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TEMPORAL VARIATION IN BIRD AND RESOURCE ABUNDANCE ACROSS AN ELEVATIONAL GRADIENT IN HAWAII

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Abstract.—We documented patterns of nectar availability and nectarivorous bird abundance over ~3 years at nine study sites across an 1,800-m elevational gradient on Hawaii Island to investigate the relationship between resource variation and bird abundance. Flower density (flowers ha^{-1}) and nectar energy content were measured across the gradient for the monodominant `Ōhi`a (*Metrosideros polymorpha*). Four nectarivorous bird species were captured monthly in mist nets and surveyed quarterly with point-transect distance sampling at each site to examine patterns of density and relative abundance. Flowering peaks were associated with season but not rainfall or elevation. Bird densities peaked in the winter and spring of each year at high elevations, but patterns were less clear at middle and low elevations. Variability in bird abundance was generally best modeled as a function of elevation, season, and flower density, but the strength of the latter effect varied with species. The low elevations had the greatest density of flowers but contained far fewer individuals of the two most strongly nectarivorous species. There is little evidence of large-scale altitudinal movement of birds in response to `Ōhi`a flowering peaks. The loose relationship between nectar and bird abundance may be explained by a number of potential mechanisms, including (1) demographic constraints to movement; (2) nonlimiting nectar resources; and (3) the presence of an "ecological trap," whereby birds are attracted by the high resource abundance of, but suffer increased mortality at, middle and low elevations as a result of disease. *Received 10 February 2010, accepted 21 October 2010.*

Key words: bird density, ecological trap, flower density, flower phenology, Hawaiian Honeycreeper, *Metrosideros polymorpha*, nectarivore.

Variación Temporal de la Abundancia de Aves y Recursos en un Gradiente Altitudinal en Hawai

Resumen.—Documentamos los patrones de disponibilidad de néctar y la abundancia de aves nectarívoras por cerca de tres años en nueve sitios de estudio a lo largo de un gradiente altitudinal de 1800 m en la isla de Hawai para investigar la relación entre la variación en los recursos y la abundancia de aves. La densidad de flores (flores ha–1) y el contenido energético del néctar de la planta monodominante llamada *Metrosideros polymorpha* fueron medidos a lo largo del gradiente. Cuatro especies nectarívoras fueron capturadas mensualmente con redes de niebla y censadas cada tres meses mediante muestreos de distancia con puntos en transectos en cada sitio para examinar los patrones de densidad y abundancia relativa. Los picos de floración se asociaron con la temporada, pero no con la precipitación ni con la elevación. Las densidades de aves presentaron un pico en el invierno y la primavera de cada año en las elevaciones altas, pero los patrones fueron

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menos claros en elevaciones medias y bajas. La variabilidad en la abundancia de aves fue modelada de mejor forma como una función de la elevación, la estación y la densidad de flores, pero este último efecto fue variable de acuerdo a la especie. Las elevaciones bajas presentaron la mayor densidad de flores, pero albergaron muchos menos individuos de las dos especies más nectarívoras. Existe poca evidencia de movimientos altitudinales de gran escala por parte de las aves como respuesta a los picos de floración de *M. polymorpha*. La relación débil entre la abundancia de néctar y de aves podría explicarse por varios mecanismos potenciales, incluyendo (1) restricciones demográficas al movimento, (2) recursos de néctar no limitantes y (3) la presencia de una "trampa ecológica" consistente en que las aves son atraidas por la alta abundancia de recursos en elevaciones medias y bajas, pero allí sufren una mayor mortalidad como resultado de enfermedades.

> When the `ōhi`a is in bloom over miles of country, the food supply seems inexhaustible, but between the flowering periods it is limited, and often leads to a decided migration of the birds either from one district to another, or to different elevations in the same district. (Perkins 1903)

THE CONCEPT THAT there is a strong general relationship between resource availability and animal abundance has become widely accepted in ecology. Mobile organisms such as birds have been shown to track changes in a variety of resources, including arthropods, fruits, seeds, and nectar (reviewed in Wiens 1989). Resource variability affects local abundance on a broad scale through its influences on latitudinal migrations (Dingle and Drake 2007). Similarly, seasonal changes in resource abundance across elevational gradients have been shown to be associated with altitudinal movements of birds across much smaller spatial scales (Stiles 1988, Loiselle and Blake 1991, Levey and Stiles 1992, Chaves-Campos et al. 2003).

Movement of individuals across the landscape strengthens the ecological linkage between habitats and may provide important ecological services such as seed dispersal and pollination. This movement may also facilitate the persistence of populations when food availability is patchy in space or time or when organisms exist primarily within metapopulations (Hanski and Gilpin 1991). Conversely, movement may be detrimental to populations and the persistence of species when some of the individuals that move are known reservoirs of disease. Recent outbreaks of West Nile virus in migratory bird species in North America are an example of this on a large scale (Rappole and Hubálek 2003). Understanding the ways in which resources and animal populations, especially those that are rare or in decline, vary within and among years across the landscape may thus be critical in designing effective conservation plans (Johnson and Sherry 2001).

We examined nectar availability as a variable resource with the strong potential to drive movements of nectar-feeding birds across large spatial and temporal scales on the island of Hawaii. We focused on nectar resources and nectarivores because (1) nectarivores constitute a large proportion of both individuals and species within Hawaiian forest bird communities; (2) the density of nectarivores is often limited by their food supplies (Carpenter 1976); and (3) feeding territoriality is relatively rare, and Hawaiian nectarivores might therefore be expected to track nectar resources across the landscape in a more or less "ideal-free" manner. The potential mass movement of some of the largest and most abundant of the remaining native Hawaiian forest vertebrates has great ecological implications for both the pollination of a variety of plant species and the spread of avian disease. The latter idea is particularly important because two native honeycreepers, the `Amakihi (*Hemignathus virens virens*) and the `Apapane (*Himatione sanguinea*), have been shown to be the primary reservoirs for mosquito-transmitted avian malaria (*Plasmodium relictum*; van Riper et al. 1986). Past work has demonstrated a strong relationship between elevation and prevalence of avian malaria in Hawaiian forest birds (Warner 1968, van Riper et al. 1986). Knowledge of the patterns of food availability and other factors that shape the structure and dynamics of avian communities in Hawaii is critical if we are to understand the avian disease system, because of the great differences in susceptibility to disease both within and among species (van Riper et al. 1986, Atkinson et al. 1995) as well as likely differences in seasonal movement patterns between species (Scott et al. 1986).

Since Perkins's (1903) observations, it has been widely believed that nectar-feeding birds closely track the flowering of `Ōhi`a (*Metrosideros polymorpha*) in Hawaii (e.g., Baldwin 1953, Carpenter and Macmillen 1980, Scott et al. 1986). However, recent studies at different locations and smaller spatial scales than those described here have been rather equivocal in their support of this relationship (e.g., Carpenter 1987, Ralph and Fancy 1995). The primary hypothesis that we address in the present study is that the abundance of nectar-consuming birds is related to spatial and temporal changes in nectar availability. The main predictions are that (1) flower abundance of `Ōhi`a, the dominant tree in Hawaiian wet forests, peaks at different times at different elevations; and (2) there is a positive relationship between flower abundance and bird abundance in a given area over time. Alternatively, birds may not track the abundance of flowers because of life-history constraints (e.g., breeding or susceptibility to disease) or because nectar in flowers is generally not a limiting resource. To test these predictions, we explore patterns of both flower and bird abundance over a 3-year period at nine locations across an 1,800-m elevational gradient. We then evaluate a set of models that incorporates both biotic and abiotic variables to explain these patterns. Our approach differs from past work on this system and other systems in a number of important ways. First, our study was conducted at a very large spatial scale, incorporating nearly the entire elevational range of both `Ōhi`a and the four bird species on Mauna Loa and Kilauea volcanoes. Second, we measured flower abundance at the level of flower density per unit area of land. And third, to improve confidence in the accuracy of our estimates of bird abundance, we used two methods concurrently to measure periodic changes in the number of birds.

METHODS

Study area.—The study area comprised ~1,100 km^2 on the eastern (windward) flanks of Mauna Loa and Kilauea volcanoes on the southeast corner of the Island of Hawai`i (~19°20′ latitude; Fig. 1). We established nine 1-km^2 study sites in native forest,

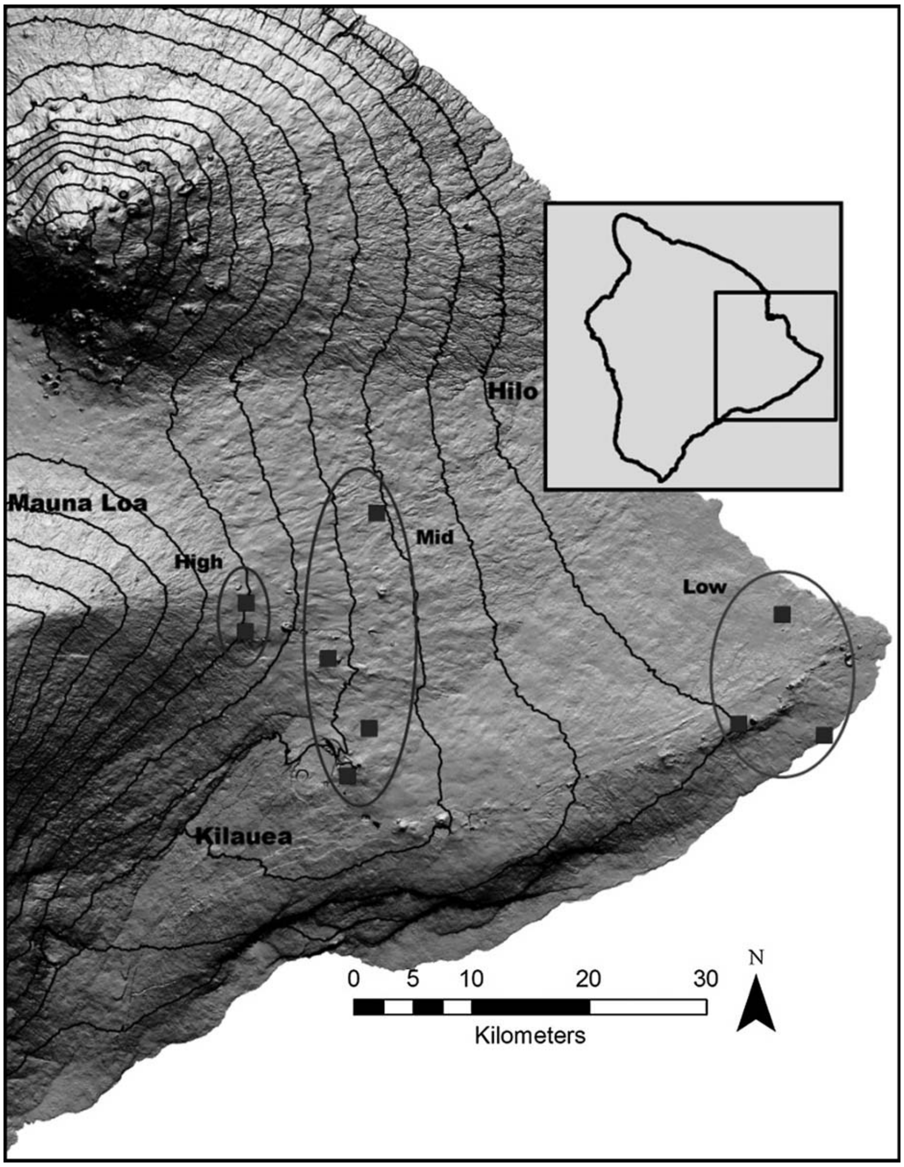

FIG. 1. Locations of nine 1-km² study sites within three elevational categories on Kilauea and Mauna Loa volcanoes, Island of Hawai`i.

each containing five 1-km-long transects spaced 200 m apart. The study sites were distributed along an elevational gradient from 25 to 1,800 m above sea level (a.s.l.) and were stratified into three elevational classes, with two replicates at high elevation (>1,650 m a.s.l.), four replicates at middle elevation (1,000–1,300 m a.s.l.), and three at low elevation (<300 m a.s.l.; Fig. 1). These classes correspond to the three major disease "zones" identified by van Riper et al. (1986). More replicates were placed at middle elevations because birds were known to be least abundant there (and most abundant at high elevations). Disease transmission varies across the elevational gradient, driven primarily by seasonal patterns in abundance of the primary vector of avian malaria, the Southern House Mosquito (*Culex quinquefasciatus*). There is year-round, intense transmission among susceptible native birds at low elevations, strongly seasonal transmission with periodic epizootics at middle elevations, and very low transmission rates at high elevations (Atkinson and LaPointe 2009).

Mean monthly temperatures ranged from 24°C at low-elevation sites to ~13°C at high-elevation sites. Because the study area spanned two active volcanoes, the substrate was relatively young basalt at all sites, ranging in age from 170 years BP to ~5,000 years BP (Wolfe and Morris 1996). All study plots were in aseasonal wet forest (1,800 mm–4,200 mm annual rainfall) dominated by `Ōhi`a, the primary canopy tree in Hawaiian forests. The understory at all sites except for two (at middle elevations) has been disturbed within the past several decades by feral pigs (*Sus scrofa*).

Study species.—The four bird species examined in our study differ in their degree of nectarivory. In `Ōhi`a-dominated forests, `I`iwi (*Vestiaria coccinea*) and `Apapane spend approximately 50% and 60% of their foraging time, respectively, on `Ōhi`a flowers and are considered true nectarivores, with the remainder of their diets being primarily foliage arthropods and, for `I`iwi, other nectar sources when available (Fancy and Ralph 1997, 1998). `Amakihi and Japanese White-eye (*Zosterops japonicus*) are both considered generalists that, in addition to foliage arthropods and fruit, consume large quantities of nectar when it is available (Ralph and Noon 1986). These birds might be expected to track nectar resources to some degree, given that nectar has far greater energy value than arthropods (Ford and Paton 1975). In `Ōhi`a-dominated forests, there is sometimes little difference in the amount of time spent foraging on `Ōhi`a flowers among `I`iwi, `Apapane, and `Amakihi (P. Hart unpubl. data).

Bird abundance.—We used two complementary methods to quantify bird populations across the elevational gradient. Constant-effort mist netting provided a measure of relative abundance and provided data on breeding activity and productivity. Bird surveys (variable-circular-plot or point-transect methods, a form of distance sampling; Reynolds et al. 1980, Scott et al. 1986) provided a means to estimate the density of our study species at each site and in each season. Each method has limitations (Karr 1981, Remsen and Good 1996, Blake and Loiselle 2001), but by using them concurrently we aimed to get the best estimates of bird populations possible.

Mist netting was conducted monthly within a 50-ha subplot in each of the nine study areas, from January 2002 through December 2004, using 18 to 24 mist nets (12 × 2.6 m, 32-mm mesh). Nets were placed at a height of 3 to 5 m on galvanized metal poles, well below the upper canopy at all sites, which ranged from ~8 m at low-elevation sites to ~20 m at some mid- and high-elevation sites. The net height was suboptimal for capturing `Apapane, which spend a large proportion of their time in the upper canopy, but was adequate for the other three species that make use of all canopy strata. Nets were operated for ~6 h each day between 0630 and 1400 hours HST, for 3 to 4 days each month at each site. Each mist-net location had a matched pair of mist nets placed within 10 m of each other, which were operated in alternate months to reduce the effects of net-shyness in birds. All captured birds were given federal bands and were aged and sexed using a combination of plumage, morphometrics, skull pneumatization, and breeding characters (Pyle 1997, U.S. Geological Survey unpubl. data). Breeding condition of captured birds was used to characterize breeding season for each elevation and species, and was determined by our assessment of the swelling of the cloacal protuberance in males and the development of a brood patch in females (Pyle 1997). Monthly changes in the relative abundance of adults of all species were estimated by comparing mist-net capture rates (captures per net hour).

Bird populations were also quantified using point-transect distance sampling at all nine study sites. We conducted these surveys quarterly (once per season) at 25 stations located 200 m apart throughout each 1-km^2 study site, for a total of 900 counts per year at 225 stations. Surveys were conducted between 0530 and 1100 hours. Each station was sampled for 8 min. Observers recorded the time, species, detection type (heard, seen, or both), and horizontal distance from the station origin to the bird as exact continuous distances. Estimates of cloud cover, rain, and wind speed were also recorded at each station.

Species-specific detection functions were modeled for all four species using DISTANCE, version 5.0, release 2 (Thomas et al. 2006). Density estimates were calculated by post-stratifying data by season, year, and site from the global detection functions pooled across strata. Covariates included cloud cover, rain, wind speed, observer, season of survey, and year of survey. Akaike's information criterion (AIC; Akaike 1973) was used to identify the best-approximating model of the data. This model-selection criterion is based on the principle of parsimony and represents a tradeoff between model fit and the number of parameters in the model (Burnham and Anderson 2002). Variances about the density estimates were derived by bootstrap methods in DISTANCE from 999 iterations (Thomas et al. 2006).

Nectar availability.—We focused on nectar resources in `Ōhi`a because >90% of the individual trees in most wet forests on the windward side of Hawai`i Island are this species (Hart 2010). The total number of inflorescences per `Ōhi`a tree was counted for 50 randomly selected trees at each study site monthly, with one tree (>5 cm diameter at breast height [dbh]) selected at each of 50 stations set at 100-m intervals along the five 1-km-long transects per study area. Estimates of flower abundance were then scaled up to density of flowers per hectare by multiplying the monthly mean number of flowers (for the 50 randomly selected trees) by the density of `Ōhi`a trees at each site. `Ōhi`a tree density was estimated by counting all trees that were >5 cm dbh within each of 25 nine-meter-radius plots set at 200-m intervals along the same five transects as above.

Because nectar availability and quality can vary with elevation, we followed protocols developed by Carpenter (1976) to measure nectar volume and calorie content in two inflorescences on each of 10 randomly selected `Ōhi`a trees at two sites per elevation across the gradient during spring and early summer 2004. We then used our estimates of inflorescence density to examine how energy (calories ha^{-1}) available to birds may vary within and among sites. Because these estimates were derived from only two seasons during one year of the study, they were not incorporated into statistical models for bird abundance.

Statistical Analyses

Modeling flower abundance.—To partition variance in flower abundance, we used generalized linear regression for repeated measures. We constructed models of flower abundance that were ranked with Akaike's information criterion adjusted for sample size in an information-theoretic framework (AIC$_c$; Akaike 1973, Burnham and Anderson 2002). The models with ΔAIC$_c$ values <2 were considered the best-approximating models, but we also considered models within 2 to 4 AIC$_c$ units of the best-approximating models.

Although we did not sample the same trees repeatedly, we sampled the same sites repeatedly, and we expect flower counts to be serially autocorrelated within a site. For regression analysis to yield valid estimates of variance, observations must be independent. If positive autocorrelation structure is ignored, estimates of variance will be biased low (e.g., Little et al. 2002) and analyses will be more likely to detect weak or spurious relationships. For the most complex model structure that we considered, we compared AIC$_c$ values of this model with no autocorrelation structure to versions with a first-order (AR[1]) and a compound symmetry (CS) autocorrelation structure (Keselman et al. 1998, Guerin and Stroup 2000).

We modeled log flower abundance with an identity link function and a normal error distribution using PROC MIXED in SAS, version 8 (SAS Institute, Cary, North Carolina). We examined the following variables: site, month, year, mean monthly rainfall, and mean monthly temperature. Although site, month, and year do not provide a biological explanation for flower abundance, they were included in analyses to account for site-level differences that are not accounted for by either rainfall or temperature. In some models, we collapsed months into seasons: December–February was classified as "winter," March–May as "spring," June–August as "summer," and September–November as "fall." We also substituted elevation for site, both as a continuous covariate and as a grouping variable where sites were classified as "low," "medium," or "high" in elevation. Finally, we examined the effect of lag times in temperature and rainfall. Lags of 1-, 2-, and 3-month durations were investigated. We assessed our predictions by interpreting patterns from the best-approximating models.

Nectar availability.—We determined the mean nectar calories available per day over the life of each inflorescence. These values were then used to estimate the mean for each of the three elevations. We performed a one-way analysis of variance (ANOVA) with a Tukey's multiple comparison (S-PLUS, version 7.0) on log-transformed data to test the null hypothesis that there was no difference in calories per inflorescence among elevations.

Modeling bird abundance.—We used the same analytical and model-selection procedures to test for differences in bird abundance as those used to test flower abundance. We constructed separate repeated-measures generalized-linear-regression model sets for bird abundance as determined by both mist-netting and point-transect methods, and then ranked models within each model set using AIC_c. Both monthly mist-net capture rates and quarterly point-transect densities were modeled with an identity link function and a normal error distribution using PROC MIXED in SAS. We examined the following explanatory factors: \`Ōhi\`a flower density (flowers ha^{-1}), elevation (measured on a continuous scale), elevation measured as a categorical variable (i.e., low, middle, high), study site, season (as described above), and breeding season. The factor "breeding season" is potentially important because movement across the landscape may be limited when individuals have an active nest. Breeding season was categorized as "yes" or "no" and was determined for each species separately as the period during which captured females possessed active brood patches.

Using restricted maximum likelihood (REML) and the global model structure (including elevation category, site nested within elevation category, flower density, and the interaction of flower density and season or breeding season), we fitted models to the following autocorrelation structures: VC (no autocorrelation structure), CS, AR(1) that was common to all sites, and AR(1) that was specific to each site. We examined the ACF and PACF plots to verify that the correct autocorrelation structure was selected. We used maximum likelihood (ML) to test for fixed effects, assuming the best variance–covariance structure.

RESULTS

Patterns of Flower and Nectar Abundance

Monthly flower density among sites and years ranged from zero to 60,739 flowers ha^{-1}. Overall, the mean (± SE) monthly flower density was highest at one of the low-elevation study sites (8,387 ± 2,431) and lowest at a middle-elevation study site (1,436 ± 354).

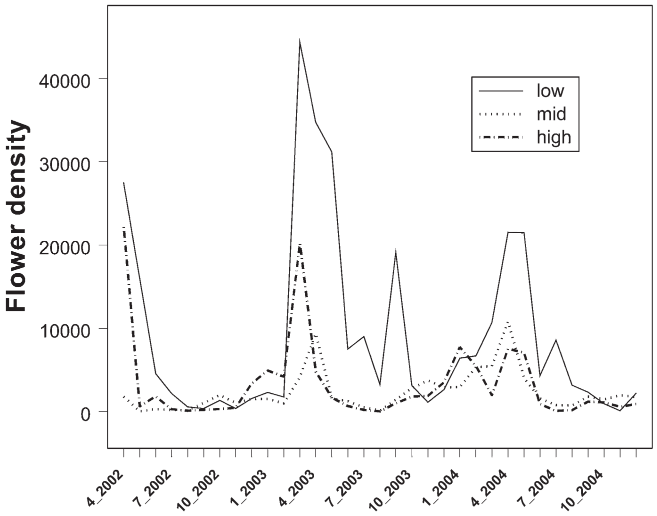

FIG. 2. Monthly \`Ohi\`a flower density (ha^{-1}) for low, middle, and high elevations on the east side of Hawai\`i Island, April 2002 to December 2004. Data represent means for all sites combined within an elevation.

There were significantly more flowers at low elevations than at either middle or high elevations, but there was no difference between mid- and high-elevation sites (one-way ANOVA with Tukey's multiple comparison, $F = 5.26$, df = 2 and 264, $P = 0.006$). The density of \`Ōhi\`a flowers generally peaked in the spring (March–May) across the elevational gradient (Fig. 2). There were a few departures from this trend. At one low-elevation site, peaks occurred in late summer (September–October) during 2 of 3 years. There was also a late-summer peak at a single study site at middle elevation. Flowering peaks were fairly consistent at high elevations.

The best model for flower density was log(flowers ha^{-1}) = site + season + site*season. This model, with an additional term for year, also provided a good fit (see Appendix 1). The factor "elevation" is notably absent from these top models.

The mean (± SE) nectar calories per \`Ōhi\`a inflorescence per day ranged from 34.9 ± 5.15 at low elevations to 28.6 ± 6.11 at middle and 23.6 ± 6.19 at high elevations. There was a significant effect of elevation on the log of nectar calories available per inflorescence per day ($F = 5.04$, df = 2 and 81, $P = 0.008$). A Tukey's multiple-comparisons test indicated that calorie content was significantly greater at low elevations than at high, but there was no difference between low and middle elevations or between middle and high. Interestingly, low-elevation sites had both the highest density of flowers and the highest nectar calorie content per flower.

Because flower (and nectar) resources may be superabundant during peaks, we also examined patterns of flower "lows." There was no difference among elevations in the number of months with <100 flowers ha^{-1} ($\chi^2 = 3.11$, df = 2, $P = 0.21$). Flowering was consistently lowest between June and November across the gradient. A single mid-elevation study area was the lone outlier to this trend, with <100 flowers ha^{-1} detected during February 2004.

Patterns of Bird Abundance

Mist netting.—We captured 737 \`Apapane, 2,245 \`Amakihi, 366 \`I\`iwi, and 3,660 Japanese White-eye (all after-hatch-year adults

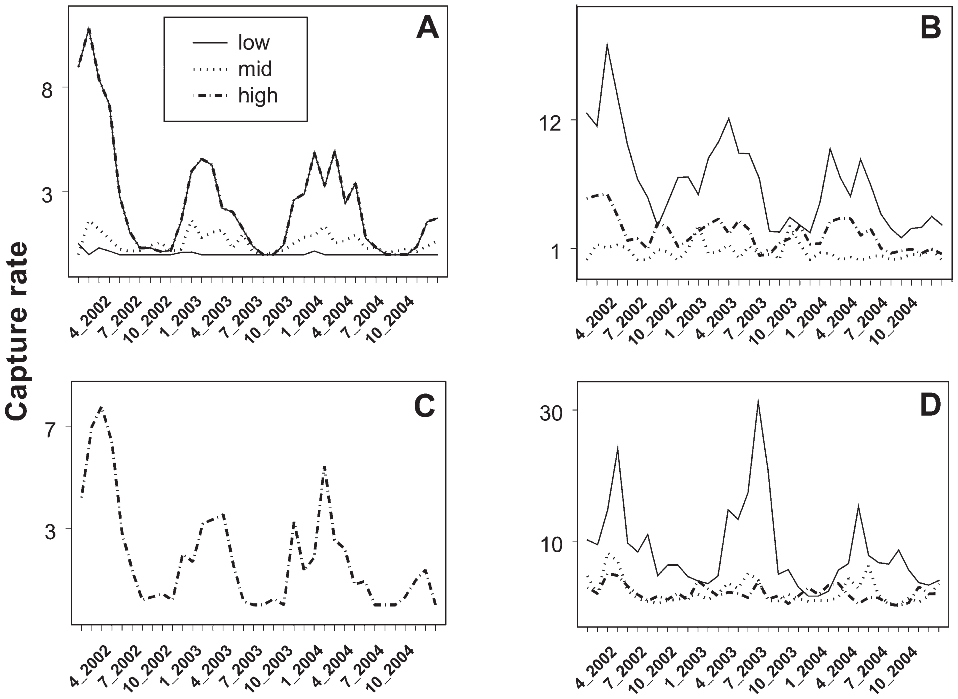

FIG. 3. Monthly mist-net capture rates (adult captures per 100 net-hours) of (A) \`Apapane, (B) \`Amakihi, (C) \`I\`iwi, and (D) Japanese White-eye on the east side of Hawai\`i Island, January 2002 to December 2004. Only \`I\`iwi captured at high-elevation study sites are included here, because of small sample sizes at other elevations. Data represent means for all sites combined within an elevation.

for each species) during 92,390 mist-net hours. Japanese White-eye were the only species commonly captured at all study sites throughout the year. \`Apapane were also present at all study sites but were relatively rare at low-elevation sites. \`Amakihi were rarely captured (or detected in surveys) at three of four mid-elevation study areas but were generally abundant at all low- and high-elevation sites. As expected, \`I\`iwi were primarily captured at the high-elevation study sites because of their susceptibility to mosquito-borne disease at lower elevations (<1,300 m).

Capture rates for adults of all species varied widely through time and across the elevation gradient. \`Apapane showed strong peaks in the spring of each year at high elevations, and weaker peaks in the spring at mid-elevation study sites (Fig. 3A). \`Amakihi capture rates peaked strongly at low elevations during each spring, but patterns were much less clear at middle and high elevations (Fig. 3B). Like those for the \`Apapane, capture rates for the \`I\`iwi peaked in the spring at each high-elevation site (Fig. 3C). Strong spring peaks were evident each year for Japanese White-eye at low and middle, but not at high, elevations (Fig. 3D).

The best models for mist-net capture rate of each species were as follows:

\`Apapane = flower density + elevation + site(elevation) + season
\`Amakihi = season
\`I\`iwi = site + flower density + breeding season
Japanese White-eye = flower density + elevation
+ breeding season

For sites combined within an elevation, \`Apapane and \`I\`iwi appear to track flower density over time at high elevations (Fig. 4A), and Japanese White-eye and \`Amakihi may track flower abundance at low elevations (Fig. 4B). Japanese White-eye are associated with flower density at mid-elevations (Fig. 4C), but the relationship between flower density and birds is less clear for \`Amakihi and Japanese White-eye at high elevations (Fig. 4D). There was variability among sites within an elevation for \`Apapane, and variability among elevations for \`Apapane and Japanese White-eye. Recapture data provided little evidence of movement between elevations for any of the four species examined here. Only one \`Apapane, two \`Amakihi, and one \`I\`iwi out of 1,566 total recaptures were ever recaptured at an elevation different from that of their initial capture.

Point-transect distance sampling.—A total of 8,705 \`Apapane, 5,108 \`Amakihi, 1,873 \`I\`iwi, and 7,847 Japanese White-eye were detected during the point-transect surveys. Annual peaks in abundance generally occurred either in the late fall, winter, or spring of each year for each species and site. There were no clear trends at any elevation for \`Apapane, \`Amakihi, or White-eye (Fig. 5A, B, D). At high elevations, abundance of \`I\`iwi peaked in the winter of each year (Fig. 5C).

The best statistical models for bird density as measured by point-transect surveys for each species were as follows:

\`Apapane = elevation + site(elevation) + season
\`Amakihi = elevation + site(elevation) + breeding season
\`I\`iwi = site + flower density
Japanese White-eye = flower density + elevation

Holding all other variables constant, locally weighted smoothing (Loess) plots show clear relationships between flower and bird abundance for \`I\`iwi (Fig. 6A), weakly positive relationships for

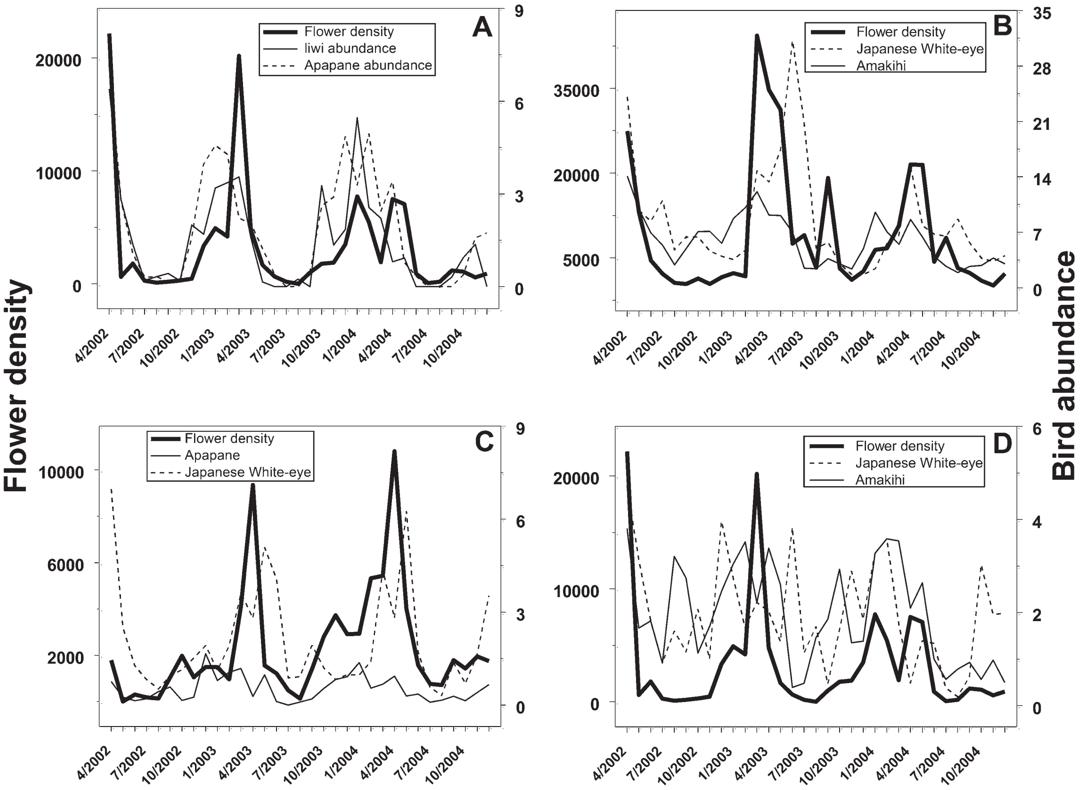

FIG. 4. The monthly relationship between flower density (flowers ha^{-1}) and bird abundance (adult captures per 100 net-hours) for (A) `I`iwi and `Apapane at high-elevation sites combined, (B) `Amakihi and Japanese White-eye at all low-elevation sites combined, (C) `Apapane and Japanese White-eye at all mid-elevation sites combined, and (D) `Amakihi and Japanese White-eye at high-elevation sites combined.

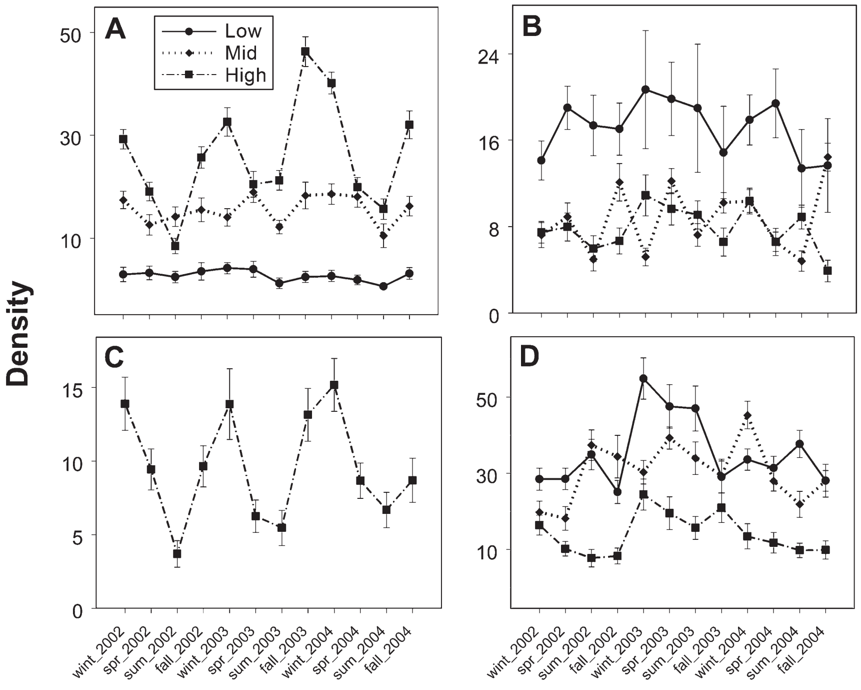

FIG. 5. Estimated bird densities (birds ha^{-1} ± SE) based on point-transect surveys for all sites combined within an elevation for (A) `Apapane, (B) `Amakihi, (C) `I`iwi, and (D) Japanese White-eye. Surveys were conducted from winter 2002 through fall 2004.

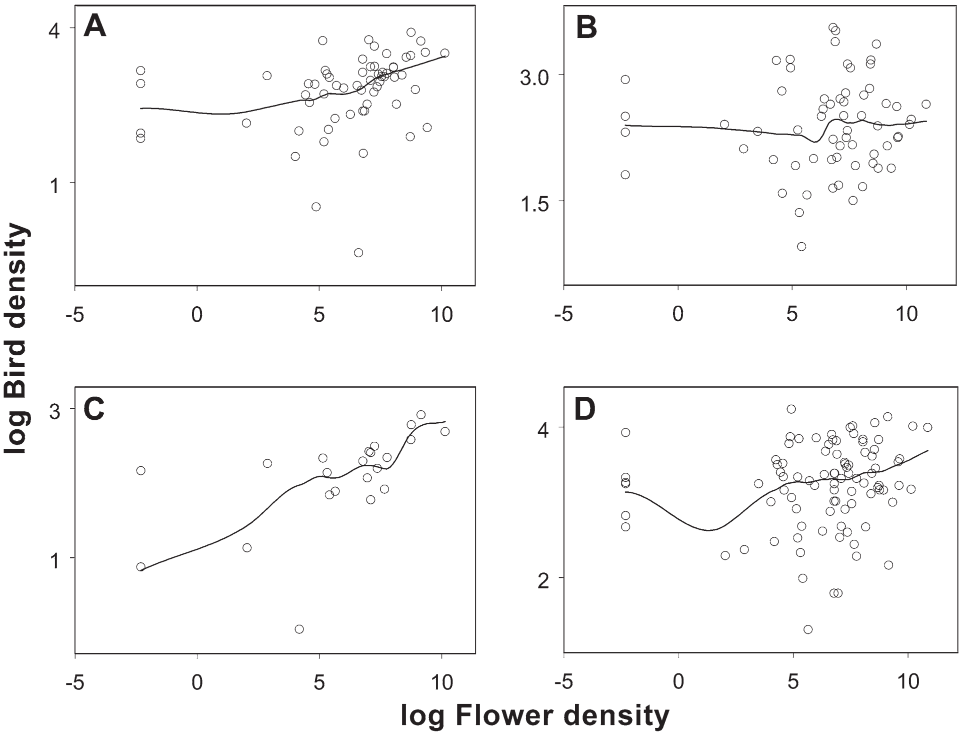

FIG. 6. Relationship between log-transformed flower density (flowers ha^{-1}) and log-transformed bird abundance (birds ha^{-1}) based on point-transect surveys for (A) `Apapane at all middle- and high-elevation sites combined, (B) `Amakihi at all low- and high-elevation sites combined, (C) `I`iwi at high-elevation sites combined, and (D) Japanese White-eye at all sites combined. Elevations at which a given species was absent or rare were not included in this analysis. Trend lines are Loess plots calculated after holding all other significant predictor variables constant.

`Apapane (Fig. 6B) and Japanese White-eye (Fig. 6C), and little relationship between flower and `Amakihi abundance (Fig. 6D).

DISCUSSION

Flowering phenology.—Despite the perception of aseasonality in the tropics, most tropical trees display distinct temporal patterns in flowering (Frankie et al. 1974, van Schaik et al. 1993). According to the "insolation-limitation hypothesis" for wet forests (van Schaik et al. 1993), flower production is maximized during peak periods of solar irradiance, generally from late spring to early summer. The finding that there are broad, seasonal (late winter and spring), and simultaneous peaks in flower abundance across the elevational gradient supports the idea that photoperiod is an important cue to flowering in `Ōhi`a. Our best statistical models included the strong effect of season (highlighting the importance of day length to flowering), along with significant effects of site. Neither rainfall nor elevation contributed significantly to flowering patterns (Appendix 1). The significant effect of the site factor likely reflects its ability to capture variation in a combination of other factors that may be site-specific, such as tree variety or substrate type. The few exceptions to the general flowering pattern (i.e., late-summer flowering peaks) at one of the low-elevation study sites may be at least partially due to genetic variation in `Ōhi`a.

Patterns of bird abundance.—Although there are inherent biases associated with both mist netting and point-transect surveys, there was broad agreement between models based on the two techniques (Appendices 2 and 3). Top models generally included an effect of elevation, flower density, and season. When "elevation" was included in either mist-net or point-transect models, it often explained a significant amount of variability in bird abundance; however, elevation by itself was never a top model for any bird species (Appendices 2 and 3). The effect of elevation in the models is likely due more to the known differences in bird density among elevations (based on disease or habitat differences such as tree size or canopy cover) than to temporal changes in density among elevations. Figure 5 provides little graphic evidence (and least-squared regressions provided no statistical evidence) that increases or decreases in the density of any species between seasons were related to changes in density of that species at adjacent elevations. This observation is further supported by the lack of recaptures between elevations for any species. Radiotelemetry is the best way to demonstrate altitudinal movement of birds, and W. Kuntz (pers. comm.) used radiotelemetry to demonstrate that some `I`iwi individuals move seasonally across ≥500 m in elevation on Mauna Kea volcano on Hawaii Island.

Flower density appeared in the top model for both mist-net and point-transect methods for the `I`iwi and Japanese White-eye, whereas flower density did not appear in the top mist-net or point-transect model for `Amakihi. For `Apapane, flower density appeared in the top mist-net model and was within 3.2 AIC$_c$ units of the best point-transect model. Although most models indicated that flower density played a role in variation in bird abundance, the effect of flower density on bird abundance was generally small. For example, the best point-transect model for `I`iwi predicted an increase of 1–3 birds ha^{-1} as flowers increased from low to high density at the high-elevation study sites. Similarly, the best mist-net model for `Apapane predicted an increase of ~1 bird ha^{-1} over the range of flower densities. Figures 4 and 6 also illustrate that this relationship may be relatively loose. For all species, there were months in which flower density was high but bird abundance low—or, perhaps more interestingly, bird abundance high but flower abundance low. Recent studies at different locations and spatial scales in Hawaii have also been rather equivocal in their support of the relationship between bird and flower abundance. For example, the relationship between nectarivorous birds and flowers was shown to be highly variable between years (Carpenter 1987), study sites (Ralph and Fancy 1995), and species (Hess et al. 2001). At high-elevation wet forest on Maui, Berlin et al. (2001) found no relationship between `Ōhi`a flowers and density of `I`iwi, `Apapane, or `Amakihi at the scale of "station," but they did find a relationship at the scale of the entire study area.

There are at least three non-mutually-exclusive mechanisms that may explain the loose relationship between nectar-feeding birds and flower abundance. First, birds may be constrained from foraging optimally on variable nectar resources by numerous factors. Second, disease and other anthropogenic disturbances are likely keeping populations below carrying capacity and nectar resources may no longer limit adults throughout much of the year. Third, the current system may be viewed through the framework of an "ecological trap."

Constraints to movement.—Most organisms are constrained from foraging in an otherwise ideal free way by factors such as territoriality, environmental tolerances, mobility, breeding, and imperfect knowledge of resource patterns. With the exception of breeding, none of these factors should generally have prevented birds in our study from tracking food availability across the landscape to maximize their energy intake. All four bird species exhibit varying degrees of territoriality around the nest site, but with the possible exception of `Amakihi (e.g., van Riper 1987), it is widely believed that movement is not constrained by territoriality outside of the nesting season.

The nesting period (January–May) for nectarivores appears to be timed to coincide with peaks in `Ōhi`a bloom. If flowering peaks occur across the gradient at about the same time, birds cannot track these peaks, because they are constrained to remain with their nests. Could these birds then be following bloom during the period when they are not constrained by breeding? The lack of recaptures between elevations does not support this idea. Also, we would have expected a significant interaction between breeding season and flower density in the models. This interaction did not appear in any of the best models for all four species.

Nonlimiting nectar resources.—Animals generally travel less when food resources are abundant in their current habitat (Pyke et al. 1977). Animals may also commonly switch to other food resources rather than travel to new areas when a particular resource becomes scarce. Most nectarivorous birds also utilize arthropods (Cotton 2007), especially during breeding periods, or have been known to switch from nectar to other carbohydrate sources or arthropods when nectar becomes scarce (Carpenter and Macmillen 1980, Paton 1980). `Ōhi`a nectar is an essential element in the diet of the three honeycreeper species included in our study, but nectar is not the sole food for any species (Perkins 1903). During periods of high flower abundance, nectar is likely a nonlimiting resource, which reduces the incentive to migrate. During periods of low `Ōhi`a flower abundance across the landscape, the birds may sometimes switch food resources rather than travel long distances to find the rare patches of high flower density. At least six other midcanopy tree and shrub species that produce nectar are common throughout our windward Hawaii study sites. Although they account for only ~10% of the trees present, they may serve to supplement nectarivore diets when `Ōhi`a nectar is scarce. In addition, arthropods contribute a significant (and variable) proportion of the diet of all species examined here. Although we did not sample arthropods or other nectar resources available to birds in the present study, future efforts to model spatial and temporal changes in bird abundance would benefit from including all food sources available to birds.

Lowland forest as an ecological trap.—The significant effects of elevation and flower density on bird abundance are consistent with the view that lower-elevation sites serve as ecological traps. Dwernychuk and Boag (1972) described an ecological trap as low-quality habitat for reproduction and survival that cannot sustain a population but is preferred over other available high-quality habitats. Ecological traps may occur when environmental change decouples the cues that individuals use to assess habitat quality from the true quality of the environment (Dwernychuk and Boag 1972, Gates and Gysel 1978). An animal's preference remains unchanged, but the positive outcome normally associated with a given cue is now reversed (Robertson and Hutto 2006). Mosquito-transmitted avian malaria primarily affects birds at low and middle elevations in Hawaii (van Riper et al. 1986). This disease can cause high mortality in the `I`iwi (Atkinson et al. 1995) and variable rates of mortality in native `Amakihi and `Apapane (van Riper et al. 1986). Some populations of `Amakihi may even be evolving resistance to malaria (Woodworth et al. 2005). Only the introduced Japanese White-eye is generally considered resistant to infection by avian malaria. If these Hawaiian species assess habitat quality primarily through flower density, there is great potential that areas at low and middle elevations with high flower density (and higher nectar calorie content) may serve, currently and/or historically, as "ecological traps" for these birds, with infection with avian malaria, reduced probability of survival, and population decline being the negative outcomes of following flowering peaks to these areas. In this scenario, low-elevation forests in Hawaii may be the first known example of an ecological trap based on disease. Of course, the relevance of the ecological-trap model varies with species, depending on their mobility and susceptibility to disease.

The movement of individuals in response to flowering may be a major factor in a handful of historical bird extinctions in Hawaii. In addition to the evolution of increased disease resistance (Woodworth et al. 2005, Atkinson and LaPointe 2009), the persistence of Hawaii's remaining forest birds that follow resources across the landscape may require behavioral adaptations to the way they assess temporal changes in habitat quality. Kokko and Sutherland (2001) discussed a number of behavioral processes that may "rescue" a population from an ecological trap. In one scenario, individuals may exhibit philopatric preferences, whereby they prefer habitat with similar characteristics to that in which they were born. This latter possibility may be particularly relevant to Hawaii and may help explain the low density of mobile individuals in some areas with abundant resources. Individuals with innate tendencies to select habitat characteristic of low- and some mid-elevation areas with high levels of disease would decline (despite high food abundance), whereas populations would remain stable for birds at higher elevations. Along with demonstrated evolution of disease resistance, behavioral adaptations may play an important role in the persistence of Hawaii's remaining forest birds.

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APPENDIX 1. A subset of ranked (based on AIC_c) regression models developed to predict log-transformed flowers per hectare. "Ele_grp" is the elevation term represented as a categorical variable (low, middle, high); "Ele_cont" is the elevation term measured on a continuous scale (m). The number of parameters (k) for a given model varies according to the correlation matrix used. Asterisk indicates interaction between terms.

Model	k	AIC_c	ΔAIC_c	w_i
Site, Season, Site*Season	37	747.4	0	0.62246
Site, Year, Season, Site*Season	39	748.4	1.0	0.37754
Ele_grp, Season, Ele_grp*Season	13	846.5	99.1	0.00000
Month, Rainfall, Temperature	13	846.7	99.3	0.00000
Ele_grp, Year, Season, Ele_grp*Season	15	847.9	100.5	0.00000
Site, Month, Year, Ele_grp, Site*Month, Site*Year, (AR(1))	37	848.7	101.3	0.00000
Site, Season	13	849.5	102.1	0.00000
Site, Year, Season	15	851.0	103.6	0.00000
Ele_grp, Season	7	864.2	116.8	0.00000
Ele_grp, Year, Season	10	865.6	118.2	0.00000
Season	5	869.3	121.9	0.00000
Ele_cont, Season	6	880.8	133.4	0.00000
Ele_cont, Year, Season	8	882.1	134.7	0.00000
Site, Month, Year, Ele_grp, Site*Month, Site*Year,	36	886.5	139.1	0.00000
Site, Month, Year, Ele_grp, Site*Month, Site*Year, (CS)	37	888.5	141.1	0.00000
Site	10	894.0	146.6	0.00000
Ele_grp	4	908.3	160.9	0.00000
Year	4	911.1	163.7	0.00000
Null	2	912.3	164.9	0.00000
Ele_cont, Season, Ele_cont*Season,	9	913.1	165.7	0.00000
Ele_cont, Year, Season, Ele_cont*Season	11	914.5	167.1	0.00000
Ele_cont	2	927.4	180.0	0.00000

APPENDIX 2. Ranked (based on AIC_c) regression models developed to predict bird abundance based on mist-net captures per 100 net-hours. "Fl_ha" represents flowers per hectare; "Ele_grp" is the elevation term represented as a categorical variable (low, middle, high); "Site(Ele_grp)" indicates site nested within elevation; "Ele_cont" is the elevation term measured on a continuous scale (m); "Br_Season" represents breeding season. Number of parameters (k) for a given model varies according to the correlation matrix used. Asterisk indicates interaction between terms.

Model	k	Log-likelihood	AIC_c	ΔAIC_c	w_i
`Apapane					
Fl_ha, Ele_grp, Site(Ele_grp), Season	16	142.2	179.9	0	0.77158
Ele_grp, Site(Ele_grp), Season	15	147.6	182.9	3.0	0.17216
Fl_ha, Ele_grp, Site(Ele_grp), Season, Fl_ha*Season	19	140.7	185.9	6.0	0.03841
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season	14	156.0	188.9	9.0	0.00857
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season, Fl_ha*Br_Season	15	154.2	189.5	9.6	0.00635
Fl_ha, Ele_grp, Br_Season	10	168.6	192.1	12.2	0.00173
Season	10	169.5	193.0	13.1	0.00110
Ele_grp, Site(Ele_grp), Br_Season	13	167.7	198.2	18.3	0.00008
Br_Season	8	183.6	202.6	22.7	0.00001
Fl_ha	8	188.1	207.1	27.2	0.00000
Fl_ha, Ele_grp	9	187.7	208.9	29.0	0.00000
Fl_ha, Ele_grp, Site(Ele_grp)	13	179.1	209.6	29.7	0.00000
Ele_grp, Site(Ele_grp)	12	193.7	221.9	42.0	0.00000
Ele_grp	8	204.2	223.2	43.3	0.00000
`Amakihi					
Season	10	206.0	229.5	0	0.93689
Ele_grp, Site(Ele_grp), Season	15	200.6	235.8	6.3	0.04015
Fl_ha, Ele_grp, Site(Ele_grp), Season	16	199.5	237.1	7.6	0.02096
Fl_ha, Ele_grp, Site(Ele_grp), Season, Fl_ha*Season	18	197.1	242.1	12.6	0.00172
Fl_ha	8	227.7	246.7	17.2	0.00017
Fl_ha, Ele_grp	10	225.7	249.2	19.7	0.00005
Br_Season	8	231.5	250.5	21.0	0.00003
Fl_ha, Ele_grp, Br_Season	11	225.2	251.0	21.5	0.00002

(continued)

APPENDIX 2. Continued.

Model	k	Log-likelihood	AIC_c	ΔAIC_c	w_i
`Amakihi					
Ele_grp	9	230.8	252.0	22.5	0.00001
Fl_ha, Ele_grp, Site(Ele_grp)	13	224.3	254.8	25.3	0.00000
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season	14	224.0	256.8	27.3	0.00000
Ele_grp, Site(Ele_grp)	12	229.9	258.0	28.5	0.00000
Ele_grp, Site(Ele_grp), Br_Season	13	228.3	258.7	29.2	0.00000
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season, Fl_ha*Br_Season	15	223.9	259.1	29.6	0.00000
`I`iwi					
Site, Fl_ha, Br_Season	4	94.6	105.6	0	0.36980
Site, Fl_ha, Br_Season, Fl_ha*Br_Season	5	93.4	106.9	1.3	0.19305
Fl_ha, Br_Season	3	98.5	107.2	1.6	0.16616
Fl_ha, Br_Season, Fl_ha*Br_Season	4	96.1	107.3	1.7	0.15806
Br_Season	2	103.4	109.8	4.2	0.04528
Site, Fl_ha, Season,	6	94.8	110.7	5.1	0.02887
Fl_ha, Season, Fl_ha*Season	8	91.0	112.2	6.6	0.01364
Fl_ha, Season,	5	98.9	112.4	6.8	0.01234
Site, Fl_ha, Season, Fl_ha*Season	9	89.8	113.8	8.2	0.00613
Season	4	102.9	113.9	8.3	0.00583
Fl_ha	2	112.4	118.8	13.2	0.00050
Site, Fl_ha	3	110.9	119.6	14.0	0.00034
Japanese White-eye					
Fl_ha, Ele_grp, Br_Season	14	417.8	449.6	0	0.76999
Br_Season	11	427.5	452.7	3.1	0.16343
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season	20	409.6	455.2	5.6	0.04682
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season, Fl_ha*Br_Season	21	409.4	457.4	7.8	0.01559
Ele_grp, Site(Ele_grp), Br_Season	19	417.5	460.7	11.1	0.00299
Season	13	434.4	464.0	14.4	0.00057
Fl_ha, Ele_grp, Site(Ele_grp), Season	22	414.8	465.1	15.5	0.00033
Fl_ha, Ele_grp, Site(Ele_grp), Season, Fl_ha*Season	25	408.3	465.9	16.3	0.00022
Fl_ha	11	444.6	469.8	20.2	0.00003
Ele_grp, Site(Ele_grp), Season	21	424.6	472.6	23.0	0.00001
Fl_ha, Ele_grp	13	444.3	473.9	24.3	0.00000
Fl_ha, Ele_grp, Site(Ele_grp)	19	436.7	480.0	30.4	0.00000
Ele_grp, Site(Ele_grp)	18	459.4	500.3	50.7	0.00000
Ele_grp	12	468.5	594.8	145.2	0.00000

APPENDIX 3. Ranked (based on AIC_c) regression models developed to predict bird densities based on point-transect sampling (please see Appendix 2 caption for description of terms).

Model	k	Log likelihood	AIC_c	ΔAIC_c	w_i
`Apapane					
Ele_grp, Site(Ele_grp), Season	21	77.7	136.1	0	0.59833
Ele_grp, Site(Ele_grp), Br_Season	19	87.5	139.1	3.0	0.13351
Fl_ha, Ele_grp, Site(Ele_grp), Season	22	77.3	139.3	3.2	0.12080
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season	20	86.7	141.7	5.6	0.03638
Ele_grp	12	111.4	142.1	6.0	0.02979
Fl_ha, Ele_grp, Site(Ele_grp)	19	91.2	142.9	6.8	0.01997
Ele_grp, Site(Ele_grp)	18	95.3	143.7	7.6	0.01339
Fl_ha, Ele_grp	13	110.4	143.8	7.7	0.01273
Fl_ha, Ele_grp, Site(Ele_grp), Season, Fl_ha*Season	25	70.5	143.8	7.7	0.01273
Fl_ha, Ele_grp, Br_Season	14	108.1	144.3	8.2	0.00992
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season, Fl_ha*Br_Season	21	86.0	144.5	8.4	0.00897
Season	13	113.0	146.4	10.3	0.00347
Br_Season	11	131.0	158.9	22.8	0.00001
Fl_ha	11	131.5	159.4	23.3	0.00001

(continued)

Appendix 3. Continued.

Model	*k*	Log likelihood	AIC$_c$	ΔAIC$_c$	w_i
		\`Amakihi			
Ele_grp, Site(Ele_grp), Br_Season	8	17.9	35.4	0	0.53963
Ele_grp, Site(Ele_grp)	7	21.6	37.1	1.7	0.23065
Fl_ha, Ele_grp, Site(Ele_grp)	8	17.8	38.6	3.2	0.10895
Fl_ha, Ele_grp Site(Ele_grp), Br_Season	9	16.4	39.9	4.5	0.05688
Fl_ha, Ele_grp, Site(Ele_grp), Season, Fl_ha*Season	14	3.3	41.6	6.2	0.02431
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season, Fl_ha*Br_Season	10	15.8	42.1	6.7	0.01893
Ele_grp, Site(Ele_grp), Season	10	16.5	42.7	7.3	0.01403
Fl_ha, Ele_grp, Site(Ele_grp), Season	11	15.0	44.2	8.8	0.00663
Ele_grp	3	150.8	159.4	124.0	0.00000
Fl_ha, Ele_grp	4	150.6	161.5	126.1	0.00000
Fl_ha, Ele_grp, Br_Season	5	150.4	163.7	128.3	0.00000
Fl_ha	2	205.7	212.1	176.7	0.00000
Br_Season	2	205.6	212.2	176.8	0.00000
Season	4	205.2	216.1	180.7	0.00000
		\`I\`iwi			
Site Fl_ha	7	29.2	51.2	0	0.82402
Site Fl_ha, Br_Season	8	29.2	55.0	3.8	0.12325
Site Fl_ha Season,	10	23.3	57.9	6.7	0.02891
Site, Fl_ha Br_Season, Fl_ha*Br_Season	9	28.9	58.9	7.7	0.01754
Fl_ha	5	46.5	61.7	10.5	0.00432
Fl_ha, Br_Season	6	46.1	64.6	13.4	0.00101
Br_Season	5	50.6	65.8	14.6	0.00056
Fl_ha Br_Season, Fl_ha*Br_Season	7	46.0	68.0	16.8	0.00019
Site Fl_ha Season, Fl_ha*Season	13	18.4	69.8	18.6	0.00008
Fl_ha Season	8	44.2	70.0	18.8	0.00007
Season	7	48.3	70.3	19.1	0.00006
Fl_ha Season, Fl_ha*Season	11	42.4	82.0	30.8	0.00000
		Japanese White-eye			
Fl_ha, Ele_grp	13	68.4	101.8	0	0.58472
Fl_ha, Ele_grp, Br_Season	14	67.8	104.0	2.2	0.19464
Ele_grp	12	74.4	105.0	3.2	0.11805
Fl_ha	11	78.3	106.2	4.4	0.06479
Br_Season	11	80.0	107.9	6.1	0.02769
Season	13	77.2	110.5	8.7	0.00755
Ele_grp, Site(Ele_grp), Br_Season	19	69.0	113.0	11.2	0.00216
Fl_ha, Ele_grp, Site(Ele_grp)	19	66.0	117.6	15.8	0.00022
Fl_ha, Ele_grp Site(Ele_grp), Br_Season	20	65.3	120.3	18.5	0.00006
Fl_ha, Ele_grp, Site(Ele_grp), Season, Fl_ha*Season	25	47.3	120.6	18.8	0.00005
Ele_grp, Site(Ele_grp)	18	72.8	121.2	19.4	0.00004
Fl_ha, Ele_grp, Site(Ele_grp), Br_Season, Fl_ha*Br_Season	21	64.2	122.6	20.8	0.00002
Ele_grp, Site(Ele_grp), Season	21	65.0	123.4	21.6	0.00001
Fl_ha, Ele_grp, Site(Ele_grp), Season	22	61.4	123.4	21.6	0.00001