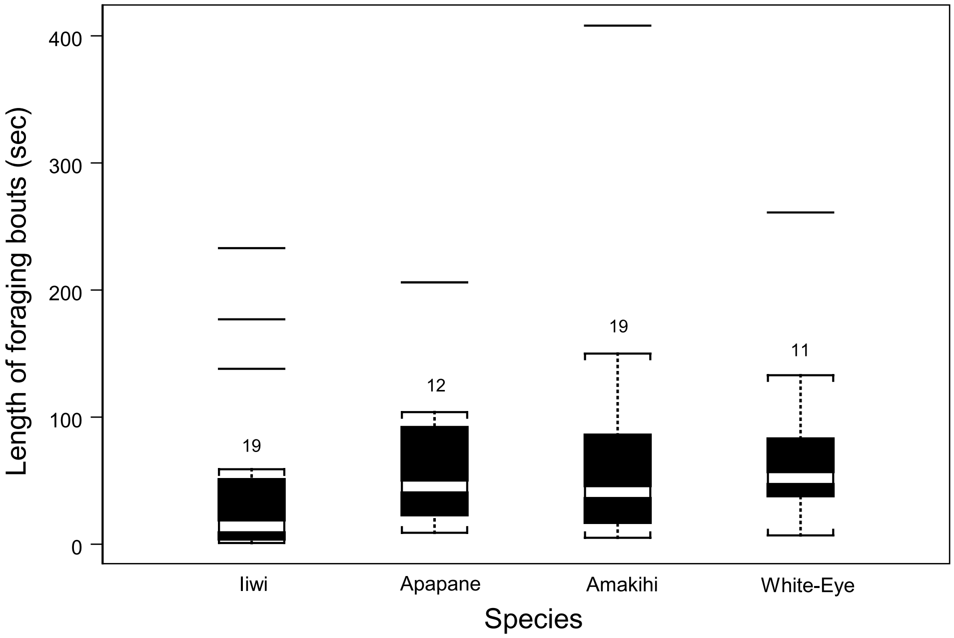

Fig. 13. Box-plots of white-eye and native bird time in ohia foraging substrates. Data are times of foraging bouts of individual birds (sample sizes above caps) in six trees, one hour of observation per tree. The three honeycreepers are the species with highest densities in the study site. Box-plots have the same components as in Fig. 2, with horizontal lines indicating outliers. The Kruskal-Wallis rank sum test showed that at least one of the species (iiwi) differed from the rest ($P = 0.04$). The length of foraging bouts of white-eye in ohia trees is indistinguishable from those of apapane and amakihi.

parent and followed their parents continuously. In the past, fledglings tended to be relatively stationary: a parent would go to a begging fledgling, which would approach the parent when the parent was 1–2 m away.

Other endangered birds disappeared from some sites or became rare during 2008. The akiapolaau was not detected at the 1900 m site during the first 6 months of 2008. At the 1770 m site in May, no Hawaii creepers were detected during 4 hours of good weather, and only three Hawaii amakihi, a normally common honeycreeper, were detected during that time period. Both creeper and amakihi were detected in greater numbers before and after, at the nearby 1900 m site, the same day. Normally common iiwi were rare at both sites and, for the first time, some had orange rather than red plumage.

DISCUSSION

The akepa population crash is different from those documented in other birds and mammals. For these, crashes were caused by harsh winter weather (Arcese *et al.*, 1992; Grenfell *et al.*, 1998; Coulson *et al.*, 2001; Cowley and Siriwardena, 2005; Berryman and Lima, 2006), droughts (Gordon *et al.*, 1988; Young, 1994), oceanographic conditions that affect food availability (Laurie, 1990; Laurie and Brown, 1990), and epizootics (Young, 1994; Caffrey *et al.*, 2005). In these examples, populations recovered because the environmental event that led to the crash was ephemeral, and no community-wide effects were observed or documented. The problem facing the akepa is that the event,

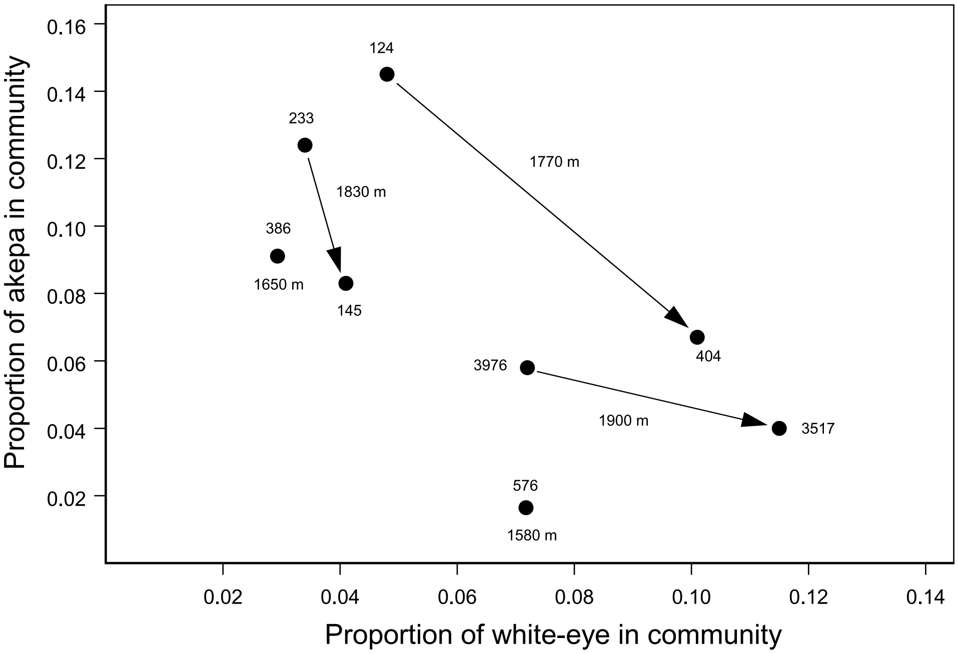

Fig. 14. Changing relationships between Japanese white-eye and Hawaii akepa over time in three different study areas used before 2000 (origin of arrow) and after 1999 (arrowhead). Isolated points are sites in which banding only occurred after 1999. Sites are identified by elevation. Sample sizes indicate the total number of individual birds captured over the relevant years in the time period. The isolated point site with lowest proportion of white-eye is the most viable based on fledgling quality (see text). The isolated site with the lowest proportion of akepa has been this way since the Hawaii Forest Bird Survey in the 1970s (Scott *et al.*, 1986).

consisting of two sets of introduced species, is a permanent environmental change. Other native species are beginning to decline as well from exposure to the same change. Introductions can reveal processes in natural communities (Strauss *et al.*, 2006). Here, the community was not strongly food limited before the white-eye increase, and the higher connectance in the community contributed by white-eyes made the community unstable following the increase.

The declines are based on food limitation. Lower fat levels during the winter months and a high prevalence of fault bars from summer moult indicate that food limitation exists throughout the year (Freed *et al.*, 2008). The changes in foraging movements within and between trees, of surviving akepa in 2006–2008, are consistent with expectations of resource depletion (Charnov *et al.*, 1976). The changes in mate calling and female begging in the akepa, and in fledgling begging and behaviour in the creeper, are the first time these types of changes have been reported in birds. Studies of nestling begging in other species indicate that changes in begging occur when nestlings are food stressed (Kilmer and Johnstone, 1997; Wright and Leonard, 2002). It is likely that the changes in calling and begging by adults and fledglings also reflect food stress. Akepa females showed variable changes, greater begging in 2006, and no begging or simpler begging in 2008. It appears that the lack of calling and the drop in begging syllables are to conserve energy, suggesting that food conditions in 2008 worsened further. Below we discuss the many issues associated with food limitation.

The causes of food limitation

Issues with food limitation must consider the relation between food availability and food requirements. Ectoparasites increase food requirements because birds must replace heat lost through degraded plumage (Booth *et al.*, 1993), and flight may become more costly (Barbosa *et al.*, 2002). In addition, ectoparasites can reduce adult survival by one year of reproductive life (Brown *et al.*, 1995). Increased white-eyes must decrease food availability in all the foraging substrates used. Together, ectoparasites and white-eyes are expected to cause every bird species in the community to experience the combination of more food required but less food available. That was evidenced by lower recapture of individuals with ectoparasites in all species except the largest one, where heat loss would be less, and a higher prevalence of major fault bars in parasitized individuals across all species (Freed *et al.*, 2008). The detrimental effect of ectoparasites is greater during adverse food conditions (de Lope *et al.*, 1993), so a synergism may be involved (Pimm, 1996). The 1770 m site, where the greatest akepa declines occurred, including disappearance of the Hawaii creeper and rarity of the Hawaii amakihi, had a higher prevalence of ectoparasites (Freed *et al.*, 2008) as well as a greater increase in white-eyes than the 1900 m site. However, the high adult mortality of the akepa during the crash included many individuals without ectoparasites. Thus, ectoparasites primarily exacerbated the more general effect of reduced food availability.

Other factors that could affect food requirements were unlikely to play a significant role in the decline in numbers and changes in condition. Unusually cold, wet weather can increase food requirements, but there was nothing exceptional about the weather either since 2000 or during the akepa crash in 2006. The cost of mounting an immune defence from a disease like malaria can also increase food requirements (Sheldon and Verhulst, 1996; Lochmiller and Deerenberg, 2000; Norris and Evans, 2000; Martin *et al.*, 2002). However, it is difficult to imagine how a rare bird like the akepa between 2005 and 2006 could have 55% prevalence of malaria with 100% mortality, while air temperatures were still too low for sporogony of the parasite to occur in the mosquito vector (Benning *et al.*, 2002; Freed *et al.*, 2005), no mosquitoes were detected in attractive oviposition buckets during the first 6 months of 2005, and there was no increase in pox virus in the community that would indicate greater presence of a disease vector. These levels of prevalence of malaria have never been documented at upper elevation in Hawaii (Feldman *et al.*, 1995; Woodworth *et al.*, 2001; Freed *et al.*, 2005).

It is possible that food was also made less available independent of increased numbers of white-eyes. Introduced arthropod predators and parasitoids could be involved. Western yellowjacket wasps (*Paravespula pensylvanica*) have been introduced to Hawaii (Gambino *et al.*, 1987), and nests were detected on the study site almost every year during the 1990s. However, due to active control measures, wasps were less conspicuous from 2000 to 2006 and no nests were detected. In addition, the wasps are surface gleaners and are unlikely to forage on arthropods in lichen, which are hidden relative to foliage arthropods. The escape of parasitoids from biological control programmes has been suspected of lowering arthropod food (Howarth, 1985, 1991), but parasitoids introduced to Hawaii specialize on caterpillars, not spiders. Spiders were several orders of magnitude more numerous in ohia foliage samples than caterpillars (Fretz, 2002), although parasitized caterpillers could be indirectly reducing spiders. The rarity of geometrid caterpillars in 2002, which were common in samples collected during 1994–1997 (Fretz, 2002), might have been due to escaped parasitoids. Alternatively, they could have been consumed by increased white-eyes. A few species of spider wasps (Pompilidae) have been adventitiously introduced to Hawaii (Nishida, 1992).

However, these wasps mainly capture spiders on the ground (Evans, 1953), and were not present in tree fogging in Hawaii (Gagne, 1979), or in experimental studies of ohia arthropods in relation to fertilization (Gruner, 2004). The native flies in the genus *Titanochaeta* parasitize spider eggs (Hardy, 1965), but little is known of their natural history. No native insects are known to have increased.

The problem with independent reduction of food is that levels would have to have been lower in all foraging substrates throughout the year. This is because most species had lower fat levels during the winter months and all species had fault bars acquired during the summer months (Freed *et al.*, 2008). The lack of change in air temperature and precipitation means that productivity was not lower for climatic reasons.

The decline of *Carposina* caterpillars might address the special collapse of the akepa. The lower abundance of the caterpillars in the site with akepa in 1995, compared with the site without akepa, was likely due to regulation of caterpillar numbers through predation by the akepa. The parasitoids detected in the sample in 2001 (in the site without akepa) were not identified, but *Odynerus* parasitoid wasps have long been associated with these caterpillars (Perkins, 1913), before any biological control introductions. It is possible that a recently escaped parasitoid from biological control may also use *Carposina* as hosts. However, the fact that the decline in *Carposina* was detected in 2001 means that akepa adult survival was maintained at a high level for several years (2001–2005) with lower abundance of *Carposina*. This implies that the rest of akepa foraging substrates were sufficient to avoid a population crash during this time period. Stomach samples from akepa reveal a diversity of prey, including spiders, caterpillars, psocids, psyillids, and delphacids (Perkins, 1903; Fretz, 2002). These are all found in ohia foliage samples (Freed *et al.*, 2007).

The decline in *Carposina* raises an important issue in the dichotomy between generalization and specialization. Specialization in relation to loss of a rich nectar source has been recognized as a cause of extinction in some nectarivorous Hawaiian birds (Pimm and Pimm, 1982). The akepa is considered a specialist insectivore because of its laterally asymmetric jaws and legs for opening ohia leaf buds (Richards and Bock, 1973; Knox, 1983; Hatch, 1985). The bird can also use morphology and behaviour to open tightly packed clusters of leaves, but almost any generalized insectivorous bill could be used for that activity. The foraging behaviour of the akepa before 2000 was typically slow and deliberate movement through the foliage. During such foraging bouts, the birds could take prey as encountered, including *Carposina* larvae detected by necrotic tissue on ohia leaf buds. The foraging specialization of the akepa may thus be more its reliance on the most common and frequently used foraging substrate rather than any particular prey item. Since all native birds use multiple foraging substrates, specialization may mean using relatively few substrates. Rapid foraging movements observed after the crash are much more energetically expensive than slow movements, and may have represented risk-prone foraging for larger prey to avoid starvation. They would likely engage in this shift only if small prey were of insufficient supply.

Interspecific competition with Japanese white-eyes

The timing of the white-eye increase and food limitation in all species of native birds implicates exploitative competition between white-eyes and the entire community. The white-eye overlaps some foraging substrates of every native species. Changes in condition of most species, and initial non-viability of the akepa, coincided precisely with the increase in white-eyes; conditions worsened and the akepa crashed with continued exposure. The declines in other endangered and common species, and changes in begging behaviour in the akepa and Hawaii creeper, occurred with further exposure. Because chewing lice on all bird species exacerbated food limitation caused by competition, after the louse increase in 2003, the competition became parasite-mediated (Price *et al.*, 1988; Hudson and Greenman, 1998).

The white-eye may be generating indirect effects as well as directly depleting food resources (Wootton, 1994). One major indirect effect is that the white-eye may be reducing *Carposina* larvae by consuming the adult moths, as has been documented for Hawaii elepaio and Hawaii creeper (Perkins, 1913). Additional indirect effects of competition may result from white-eyes altering arthropod predator/prey ratios in different foraging substrates.

Interspecific competition between introduced and native birds in Hawaii has been anticipated for some time (Conant, 1981; Mountainspring and Scott, 1985; Scott *et al.*, 1986; Pimm, 1996). Negative correlation in density, based on the Hawaii Forest Bird Survey (Scott *et al.*, 1986), is the basis for recognizing the potential for competition (Newton, 1998). However, competition between introduced and native species, in Hawaii or elsewhere, has never been known to contribute to a complete demographic collapse as documented for the akepa. Our study demonstrates how strong exploitative competition between an introduced and native species can be, and shows how quickly and strongly exploitative competition can change the condition of all species in the community. No other introduced bird species has been found to be as generalized as the white-eye, with the potential to compete with every species of native bird because of shared foraging substrates. The effects of a single species of introduced fish on the community of native fish in Lake Victoria (Ogutu-Ohwayo, 1990) come closest to the community-wide effect of the white-eye on the native Hawaiian avifauna.

There are two reasons why the akepa is the most susceptible native species to competition from the white-eye. First, the two species are ecologically similar in morphology and foraging substrates. The theory of limiting similarity (Hutchinson, 1959; MacArthur and Levins, 1967; Abrams, 1983), which has been successfully applied to co-existence of introduced birds in Hawaii (Moulton, 1985), is relevant. Bill length ratios of small honeycreepers that feed on ohia foliage match theoretical expectations. Because of their similarities, the increase in white-eye and decrease in akepa over time suggests that the white-eye is replacing the akepa as the shortest-billed insectivore in the community. Its slightly longer bill gives it an advantage over the akepa. That bill enables it to feed on all prey sizes consumed by akepa and also larger size prey that could not be handled efficiently by the akepa (Wilson, 1975). The use of more substrates than the akepa, and a lower prevalence and intensity of lice (Freed *et al.*, 2008), confer additional advantages.

The second reason the akepa is most susceptible is that the late breeding season of the akepa, compared with white-eyes and common honeycreepers, constrains it to consume ‘leftovers’. There is a seasonal decline in food extending from January to July, and the akepa is constrained by small size in a cool environment to breed during the warmer months of March–June (Freed *et al.*, 2007). The other species can begin breeding as early as the previous December. The specific adaptations shaped by the seasonal decline in food are nestling overgrowth (Freed *et al.*, 2007) combined with mass-related fledgling quality (Medeiros and Freed, in press), and seasonal variation in sex allocation for longer lifespan of sons (Freed *et al.*, in press). These have been dismantled by food limitation associated with interspecific competition. There are now fewer leftovers with the increase in white-eye.

Evolutionary responses to the new exploitative competition are extremely limited because the white-eye uses all but the foraging substrates that require extreme morphological and behavioural specialization. The only possible response of the akepa to this new competition would be a shorter bill to concentrate on smaller prey or exploit a previously unused food resource if one exists. For either alternative, the akepa is now in an evolutionary trap (Schlaepfer *et al.*, 2002, 2005). It is already the shortest-billed of all historically known and fossil honeycreepers (Amadon, 1950; James and Olson, 1991). There have been multiple opportunities from colonizing new islands for a shorter-billed ecomorph to evolve (Freed, 1999). The absence of this suggests that there is no niche available in native forests for a shorter billed honeycreeper. In addition, there are no known prey items that are unused by native birds. If such prey existed, they would also be available to the white-eye.

We can use replacement of the akepa by the white-eye to reinterpret the static results of the Hawaii Forest Bird Survey (Scott *et al.*, 1986). Hakalau Forest National Wildlife Refuge exists in a pocket of low white-eye density surrounded on three forested sides by high-density populations. White-eyes greatly outnumber akepa in the pocket. Areas of vanishingly rare akepa are within higher-density areas of white-eyes. The highest-density region of akepa corresponded to the lowest-density region of white-eye in the refuge from the 1970s. This site, with increased white-eyes, is now approaching much lower-density sites of the akepa. Even outside the refuge, akepa are rare or absent where white-eye are common. Exploitative competition with white-eye may have shaped akepa distribution and abundance documented by Scott *et al.* (1986). Such competition may even explain distributional anomalies, based on rarity or absence of the bird in apparently suitable habits, for the akepa and other species identified by Scott *et al.* (1986). Disease was the previously favoured hypothesis (Scott *et al.*, 1986; Woodworth *et al.*, 2001; Freed *et al.*, 2005).

Why did the white-eye increase?

The increase in white-eyes was temporally associated with regeneration and restoration. Feral cattle and pigs were removed in the study site and contiguous areas during the 1990s. This meant that understory plants were no longer eaten by cows or uprooted by pigs. The result was an increase in food resources that could be used by white-eyes and other native birds that frequently forage in the understory. At the same time, the refuge planted hundreds of thousands of koa trees in pastures outside of the forest. A survey during the summer of 2006 detected white-eyes at almost every station in the restoration area (L. Pejchar, personal communication). During November 2006, we observed a flock of at least 40 white-eyes move from one koa tree to another to take advantage of a Scotorhythrid (Geometridae) caterpillar emergence (R. Peck, personal communication), and have heard them sing in the area during the breeding season. White-eyes do not forage in open pasture, and there were no other land-use changes in the area. We thus suspect that attempts to regenerate and restore the forest, clearly for the benefit of native birds, are having the unintended consequence of increasing the range and number of white-eyes at upper elevation. The population in the range expansion provides the most likely source of immigrants into the forest. Restoration outside of the forest may be giving white-eyes in the forest an additional advantage in competition with the akepa and other native birds.

Restoration problems involving exotic plants are well known (D'Antonio and Meyerson, 2002). This is the first case where problems from an exotic bird have been documented. The site at 1650 m in pristine forest has the lowest number of white-eyes. They may be relatively rare there because of greater distance from restoration sites, although further research is necessary to determine if the more pristine nature of the site is less suitable for white-eyes. For now, it is the only portion of the refuge that may have a viable akepa population.

White-eyes may also be affecting akepa in the Kau Forest Reserve on Mauna Loa, the only other significant population (Scott *et al.*, 1986). The bird has increased in numbers there (R. Camp, personal communication). During 2006, we banded in the Kau for the first time in 19 years (Freed, 1988). The birds appear to be having similar problems maintaining numbers there, based on the observation that an akepa in May had no fat and required a chemical heat pad to alleviate stress. In addition, only two of five colour-banded females had fledglings, a proportion comparable to the poor five of 11 at Hakalau that year.

CONCLUSION

This study has shown that the combination of ectoparasites and exploitative interspecific competition with the introduced bird has put the high-density Mauna Kea population of Hawaii akepa on a rapid trajectory of extinction with a major loss of adults and a severe shortage of young females. The endangered Hawaii creeper and akiapolaau are also affected. The problem is even extending to species of concern like iiwi and unlisted species like the Hawaii amakihi. These impacts of food limitation have not been previously acknowledged (Simberloff, 1981, 1996; van Riper and Scott, 2001). The combination makes *all* native birds conservation-reliant (Scott *et al.*, 2005), meaning that the threats will need to be actively managed.

Control of white-eyes in an experimental study to test for the effect of white-eyes on akepa condition and demographics should thus be the highest priority management for the akepa and other native birds at Hakalau. The site of former high density for the akepa had valuable characteristics of an old-growth forest, including the highest density of large trees with cavities that the birds depend on for nesting (Freed, 2001), and trees with a broader canopy from growing in the absence of close neighbours. These have greater foraging surfaces. The birds are disappearing from the site that best provided their niche requirements in one of the last remaining populations. White-eyes are also abundant in other significant portions of the State for native birds, such as the Alakai Swamp on Kauai and Hanawi Natural Area Reserve on Maui (Scott *et al.*, 1986). Control is likely important in those sites as well.

White-eye control will represent experimental community ecology in a changing world (Lawton, 2000), much like control of native brood parasitic cowbirds (*Molothrus* spp.) to manage endangered and threatened hosts (Kus and Whitfield, 2002), control of introduced fish for the benefit of a declining amphibian (Vredenburg, 2004), and control of introduced common mynas (*Acridotheres tristis*) in New Zealand, with beneficial effects to an entire avifauna (Tindall *et al.*, 2007). Such control is even necessary for future threats. Avian malaria is expected to increase at upper elevation in Hawaii as climate changes (Benning *et al.*, 2002; Harvell *et al.*, 2002). Individuals must be in the best nutritive condition to cope with this disease, especially if they are simultaneously coping with chewing lice.

ACKNOWLEDGEMENTS

We thank the many graduate students, undergraduates, and interns who assisted with data collection, especially Patrick Hart for the forest structure study; Matthew Medeiros, Jansen Santos, Morgan Galland, Alex Frank, Erica Westerman, and Beth Story for re-sighting; Liba Pejchar and Jack Jeffrey for identifying foraging substrates; Liba Pejchar and Robert Peck for sharing data; and two sessions of the Quantitative Field Ecology Course at the University of Hawaii. We appreciate discussion of the issues with Michael Rosenzweig, Stuart Pimm, Ian Newton, Sam Bader, Ed Lempinen, and Barry Stieglitz. The manuscript was improved with comments from Walt Koenig, Erica Westerman, and

Stuart Pimm. Special use permits were provided by Hakalau Forest National Wildlife Refuge. Funding and other support was provided by the MacArthur Foundation World Environment and Resources Program, National Center for Environmental Research (Science to Achieve Results, Environmental Protection Agency R82-9093) to L.A.F. and R.L.C., NSF Graduate Research Scholarship to G.R.B., and Australian Research Council Discovery-Project Grant DP451402 to L.A.F. (Partner Investigator; H. McCallum, Chief Investigator). This paper is dedicated to the memory of Alice W. Freed, who the USFWS would not allow to visit the refuge.

REFERENCES

Abrams, P. 1983. The theory of limiting similarity. *Annu. Rev. Ecol. Syst.*, **14**: 359–376.

Amadon, D. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). *Bull. Am. Mus. Nat. Hist.*, **95**: 151–262.

Arcese, P., Smith, J.M.N., Hochachka, W.M., Rogers, C.M. and Ludwig, D. 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. *Ecology*, **73**: 805–822.

Barbosa, A., Merino, S., de Lope, F. and Moller, A.P. 2002. Effects of feather lice on flight behavior of male barn swallows (*Hirundo rustica*). *Auk*, **119**: 213–216.

Benning, T.L., LaPointe, D., Atkinson, C.T. and Vitousek, P.M. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proc. Natl. Acad. Sci. USA*, **99**: 14246–14249.

Berryman, A. and Lima, M. 2006. Deciphering the effects of climate on animal populations: diagnostic analysis provides new interpretation of Soay sheep dynamics. *Am. Nat.*, **168**: 784–795.

Bonser, R.H.C. 1995. Melanin and the abrasion resistance of feathers. *Condor*, **97**: 590–591.

Booth, D.T., Clayton, D.H. and Block, B.A. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proc. R. Soc. Lond. B*, **253**: 125–129.

Bortolotti, G.R., Dawson, R.D. and Murza, G.L. 2002. Stress during feather development predicts fitness potential. *J. Anim. Ecol.*, **71**: 333–342.

Brown, C.R., Brown, M.B. and Rannala, B. 1995. Ectoparasites reduce long-term survival of their avian host. *Proc. R. Soc. Lond. B*, **262**: 313–319.

Buckland, S.T., Anderson, D.R., Burnham, K.P. and Laake, J.L. 2001. *Introduction to Distance Sampling*. New York: Oxford University Press.

Caffrey, C., Smith, S.C.R. and Weston, T.J. 2005. West Nile virus devastates an American crow population. *Condor*, **107**: 128–132.

Case, T.J. 2000. *An Illustrated Guide to Theoretical Ecology*. New York: Oxford University Press.

Case, T.J. and Bolger, D.T. 1991. The role of introduced species in shaping the abundance and distribution of island reptiles. *Evol. Ecol.*, **5**: 272–290.

Caswell, H. 2001. *Matrix Population Models*, 2nd edn. Sunderland, MA: Sinauer Associates.

Charnov, E.L., Orians, G.H. and Hyatt, K. 1976. Ecological implications of resource depletion. *Am. Nat.*, **110**: 247–259.

Conant, S. 1981. Recent observations of endangered birds in Hawaii's national parks. *'Elepaio*, **41**: 55–61.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H. *et al.* 2001. Age, sex, density, winter weather, and population crashes in soay sheep. *Science*, **292**: 1528–1531.

Cowley, E. and Siriwardena, G.M. 2005. Long-term variation in survival rates of sand martins *Riparia riparia*: dependence on breeding and wintering ground weather, age and sex, and their population consequences. *Bird Study*, **52**: 237–251.

D'Antonio, C. and Meyerson, L.A. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecol.*, **10**: 703–713.

Davis, M. 2003. Biotic globalization: does competition from introduced species threaten biodiversity. *Bioscience*, **53**: 481–489.

de Lope, F., Gonzalez, G., Perez, J.J. and Moller, A.P. 1993. Increased detrimental effects of ectoparasites on their bird hosts during adverse environmental conditions. *Oecologia*, **95**: 234–240.

Diamond, J.M. 1984. Historic extinctions: a rosetta stone for understanding prehistoric extinctions. In *Quaternary Extinctions: A Prehistoric Revolution* (P.S. Martin and R.G. Klein, eds.), pp. 824–862. Tucson, AZ: University of Arizona Press.

Ebert, T.A. 1999. *Plant and Animal Populations: Methods in Demography*. San Diego, CA: Academic Press.

Evans, H.E. 1953. Comparative ethology and the systematics of spider wasps. *Syst. Zool.*, **2**: 155–172.

Fancy, S.G. 1997. A new approach to estimating densities from variable circular-plot counts. *Pacific Sci.*, **51**: 107–114.

Fancy, S.G. and Ralph, C.J. 1997. ‘Apapane (*Himatione sanguinea*). In *The Birds of North America*, No. 296 (A. Poole and F. Gill, eds.). Washington, DC: The Academy of Natural Sciences and The American Ornithologists’ Union.

Fancy, S.G. and Ralph, C.J. 1998. ‘I‘iwi (*Vestiaria coccinea*). In *The Birds of North America*, No. 327 (A. Poole and F. Gill, eds.). Philadelphia, PA: The Birds of North America, Inc.

Feldman, R.A., Freed, L.A. and Cann, R.L. 1995. A PCR test for avian malaria in Hawaiian birds. *Molec. Ecol.*, **4**: 663–673.

Freed, L.A. 1988. Demographic and behavioral observations of the Hawaii akepa. ‘*Elepaio*, **48**: 37–39.

Freed, L.A. 1999. Evolution and extinction of Hawaiian honeycreepers: a comparative study. In *Genetics and the Extinction of Species* (L. Landweber and A. Dobson, eds.), pp. 137–162. Princeton, NJ: Princeton University Press.

Freed, L.A. 2001. Significance of old-growth forest to the Hawaii akepa. *Stud. Avian Biol.*, **22**: 173–184.

Freed, L.A., Cann, R.L., Goff, M.L., Kuntz, W.A. and Bodner, G.R. 2005. Increase in avian malaria at upper elevation in Hawaii. *Condor*, **107**: 753–764.

Freed, L.A., Fretz, J.S. and Medeiros, M.C. 2007. Adaptation in the Hawaii akepa to breed and moult during a seasonal food decline. *Evol. Ecol. Res.*, **9**: 157–167.

Freed, L.A., Medeiros, M.C. and Bodner, G.R. 2008. Explosive increase in ectoparasites in Hawaiian forest birds. *J. Parasitol.*, **94**: 1009–1021.

Freed, L.A., Cann, R.L. and Diller, K. in press. Sexual dimorphism and the evolution of seasonal variation in sex allocation in the Hawaii akepa. *Evol. Ecol. Res*.

Fretz, J.S. 2002. Scales of food availability for an endangered insectivore, the Hawaii Akepa. *Auk*, **119**: 166–174.

Futuyma, D.J. 1998. *Evolution*, 3rd edn. Sunderland, MA: Sinauer Associates.

Gagne, W.C. 1979. Canopy-associated arthropods in Acacia koa and Metrosideros tree communities along an altitudinal transect on Hawaii Island. *Pacific Insects*, **21**: 56–82.

Gambino, P., Medeiros, A.C. and Loope, L.L. 1987. Introduced vespids *Paravespula pensylvanica* prey on Maui’s endemic arthropod fauna. *J. Trop. Biol.*, **3**: 169–170.

Goodman, L.A. 1962. The variance of the product of *K* random variables. *Am. Stat. Assoc. J.*, **57**: 54–60.

Gordon, G., Brown, A.S. and Pulsford, T. 1988. A koala (*Phascolarctos cinereus goldfuss*) population crash during drought and heatwave conditions in south-western Queensland. *Aust. J. Ecol.*, **13**: 451–461.

Grenfell, B.T., Wilson, K., Finkenstadt, B.F., Coulson, T.N., Murray, S., Albon, S.D. *et al.* 1998. Noise and determinism in synchronized sheep dynamics. *Nature*, **394**: 674–677.

Gruner, D.S. 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. *Ecology*, **85**: 3010–3022.

Guest, S.J. 1973. A reproductive biology and natural history of the Japanese white-eye (*Zosterops japonicus japonicus*) in urban Oahu. US Technical Report #29, IBP Ecosystems and MS thesis, University of Hawaii.

Gurevitch, J. and Padilla, D.K. 2004. Are invasive species a major cause of extinctions? *Trends Ecol. Evol.*, **19**: 470–474.

Hardy, D.E. 1965. *Insects of Hawaii, Vol. 12, Diptera: Cyclorrhapha*. Honolulu, HI: University of Hawaii Press.

Hart, P.J. and Freed, L.A. 2003. Structure and dynamics of interspecific flocks of Hawaiian birds. *Auk*, **120**: 82–95.

Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A., Ostfield, R.S. *et al.* 2002. Climate warming and disease risks for terrestrial and marine biota. *Science*, **296**: 2158–2162.

Hatch, J.J. 1985. Lateral asymmetry of the bill of *Loxops coccineus* (Drepanidinae). *Condor*, **87**: 546–547.

Hoelzel, A.R. and Dover, G.A. 1991. Genetic differentiation between sympatric killer whale populations. *Heredity*, **66**: 191–195.

Howarth, F.G. 1985. Impacts of alien land arthropods and mollusks on native plants and animals in Hawaii. In *Hawaii's Terrestrial Ecosystems: Preservation and Management* (C.P. Stone and J.M. Scott, eds.), pp. 149–179. Honolulu, HI: Cooperative National Park Resources Study Unit, University of Hawaii.

Howarth, F.G. 1991. Environmental impacts of classical biological control. *Annu. Rev. Entomol.*, **36**: 485–509.

Hudson, P. and Greenman, J. 1998. Competition mediated by parasites: biological and theoretical progress. *Trends Ecol. Evol.*, **13**: 387–390.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals. *Am. Nat.*, **93**: 145–159.

James, H.F. and Olson, S.L. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part II. Passeriformes. *Ornithol. Monogr.*, **46**: 1–88.

Kilmer, R. and Johnstone, R.A. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.*, **12**: 11–15.

Knox, A.G. 1983. Handedness in crossbills *Loxia* and the akepa *Loxops coccinea. Bull. Br. Ornithol. Club*, **103**: 114–118.

Koenig, W.D. 2003. European starlings and their effect on native cavity-nesting birds. *Conserv. Biol.*, **17**: 1134–1140.

Krebs, C.J. 1999. *Ecological Methodology*, 2nd edn. New York: Benjamin Cummings.

Kus, B.E. and Whitfield, M.J. 2002. Parasitism, productivity, and population growth: response of least bell's vireos (*Vireo bellii pusillus*) and southwestern willow flycatchers (*Empidonax traillii extumus*) to cowbird (*Molothrus* spp.) control. *Ornithol. Monogr.*, **57**: 16–27.

Laurie, W.A. 1990. Population biology of marine iguanas (*Amblyrhynchus cristatus*). 1. Changes in fecundity related to a population crash. *J. Anim. Ecol.*, **59**: 515–528.

Laurie, W.A. and Brown, D. 1990. Population biology of marine iguanas (*Amblyrhynchus cristatus*). 2. Changes in annual survival rates and the effects of size, sex, age, and fecundity in a population crash. *J. Anim. Ecol.*, **59**: 529–544.

Lawton, J.H. 2000. *Community Ecology in a Changing World*. Oldendorf, Germany: Ecology Institute.

Lepson, J.K. and Freed, L.A. 1995. Variation in male plumage and behavior of the Hawaii akepa. *Auk*, **112**: 402–414.

Lepson, J.K. and Freed, L.A. 1997. 'Akepa (*Loxops coccineus*). In *The Birds of North America*, No. 294 (A. Poole and F. Gill, eds.). Washington, DC: The Academy of Natural Sciences and The American Ornithologists' Union.

Lepson, J.K. and Woodworth, B.L. 2001. Hawai'i Creeper (*Oreomystis mana*). In *The Birds of North*

America, No. 680 (A. Poole and F. Gill, eds.). Philadelphia, PA: The Birds of North America, Inc.

Lindsey, G.D., VanderWerf, E.A., Baker, H. and Baker, P.E. 1998. Hawai'i (*Hemignathus virens*), Kaua'i (*Hemignathus kauaiensis*), O'ahu (*Hemignathus chloris*), and Greater 'Amakihi (*Hemignathus sagittirostris*). In *The Birds of North America*, No. 360 (A. Poole and F. Gill, eds.). Philadelphia, PA: The Birds of North America, Inc.

Lochmiller, R. and Deerenberg, C. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos*, **88**: 87–98.

Lydeard, C. and Belk, M.C. 1993. Management of indigenous fish species impacted by introduced mosquitofish: an experimental approach. *Southwest. Nat.*, **38**: 370–373.

MacArthur, R.H. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, **101**: 377–385.

Marques, T.A., Thomas, L., Fancy, S.G. and Buckland, S.T. 2007. Improving estimates of bird density using multiple-covariate sampling. *Auk*, **124**: 1229–1243.

Martin, L.B., II, Scheuerlein, A. and Wikelski, M. 2002. Immune activity elevates energy expenditure of house sparrows: a link between direct and indirect costs? *Proc. R. Soc. Lond. B*, **270**: 153–158.

Medeiros, M.C. and Freed, L.A. (in press). A mass threshold greatly affects juvenile survival in the Hawaii akepa. *Auk*.

Mooney, H.A. and Hobbs, R.J. 2000. *Invasive Species in a Changing World*. Washington, DC: Island Press.

Moulton, M.P. 1985. Morphological similarity and coexistence of congeners: an experimental test with introduced Hawaiian birds. *Oikos*, **44**: 301–305.

Mountainspring, S. and Scott, J.M. 1985. Interspecific competition among Hawaiian forest birds. *Ecol. Monogr.*, **55**: 219–239.

Newton, I. 1998. *Population Limitation in Birds*. San Diego, CA: Academic Press.

Nishida, G.M., ed. 1992. *Hawaiian Terrestrial Arthropod Checklist*. Honolulu, HI: Bishop Museum Press.

Norris, K. and Evans, M. 2000. Ecological immunology: life history trade-offs and immune defense in birds. *Behav. Ecol.*, **11**: 19–26.

Ogutu-Ohwayo, R. 1990. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus. Environ. Biol. Fishes*, **27**: 81–96.

Perkins, R.C.L. 1903. Vertebrata. In *Fauna Hawaiiensis*, Vol. 1, Part IV (D. Sharp, ed.), pp. 365–466. Cambridge: Cambridge University Press.

Perkins, R.C.L. 1913. Introduction to *Fauna Hawaiiensis*. Cambridge: Cambridge University Press.

Petren, K. and Case, T.J. 1996. An experimental demonstation of exploitation competition in an ongoing invasion. *Ecology*, **77**: 118–132.

Pimm, S.L. 1996. Lessons from a kill. *Biodivers. Conserv.*, **5**: 1059–1067.

Pimm, S.L. and Pimm, J.W. 1982. Resource use, competition and resource availability in Hawaiian honeycreepers. *Ecology*, **63**: 1468–1480.

Poole, A., ed. 2005. *The Birds of North America, Online*. Ithaca, NY: Cornell Laboratory of Ornithology.

Pounds, J.A., Fogden, M.P.L. and Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature*, **398**: 611–615.

Pratt, T.K., Fancy, S.G. and Ralph, C.J. 2001. 'Akiapōlā'au (*Hemignathus munroi*) and Nukupu'u (*Hemignathus lucidus*). In *The Birds of North America*, No. 600 (A. Poole and F. Gill, eds.). Philadelphia, PA: The Birds of North America, Inc.

Price, P.W., Westoby, M. and Rice, B. 1988. Parasite-mediated competition: some predictions and tests. *Am. Nat.*, **131**: 544–555.

Richards, L.P. and Bock, W.J. 1973. Functional anatomy and adaptive evolution of the feeding apparatus in the Hawaiian honeycreeper genus *Loxops* (Drepanididae). *Ornithol. Monogr.*, **15**: 1–173.

Roeder, K., Dennis, B. and Garton, E.O. 1987. Estmating density from variable circular plot censuses. *J. Wildl. Manage.*, **51**: 224–230.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. and Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature*, **421**: 57–60.

Ross, S.T. 1991. Mechanisms structuring stream fish assemblages: are there lessons from introduced species? *Environ. Biol. Fishes*, **30**: 359–368.

Schlaepfer, M.A., Runge, M.C. and Sherman, P.W. 2002. Ecological and evolutionary traps. *Trends Ecol. Evol.*, **17**: 474–480.

Schlaepfer, M.A., Sherman, P.W., Blossey, B. and Runge, M.C. 2005. Introduced species as evolutionary traps. *Ecol. Lett.*, **8**: 241–246.

Schoenherr, A.A. 1981. The role of competition in the replacement of native fishes by introduced species. In *Fishes in North American Deserts* (R.J. Naiman and D.L. Soltz, eds.), pp. 173–204. New York: Wiley.

Scott, J.M., Mountainspring, S., Ramsey, F.L. and Kepler, C.B. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. *Stud. Avian Biol.*, **9**: 1–431.

Scott, J.M., Goble, D.D., Wiens, J.A., Wilcove, D.S., Bean, M. and Male, T. 2005. Recovery of imperiled species under the endangered species act: the need for a new approach. *Frontiers Ecol. Environ.*, **3**: 383–385.

Sheldon, B. and Verhulst, S. 1996. Ecological immunology: costly parasite defenses and trade-offs in evolutionary ecology. *Trends Ecol. Evol.*, **11**: 317–321.

Simberloff, D. 1981. Community effects of introduced species. In *Biotic Crises in Ecological and Evolutionary Time* (M.H. Nitecki, ed.), pp. 53–81. New York: Academic Press.

Simberloff, D. 1996. Impacts of introduced species in the United States. *Consequences*, **2**: 1–13.

Slagsvold, T. 1982. Sex, size, and natural selection in the hooded crow *Corvus corone cornix. Ornis Scand.*, **13**: 165–175.

Strauss, S.Y., Lau, J.A. and Carroll, S.P. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecol. Lett.*, **9**: 357–374.

Thompson, B.C., Knadle, G.E., Brubaker, D.L. and Brubaker, K.S. 2001. Nest success is not an adequate comparative estimate of avian reproduction. *J. Field Ornithol.*, **72**: 527–536.

Tindall, S.D., Ralph, C.J. and Clout, M.N. 2007. Changes in bird abundance following common myna control on a New Zealand island. *Pacific Conserv. Biol.*, **13**: 202–212.

VanderWerf, E.A. 1993. Scales of habitat selection by foraging elepaio in undisturbed and human altered habitat. *Condor*, **95**: 980–989.

VanderWerf, E.A. 1998. ‘Elepaio (*Chasiempis sandwichensis*). In *The Birds of North America*, No. 344 (A. Poole and F. Gill, eds.). Philadelphia, PA.: The Birds of North America, Inc.

van Riper, C., III and Scott, J.M. 2001. Limiting factors affecting Hawaiian native birds. *Stud. Avian Biol.*, **22**: 221–233.

van Riper, S.G. 2000. Japanese white-eye (*Zosterops japonicus*). In *The Birds of North America*, No. 487 (A. Poole and F. Gill, eds.). Philadelphia, PA: The Birds of North America, Inc.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. and Melillo, J.M. 1997. Human domination of earth’s ecosystems. *Science*, **227**: 494–499.

Vredenburg, V.T. 2004. Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. *Proc. Natl. Acad. Sci. USA*, **101**: 7646–7650.

Wakelee, K.M. and Fancy, S.G. 1999. ‘Ōma‘o (*Myadestes obscurus*), Kāma‘o (*Myadestes myadestinus*), Oloma‘o (*Myadestes lanaiensis*), and ‘Āmaui (*Myadestes woahensis*). In *The Birds of North America,* No. 460 (A. Poole and F. Gill, eds.). Philadelphia, PA: The Birds of North America, Inc.

White, G.C. and Burnham, K.P. 1999. Program MARK: survival rate estimation from both live and dead encounters. *Bird Study*, **46** (suppl.): S120–S139.

Williams, B.K., Nichols, J.D. and Conroy, M.J. 2002. *Analysis and Management of Animal Populations*. San Diego, CA: Academic Press.

Wilson, D.S. 1975. The adequacy of body size as a niche difference. *Am. Nat.*, **109**: 769–784.

Woodworth, B.L., Nelson, J.T., Tweed, E.J., Fancy, S.G., Moore, M.P., Cohen, E.B. *et al.* 2001. Breeding productivity and survival of the endangered Hawaii creeper in wet forest refuge on Mauna Kea, Hawaii. *Stud. Avian Biol.*, **22**: 164–172.

Wootton, J.T. 1987. Interspecific competition between introduced house finch populations and two associated passerine species. *Oecologia*, **71**: 325–331.

Wootton, J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.*, **25**: 443–466.

Wright, J. and Leonard, M.L., eds. 2002. *The Evolution of Begging*. New York: Kluwer Academic.

Young, T.P. 1994. Natural die-offs of large mammals: implications for conservation. *Conserv. Biol.*, **8**: 410–418.

APPENDIX: LIMITATION OF SURVEY METHODOLOGY COMPARED WITH DEMOGRAPHY AND MIST-NETTING

There are many situations in biology where different methodologies produce different results. For example, indirect analysis of proteins by electrophoresis and direct comparisons of DNA sequences have led to different conclusions about genetic population structure (Hoelzel and Dover, 1991). In this Appendix, we will cover methodologies that have produced contradictory results over the population dynamics within and between the Hawaii akepa and Japanese white-eye.

We documented a significant decline in the endangered Hawaii akepa beginning in 2000 at upper elevation in the core area of its distribution on Mauna Kea, a significant increase in Japanese white-eye at the same time, and significant evidence that the white-eye was replacing the akepa in three study sites that spanned a distance of 2 km. An unpublished analysis of survey data collected during the years 1987–2007 shows no change in numbers of the akepa and the white-eye, and no interaction in numbers between the two species (R. Camp, personal communication). This has prompted the USFWS to favour survey data over demographic data, devalue data indicating increasing food limitation based on fat, mass, fault bars, and stunted growth, and deny permits to continue research. It is thus critical to determine why a discrepancy exists between the two methods. We offer several reasons that may be widely applicable to population biology in a changing world.

Possible reasons for the discrepancy between survey and demographic data include: (1) the dispersion and behaviour of the akepa violate major assumptions of the model used to analyse the survey data; (2) the methodology is too insensitive to detect sudden changes of density in a declining population; (3) the methodology produces artifacts when homogenizing data over a large area; and (4) trend analysis may require new approaches for detecting recent declines. In addition to discrepancies with mist-netting data, survey observations seem incongruous – during 2006, the year of the akepa crash, survey personnel commented on the rarity of akepa detections at upper elevations. This makes it difficult to accept the analysis of survey data that showed no change in numbers of akepa and no change in numbers of white-eye. The observation of silent akepa during recent years (since 2006) further calls the results into question.

The doctrine of survey methodology is that detection of birds decreases with distance and some adjustment must be made to account for individuals missed at a survey station that are likely present (Buckland *et al.*, 2001). The methodology used for Hawaiian forest birds is the variable circular plot (Scott *et al.*, 1986), a variant of a point count. It is based on a detection function that decreases with distance from the centre of the plot where the observer is stationed. Basic assumptions of the detection function are that birds detected closer to the centre of the plot will contribute more to the density estimate than birds detected at greater distances, and that detection probability at the station centre should be perfect (Williams *et al.*, 2002). The detection function is used to calculate the effective area sampled. Then the observed numbers at each station within the effective area can be converted to density (Roeder *et al.*, 1987).

One additional assumption that the Hawaii akepa almost certainly violates is that individuals detected at a station are independent. The akepa is non-territorial, and colourful males have noisy and flashy group displays around females during survey months (Lepson and Freed, 1995). We know that individual males will move more than 100 m to participate in a group display around a female in her fertile period. In this case, a female within the detection envelope will attract many conspicuous birds that would otherwise be outside of the detection envelope. It is important to know the extent to which group displays are encountered during the survey because they falsely increase the counts in the effective area surveyed. This means that birds will be counted that would otherwise not be included.

The assumption of perfect detection at the station centre is considered most important (Buckland *et al.*, 2001). This is where the changing vocalizations over time may be problematical. The surveys involve 8-min counts of all species of birds at the station. The akepa were likely more detectable when females were begging for extended periods of time, and less detectable when silent for 8 min or more. Temporally variable violation of the assumption will bias trend analysis.

In general, there are several advantages for combining data over large areas (Fancy, 1997), and some analyses of survey data combined data from all stations within the refuge for estimating a global detection function. We think this has produced problems recognized as Simpson's paradox, where the analysis of the parts does not add up to the analysis of the whole. For example, analysis of survey data from 1987 to 2005 in the high-density area, which was effectively sampled by two mist-netting study sites, showed that akepa were declining and white-eye were increasing, in agreement with our findings. However, analysis of data over the entire refuge showed no change in either species. The implication was that akepa were increasing and white-eye were decreasing in the part of the refuge outside the high density area. A problem with analysis of data over the entire refuge is that there is extraordinary spatial variation in density of both species (Scott *et al.*, 1986). This spatial variation may include differences in phenology or behaviour. We think that resolution of the paradox should be an important objective of distance sampling. In the meantime, for endangered species, a conservative approach would favour determining changes independently in areas that differ in bird density or habitat.

The manner in which trend analysis is conducted will also shape interpretations of the results. Density estimates are highly variable, so standard regression and time-series approaches may not detect a change unless the change is large and persists for many years. We let the birds inform us that changes occurred at 2000 to use as a break point. The coincidence of the 4-year increase of white-eyes and 4-year failure to capture akepa fledglings is unlikely to be due to chance (16 ways of choosing run of 4 years for each series,

$P = 0.004$ of runs coinciding by chance). Survey data alone are unlikely to identify break points. The use of break points based on changes in condition of the birds can and should be incorporated into regression analyses. For example, the analysis in the core area of endangered birds annualized the trend from 1987 to 2005. It would have been more appropriate to use a break point at 2000 to determine if survey data were consistent with our mist-net data. In general, unless break points are considered, the longer the time-series the more likely that recent trends will be masked by older data.

This problem can also be illustrated by some recent density analyses of birds on the refuge presented at a workshop sponsored by the US Fish and Wildlife Service (Implementing Recovery for Endangered Forest Bird Species in Hawaii, Hilo, Hawaii, 8–10 October 2008). For these, the refuge has been partitioned into elevational strata, and the detection function is based on the current year's data. Standard trend analysis from 1987 to 2007 for middle-elevation birds, which includes our 1900 m site, shows stable to increasing populations of all native birds, as well as the white-eye. However, what was identified as 'short-term trajectories' from 1999 to 2007 showed a decline at middle elevation for all native species (some significant), and a slight increase in white-eye. The same pattern in all eight native species indicates that the decline is unlikely to be due to chance (sign test, $P = 0.008$). It is also informative that the white-eye was the only bird not to show a decline. By performing two regressions, with partially overlapping years, the short-term trajectory was dismissed because of its length. However, a single regression with a break point at 1999 (or 2000 to be consistent with our break point) could be compared with the standard regression without a break point. If the fit were improved with the break point, our demographic conclusions for the akepa would be supported by the survey data, as well as our documentation that other species were similarly affected.

Finally, it is important to consider the problem of pooling viable and non-viable populations in a survey analysis. In a declining population, the birds that formerly were present but missed may no longer be present. In an expanding population, there may be even more birds present but missed. Density estimates can be improved by incorporating covariates (Marques *et al.*, 2007), but the pooling problem may not be improved, unless the covariates relate to the viability. Covariates are used to reduce variability, rather than distinguish sub-populations with different trends.

In conclusion, pooling data across space and the type of analysis employed may mask real demographic trends. Survey and mist-netting operate at different scales. It is a *non-sequitur* to assert that survey results at a large scale mean that demographic results at a smaller scale are wrong. There is a central role for mist-netting in multiple sites to deal with these problems of scale, because a survey alone cannot inform of important changes in condition, such as lower fat, lower mass, novel parasites, degraded plumage, and stunted growth, that precede the shift of a viable population to non-viable. Mist-netting can also document changes in viability more rapidly.