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Authors: Freed, Leonard A., Medeiros, Matthew C., and Bodner, Gustav R.

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EXPLOSIVE INCREASE IN ECTOPARASITES IN HAWAIIAN FOREST BIRDS

Leonard A. Freed, Matthew C. Medeiros, and Gustav R. Bodner
Department of Zoology, University of Hawaii at Manoa, Honolulu, Hawaii 96822 *e-mail: lfreed@hawaii.edu*

ABSTRACT: Ectoparasites, particularly chewing lice in the Phthiraptera (Insecta), affect the ecology of numerous host species. Most lice are highly host-specific, and there are no documented cases of major increases of chewing lice, within populations, over years. During continuous study from 1987–2005 at upper elevation forests on the island of Hawaii, chewing lice were exceedingly rare and, until 2003, were found in just 2 of 12 species of native and introduced birds. From 2003–2005, there was an explosive increase in the prevalence of chewing lice in all host species. There was no change in humidity, or in behavior of hosts, that could have caused an ecological release of existing lice. Based on reduced fat levels and increases in broken wing and tail feathers for most host species, there was apparently a food limitation that preceded the increase. The increase coincided temporally with detection of a nonnative bird that had recently been found in elevations below the study sites. Although there were isolated sightings of this bird on the study sites, seasonal movements and behavior of some species of native birds could also have allowed greater transmission to study sites. Both prevalence and intensity of infection, indexed by number of body regions parasitized, were lower in native species with greater bill overlap, a character that could help birds control lice. Seasonality of prevalence indicated that low prevalence preceded molt and high prevalence occurred after molting of hosts. The number of major fault bars in wing and tail feathers, a sign of nutritive stress, was correlated with intensity of infection, indicating an indirect cost to the hosts of being parasitized. In addition, birds with lice were less likely to be recaptured than birds without lice.

Ectoparasites have played a major role in the ecology and evolution of birds and other host species (Marshall, 1981; Loye and Carroll, 1995; Moller, 1997). They influence nest-site selection (Loye and Carroll, 1998), mate choice (Clayton, 1991; Moller, 1994), nesting success and the ability of parents to efficiently provide care (Moller et al., 1990; Lehmann, 1993; Moller, 1993; Richner et al., 1993; Tompkins et al., 1996; Fitze et al., 2004), and adult survival (Brown et al., 1995). Chewing lice (Phthiraptera) reduce insulation of plumage and force the host to increase metabolism to replace lost heat (Booth et al., 1993). However, despite the importance of ectoparasites to host ecology, there is no evidence of large-scale change in prevalence within a host population or community over a time scale of several years (Johnson and Clayton, 2003; Poulin, 2007). This is especially well-documented for chewing lice, for which known changes in prevalence are normally seasonal (Foster, 1969; Kettle, 1983; Martin et al., 2007). Most avian hosts have them (Johnson and Clayton, 2003), with high host-specificity implying cospeciation (Page, 1993; Hoberg et al., 1997; Paterson and Gray, 1997). Therefore, large-scale changes beyond seasonality would be unusual. Here, we document the first case of an explosive increase in prevalence of chewing lice. The increase proceeded from an initial null condition, for most host species, to a spread throughout a host community of both native Hawaiian birds and established, introduced birds.

The history of chewing lice in Hawaii is confusing. The assumption that each species of native birds has its own species of lice is not supported by early studies. Ectoparasites on endemic land birds have been reported only from the island of Hawaii, where 4 endemic species of chewing lice have been documented for passerines (Price et al., 2003). Each of two common species of Hawaiian honeycreepers (Drepanidinae), iiwi (*Vestiaria coccinea*) and Hawaii amakihi (*Hemignathus virens virens*), had a species of Ischnocera and Amblycera, respectively, in the early twentieth century (Kellogg and Chapman, 1902). However, at that time studies at low elevation on the island also indicated that another honeycreeper, the apapane (*Himatione sanguinea*), shared lice with the iiwi and amakihi, and that some lice ''species'' were shared among sea birds, water birds, shore birds, native passerines, and diverse introduced birds (Kellogg and Chapman, 1902; Zimmerman, 1948; Alicata, 1969). Lice found on the apapane were not included by Price et al. (2003). In addition to the taxonomic shortcomings that these studies admit, there was no mention of lice in the numerous other species of native passerine birds on the island of Hawaii or on the other main Hawaiian islands.

More recent field studies have not clarified the situation. In the 1970s, mites (Acari) and lice were detected among species of native and introduced birds along an elevational gradient on Mauna Loa on the island of Hawaii, but no details were provided on the association of lice and mites with species of hosts (van Riper et al., 2002). More importantly, a comprehensive comparison of amakihi parasites in dry and wet forests, within the same time period, documented 9 species of mites but no lice (van Riper, 1991). The wet-forest site in van Riper (1991) was located close to a site in van Riper et al. (2002). Absence of reports of chewing lice in a native Hawaiian forest bird at mid and upper elevations, as part of a comprehensive parasitological study, suggests that they either were not there or were not common there.

The data reported here are from a 19-yr study of Hawaiian birds in montane forest in a national wildlife refuge, with sites at elevations ranging from 1,585 to 1,900 m. Because we were not permitted by the U.S. Fish and Wildlife Service to collect ectoparasites for identification, we cannot address their origin or association among host species. However, we can document that there has been a recent and explosive increase in lice over the entire host community, and we address these issues in terms of ectoparasite ecology. By comparing prevalence in adult and young birds, and among host species that differ in behavior and life history, we reveal patterns of vertical and horizontal transmission, as well as the intensity of infection, in an entire community of hosts. We also show that differences in bill morphology among hosts explained the variation in intensity of infection, and that ectoparasite prevalence was related to seasonality of molt. In addition, we identify costs of ectoparasitism borne by almost the entire community of hosts, costs that increased with intensity of infection.

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TABLE I. Host species, abbreviations, and mass.

Species	Abbreviation	Mass (g)
Native birds: Drepanidinae		
Akiapolaau (*Hemignathus munroi*)	AKIP	29
Hawaii akepa (*Loxops coccineus coccineus*)	AKEP	11
Hawaii creeper (*Oreomystis mana*)	HCRE	14
Hawaii amakihi (*Hemignathus virens virens*)	HAAM	14
Apapane (*Himatione sanguinea*)	APAP	16
Iiwi (*Vestiaria coccinea*)	IIWI	20
Native bird: Monarchidae:		
Hawaii elepaio (*Chasiempis sandwichensis ridgwayi*)	ELEP	15
Native bird: Turdidae		
Omao (*Myadestes obscurus*)	OMAO	50
Established introduced species captured on study site		
Northern cardinal (*Cardinalis cardinalis*)	NOCA	39
House finch (*Carpodacus mexicanus*)	HOFI	21
Japanese white-eye (*Zosterops japonicus*)	JAWE	11
Red-billed leiothrix (*Leiothrix lutea*)	RBLE	22
Established introduced species not captured on study site		
Common myna (*Acridotheres tristra*)		110
Kalij pheasant (*Lophura leucomelanos*)		800
New introduced species		
Japanese bush-warbler (*Cettia diphone*)		14

MATERIALS AND METHODS

Host species and study sites

The host species, with common and scientific names, are identified in Table I along with body-mass data. (Further reference to species in the text will be by common name.) All but 1 host are passerine songbirds. The native species include 6 Hawaiian honeycreepers (Fringillidae: Drepanidinae), 1 flycatcher (Monarchidae), and 1 thrush (Turdidae). The long-established introduced species from different areas of the world represent the families Fringillidae, Emberizidae, Zosteropidae, and Timaliidae. These have been present at the study sites since at least the mid-1970s (Scott et al., 1986), when censuses were first conducted. The introduced Japanese bush-warbler (Sylviidae) was only recently established on the island of Hawaii (Nelson and Vitz, 1998). Additional introduced species were observed, but were not captured in mist-nets. Mass for these species is from Dunning (1993).

The study was focused at Hakalau Forest National Wildlife Refuge on the windward slope of Mauna Kea, island of Hawaii, from 1987–2005 and during part of 2006. All study sites were in old-growth ohia–koa (*Metrosideros polymorpha–Acacia koa*) forest (Freed, 2001) ranging in elevation from 1,585 to 1,900 m. Five of the 6 sites had the same species of native and introduced birds. The other site lacked 1 of the endangered honeycreepers. Most mist nets for capturing birds were aerial, 15–20 m above ground. Bird holding-bags were used once per bird and sterilized before re-use by soaking in a 1% bleach solution for 10 min.

Site use varied from year to year, although the long-term site at 1,900 m was used in all years beginning in 1987. From 1993–1998, 3 sites at different elevations (1,900, 1,707, and 1,585 m), along a 12-km north-northeast transect from the 1,900-m site, were used for comparison of prevalence among elevations where there was a decrease in density of endangered birds. From 1999–2003, only the 1,900 m site was used. During 2004–2005, 4 sites at different elevations (1,900, 1,768, 1,646, and 1,585 m) were used throughout the year so that time and elevation could be evaluated along with seasonality of prevalence, age of host, and variation among all host species. The uppermost 3 of these sites were along a transect extending east from the edge of the forest, at 1,900 m, into increasingly pristine forest. The fourth site, at 1,585 m, was 9 km north-northeast of the 1,900 m site, in moderately disturbed forest, and afforded an additional 2004–2005 site at the same elevation used during 1993–1998.

Inspection for ectoparasites

Captured birds were routinely inspected for health and condition, including detailed inspection of wing, tail, and body feathers for molt and wear. Body feather regions included head, throat, back, breast, flank, vent, and eye ring. The inspection included blowing on feathers to search for emerging pin feathers close to the skin. Wing and tail feathers were spread and inspected closely for both gaps and pin feathers. In addition, the bird was inspected for poxlike lesions on toes, bills, and wings. These inspections lasted approximately 2 min, allowing close scrutiny of all parts of these small birds. In addition, standard measurements were taken that involved additional opportunity to detect ectoparasites. During every year of the study, there were researchers who had banded birds in other parts of the world and were familiar with mites and lice; there were also banders with no prior experience. The number of banders ranged from 2 to 10 per yr. The highest numbers were for 2002–2005; these years, along with 1994, contained the highest proportion of less-experienced banders. All new banders were shown birds that had ectoparasites so that they could have a mental image with which to recognize them.

Beginning in 1994, 'ectoparasite' was a dedicated column in the banding book. Prior to that, they were mentioned in a note column. Until 2003, documentation of ectoparasites was mainly for presence–absence. Because ectoparasites became more common around 2003, we began to record more detailed data, such as identifying which body regions were parasitized and whether eggs or posthatching stages were seen. A $\times 20$ hand lens was frequently used to inspect the feathers. In addition, the ears of the birds were examined.

Until 2002, mostly mites were detected. These were identified by their round body form on the host and on our hands, as well as by the observation of 8 legs. The presence of feather mites was inferred by the tiny size of the mites and by any small holes in wing and tail feathers that could be attributed to mites. We identified posthatching lice based on elongated shape and, less commonly, by the observation of 6 legs. After 2002, when eggs were first observed, we used egg morphology to infer that both Ischnocera and Amblycera lice were present. Ischnocera lice have numerous small eggs arranged along the base of barbs on contour feathers of the host; Amblycera lice have larger and more-isolated eggs that extend away from the plane of the feather (Marshall, 1981). Although lice were observed attached to wing, tail, and body contour feathers, they were also observed moving on the skin, including orbital skin around the eye, and in the ears; the 2 orders of chewing lice generally could not be distinguished on hosts, so analyses with lice combine Ischnocera and Amblycera.

The number of regions of the body with ectoparasites is 1 component of infection intensity. We distinguished between 1, 2, 3, and 4-or-more regions. The distribution of regions for each host species was compared with a Poisson distribution and then a negative binomial distribution. The latter is commonly observed in parasitological studies (Poulin, 2007). The proportion of individuals in combined classes 3- and 4-or-more was considered an index of intensity for a species. Only chewing lice were used for this index, because most mites were not seen directly but were inferred from small holes in feathers.

Related data

Because bill morphology of avian hosts is considered important for controlling ectoparasites (Clayton and Walter, 2001; Clayton et al., 2005), we measured bill overhang and bill overlap of native host species from specimens in the B. P. Bishop Museum in Honolulu. Measurements were taken using digital calipers accurate to 0.01 mm. Overhang was measured in 2 native species in which the upper and lower bills are not parallel along their entire length; we measured the distance along the upper bill, from the tip to where the closed lower bill met the upper one. Overlap, which is characteristic of Hawaiian honeycreepers, occurs when the upper and the lower bills are parallel, but the lower one is shorter. Overlap was measured along the upper bill, from its tip to the

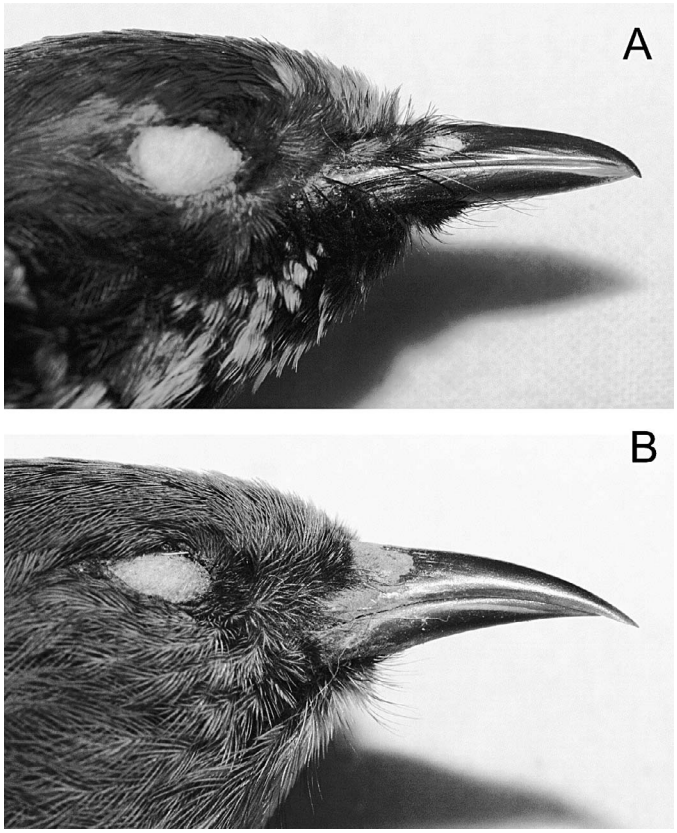

FIGURE 1. Illustration of bill overhang and bill overlap in Hawaiian birds. (**A**) Hawaii elepaio, a monarchine flycatcher. Here the upper bill extends downward in front of the end of the lower bill, illustrating bill overhang. (**B**) Hawaii amakihi, a Hawaiian honeycreeper. The upper and lower bills are parallel, but the lower bill is shorter than the upper bill; this illustrates bill overlap. The overlap is the bill morphology of all Hawaiian honeycreepers. The birds can move the tips of the upper and lower bills together for gleaning. The downward and then forward movement of the lower bill can, in principle, create a force against the upper bill that has a horizontal component analogous to that of simple forward movement of the lower bill of birds with bill overhang.

tip of the lower one. An overhang bill and an overlap bill are illustrated in Figure 1.

Maximum and minimum relative humidity, air temperature, and precipitation were obtained from the MESOWEST web site (http://raws.wrh.noaa.gov). Data were collected by an automatic station at the 1,940-m elevation, approximately centered above all study sites. The data were used to determine if weather changes were associated with the increase in ectoparasites (Moyer, Drown, and Clayton, 2002).

The following data were used to determine if changes in host condition were caused by, or preceded, the increase in ectoparasites: Change in body condition of all hosts was documented by the presence of broken wing and tail feathers, or by changes in fat levels of males, or both. The broken feathers were associated with fault bars lacking melanin (Fig. 2), which gives strength to feathers (Burtt, 1986; Bonser, 1995). Fault bars can be caused by nutritional stress at the time of molting and also by the stress of handling, as well as by inclement weather (King and Murphy, 1984; Negro et al., 1994). We address stress-of-handling in the statistical analyses. Inclement weather can be ignored because molting occurs during the warmer summer months (Freed et al., 2005). Fat levels of males of all species during the colder winter and early spring months (January–April) were compared from 1987–2006. Fat levels in the furcular cavity were scored as 0 (no fat), 0.1 (trace of fat), 1 (partially full), and 2 (full). Lower fat levels reflect food limitation (Brown, 1996). Additional data on change in condition of 1 host, the Hawaii akepa, an endangered Hawaiian honeycreeper,

FIGURE 2. Broken feather, major fault bars, and minor fault bars in tail feathers of the iiwi, a Hawaiian honeycreeper. Note the horizontal orientation in the fault bars and the same orientation in the broken feather. Melanin is lacking in the nonpigmented areas, formed when the bird last molted, and this has created zones of weakness. The major fault bars are generally wider (extending to or almost to the shaft of the feather). The minor fault bars are generally narrower and extend over fewer barbs. It is the level of damage to the barbules that connect contiguous barbs that formally distinguishes major fault bars from the others.

involve the loss of fledglings during 2002–2003. This was documented by following family groups with color-banded parents from time of fledging in May, June, and July.

During 2003–2005, special attention was directed at documenting fault bars in wing and tail feathers of all host species. Sharply defined lines perpendicular to the axis of the feather, and the presence of degraded structural articulations between barbs of the feathers, were classified as major fault bars. Lines with reduced or absent melanin, but structurally intact, were classified as minor fault bars (Fig. 2).

Statistical analyses

Community-wide prevalence of ectoparasites, by year, was estimated by lumping birds of all species. Each bird was counted once in each year captured because an individual, in principle, might gain or lose ectoparasites between years. Prevalence over multiple years was calculated as the sum of numerators and denominators of individual years, reflecting the pool of hosts and ectoparasites over that time period. Direct tests of proportions were used for comparisons of time periods and study areas; for these, an individual was only counted once in each time period. An individual was considered positive within a time period if observed with ectoparasites at least once. Morisita's index of similarity (Krebs, 1999) was used to compare relative abundances of host species between time periods.

Because a large number of personnel were involved in the study, the following test was performed to determine if the increase in prevalence was simply based on more-experienced or -alert researchers: Within each of the 2 time periods, i.e., 1987–2002 and 2003–2005, many individual birds were captured and inspected more than once. An error was defined as a bird that had ectoparasites on a particular capture, but did not have ectoparasites on the next capture. This could result both from observer error or loss of ectoparasites. Assuming that loss of ectoparasites does not vary from year to year, a difference in error rate between time periods could be attributable to observers. A test of proportions was used to compare error rate between the time periods.

Logistic regression was used to analyze prevalence of ectoparasites in individual host species in 2004 and 2005, when comparable banding efforts were conducted in 4 study sites (each having the same host

TABLE II. First detection of ectoparasites by host species.

Species	Yr initially detected	Individuals inspected before initial detection
AKEP	1987	22
OMAO	1987	31
HAAM	1988	88
HOFI	1989	24
APAP	1989	332
IIWI	1989	340
HCRE	1994	74
RBLE	1994	82
JAWE	1994	194
ELEP	1996	148
NOCA	2000	9
AKIP	2005	24

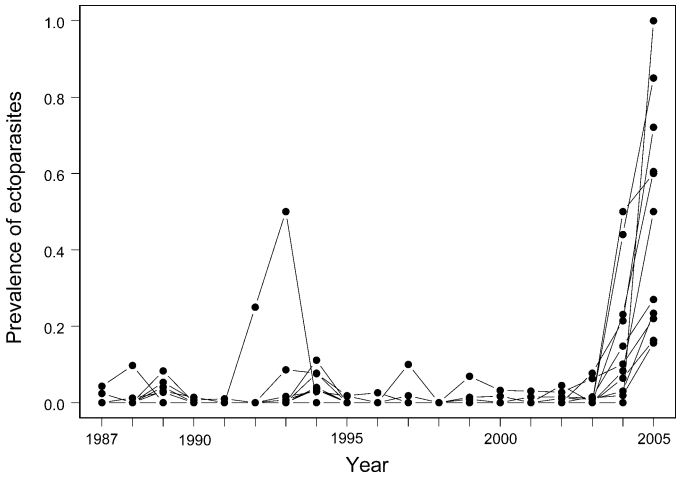

FIGURE 3. Ectoparasite prevalence of 11 species of native and introduced birds for each year from 1987–2005. All cases, except 2, before 2002 involve mites.

species). The model included effects of species, site, year, and the associated interactions. A second analysis classified each individual as an adult or juvenile. This model included effects of species, age, year, and the associated interactions. Analysis of deviance was used for testing effects.

Through logistic regression, we tested the effects of both bill morphology and prevalence on the variation in intensity among host species. Bill overlap–overhang and prevalence in 2005 were explanatory variables in the regression, which used all native species except the akiapolaau. In this species, the lower bill is half the length of the upper bill and is specialized for excavating wood. The bill overlap is too extreme to be useful for controlling ectoparasites. In addition, the sample size for this rare bird was too small to estimate intensity of ectoparasites.

Seasonality of prevalence was analyzed by month during 2004–2005. Each individual was given a monthly score of ectoparasites, i.e., present or not present. The logistic regression model included effects of month, year, and the month-by-year interaction. An effect of month without a significant interaction would reflect seasonality (e.g., Freed et al., 2007).

Changes in fat levels, and in prevalence of broken wing and tail feathers, were analyzed through logistic regression. Effects in each model included species, time period, and the species-by-time-period interaction. One model used 1987–1999 and 2000–2002 as the time periods. This model was to determine if the change occurred before the increase in ectoparasites. A second model used 2000–2002 and 2003–2006 as the time periods, in order to determine if additional change was coincident with the increase in ectoparasites.

Costs of ectoparasitism were tested in 3 ways. First, through logistic regression, prevalence of major fault bars (including broken feathers) was regressed on presence or absence of ectoparasites, host species, and the interaction. Second, for those individuals with ectoparasites, the proportion with 3 or more major fault bars (arcsin transformed) was least-square regressed based on the number of body regions with lice (1, 2, and combined 3 and 4- or more). Third, for each species with lice and sufficient sample sizes, a paired sample Wilcoxon signed-rank test was used to compare the proportion of individuals recaptured with an initial infection status of 'present' versus an initial status of 'absent'. Within the infected birds, a comparison was made between recapture and intensity. A sign test was used to determine if lower recapture of individuals with 3 or more body regions with lice was widespread among species.

RESULTS

During the first 16 of 19 yr, at an elevation of 1,900 m, we detected ectoparasites every year except 1998 and a low overall prevalence of 1.0% (96/8,345). For most species, it took many years and many individuals for the first ectoparasites to be detected (Table II). Community-wide prevalence almost doubled from the 1987–2002 to the 2003 data (1.7% to 2.9%, test of proportions, $P = 0.013$), tripled between 2003 and 2004 (2.9% to 10.0%, $P < 0.0001$), and almost tripled again between 2004 and 2005 (10% to 28%, $P < 0.0001$). All species had increased prevalence of ectoparasites from 2002 to 2005 (Fig. 3). The proportion of birds with ectoparasites, later captured without ectoparasites (combined observer error and genuine loss of ectoparasites), did not differ significantly from 1987–2002 (n = 26 of 135) and 2003–2005 (n = 135 of 864) (19.0% vs. 16.0%, test of proportions, $P = 0.35$). The overall pattern of very few ectoparasites in early years and very many in later years was noted anecdotally by 5 personnel with experience banding birds outside of Hawaii. Those present during the 2002 increase and the 2003–2005 increase were quite surprised at the magnitude of the increase.

The types of ectoparasites differed before and after the increase. Mites were predominant from 1987–2000 (95.2% of 42 records with type of ectoparasite identified), and lice were predominant from 2004–2005 (88.8% of 196 records with type of ectoparasite identified, test of proportions, $P < 0.0001$). Most mites during 2004–2005 were feather mites. Only 2 host species, the Hawaii akepa and omao, had lice prior to 2003, and these cases were isolated for each host within a single year. In 2002, the iiwi was the first bird on the study site observed with chewing lice. Despite extensive inspection of feathers for molt throughout the study, Ischnocera lice eggs were not noted until 2003, and Amblycera lice eggs until 2004; most observations in 2004–2005 were of eggs (699 observations with just eggs and 126 observations were of posthatch individuals). No hippoboscid flies, which can transmit lice from one host to another (Johnson and Clayton, 2003), were detected at any point in the study.

There was no change in community structure of host species captured between the time periods (Morisita's index of similarity = 0.97, 0.98, 0.97 between time periods). In addition, ectoparasites were initially rare in all species (Fig. 3). If all species had hosted chewing lice or mites from 1987–2002, there should have been a correlation between year of first detection and number of individuals sampled before that time. No such correlation existed (rho = −0.26, $P = 0.42$; Table II). There

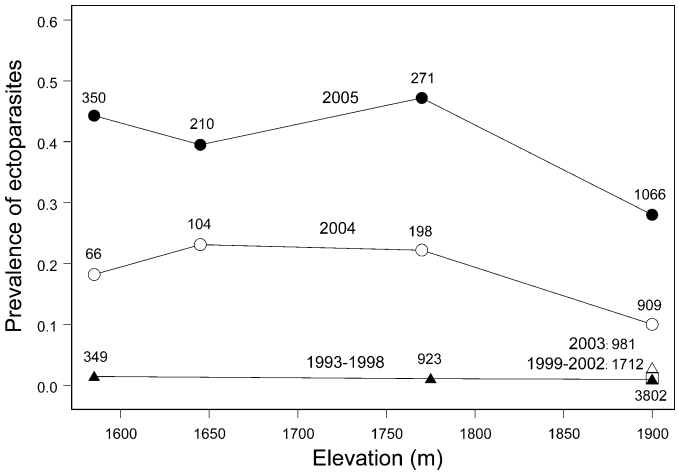

FIGURE 4. Prevalence of ectoparasites by elevation and time. The lower elevation site used during 1993–1998 was 12 km north-northeast of the 1,900-m elevation site. The mid-elevation site in 1993–1998 was 4 km north from the 1,900-m site. The 4 sites used in 2004–2005 are described in the text. Open box represents 1999–2002 prevalence and open triangle represents 2003 prevalence, both at the 1,900-m site.

was also no correlation between 2005 prevalence and the year when species were first detected with ectoparasites (rho = 0.07, $P = 0.83$; data from Fig. 3, Table II). No changes in scratching behavior were noted until 2006.

The increase occurred over a large area (Fig. 4). Three study sites were used from 1993–1998, including the long-term site. These sites spanned an elevational gradient of 330 m over a distance of 12 km. Prevalences of ectoparasites were consistently low, but marginally significantly higher, at the lower elevation (test of proportions, $P = 0.052$). Prevalences were over an order of magnitude higher in 4 study sites, spanning the same elevational gradient and a distance of 9 km, in 2004 (0.13 vs. 0.01, $P < 0.0001$). The increase between 2004 and 2005 occurred across all study sites, with an almost tripling of prevalence (0.36 vs. 0.13, $P < 0.0001$). Logistic regression for 2004–2005 had significant effects for all factors and interactions. The lowest prevalence was at the upper-elevation site.

TABLE III. Analysis of deviance table of logistic regression of 2004–2005 increase in prevalence.

Factor	Degrees of freedom (df)	Deviance	Residual df	Residual deviance	P value (χ^2)
Null	85	740.31			
Site	3	53.58	82	686.74	<0.0001
Species	11	319.72	71	367.02	<0.0001
Year	1	173.55	70	193.47	<0.0001
Site: year	3	29.66	67	163.82	<0.0001
Species: year	11	27.42	56	136.40	0.0040
Site: species	30	92.41	26	43.99	<0.0001

The widespread increase in prevalence affected all 8 native, and 4 long-established, introduced bird species. The logistic regression indicated significant differences among species, age classes, year, and all 2-way interactions. Figure 5 shows the results analogous to interaction plots. All species except the cardinal had higher adult prevalence in 2005 than in 2004. All species except the akiapolaau, elepaio, and amakihi had higher prevalences in young birds in 2005 than in 2004. Overall, adult

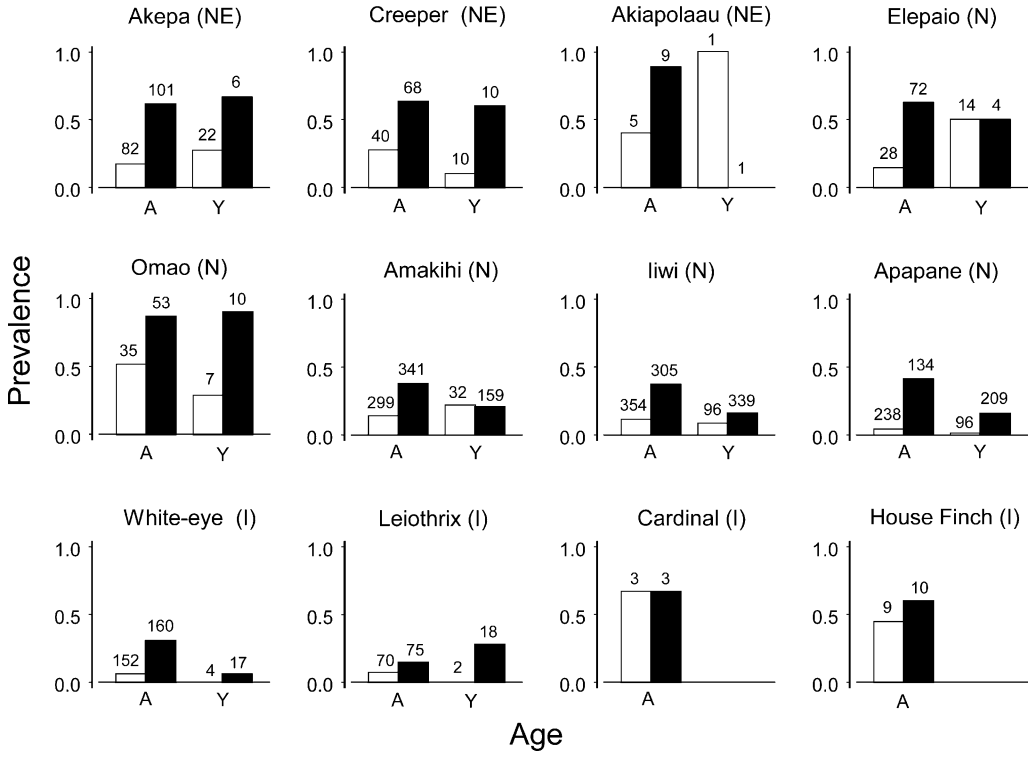

FIGURE 5. Comparison of ectoparasite prevalence among species by age class (A = adults, Y = young) between 2004 (open bars) and 2005 (filled bars). Sample sizes above bars. NE = native, endangered host; N = native host; I = introduced host.

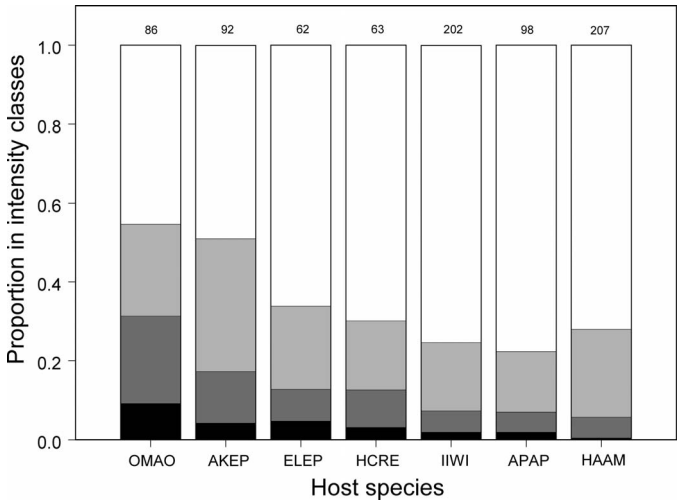

FIGURE 6. Distribution of number of body regions infected by chewing lice of the 7 native species with sufficient sample size. The top of each bar represents 1 region (white), followed by 2 regions (light gray), 3 regions (dark gray), and more than 3 regions (black). All species show aggregation of ectoparasites. An indicator of intensity used for analyses is the proportion of individuals with 3 or more body regions infested.

birds had a higher prevalence than young birds, but in 6 species (akepa, akiapolaau, elepaio, omao, amakihi, and leiothrix), young birds had higher prevalence than adults during 1, or both, years. More-focused analyses revealed that native species had higher prevalence than introduced species (50.0% vs. 20.0%, $P < 0.0001$) and, within the native birds, endangered species had higher prevalence than the unlisted species (57% vs. 46%, $P < 0.0001$).

All species of native birds for which intensity was estimated based on body regions revealed lower proportions of individuals with a greater number of body regions infested (Fig. 6).

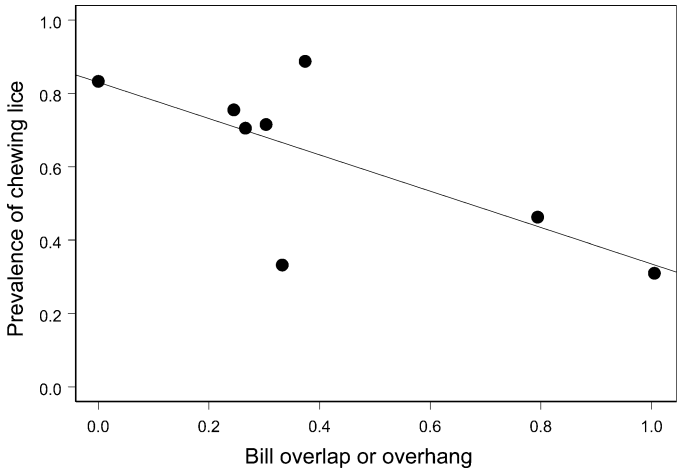

FIGURE 7. Relationship among native host species between prevalence of ectoparasites and bill overlap or overhang. The akiapolaau, with its unusual bill morphology, was assigned an overlap value of 0.0. The outliers are the omao, with higher prevalence than expected, and the apapane, with lower prevalence than expected. The line shown is a least-squares regression line, but the analysis included intensity and prevalence in a logistic regression. The akiapolaau was excluded from that analysis because of a too-low sample size for estimating intensity.

TABLE IV. Analysis of deviance table of logistic regression of bill overlap and prevalence on intensity of ectoparasitic infection.

Factor	Degrees of freedom (df)	Deviance	Residual df	Residual deviance	P value (χ^2)
Null	6	40.96			
Overlap-overhang	1	15.56	5	25.41	<0.0001
Prevalence	1	18.99	4	6.41	<0.0001
Overlap: prevalence	1	0.61	3	5.81	0.44

The Poisson distribution was rejected for each species (all $P < 0.01$), reflecting aggregation. When sample size permitted analysis, the negative binominal model adequately described the observed frequency distribution. There was significant correlation between prevalence and intensity (rho = 0.84, $P = 0.018$).

Bill overlap and overhang, treated as a single character, varied among species and was closely related to prevalence (Fig. 7). Logistic regression showed that intensity varied with both overlap–overhang ($P < 0.0001$) and prevalence ($P < 0.0001$), when overlap–overhang was entered into the model first (Table IV). Overlap–overhang in the model alone accounted for approximately 50% of the lack of fit for the nonparameterized (null) model.

The increase of prevalence in 2004–2005 was seasonal (Fig. 8). Logistic regression had significant effect for mo ($P < 0.0001$) as well as yr ($P < 0.0001$). The interaction was just marginally significant ($P = 0.05$), suggesting a seasonality signal that persisted during the increase. Several patterns stand out: First, in both years, highest prevalances were during the months of October–December. During 2004, 8 of 10 species, and during 2005, 7 of 10 species, had their highest prevalences during these months, so the seasonality is widespread in the community. Second, during both years, lowest prevalence was during July. Both adult and young birds contributed to the low prevalence (logistic regression, age effect, $P = 0.67$).

Molt and breeding data of host species are shown in Figure 9. The seasonal low point of prevalence coincides with the last nesting month and the first month of main molting for these years. The seasonal high point occurred late in the molting sea-

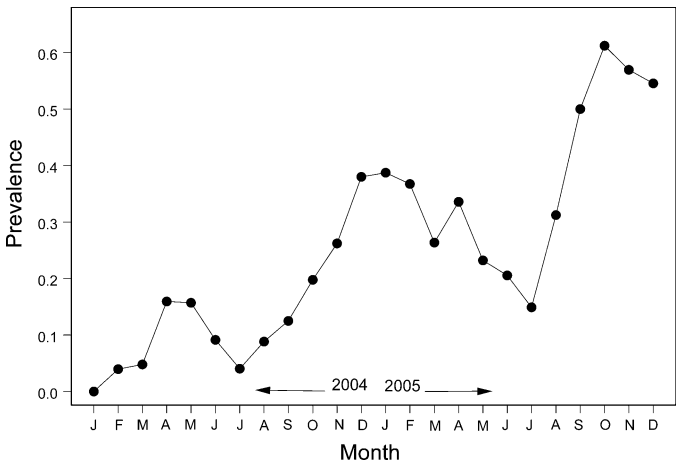

FIGURE 8. Seasonality reflected by monthly community-wide prevalence on adult hosts during 2004–2005.

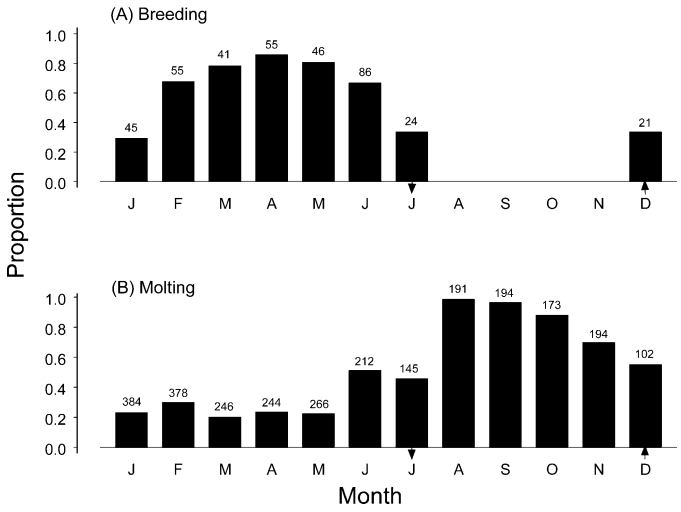

FIGURE 9. Breeding and molting phenology of adult hosts during 2004–2005, combined. Breeding data are from females with a brood patch. The molting during months before June represents mainly individuals from the previous year that did not finish their molt. Generally, adults begin to molt in June and finish in November or December. Downward and upward pointing arrows indicate seasonal low and high prevalence of ectoparasites from Figure 8.

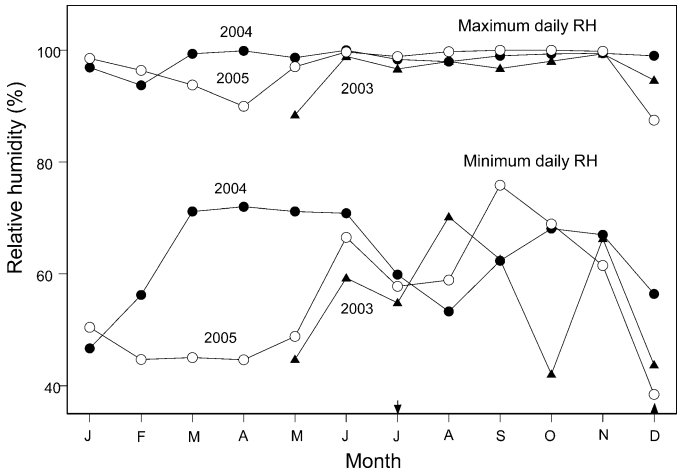

FIGURE 10. Maximum and minimum relative humidity from mid-2003 through 2005. Points are monthly means from daily records. Downward and upward pointing arrows indicate seasonal low and high prevalence of ectoparasites from Figure 8.

son. Most wing and tail feathers were molted during June–October, at which time there was continuous molt of small body feathers. The seasonal high point occurred when hosts had predominantly fresh feathers.

Climatic factors were not associated with the increase in prevalence. Relative humidity varied significantly among month and year ($P < 0.0001$ for mo and yr for both maximum and minimum relative humidity), but levels never reached xeric conditions at any time from 2003–2005 (Fig. 10). During the larger 2004–2005 increase, there was no correlation between monthly prevalence and high humidity (rho = −0.14, $P = 0.50$), low humidity (rho = −0.12, $P = 0.58$), high air temperature (rho = −0.03, $P = 0.87$), low air temperature (rho = −0.17, $P = 0.43$), or precipitation (rho = −0.09, $P = 0.66$).

Changes in biological condition of hosts preceded the increase in ectoparasites, and further changes occurred during the increase. After 2000, males of most species had significantly lower fat levels during the months of January–April (Fig. 11a; logistic regression with effects of time period [$P < 0.0001$], species [$P < 0.0001$], and the interaction between time period and species [$P = 0.003$]). There was also a significant increase in broken wing and tail feathers during 2000–2006 compared with previous years (Fig. 11b; logistic regression with effects of time period [$P < 0.0001$], species [$P = 0.0001$], and the interaction between time period and species [$P = 0.84$]). Further analyses showed that more birds had lower fat levels, and more birds had broken feathers, from 2000–2002 than from 1987–1999 (period effect for each analysis, $P < 0.0001$). The changes in fat partially reversed from 2003–2006 ($P < 0.0001$), but fat levels were still lower than for 1987–1999 ($P < 0.0001$). Changes related to broken feathers increased further from 2003–2006 ($P < 0.0001$). In addition, during 2002–2003, there was a loss of Hawaii akepa fledglings, from a minimum of 6 families, at least 2 mo before the normal termination of parental care; thus no fledglings were captured in mist nets. This was unprecedented, based on captures of fledglings in comparable months during previous years with equivalent mist-netting effort.

Another biological change was the addition of a new, introduced host species. In 2005, a Japanese bush-warbler was observed on the 1,900-m study site for the first time; however, no bush-warblers were captured in mist nets or appeared to be established on the site.

There was an indirect cost to being parasitized. While host species differed in prevalence of major fault bars (Fig. 12; logistic regression, $P < 0.0001$) for all species, parasitized individuals were more likely to have major fault bars, including broken wing and tail feathers (Fig. 12; $P < 0.0001$). The av-

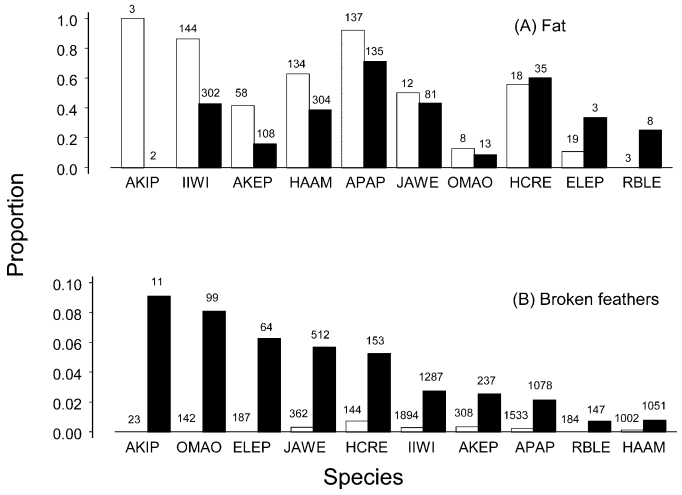

FIGURE 11. (**A**) Changes in fat levels among males during the cold months of January–March from 1987–1999 (open bars) and from 2000–2006 (filled bars). Data are proportion of males that have more than minimal fat. (**B**) Changes in proportion of individuals that have broken wing or tail feathers (see Fig. 2) before 2000 (open bars) and from 2000–2006 (filled bars). Species are ranked from left-to-right by magnitude of decreasing change (including reversal) in (**A**) and magnitude of increasing change in (**B**). Sample sizes are shown above bars.

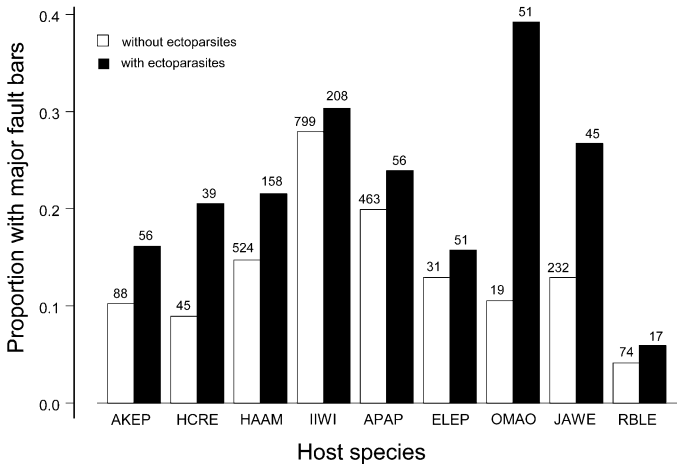

FIGURE 12. Comparison of proportion of individuals with major fault bars of each species in relation to being infected with chewing lice. White bars indicate birds without ectoparasites. Black bars indicate birds with ectoparasites. Data are from 2003–2005.

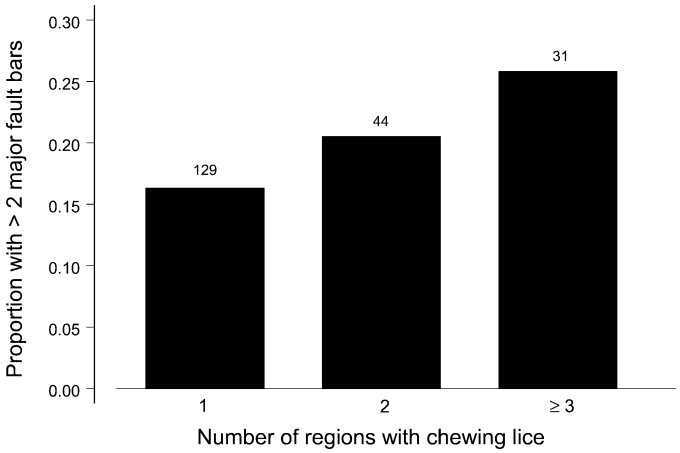

FIGURE 13. Comparison of intensity of major fault bars in relation to number of regions infested with chewing lice. All native species, and 1 introduced species, were involved in the analysis. Data are from 2003–2005.

erage increase in proportion associated with ectoparasitism was 58%. There was also a positive relationship between number of body regions parasitized and the proportion of parasitized birds with 3-or-more fault bars (Fig. 13; regression, $P = 0.04$). Initially captured birds had a higher proportion of fault bars than recaptured birds (0.71 of 3,608 vs. 0.62 of 1,324 individuals, test of proportions, $P < 0.0001$), indicating that handling of birds did not promote fault-bar formation.

Birds with chewing lice were less likely to be recaptured than birds without chewing lice (Fig. 14; Wilcoxon test, $P = 0.006$). This pattern occurred in 9 of 10 species. Using just birds with lice, those that had 3 or more regions were less likely to be recaptured, but not significantly so, than those with 1 or 2 regions (Wilcoxon test, $P = 0.32$). However, 8 of 10 species had lower recapture probabilities of individuals with high-intensity infections, suggesting that intensity may be relevant (sign test, $P = 0.054$).

DISCUSSION

The increase of chewing lice reported here is the most explosive community-wide increase known for any parasite of wild animals (Poulin, 2007), from near 0 to levels comparable to colonial sea birds (Eveleigh and Threlfall, 1976) and Neotropical birds (Clayton et al., 1992), in just 3 yr. The only other increases of this magnitude in parasites are those of a single species of cyprinodont fish with significant inter-year variation in prevalence associated with abiotic factors (Janovy et al., 1997). Ectoparasites are macroparasitic (Anderson and May, 1979), yet in our study, their increase had all the characteristics of a major microparasitic epizootic, with low resistance among hosts and rapid transmission (Dobson and Hudson, 1995). Despite having many inexperienced personnel associated with the study, the proportion of missed detections was similar before and during the increase, so the increase cannot be attributable to better detection during that time. Here, we discuss problems associated with the origin of the lice, the transmission dynamics, variation in prevalence among host species, the emerging pattern of seasonality, and the costs to the hosts.

The explosive increase is without precedent and draws attention to the lack of basic knowledge of avian chewing lice population dynamics in long-term studies. Any hypothesis to account for such an increase is difficult to reconcile with the short time-span of the increase, its synchronous occurrence across all species and in all study sites, and with the apparent lack of host specificity. However, we propose 2 hypotheses, i.e., one based on ecological release and the other on host-switching. The ecological release hypothesis assumes that each species of native and introduced bird on the study site had lice, and that there was a contemporaneous increase in prevalence of each species due to a change in some underlying limiting factor. For an ectoparasite, that factor could involve changes in behavior of hosts that facilitated transmission, or a higher intensity on hosts

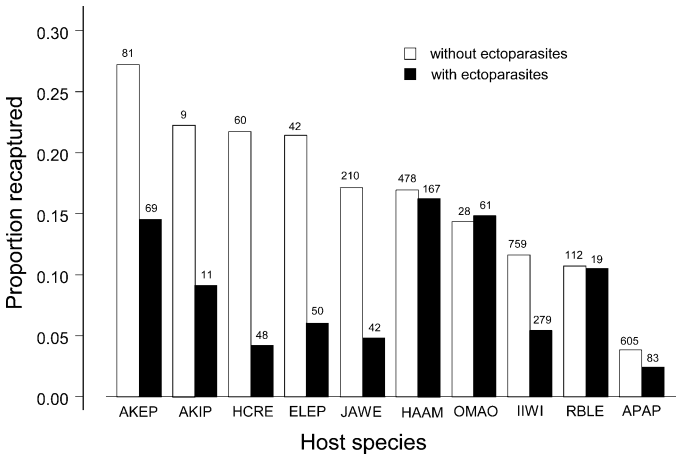

FIGURE 14. Recapture of individual birds identified without ectoparasites (white bars) and those with ectoparasites (black bars). Data come from the 4 study sites used during 2003 to mid-2006. Too few years are involved for formal mark-recapture analysis, especially because many birds were not recaptured for 3 or 4 yr after initial capture. Therefore, the proportions should not be considered estimates of survival. Rather, it is the difference between proportions that addresses the potential cost of ectoparasitism. The species are ranked by proportion of recaptures of individuals without ectoparasites. Sample sizes are indicated for each category. Ectoparasites are exclusively chewing lice.

that could increase the likelihood of intraspecific transmission. There is not a requirement that each host species has its own lice. The host-switching hypothesis assumes that each species on the study site originally lacked chewing lice, or had very few, and that each host acquired lice species from a new source. It is important to realize that these hypotheses are based entirely on existing empirical patterns, with notable exceptions (Poulin, 2007).

The assumption of the ecological release hypothesis, i.e., that each host species already had lice, has the problem of explaining why those lice species were so rarely detected, and in only 2 host species, in 15 yr of study by experienced researchers. Extensive behavioral observations of Hawaii akepa were documented each year since 1987 (e.g., Lepson and Freed, 1995). Like most birds, regular preening involves the bird scratching the back of its head with its foot. A novel scratching behavior was only observed in 2006; the bird would lift a foot, rotate it inward, stroke the breast from anterior to posterior on the opposite side, and repeat with the other foot. Any distinctive and conspicuous behavior, such as the akepa scratching, should have been observed throughout the study if the birds had been hosting chewing lice all along. The early years of the study were also consistent with the comprehensive parasitological study of Hawaii amakihi by van Riper (1991), in which no lice were documented.

An absence of lice may not be as surprising for Hawaii as for some other places. ''Missing the boat,'' meaning loss of ectoparasites associated with founder events, is known to occur in chewing lice–host co-evolution (Paterson and Gray, 1997; Paterson et al., 1999). For native birds on the island of Hawaii, there have been multiple opportunities for ectoparasites to be lost from initial colonization of the oldest island, Kauai, followed by a minimum of 3 founder events to the island of Hawaii through Oahu and Maui (Cann and Douglas, 1999; Freed, 1999). There may be a problem in identifying endemic lice for iiwi and amakihi (Price et al., 2003), because Kellogg and Chapman (1902) identified lice on these species, and also on the apapane and diverse other native and introduced birds, at low elevations on the island of Hawaii.

Despite the significant relationship between intensity of parasitism and bill overlap–overhang, the association does not support the assumption of the ecological release hypothesis, i.e., that the birds had chewing lice all along. There is no evidence that any of the host species had bill overlap or overhang that evolved for the purpose of controlling ectoparasites. The 3 species of native birds with low intensity and more overlap are primarily nectarivorous. The overlap is associated with manipulating flowers to expose the nectar pool or to guide the tongue into the nectar pool. The micro-evolutionary change in iiwi bills is associated with a switch to ohia flowers without corollas, leading to a shortening of the upper bill but not the lower bill, thereby effectively reducing the overlap (Smith et al., 1995). Cranial kinesis enables the birds to extend the lower bill for use as pincers, with the upper bill used for gleaning arthropods on foliage or bark. This movement, evolved for feeding, could be available for controlling ectoparasites because the tip of the upper bill could be placed in front of the ectoparasite, and the lower bill could exert a force on the upper bill that could be partitioned into a horizontal as well as a vertical component. The horizontal component would effectively crush, dislodge, or puncture the louse, as is hypothesized for birds with sufficient overhang (Clayton et al., 2005). Sufficient bill overhang or overlap could help control ectoparasites, but the relation between intensity and bill overhang or overlap does not involve primary adaptation for controlling ectoparasites in these birds.

There were changes in host condition that could potentially lead to ecological release of existing ectoparasites, but they did not come at the right time period to explain the increase in ectoparasites. The changes in fat levels and broken feathers reflect food limitation, as does the early loss of fledgling akepa in 2002–2003. The birds may have suffered food limitation, directly or indirectly, because they spent more time preening than feeding. However, the changes in fat levels and broken feathers during 2000–2002 preceded the increase in chewing lice by 3–4 yr, and the loss of fledglings preceded the increase by 1–2 yr. If the birds already had chewing lice, the increase in prevalence should have been observed sooner. There is no support for the ecological release hypothesis based on changes in condition of the birds.

The rare presence of chewing lice in 2 native species before 2002 was not consistent with the ecological release hypothesis and does have alternative explanations. The case with the akepa, having a body mass of 11 g, was in 1988, a rare year in which the common myna (110 g), a species with lice (Kellogg and Chapman, 1902), nested briefly in cavities used by the akepa. In 2004–2005, we also captured some myna outside of the forest that had a high intensity of lice. The case with the omao (49 g) was in 1995. This frugivorous bird is occasionally captured close to the ground in the lower trays of pole-based nets near fruit. The Kalij pheasant (800 g) feeds on fruit close to the ground; this pheasant is known to have lice (Lewin and Mahrt, 1983). The size differentials of the species pairs are an order of magnitude different, and this would make it difficult for transferred lice to persist on new hosts (Tompkins and Clayton, 1999; Clayton et al., 2003; Bush and Clayton, 2006). Lice were not found on these species again until 2002, despite numerous captures and inspections, implying that the lice were lost from the few host individuals in the earlier years.

The host-switching hypothesis, i.e., that the chewing lice were from a new, introduced species of bird, is unlikely if most lice are host-specific; narrow host-specificity appears to be common in avian chewing lice (Price et al., 2003). However, numerous cases exist for host-switching and host-sharing (Clayton et al., 2004; Poulin, 2007). Indeed, the majority of the study species are close to the size of the recently colonized, introduced Japanese bush-warbler (Nelson and Vitz, 1998), i.e., they are mostly within the 25% difference in size (Table I) required for successful transfer, a difference based on much-larger columbiform birds (Bush and Clayton, 2006). The greatest problem for the host-switching hypothesis is that the omao, with the highest prevalence, is much more than 25% larger than the next-largest species. However, these are all passerine species and all are much smaller than columbiformes. For small passerine birds, the absolute-size difference may be more important than relative-size difference. The size difference for effective transfer may be much larger than 25% for smaller birds. This is a problem that requires experimental work.

Although the bush-warbler was detected only rarely in the study sites, this does not pose a problem for the host-switching hypothesis because both the iiwi and apapane left the study sites

during both the nonbreeding months and during the time that the iiwi is territorial (Carpenter and McMillen, 1976). We have observed frequent interspecific territoriality; therefore, physical contact with a species with chewing lice, either on or off the study site, is possible. In addition, both sympatry and shared microhabitats have been indicated as factors for the sharing of ectoparasites (Price and Clayton, 1983; Clayton, 1990), so the relatively simple ohia–koa forest (Freed, 2001) may contribute to close contact among species as they forage.

Collection of lice for identification is essential for distinguishing the ecological release and host-switching hypotheses. Either would be the first such examples, at this scale, in avian ectoparasite ecology. In addition, the empirical pattern indicating that introduced species typically lose their parasites (Paterson and Gray, 1997; Paterson et al., 1999; Torchin et al., 2003) apparently does not apply to all introduced Hawaiian birds. All 4 introduced passerines established on the study site showed the same increases as the native host species, so this particular subset may fit the empirical pattern. However, recent studies of native and introduced birds on the island of Oahu have revealed that all 13 passerine species captured thus far, including 11 introduced species, have chewing lice (identification pending). There were 140 species of introduced birds from at least 5 continents in Hawaii (Moulton et al., 2001). There is a possibility that generalist lice from one or more of these species, even those that were not successfully naturalized, could become established on both introduced and native species with appropriate body size. Study of the Japanese bush-warbler at lower elevations indicated high prevalence and intensity of ectoparasites (J. Foster, pers. comm.). Rare events involving mixing of hosts must have occurred during the evolutionary history of lice; Hawaii might be an example of such events.

Regardless of the origin of ectoparasites, horizontal transmission within species is necessary for such an explosive increase in prevalence. Such transmission involves fights between males and copulations between mates, events universally observed in birds. Hawaiian birds also show some behavior that is less universal. Within all species of native Hawaiian birds, for example, fighting males are known to interlock and fall to the ground. While rare, but observed several times per year per species, such prolonged contact provides greater opportunity for successful transmission. This behavior could account for an explosive increase, even in rare species. In addition, 3 of the rare species are commonly found, in flocks with their offspring, for 4 mo of the year, along with other native and introduced species (Hart and Freed, 2003). Horizontal transmission between adults of the same species might be enhanced by the social behavior of flocking.

The variation in prevalence among young birds in the various host species suggests variation among species in the strength of vertical transmission. The high prevalence of ectoparasites in young birds is concentrated in the 3 species of endangered honeycreepers, as well as in the native omao and elepaio (Fig. 5). The endangered honeycreepers (Hawaii creeper, Hawaii akepa, and akiapolaau) have lengthy fledgling periods, ranging up to 8 wk, 12 wk, and 1 yr, respectively (Freed, 1999). The omao has postfledging care lasting for 40–45 days (Wakelee and Fancy, 1999), and postfledging care in the elepaio extends for more than 1 mo (VanderWerf, 1998a). All other species, with a lower prevalence of ectoparasites in young birds, have fledgling periods that are 1 mo or less. The extended parental care of species with a high prevalence of ectoparasites in young birds provides greater opportunity for transmission from parents to offspring.

Long fledgling periods can even result in a different type of vertical transmission. Vertical transmission in birds is assumed to occur in the nest (Johnson and Clayton, 2003). However, generation time of lice, based on incubation of eggs (4–10 days) and 3 nymphal stages (3–12 days for each), is about a month (Marshall, 1981; Johnson and Clayton, 2003). For host species with fledgling periods longer than louse-generation time, parents that are uninfected during the nestling period may acquire lice during the fledgling period and then transmit them vertically to their fledglings. Lengthy fledgling periods are characteristic of tropical birds (Ricklefs, 1969; Stutchbury and Morton, 2001). The 2 patterns of vertical transmission, i.e., to nestlings and to fledglings, may explain why high prevalence may be sustained in Neotropical species (Clayton et al., 1992).

Horizontal transmission between species is possible, because lice are known to be shared among host species elsewhere, based on sympatry, similar microhabitat, and similar body size (Price and Clayton, 1983; Clayton, 1990; Tompkins and Clayton, 1999; Bush and Clayton, 2006), assuming that the lice can escape from new host species defenses (Clayton et al., 2003). The old growth ohia–koa forest, in which the increase in prevalence occurred rapidly, consists predominantly of ohia trees (Freed, 2001). Native host species glean arthropods from the foliage, twigs, and bark, and many species are found in the same tree at the same time. In addition, we have observed territorial iiwi physically contact Hawaii akepa, Hawaii creeper, Hawaii amakihi, apapane, and Hawaii elepaio on ohia trees, and Japanese white-eye and amakihi on flowering raspberry bushes (*Rubus sandwichensis*). Akiapolaau defend sap trees from amakihi and Japanese white-eye (Pejchar and Jeffrey, 2005), resulting in occasional physical contact. Additional behavior supporting horizontal transmission between species involves re-using or stealing of nesting material (Fey et al., 1997); this occurs in Hawaiian birds. Omao re-use apapane nests (Wakelee and Fancy, 1999), Hawaii elepaio take nesting material from akepa nests in cavities, and apapane remove material from active Hawaii creeper nests (VanderWerf, 1998b). There may be more opportunities for horizontal transmission between species in the Hawaiian bird community than in other avian communities.

Existing data on ectoparasite seasonality in tropical birds are limited to 1 study of 1 species, the house sparrow (*Passer domesticus*), a nontropical bird that was introduced to tropical environments (Martin et al., 2007). The seasonality in the current study is community-wide, indicating similar host–parasite interactions. Both the low and high months of prevalence were essentially postbreeding, whereas in the house sparrow, only the high months of prevalence were postbreeding. The low prevalence in July is associated with an intensive molt of wing and tail, as well as body, feathers; thus the ectoparasites may have been less conspicuous within the rolled pin feathers, as has been documented for other species (Moyer, Gardiner, and Clayton, 2002). The high prevalence in October–December is during the molting period, but fewer wing and tail feathers are molted in October, and fewer body feathers are molted in November and December. The high prevalence during these months may reflect fresher feather resources arising from recent

molting. The fresh-feather hypothesis may link the house sparrow and Hawaiian bird studies, in terms of the seasonality of ectoparasites associated with molting in tropical environments. With our data, there may be a real difference in seasonality of prevalence between tropical and temperate birds, wherein the highest prevalence is associated with breeding (Foster, 1969; Kettle, 1983; Martin et al., 2007).

In the present study, we show an indirect cost to hosts of being parasitized because fault bars were not associated with handling, and the increase in prevalence of ectoparasites was not correlated with change in weather. There is a greater likelihood of nutritional stress while molting, leading to major fault bars and broken wing and tail feathers. Such feathers will cause flight to be more energetically expensive because aerodynamic efficiency will be reduced. Chewing lice alter the flight efficiency in barn swallows (*Hirundo rustica*) by chewing holes in portions of the tail feathers lacking melanin (Kose and Moller, 1999; Barbosa et al., 2002). However, the fault bars in Hawaiian birds apparently are not caused by the direct effect of chewing because individuals without ectoparasites also had them. Moreover, chewing is unlikely to exhibit as a sharp, straight line perpendicular to the shaft of the feather. Previous work on other birds has shown that the effect of ectoparasites is stronger when hosts are stressed, based on nestling weight and survival (de Lope et al., 1993). Our study shows that the nutritional stress preceded the increase in prevalence of ectoparasites, based on feather condition (and fat), and that feather condition worsened with intensity of infection. This is evidence that an indirect cost can increase with intensity of infection.

The lower recapture success of birds with ectoparasites suggests that there might be higher mortality in birds with ectoparasites. However, it may be that the difference in recapture success is due to the possibility that individuals with ectoparasites fly less, and thus are less likely to be captured in aerial mist nets; they could be spending more time controlling ectoparasites (Lehmann, 1993; Johnson and Clayton, 2003). In addition, because all species were food-limited, any individuals with ectoparasites (and extra food requirements to replace lost heat) may have spent more time foraging within single trees before flying to other trees. Both the mortality in adults and juveniles, and the change in foraging behavior, would be the first-reported cases of these effects from chewing lice in wild birds. The only species (omao) that deviated from this pattern of lower recapture with ectoparasites was the largest bird in the community. Its body size may have made the effects of heat loss from degraded plumage less costly. Whatever factors resulted in lower recapture success appear to have increased with intensity of infection. A great deal of additional investigation is necessary to determine how much mortality was involved, but further research has been halted by the U.S. Fish and Wildlife Service.

The present study provides several opportunities to address the cost of ectoparasitism in the context of food limitation. For the young Hawaiian birds captured as fledglings or independent juveniles, fault bars would have developed during wing and tail feather growth in the nest during the months of January–June. For the adults, fault bars would have developed during June–September, the months of heavy molting of wing and tail feathers. For young birds that are heat-subsidized by parental brooding in the nest, and not handled by researchers, the fault bars would arise strictly from food limitation. Akepa nestlings were only handled after their flight feathers had largely matured, but were underweight beginning in 2000 (data not shown), 3 yr before the increase, so this appears to be resource-based food limitation. For the adult birds, fault bars in 2003 would also have arisen because of food limitation, with minimal interaction with ectoparasites.

After 2003, the resource-based limitation could be exacerbated by ectoparasites in 4 ways. First, insulation against the cool temperatures at night in upper-elevation forests, during the months of molting, could be lowered by plumage degraded by chewing lice. Second, blood consumed by Amblycera lice would need to be replaced. Third, birds could spend more time controlling ectoparasites or relieving irritation, and less time feeding. Fourth, the contribution of ectoparasites to major fault bars and broken feathers would increase the costs of flying. Any of these mechanisms, singly or in concert, could increase food-limitation effects beyond just the decreased amount of food available in the environment.

Indirect costs of ectoparasites lead to host mortality when the host cannot compensate for the increased costs. Host mortality is considered a direct cost, but to use the term ''cost'' in both contexts may be confounding a physiological effect with a demographic consequence. Most parasites, and especially ectoparasites, cannot cause a direct cost unless some pathology occurs. Without the pathology, the frequently observed association of mortality in hosts with the highest infestations (Poulin, 2007) is associated with higher indirect costs. In our study, this may have occurred in 8 of the 10 species, with lower recaptures of individuals with the highest intensities. There was possibly an ectoparasite-driven mortality even in individuals with lesser infestations. The effect should become stronger if food becomes more limiting. Thus, if causes of food limitation are managed, the indirect and demographic costs due to ectoparasites may decrease. Without management, they may increase.

Future work is necessary to identify the ectoparasites and to investigate host specificity. The only way that progress can be made in distinguishing the ecological release and the host-switching hypotheses is to identify lice on all species of birds on the island of Hawaii. In addition, work is needed to track the phenomenon, as there was no indication through 2005 that the increase in prevalence had reached an equilibrium, either within species or in the entire community of hosts. Ectoparasites have essentially been ignored in the conservation literature for Hawaiian birds (Scott et al., 1986; van Riper and Scott, 2001). Now, in addition to introduced predators, competitors, and pathogens (Scott et al., 1986), they have to contend with chewing lice. At a minimum, chewing lice will increase food requirements of hosts. This indirect cost may be especially relevant because it will negatively impact the ability of hosts to mount a sufficient immune defense against diseases like avian malaria and pox virus (Freed et al., 2005). Finally, the ectoparasites may also be directly contributing to mortality of hosts, although more research is necessary to determine if this actually occurs.

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