Forest Bird Distribution, Density and Trends in the Ka`ū Region of Hawai`i Island

By P. Marcos Gorresen, Richard J. Camp, and Thane K. Pratt

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Executive Summary

In the Ka`ū District on the Island of Hawai`i lies perhaps the largest intact stretch of native rainforest in the state, one of critical importance to the conservation of Hawaiian forest birds. The original vegetation of this 47,408 ha (474 km^2) tract is native forest, woodland, and shrubland, although the southwest and subalpine margins have been historically grazed and are pasture to varying degrees. The tract is centered on the Ka` ū and Kapāpala Forest Reserves owned and managed by the State of Hawai`i, and include inholdings belonging to Kamehameha Schools and The Nature Conservancy. Recently, Kahuku Ranch to the north and southwest was incorporated into Hawai`i Volcanoes National Park. Together these lands harbor the second largest concentration of native forest birds on Hawai`i Island, including populations of three endangered Hawaiian honeycreepers.

To understand the status of forest birds in the Ka`ū forest, it has been a conservation goal to survey and monitor their populations. This report presents analysis of the 30-year history of monitoring in this important bird habitat. The objectives of the study were to (1) examine the distribution of native and exotic forest birds; (2) estimate population sizes; and (3) estimate trends in population density. The five forest bird surveys analyzed herein were conducted between 1976 and 2005 by the State of Hawai`i Division of Forestry and Wildlife, the National Park Service, U.S. Geological Survey, and U.S. Fish and Wildlife Service, and include a total of 54 transects and 1,952 stations. The most recent of these surveys, in 2005, sampled bird populations at a much finer scale than previous surveys, and although limited to elevations above 1,500 m, these surveys are the first to give up-to-date information at greater accuracy for bird populations in habitat above the elevational zone afflicted by mosquito-borne bird diseases (Tweed *et al*. In review). Species-habitat models were developed to predict densities for the entire study area for 7 of the 11 species treated herein.

The distributions of the three endangered species - `Akiapōlā`au, Hawai`i Creeper, Hawai`i `Ākepa – are restricted to a narrow (3 – 4 km) band of forest and adjacent woodland above 1,500 m. These species show no trend in density at high elevations, but have been extirpated from habitat below 1,500 m since the 1976 Hawaii Forest Bird Survey. Current population estimates for `Akiapōlā`au are 1,073 (± 307 SE) birds, for Hawai`i Creeper, 2,268 (± 797 SE), and for Hawai`i `Ākepa, 2,556 (± 863 SE).

With a population numbering about 14,600 (± 4,300 SD) birds, the Hawai`i `Elepaio also exhibits a restricted distribution and is mostly concentrated towards the

northeastern third of the study area. There is tentative evidence of a contraction in the species' range and a decline in density since 1976. Encouragingly, about two-thirds of its population occurs below 1,500 m and may indicate that Hawai`i `Elepaio are either to some degree resistant to avian malaria or the disease may not be as prevalent in this area as it is in other montane habitats.

`I`iwi are common within much of the forest habitat in the study area, and the population size was estimated at about 78,000 (± 9,000 SD) individuals. As much as 40% of the `I`iwi population may be seasonally present below 1,500 m. The greater part of this low elevation distribution occurs in drier forest in the northeastern third of the study area. Given the observed decline in `I`iwi in Ka`ū (and elsewhere) and the species' susceptibility to avian malaria, the population would likely benefit from habitat restoration and protection in this area.

Ōma`o, Hawai`i `Amakihi, and `Apapane are widely distributed in the study area, and have sizable populations (about 82,000 [± 7,000 SD], 155,000 [± 9,000 SD], and 492,000 [± 24,000 SD], respectively). The proportion of these species' populations observed and predicted to occur below 1,500 m ranged from 34% (Hawai`i `Amakihi) and 41% (`Apapane) up to 64% (Ōma`o). Their occurrence, in places down to 700 m, indicates that these birds may be survivors of prior malaria infections. The apparent downward trends detected for Ōma`o and Hawai`i `Amakihi are in doubt given the observed high variability in density. The upward trend in `Apapane density at low elevations appears reliable.

The densities of non-native birds appear stable and relatively low at upper elevations. Red-billed Leiothrix is the only non-native species to demonstrate an upward trend at low elevations. The population size of Red-billed Leiothrix, Japanese White-eye and Northern Cardinal were estimated at about 39,000 (± 5,000 SD), 245,000 (± 33,000 SD), and 11,000 (± 2,500 SE) birds, respectively.

The difficulty in reliably discerning trends in density and changes in the extent of a species' range indicate that the current survey program should be reevaluated. We propose the establishment of a comprehensive monitoring framework that intensively samples select areas and extensively samples a larger region to provide both the "close-ups" and the "big picture" needed to anticipate and follow changes in bird numbers, occurrence and distribution. The relative uncertainty associated with densities predicted by species-habitat models is greatest in under-sampled habitats and where observed density is low and variable. Surveys should be designed to provide a broader coverage of sampled habitats or specific areas within selected species' range. To a large extent, such a program can build on recent surveys in the region.

The current practice of conducting surveys in late winter and spring is supported by the data, which show that mid-spring counts coincide with the period when the majority of species are most vocal in Ka`ū. For trend analyses, it is important to maintain as consistent a survey schedule as logistically feasible to minimize measurement error.

Variable circular-plot and other count methods are relatively ineffective at tracking trends of rare species such as `Akiapōlā`au, Hawai`i Creeper and Hawai`i `Ākepa. Demographic studies for these species should be considered in the Ka`ū study area.

Introduction

An accurate and current measure of population status and trend is necessary for conservation and management efforts. Scott and Kepler (1985) provided a comprehensive review of the status of native Hawaiian birds based on the extensive Hawaii Forest Bird Survey (HFBS) of the main islands (Scott *et al*. 1986). At that time, they documented declining populations and decreasing ranges for most species, and the extinction of several species over the previous 50 years. Many native bird species continue to decline throughout Hawai`i (Camp *et al*. In review, Gorresen *et al*. In prep.).

The focus of this study is the mid-to-high elevation rainforest on the southeast windward slopes of Mauna Loa Volcano (Figure 1). Known as Ka`ū, the region encompasses forest lands protected by Kamehameha Schools, The Nature Conservancy, Hawai`i Volcanoes National Park (HVNP), and the State of Hawai`i'’s Ka`ū Forest Reserve, Kapāpala Forest Reserve and Kapāpala Cooperative Game Management Area,. Together these lands support one of three main concentrations of native forest birds on the Hawai`i Island (the other two being centered on the Hakalau Forest National Wildlife Refuge and Kūlani-Keauhou area in the north and central windward part of the island, respectively.)

Because this region harbors important populations of native and endangered forest birds in some of the best remaining forest habitat on the island, it has been a focus of forest bird surveys since the 1970s. The Ka`ū region was first quantitatively surveyed in 1976 by the Hawaii Forest Bird Survey (Scott *et al*. 1986). Surveys were conducted by State of Hawai`i Division of Forestry and Wildlife in 1993 and 2002 and by the U.S. National Park Service and the U.S. Geological Survey in 2004 and 2005.

In this report, we present analyses of the density, distribution and trends of native and introduced forest bird within the Ka`ū region of Hawai`i Island. The analyses cover only those species with sufficient detections to model detection probability and calculate density. These include three endangered native passerines: `Akiapōlā`au (*Hemignathus munroi*), Hawai`i Creeper (*Oreomystis mana*), and Hawai`i `Ākepa (*Loxops coccineus*); five more common native passerines: the Hawai`i `Elepaio (*Chasiempis sandwichensis*), `Ōma`o (*Myadestes obscurus*), Hawai`i `Amakihi (*Hemignathus virens*), `I`iwi (*Vestiaria coccinea*) and `Apapane (*Himatione sanguinea*); and three non-native species: Red-billed Leiothrix (*Leiothrix lutea*), Japanese White-eye (*Zosterops japonicus*), and Northern Cardinal (*Cardinalis cardinalis*).

Methods

Study Area

The 47,408 ha (474 km^2) region comprising the Ka`ū study area lies just east of the South Rift Zone on the southeast windward slope of Mauna Loa Volcano on Hawai`i Island, and is located between 600 and 2,400 m elevation (Figure 2). Forest bird habitat consists of four general landcover types (excluding exposed lava terrain, fallow caneland, open pasture and exotic tree plantations): 1) native forest, 2) forested pasture, 3) sub-alpine woodland, and 4) sub-alpine scrubland. The native forest is comprised primarily of mature mesic and wet `ōhi`a (*Metrosideros polymorpha*) vegetation associations that include varying amounts of koa (*Acacia koa*) and understory components such as tree-fern (hāpu`u [*Cibotium glaucum*]) and matted-fern (uluhe; primarily *Dicranopteris* *linearis*). Forested pasture makes up much of the vegetation along the southern portion of the study area. The area largely has been used for cattle ranching over the past 150 years, and the canopy cover and understory composition has been altered considerably from its original condition as mesic and wet koa-`ōhi`a forest. Currently, the area consists of pasture with isolated trees and small stands of native forest. The dry sub-alpine woodland and shrubland at the northwestern and upland edge of the study area is dominated by `ōhi`a, pukiawe (*Leptecophylla tameiamaeiae*) and other shrub species.

Bird Sampling

As elsewhere in much of Hawai`i, the HFBS established the basis for long-term population monitoring with survey transects throughout the Ka`ū study area (Scott *et al*. 1986). The HFBS in Ka`ū was conducted in 1976, and spanned almost the entire elevation gradient (600-2,300 m) of forest habitat in the region (Figure 3). Within the study area, the HFBS sampled a total of 874 stations established at 100 m intervals and along transects spaced about 3 km apart. Surveys subsequent to the HFBS were carried out in 1993, 2002, 2004 and 2005 across smaller portions of the study area. The 1993 and 2002 surveys were carried out by the Hawai`i Division of Forestry and Wildlife (DOFAW) for the central part of the study area (Camp *et al*. In review). Stations were established at 150 m intervals along five of the 1976 HFBS transects, and totaled to 232 and 214 stations in 1993 and 2002, respectively. In 2004, the U.S. Geological Survey (USGS) conducted a survey of 147 stations within the Kapāpala Forest Reserve and adjacent Kapāpala Cooperative Game Management Area. Both stations and transects for this survey were spaced at 200 m intervals. In 2005, the USGS and National Park Service jointly surveyed parts of the Kahuku Unit (newly acquired by HVNP) and the adjacent Ka`ū Forest Reserve (Tweed *et al*. In review). This survey sampled stations established at 200 m intervals and along transects spaced 1 km apart. In 2005, the USGS also sampled an area in southern Ka`ū not surveyed since the 1976 HFBS. This survey was comprised of a single transect running the entire elevation gradient of forest habitat and stations spaced at 200 m intervals.

All surveys were conducted using variable circular-plot (VCP) count methodology (Reynolds *et al*. 1980). VCP counts are a form of distance sampling used to correct abundance estimates for individuals that go undetected as a function of the distance between observer and birds. VCP counts are recorded at observation points (i.e., stations) that serve as the centers for estimating radial distances to birds during a count period.

Accounting for the distance-related decline in bird detectability is complicated by the variable effects of "nuisance" factors such as observer ability and weather conditions. Nuisance factors related to observer ability were minimized by calibration and training in identification of species and the estimation of distances to detected birds. Observers recorded the species, detection type (auditory, visual, or both), and distance from the station center point to birds detected during eight-minute counts. Time of sampling and weather conditions were also recorded, and surveying was halted when conditions hindered the ability to detect birds (i.e., heavy rain, and wind and gust >20 kph). The survey data used for analyses excluded observations located outside of the study area and those not conducted during the breeding season (December to July).

Measures of Bird Abundance and Density

Bird count data were prepared with one of two approaches depending on whether they were used for trend assessment or species-habitat modeling. Both approaches used distance-sampling models to correct abundance estimates for detectability. The difference between approaches lay in the stage at which the corrections were applied. Count data were adjusted for detectability *prior* to carrying out trend analyses. In contrast, bird detections were directly used to develop species-habitat models, and the predicted abundances derived from the models were *subsequently* adjusted to account for unobserved birds; the rationale is described more fully in the section "*Modeling Bird Distribution*".

The program Distance 4.1 (Thomas *et al*. 2003) was used to develop distance-based models of bird detectability for the purpose of calculating the area effectively sampled for each species (referred herein as "detectability models"). Bird counts were initially examined to derive truncation distances for excluding very distant and unreliable observations, and to avoid double-counting birds. Data were truncated at the point where the detection probability was approximately 0.10 (i.e., corresponding to the most distant observations at the "tail" of the data distribution). A detection function was fit to the remaining bird observations following the model selection methods described by Buckland *et al*. (2001, 2004) and Thomas *et al*. (2003). Model selection was limited to half normal and hazard-rate detection functions with expansion series of two orders. These models are most appropriate for VCP counts and permit assessment of the relative effects of such factors as survey observer, time of day, cloud cover, rain, wind, gust, year, and month. Histograms of the count data and the detection function were plotted, and the fit of the function was examined. If necessary, distant observations were further truncated to improve the fit of the detection function. Models with varying combinations of covariates were compared to identify the best fit of detection function and count data. Selection of the final model for each species was based on that with the lowest Akaike's Information Criterion (AIC) score. The final detectability models developed for each species, including covariates, truncation distances and effective detection radius (i.e., area sampled), are detailed in Appendix 1. The variance estimates for all detection radius estimates are reported as standard errors (SE).

Mean annual density and variance estimates were obtained by a bootstrap method in Distance (Buckland *et al*. 2001). The method involves taking a random sample with replacement of the detections observed at stations in each study area, and re-running the analysis to estimate densities for each of 999 iterations. The 95% confidence intervals (CI) for the mean annual density estimates were derived from the 5th and 95th percentiles of the bootstrapped estimates. The variance estimates for all density estimates are reported as standard errors.

Measures of Bird Habitat Attributes

The 47,408 hectare Ka`ū study area was delineated with a minimum concave polygon extending up to 1-kilometer around all survey stations. This restricted delineation ensured that density predictions were not generated from habitat values much beyond the range of those used to fit the species-habitat models. We selected habitat variables for investigation based on published ecological studies in Hawai`i and elsewhere (e.g., Scott *et al.* 1986, Dettmers *et al.* 2002), knowledge of the prominent features of Hawaiian forests, and discussions with other biologists. However, we were limited to using only those variables for which digital maps at the landscape scale were available. These variables included vegetation information produced from the classification of a Landsat ETM satellite image (path/row: 63/47; date: Feb 5, 2000) with the program Imagine (ERDAS 1999). Classification was accomplished with a supervised method that involved identifying sets of spectral signatures characteristic of specific landcover and vegetation types. Classification incorporated “training” samples derived from site visits (i.e., “ground-truth”) and image interpretation of ancillary data such as high-resolution imagery acquired by aircraft (e.g., USDA Emerge Program Digital Orthophotos) and digital vegetation maps (e.g., Jacobi 1989). Landcover classification yielded information on the dominant vegetation types (i.e., `ōhi`a, shrubland, grassland, and exotic vegetation types), the presence/absence of major understory components (i.e., matted-ferns, native shrubs), canopy closure (closed: >60%; open: >25-60%; sparse: 1-25%; none; see Jacobi 1989), canopy height (high: >10 m; mid: >5-10 m; low: 2-5 m; none), and the diversity of landcover types (i.e., variety within an area). The presence/absence of koa and tree-fern landcover components were obtained from maps of aerial photograph interpretation (Jacobi 1989). Species-habitat models also included the abiotic variables elevation, slope, rainfall, and temperature. Elevation and slope were obtained from 10 m resolution USGS Digital Elevation Model layers. Squared elevation values were also used to characterize unimodal relationships with bird abundance. Mean annual rainfall and temperature were derived from the PRISM layers produced by the Spatial Climate Analysis Service at the Oregon State University at a resolution of 15 arc-seconds (~ 450 m).

Habitat values were generated as either point- or area-based measures centered at each of the 1,952 distinct VCP station locations sampled within the study area (Table 1). In addition to the survey stations, habitat values were derived for a lattice of points used for the prediction of densities for the entire study area. The lattice points were established on a 100-meter spacing so as to match the 1-hectare (i.e., 100 x 100 meter) resolution used for bird density estimation. Point-based values were obtained by querying the rainfall and temperature layers with the station and lattice layer. Queries were performed with the Spatial Analyst module of ArcGIS 8.0 (ESRI 2002). Area-based measures used a 90-meter radius area (= 25,447 m^2 [2.5 hectare] circular sample) centered on each lattice point to quantify values for all other habitat variables. This radius was calculated as one-half the mean nearest neighbor distance among the survey stations. This radial extent was a compromise between sampling habitats across either too large or too small an area. More specifically, the extent of the area used for habitat sampling ensured that it exceeded the spatial resolution of digital grid-based imagery (900 square meters). The limited extent of the sample area also reduced the amount of overlap (and therefore autocorrelation) in habitat measures between neighboring stations.

Area-based measures of habitat were based on either the proportion or the dominant characteristic identified within the sample area radius. The dominant characteristic was used when a categorical variable displayed more than one state (e.g., closed, open and sparse canopy closure). The average of all values within the sample area radius was used for quantitative variables (e.g., the mean of elevation values from all 10 x 10 m cells within the 90-meter radius sample). The set of values for each habitat layer were standardized to have a zero mean and unit variance so as to improve statistical performance of species-habitat models and permit the comparative assessment of variable contribution in accounting for bird abundance (Gilks and Roberts 1996).

Accuracy assessment of the classified landcover image was carried out by calculating the proportion of ground-truth samples that correctly matched the landcover class. For logistical reasons (i.e., high cost of traveling to widely dispersed locations by helicopter), ground-truth samples of vegetation were not randomly selected for accuracy assessment from the study area. Instead, samples were acquired by traversing the study area along a linear path by helicopter and regularly (i.e., every few minutes) describing vegetation attributes at point locations from a low altitude ($\leq$ 50 m). Vegetation was also described from locations on the ground reached by foot or vehicle. Moreover, ancillary data (i.e., high resolution aerial [Emerge] and satellite [Ikonos] imagery) was used to provide additional "samples" of landcover features for the assessment of classification accuracy.

Landcover classes are made up from a number of attributes related to plant community composition and physical structure. Therefore, we felt that an assessment of the accuracy of a classified image would be most informative if it were separately performed on the distinct attributes of the landcover classes. The four general attributes comprising the landcover classes included the dominant vegetation type, subcanopy vegetation type (if applicable), canopy closure (if applicable), and physiognomic stature. These components were correctly classified in 98%, 78%, 73% and 73% of the 170 available ground-truth samples, respectively, with an average accuracy of 81% for all four components.

Assessing Trends in Density

For the purpose of assessing trends, the bird survey data was initially subset to address inconsistencies in temporal and spatial sampling and to ensure that analyses were not biased by the inclusion of data for areas sampled in one period but not another. Survey stations sampled in each year were delineated to identify an area coincident to all surveys. This area was further subset to assess trends in upper and lower elevation habitat (defined by the 1,500 m contour, an elevation threshold below which mosquito-borne bird diseases are prevalent; Atkinson *et al*. 2001, 2005; Figure 4). A total of 396 stations along 6 transects from the 1976 HFBS were used for density trend analyses. Analysis of the 1993, 2002 and 2005 surveys used 232, 214, and 213 stations along 5, 5, and 15 transects, respectively.

Trends in bird density were assessed with equivalence tests (Dixon and Pechmann 2005). The method is particularly useful for distinguishing between cases in which there actually was no trend from the inability to *statistically* detect a trend because of high variability in densities or small sample size. In contrast, conventional approaches to trend analysis are not readily able to provide conclusive evidence that a trend is near or at zero.

Equivalence tests were applied in combination with z-tests. A two-sample z-test was used to examine the significance of a "presumed" slope given the combined within-year variance in the densities of the 2 years under comparison (i.e., "signal" relative to "noise"). The term "presumed" was used to highlight the uncertainty inherent in inferring a trend from only two periods. Regression approaches to calculating slope are possible for data sets with a greater number of samples (at least 5 years) than available and analyzed here (e.g., see Dixon and Pechmann 2005).

To assess the significance of a trend we chose the fairly conservative threshold corresponding to an annual rate of change of |0.0270| used by the Breeding Bird Survey in North America (Peterjohn *et al*. 1995). An observed slope greater than 0.0270 or less than -0.0270 would result in the doubling or halving of a population in 25 years, respectively. Conversely, the range that encompasses these values (i.e., from <0.0270 to >-0.0270) is the "equivalence region" from which a stable or negligible trend may be inferred in an equivalence test.

Contrary to the standard approach in statistical tests, the null hypothesis (*H*) of the equivalence test assumes that the densities are substantially *different*, and the alternative hypothesis (*K*) states that the presumed slope lies within the lower (θ_L) and upper (θ_U) thresholds of the equivalence region (Manly 2001:179, MacKenzie and Kendall 2002). The rationale for this approach lies in the fact that an actual trend is seldom likely to be exactly zero, and the more relevant question is whether the trend, if present, is biologically negligible.

The trend analysis first calculates the presumed slope as the difference in the mean densities $\hat{D}_1$ and $\hat{D}_2$ over the time spanned by the surveys T_1 and T_2. The variance around the slope is calculated as the standard error of the difference in mean densities divided by the length of the time period

$$SE_{SLOPE} = SE\left(\hat{D}_2 - \hat{D}_1\right)/\left(T_2 - T_1\right),$$

where the standard error of the difference in mean densities is estimated as

$$SE(\hat{D}_2 - \hat{D}_1) = \sqrt{\left\{SE\left(\hat{D}_1\right)\right\}^2 + \left\{SE\left(\hat{D}_2\right)\right\}^2}.$$

The presence of a trend in density is then examined with a one-sided test of each the following two sub-hypotheses:

H_{LOWER}: $\hat{D}_1 - \hat{D}_2 \leq \theta_L$ K_{LOWER}: $\hat{D}_1 - \hat{D}_2 > \theta_L$

H_{UPPER}: $\hat{D}_1 - \hat{D}_2 \geq \theta_U$ K_{UPPER}: $\hat{D}_1 - \hat{D}_2 < \theta_U$.

That is, the tests of the sub-hypothesis separately ask whether the trend exceeds the lower and upper thresholds.

The test statistics for the lower and upper sub-hypothesis tests (as adapted from Manly [2001:185] for the use of z-tests) are calculated as

$$\frac{(\hat{D}_2 - \hat{D}_1) - \theta_L}{\sqrt{\left\{SE\left(\hat{D}_1\right)\right\}^2 + \left\{SE\left(\hat{D}_2\right)\right\}^2}}$$

and

$$\frac{\theta_U - (\hat{D}_2 - \hat{D}_1)}{\sqrt{\left\{SE\left(\hat{D}_1\right)\right\}^2 + \left\{SE\left(\hat{D}_2\right)\right\}^2}},$$

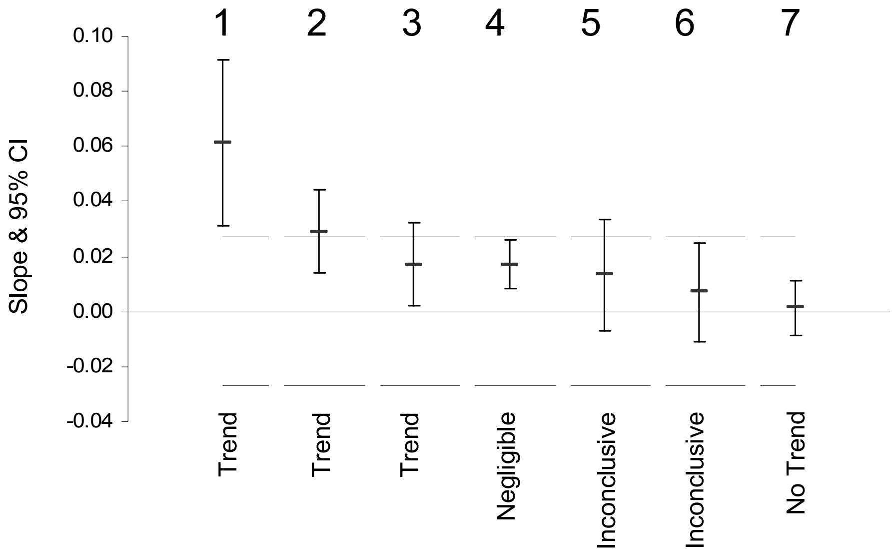
respectively.

Each of the null sub-hypotheses are rejected when the *P*-value of its test statistic is less than the pre-specified α level (set here at 0.05). Adjustments for multiple comparisons are not required for this type of equivalence testing (Manly 2001:185).

Finally, the significance of difference in mean densities for the 2 years is also assessed with a two-sample z-test. The results of the combined z-test and equivalence test yield one of four possible trend outcomes - three conclusive and one inconclusive – as diagrammed below (adapted from Dixon and Pechmann 2005):

		Z-test	
		Do Not Reject Null	Reject Null
Equivalence Test	Reject Null if both *P*-values < α (i.e. within equivalence region)	Conclusive evidence of no biologically significant trend (i.e., stable population).	Conclusive evidence that a trend is present but is biologically negligible.
	Do Not Reject Null if one or both *P*-values > α (i.e., not within equivalence region)	Population may be changing or stable (i.e., inconclusive result).	Conclusive evidence of a biologically significant trend.

We conclude that the population is "stable" when the difference in densities is not statistically different from 0 and the presumed slope is inside the equivalence region (i.e., between -0.0270 and 0.0270; both null sub-hypotheses rejected and, consequently, the equivalence null hypothesis rejected). In contrast, there is conclusive evidence of a biologically significant trend when the difference in densities is statistically different from zero and the presumed slope was outside the equivalence region (i.e., less than -0.0270 or greater than 0.0270; one of the null sub-hypotheses rejected; consequently, equivalence null hypothesis not rejected). The outcomes leading to the above conclusions of "trend" and "no trend" are illustrated in cases 1 and 7 diagrammed below (for clarity, shown only for positive or non-trend outcomes):



However, there are a range of outcomes (cases 2 to 6) that may be obtained depending on the magnitude and reliability of the estimated slope. Where the mean of the presumed slope lies just above or below the threshold and the confidence interval of the slope is broad but does not bracket zero (Cases 2 and 3), the outcome is necessarily mixed; i.e., “the trend is stable *or* increasing”. Although cases 2 and 3 reflect the uncertainty surrounding the estimated slope, they may be distinguished from “inconclusive” outcomes because they do not include the possibility of an opposite trend.

A conclusion of “negligible trend” (Case 4) results when the difference in densities is significantly different from zero, but the equivalence test indicates that the presumed slope is within the equivalence region and near zero. This outcome may occur when the variance of the trend is sufficiently small that the confidence intervals of the slope do not include 0, but the presumed slope is deemed to be biologically unimportant. For purposes of simplifying interpretation, we considered a biologically negligible trend to be equivalent to a stable trend.

Finally, an inconclusive outcome may be obtained when the null hypotheses of both the z-test and equivalence test are not rejected. This occurs when the difference in densities is not significantly different from zero but the equivalence test does not support the conclusion that the trend is at or near zero. Together, the two tests indicate that the densities may *either* be changing or have remained stable but are indistinguishable because the variability in abundance is high. This inconclusive result is illustrated by wide confidence intervals that span zero and that may or may not lie entirely within the equivalence region (Cases 5 and 6, respectively).

Modeling Bird Distribution

Modeling approach rationale

Predicted bird abundance for the Ka`ū study area was generated with a Bayesian hierarchical model proposed by Link and Sauer (2002), and further developed by Thogmartin *et al*. (2004) for the spatial modeling of bird counts. The approach is well suited for the analysis of large data sets with complex dependencies among “higher-level” attributes associated with bird abundance (Link *et al*. 2002). For example, patterns in count data may be partly a function of such factors as spatial autocorrelation, year and seasonal effects. These patterns may be particularly prevalent in data derived from clustered populations surveyed over time and large spatial scales. Accounting for these effects with “hyperparameters” in a hierarchical model reduces the need for *ad hoc* procedures to correct for potential sources of bias and survey design inefficiencies (Link and Sauer 1998).

In addition to the effects of habitat variables and hyperparameters, factors that influence the *detectability* of birds can also influence counts and typically include “nuisance” variables such as observer ability and weather conditions (Buckland *et al*. 2001:22). These factors affect consistency in the estimation of the distance between observer and detected birds, and are usually negligible at close range and more pronounced at greater distances (i.e., detectability diminishes with distance). For instance, high wind may severely curtail the area in which birds can be detected compared to that sampled during a windless day. Moreover, observers often differ in their ability to perceive and accurately estimate the distance to birds. Detection functions (i.e., a model fit of counts by distance intervals) may show distinctly dissimilar shapes (i.e., intercept, “shoulder”, slope, and “tail”) among observers. The bias associated with an observer effect has previously been dealt with elsewhere by its incorporation as a hyperparameter in hierarchical models (e.g., Link and Sauer 2002, Thogmartin *et al*. 2004). However, this variable was not included in the hierarchical models developed for this study because few, if any, observers have surveyed more than one year in Ka`ū, and this precluded the separation of an observer effect from a year effect. Perhaps more importantly, it was felt that the observer effect, along with other “nuisance” variables relating to weather conditions, would be handled best with the program Distance (Thomas *et al*. 2003). The rationale for this lies with the program’s ability to separately model a detection function for each observer and weather condition class (e.g., heavy rain, light rain, no rain), and distill their respective effects to yield a “global” detection function applicable to an adjustment of all counts.

Detectability may also be influenced by seasonal effects related to the phenology of bird vocalization. When birds are highly vocal, the average distance at which individuals are detected may be less than that during less vocal periods. This may be caused by the “interference” of nearby and vocal birds on an observer’s ability pick out the song and calls of distant birds. However, although preliminary analysis indicated that the covariate “month” was significant, its inclusion in the distance-sampling models had little to no effect on the estimated detection radius for each species (i.e., the area effectively sampled during a survey). For example, the detection radius for `Ōma`o with and without the variable month was 54.11 m and 54.07 m, respectively; a difference of only 0.06%. The average difference in the detection radii for all species examined in this study was 0.23 m (<0.01%) and the maximum difference (for `I`iwi) was only 1.13 m (3.0%). For this reason, we chose to exclude month from the detection functions estimated for each species, and to instead model seasonal effects as a nuisance variable in the hierarchical model. This approach also allowed for a more nuanced accounting of seasonal effects by the use of survey “date”, rather than month, as an explanatory variable (described in more detail in the next section).

When inference is to be made about abundance from observed counts, it is important to account for the biases associated with imperfect detection (Royle *et al*. 2004). Towards this end, a detection function provides a “correction factor” that adjusts counts for *undetected* individuals (Buckland *et al*. 2001:20), and effectively renders count data into density by the incorporation of area sampled. However, because the detection function is simply applied as a constant, we chose to use it as a follow-up adjustment to model predictions. The alternative was to apply the detection function *before* modeling bird-habitat associations. However, such an adjustment lead to analytical problems with the less than tractable distribution of densities (i.e., it resulted in non-integer values and higher variance from a “toothed” series of values on an otherwise continuous axis; e.g., 0, 1.3, 2.6, 3.9, etc., derived from counts of 0, 1, 2, 3, etc.). The adjustment for undetected birds was made necessary by the fact that, despite it being an active field of research, there has yet to be developed a practical method for relating count data to covariates describing both bird habitat and the complex effects of hyperparameters and nuisance variables. The primary drawback to the adjustment is that the error attributable to modeling the distance-conditional effect of nuisance variables is not incorporated into the subsequent model relating bird abundance to habitat and other variables.

Model formulation

General linear models with a Poisson distribution and a log link function were initially used to relate bird counts to habitat variables. A Poisson distribution was used for modeling because bird counts are discrete positive integers with larger values being less frequent than smaller values and zeros (Sokal and Rohlf 1995:81). An approach analogous to forward stepwise selection was used to individually add variables and assess the effects of multicollinearity (e.g., coefficient sign reversal) as partly correlated variables were added to the model. Highly correlated variables (>|0.80|) were excluded as candidate variables. Variable significance was evaluated at each step with a likelihood ratio test (Neter *et al*. 1996:586). Poisson models were developed with the program S-PLUS 6 (2001).

After habitat variables were selected with general linear models, hierarchical models were developed that incorporated year, season and spatial effects. Year and seasonal effects (i.e., month) were previously assessed in Distance and determined to be significant covariates in all cases for which there was sufficient data to model their effects on bird counts (Appendix 1).

Because year effects were included in the hierarchical models as a hyperparameter, we were able to use count data for all surveys (1976, 1993, 2002, 2004 and 2005) carried out during the breeding season (December to July). Year was treated as a fixed effect under the assumption that it is measured without error. As such, models required that a year be specified in the linear predictor. We applied one of two approaches depending on whether the species showed significantly positive or negative trends in density during the 1976-2005 survey period. For those species with significant trends, we selected the latest year of survey to generate the predictions of abundance and the most current estimate of population size. For species that did not show an apparent trend, we chose a year that was closest to the mean of the coefficients for all year effects. This allowed us to avoid the influence of an “unusually” high or low year effect associated with the most recent survey and which may simply reflect sampling error. That is, we wished the models to predict bird abundance for an “average” year and to make our inference of population size for the entire survey period. The choice of year in the prediction of abundance for each species is noted in Appendix 2.

Seasonal effects were incorporated into hierarchical models by use of survey date as a random effect variable. This effect was modeled for each species by defining a unimodal relationship of bird count and date for the span of the survey period. The unimodal pattern was described with a sine and a cosine function from a Fourier series (Stolwijk 1999). More complicated functions describing multiple cycles were possible, however, observed counts plotted by date revealed either a single peak during the spring or a monotonic increase during the breeding season for all species examined (for examples see species accounts). Values from the sine and cosine functions were calculated for all dates associated with survey observations and the functions were included as parameters in the hierarchical model for each species. However, the application of a model for predictive purposes entailed specification of a date in the linear predictor for each species. We chose a date at which the seasonal effect upon count was at its maximum (e.g., `Ōma`o counts peaked on survey date 138 [mid-May]). This generated predictions for the period at which the highest proportion of a population was vocal and the fewest number of birds remained undetected.

Ecological features (e.g., forest) are structured by environmental factors (e.g., rainfall) and naturally result in the spatial autocorrelation of other ecological features such as bird distribution (Legendre 1993). Correct inference of bird abundance and distribution in such conditions requires the proper accommodation of spatial autocorrelation. Spatial effects were incorporated into the hierarchical model with a Gaussian conditional autoregressive prior based on the spatial neighborhood of point and area locations (i.e. survey stations and map layer cells; Speigelhalter *et al*. 2000). The spatial neighborhood was defined by the adjacency of 2,030 grid cells delineated at a 500 m resolution across the study area. Exploratory analysis indicated that a smaller grid cell size resulted in too many cells upon which to efficiently compute a model incorporating spatial effects. For example, a total of 47,408 cells were produced from applying a grid cell resolution of 100 m (i.e., corresponding to the 1 ha cell size used to quantifying habitat values). Coarser grids reduced the number of cells (e.g., total of 539 at a 1 km resolution) and greatly improved computational efficiency, but resulted in a severe "pixelation" of the predicted surface of bird abundance. An adjacency matrix for the spatial neighborhood was generated with the GeoBUGS module in WinBUGS (Thomas *et al*. 2002). Spatial neighborhood weights were set to 1 for locations within adjacent cells and 0 otherwise.

Hierarchical models incorporating both the habitat variables and hyperparameters were developed in WinBUGS 1.4 (Speigelhalter *et al*. 2000), a statistical package for conducting Bayesian inference with Markov chain Monte Carlo (MCMC) methods (i.e., Gibbs Sampling). The overdispersed Poisson regression models were fit following the methods described by Link *et al*. (2002) and Royle *et al*. (2002:630–631). Posterior distributions of model parameters were calculated from four chains run for 25,000 iterations after discarding the values from the first 15,000 iterations (i.e., "burn-in" period). Model convergence was assessed from the posterior distribution of the remaining values. Following convergence, the model was re-run with one chain for another 1,000 iterations to compute the posterior samples of model coefficients used for generating predicted densities.

Several species (`Akiapōlā`au, Hawai`i Creeper, Hawai`i `Ākepa and Northern Cardinal) did not have sufficient detections to adequately develop the hierarchical models used to predict densities and population estimates. For the native species, population sizes were simply calculated as the product of the mean density and the area of the species' distribution in Ka`ū, and were originally reported in Tweed *et al*. (In review). The area occupied by a species was manually delineated in ArcGIS from the locations of current bird detections and known habitat associations. Population estimates were not produced for the Northern Cardinal because survey coverage did not sufficiently coincide with the species' Ka`ū range.

Bird abundance prediction and mapping

Following the development of a species' hierarchical model and the assessment of model convergence, the posterior distribution of model coefficients was extracted in WinBUGS from the CODA output for a single chain. A custom script in SAS (Release 8.02: SAS Institute 2001) was used to integrate the posterior samples of model coefficients from each of the 1,000 MCMC simulations with the values of the habitat variables and hyperparameters for all 47,408 one-ha grid cells comprising the study area. The predicted abundances obtained from each simulation were subsequently adjusted to account for "undetected" birds (see Section "*Modeling approach rationale*"). Because the adjustment incorporated an estimate of the area sampled, its application effectively converted abundance predictions into densities scaled to the one-ha grid cell resolution. That is, the area-based adjustment for unobserved birds acts to link the scale of the predictive model to that of the map resolution. The melding of distance-sampling with the species-habitat models developed herein is a modest but important improvement on previous *ad hoc* methods that translate predictive models into a map of bird abundance (e.g., Royle *et al*. 2002, Thogmartin *et al*. 2004).

A preliminary population estimate was generated for each of a species' 1,000 model simulations. Each population estimate was obtained from the sum of all 47,408 predicted densities (i.e., the predictions for all one-ha grid cells within the study area). The mean, standard deviation (SD) and 95% confidence interval of the final population estimate were calculated from all 1,000 preliminary estimates. Maps of the mean predicted densities and associated standard deviation for each 1-ha grid cell were input and converted to a raster with the Spatial Analyst extension of ArcGIS 8.0 (ESRI 2002).

Model assessment and validation

Models were validated by comparing predicted abundance to that of the observed abundance derived from a reserved dataset randomly sampled from and comprising 10% of the full dataset. Several methods were used to assess predictive model performance. A histogram of observed and predicted abundance was used to visually assess at which levels of abundance a model adequately or inadequately estimated abundance. A Wilcoxon rank sum tested the significance of the difference between validation and predicted distributions (Sokal and Rohlf 1995). An alternative test - the Kolmogorov-Smirnov two-sample test – was not used since it is overly conservative when the distribution is not normal and is not recommended for discrete data. The slope of a linear regression of observed and predicted abundance was used to indicate the degree to which they approximated a 1-to-1 correspondence (e.g., MacNally and Fleishman 2002). Predictive models with a slope between 0.66 and 1 were considered to be unbiased (i.e., do not under-predict abundance). Models with a slope between 0.33 and <0.66 were moderately biased and those with a slope <0.33 were highly biased. Finally, the strength of a correlation among observed and predicted abundances was used to evaluate the relative precision of the model. Predictive models with a significant Pearson correlation coefficient (r) between 0.66 and 1 were considered to be precise. Models with a coefficient between 0.33 and <0.66 were moderately precise and those with a coefficient <0.33 were regarded as imprecise.

The maps of predicted densities and associated standard errors provided the means for spatially evaluating the effects of sample allocation (i.e., survey station placement) in a region, and for identifying areas that may be under-sampled and contributing to a high degree of predictive uncertainty. For each species, a map of relative prediction uncertainty was derived by dividing the standard deviation by the mean predicted density for each grid cell (i.e., effectively producing a coefficient of variation at the resolution of the grid cell). Sampling efficiency was evaluated by examining the prediction uncertainty maps of an abundant and a common widespread species (`Apapane and `Ōma`o) and a common and an uncommon species with more restricted distributions (`I`iwi and Red-billed Leiothrix).

Species Accounts

Native Birds

Hawai`i `Elepaio (*Chasiempis sandwichensis*)

A total of 398 Hawai`i `Elepaio were detected during surveys (Table 2). Detection distances ranged up to 79 m (mean = 28.5 ± 13.5 m [SD]; Appendix 1). The detectability models for trend analysis and density prediction yielded effective detection radii of 37.4 ± 0.7 and 37.5 ± 0.7 m (SE), respectively.

Poisson regression was initially used to identify a suite of habitat variables correlated to Hawai`i `Elepaio density. The variables koa, tree-fern, stature, precipitation and survey date accounted for 18% of the total (null) deviance in `Elepaio density (Table 3). The factor "year 1993" was used as a fixed effect in the hierarchical species-habitat model for predicting densities (Appendix 2). Hawai`i `Elepaio counts did not exhibit a strong seasonal pattern although the gradual increase in counts peaked towards the end of the survey period (i.e., July 29; survey date 203; Figure 5). The seasonal effect was incorporated in the predictive model with sine and cosine values equal to -0.346 and -0.938, respectively.

A visual comparison of the predictions of the hierarchical model with that of the validation dataset (i.e., reserved subset of observations) appeared to show a moderately close approximation of observed and predicted counts (Figure 6). However, the Wilcoxon test of the difference in means between the count distributions was marginally significant ($Z = 2.095$; $P = 0.036$; Table 3) and indicates that the correspondence of model predictions and observed counts were not closely matched. In addition, the regression slope was only 0.25 (Figure 6) and reveals that the model was under-predicting the abundance of Hawai`i `Elepaio. Moreover, the correlation among observed and predicted counts was 0.39 ($P < 0.001$), a fairly low level of precision.

In general, Hawai`i `Elepaio were concentrated in the drier northeastern part of the Ka`ū study area, and birds were notably absent in the southern-most portion of forested habitat (Figure 7). The density of Hawai`i `Elepaio was also relatively low compared to other regions in its island range, and surprisingly, density was also somewhat higher at lower elevations. For example, the mean density in 2002 was 0.3 ± 0.1 and 0.7 ± 0.1 birds/ha in forest >1,500 m and <1,500 m, respectively (Table 4). In comparison, mean density was 2.2 ± 0.1 birds/ha in the Kūlani-Keauhou region (Gorresen *et al*. 2005). Despite the predictive under-performance of the models, the predicted distribution of densities (Figure 8) spatially corresponded with that observed. The population of Hawai`i `Elepaio was estimated at 14,621 birds (SD = 4,279; 95% CI = 8,388 – 22,711; Table 5). About 4,677 individuals or 32% of the predicted total Hawai`i `Elepaio were estimated to occur ≥1,500 m.

`Elepaio occur from low to high elevations on the islands of Hawai`i, Kaua`i and O`ahu (VanderWerf 1998). However, recent evidence indicates that the densities of regional populations on Hawai`i Island (and O`ahu) are declining and the species' range may be contracting at low and mid-elevations (Reynolds *et al*. 2003, Camp *et al*. In review, Gorresen *et al*. 2005, Gorresen *et al*. In prep.). The species was relatively widespread throughout the southern-most portion of its Ka`ū range in 1976; however, few detections were made in this area when it was resurveyed in 2005 (Figure 9).

Although there was a moderate decrease in the mean annual densities of Hawai`i `Elepaio above 1,500 m, trend analysis concluded that the densities observed above and below 1,500 m were not different (presumed slope above 1,500 m = -0.008; 95% CI = -0.018 to 0.001; *P* = 0.089; presumed slope below 1,500 m = 0.001; 95% CI = -0.012 to 0.013; *P* = 0.936; Figure 10; Tables 4 and 6).

`Ōma`o (*Myadestes obscurus*)

A total of 3,893 `Ōma`o was detected during surveys (Table 2). Detection distances ranged up to 213 m (mean = 43.8 ± 20.2 m [SD]; Appendix 1). The detectability models for trend analysis and density prediction both yielded an effective detection radius of 54.1 ± 0.4 m (SE).

Poisson regression was initially used to identify a suite of habitat variables correlated to `Ōma`o density. The variables canopy stature, tree-fern, canopy closure, koa, precipitation, slope, and survey date accounted for 24% of the total (null) deviance in `Ōma`o density (Table 3). The factor "year 1993" was used as a fixed effect in the hierarchical species-habitat model for predicting densities (Appendix 2). `Ōma`o counts exhibited a moderately strong seasonal pattern that peaked in mid-May (i.e., survey date 124; Figure 11). The seasonal effect was incorporated in the predictive model with sine and cosine values equal to 0.845 and -0.534, respectively.

The abundance predicted by the hierarchical model moderately approximated that of the validation dataset (Figure 12). The Wilcoxon test of the difference in means between the count distributions was not significant (Z = -1.743; *P* = 0.081; Table 3) and indicated that the correspondence of model predictions and observed counts was marginally adequate. The regression slope was 0.47 (Figure 12) and revealed that the model was, to a small extent, under-predicting the abundance of `Ōma`o. However, the correlation among observed and predicted counts was 0.71 (*P* < 0.001) and showed that the model was fairly precise.

`Ōma`o was the second-most abundant native species, and was widespread in forest habitat (Figure 13). The species was also present in the degraded forest and pasture in the southern-most portion of the study area, and encouragingly, densities were also fairly high at lower elevations. For example, the mean density in 2002 was 4.1 ± 0.2 and 2.4 ± 0.2 birds/ha in forest >1,500 m and <1,500 m, respectively (Table 4). The spatial distribution of the predicted counts corresponded well with that observed (Figure 14). The population of `Ōma`o was estimated at 82,378 birds (SD = 7,493; 95% CI = 70,519 – 94,578; Table 5). Of this total, about 29,781 individuals or 36% of the predicted population were predicted to occur ≥1,500 m.

`Ōma`o occurs from mid to high elevations on windward Hawai`i Island (Wakelee and Fancy 1999). However, densities appear to have decreased in the central and east windward regions (i.e., eastern Mauna Loa and Kīlauea Volcano) since the 1977 and 1979 HFBS (Reynolds *et al*. 2003, Camp *et al*. In review, Gorresen *et al*. 2005, Gorresen *et al*. In prep.). The picture of `Ōma`o trends in Ka`ū is mixed. Although the 1976 and 2005 densities above 1,500 m were not different (presumed slope = -0.008; 95% CI = -0.021 to 0.004; *P* = 0.174; Figure 15; Tables 4 and 6), the 1993 and 2002 data indicated that estimated `Ōma`o abundance was highly variable and the conclusion of "no change" may not be warranted. In contrast, the density of `Ōma`o below 1,500 m was significantly less in 2002 than that observed in 1976 (presumed slope = -0.029; 95% CI = -0.046 to -0.012; *P* < 0.001).

Hawai`i `Amakihi (*Hemignathus virens*)

A total of 2,961 Hawai`i `Amakihi was detected during surveys (Table 2). Detection distances ranged up to 157 m (mean = 30.5 ± 16.2 m [SD]; Appendix 1). The detectability models for trend analysis and density prediction yielded effective detection radii of 36.6 ± 0.3 and 36.5 ± 0.3 m (SE), respectively.

Poisson regression was initially used to identify a suite of habitat variables correlated to Hawai`i `Amakihi density. The variables temperature, matted-fern, koa, precipitation, landcover diversity and survey date accounted for 27% of the total (null) deviance in Hawai`i `Amakihi density (Table 3). The factor “year 1993” was used as a fixed effect in the hierarchical species-habitat model for predicting densities (Appendix 2). Hawai`i `Amakihi counts exhibited a weak bimodal seasonal pattern with peaks in early April and late July (Figure 16). The late July date (i.e., survey date 203) corresponding to sine and cosine values equal to -0.346 and -0.938 was used to incorporate the seasonal effect in the predictive model.

A visual comparison of the predictions of the hierarchical model with that of the validation dataset (i.e., reserved observations) appeared to show a moderately close approximation of observed and predicted counts (Figure 17). However, the Wilcoxon test of the difference in means between the count distributions was significant ($Z = -3.363$; $P < 0.001$; Table 3) and the regression slope was only 0.40 (Figure 17). These results indicate that the model under-predicted Hawai`i `Amakihi abundance. The correlation among observed and predicted counts was 0.59 ($P < 0.001$), a moderately accurate level of precision.

On Hawai`i Island, `amakihi occur from near sea-level to high elevations in a variety of native and non-native habitats (Lindsey *et al*. 1998). The species was widespread in forest habitat, and also occurred in the degraded forest and pasture in the southern-most portion of the study area (Figure 18). Hawai`i `Amakihi was the third-most abundant native species, and were even found in moderately high numbers at lower elevations. For example, the mean density in 2002 was 5.8 ± 0.4 and 2.6 ± 0.3 birds/ha in forest >1,500 m and <1,500 m, respectively (Table 4). The spatial distribution of the predicted counts corresponded well with that observed (Figure 19). The population of Hawai`i `Amakihi was estimated at 154,749 birds (SD = 9,393; 95% CI = 140,463 – 170,416; Table 5). About 102,475 individuals or 66% of the predicted total Hawai`i `Amakihi were predicted to occur ≥1,500 m.

With the exception of the population along the East Rift (i.e., eastern Kīlauea Volcano), densities of `amakihi appear to have increased or remained stable throughout most of their range on Hawai`i Island since the HFBS (Camp *et al*. In review, Gorresen *et al*. 2005, Gorresen *et al*. In prep.). Although the densities in 2005 above 1,500 m were significantly less than that observed in 1976 (i.e., presumed slope = -0.039; 95% CI = -0.068 to -0.010; $P = 0.009$; Figure 20; Tables 4 and 6), the 1993 and 2002 mean annual densities indicated that variability was high and the conclusion of a downward trend may not be warranted. Similarly, a test of the difference in densities below 1,500 m was inconclusive because of high intra-annual variability (presumed slope = -0.013; 95% CI = -0.044 to 0.018; $P = 0.404$).

\`Akiapōlā\`au (*Hemignathus munroi*)

A total of 38 \`Akiapōlā\`au was detected during surveys (Table 2). Detection distances ranged up to 122 m (mean = 47.2 ± 29.9 m [SD]), and the detectability model for trend analysis yielded an effective detection radius of 54.5 ± 4.3 m (SE; Appendix 1). \`Akiapōlā\`au counts exhibited a weak seasonal effect, with a slightly higher number of counts observed towards the beginning of the survey period (i.e., late February; Figure 21).

Hierarchical models of species-habitat associations were not developed for \`Akiapōlā\`au because of the species' very low incidence of occurrence. Population size was calculated by extrapolating the current mean density to the species' estimated range size. \`Akiapōlā\`au were detected as low as 1,300 m during the 1976 HFBS in Ka\`ū (Figure 22). However, all detections since the 1976 HFBS have occurred above 1,450 m, and the current range is estimated to cover 5,555 ha. Given this range size and the mean density of 0.19 ± 0.06 birds/ha observed in 2005, the current population of \`Akiapōlā\`au in Ka\`ū was estimated by Tweed *et al*. (In review) at 1,073 birds (95% CI = 616 – 1,869 birds; Table 5).

The mean annual density of \`Akiapōlā\`au above 1,500 m in 2005 was marginally greater than that observed in 1976 (presumed slope = 0.004; 95% CI = 0.001 to 0.006; *P* = 0.015; Figure 23; Tables 4 and 6). However, the significant "trend" may be the result of year-to-year differences in the timing of survey relative to the period when the species is most vocal (Tweed *et al*. In review). In this case, it is thought that the higher mean density observed in 2005 was the result of coincident survey and vocal periods. Trend analysis determined that the 1976 and 2002 densities detected below 1,500 m were not significantly different (presumed slope = -0.001; 95% CI = -0.003 to 0.001; *P* = 0.224). However, the "absence" of a trend was simply an artifact of the initial very low density followed by the likely extirpation of \`Akiapōlā\`au from low elevation forest.

Hawai\`i Creeper (*Oreomystis mana*)

A total of 94 Hawai\`i Creeper was detected during surveys (Table 2). Detection distances ranged up to 100 m (mean = 27.8 ± 17.8 m [SD]), and the detectability model for trend analysis yielded an effective detection radius of 27.1 ± 1.5 m (SE; Appendix 1). Hawai\`i Creeper counts exhibited a weak seasonal effect with a slightly higher number of counts observed towards the beginning of the survey period (i.e., early March; Figure 24).

Hierarchical models of species-habitat associations were not developed for Hawai\`i Creeper because of the species' very low incidence of occurrence. Population size was calculated by extrapolating the current mean density to the species' estimated range size. Although most detections of Hawai\`i Creeper in Ka\`ū have occurred above 1,500 m, four detections were made below this elevation during the 1976 HFBS (Figure 25). However, all detections since 1976 have occurred at or above 1,500 m, and the current range is estimated at 6,418 ha. Given this range size and the mean density of 0.35 ± 0.12 birds/ha observed in 2005, the current population of Hawai\`i Creeper in Ka\`ū was estimated by Tweed *et al*. (In review) at 2,268 birds (95% CI = 1,159 – 4,438 birds; Table 5).

As with other endangered bird species, the analysis of Hawai\`i Creeper trend was complicated by high intra- and inter-annual variability in density. Although the mean annual densities observed above 1,500 m in 1976 and 2005 were not significantly different (presumed slope = -0.001; 95% CI = -0.014 to 0.012; *P* = 0.827; Figure 26; Tables 4 and 6), intra- and inter-annual variability was high and the conclusion of “no change” may not be warranted. The 1976 and 2002 densities detected below 1,500 m were also not significantly different (presumed slope = -0.001; 95% CI = -0.004 to 0.001; *P* = 0.175). As with `Akiapōlā`au, the “absence” of a trend was simply an artifact of the initial very low density followed by the likely extirpation of Hawai`i Creeper from low elevation forest.

Hawai`i `Ākepa (*Loxops coccineus*)

A total of 256 Hawai`i `Ākepa was detected during surveys (Table 2). Detection distances ranged up to 111 m (mean = 33.2 ± 16.7 m [SD]), and the detectability model for trend analysis yielded effective detection radius of 41.6 ± 1.7 m (SE; Appendix 1). Hawai`i `Ākepa counts exhibited a modest seasonal effect, with a higher number of counts observed towards the middle of the survey period (i.e., end April; Figure 27).

Hierarchical models of species-habitat associations were not developed for Hawai`i `Ākepa because of the species’ very low incidence of occurrence. Population size was calculated by extrapolating the current mean density to the species’ estimated range size. Several observations of Hawai`i `Ākepa during the 1976 HFBS in Ka`ū occurred as low as 1,250 m; however, all detections since the 1976 HFBS have occurred within forest habitat between 1,550 and 2,200 m. The current range in Ka`ū is estimated to cover 7,958 ha and to no longer extend below 1,500 m (Figure 28). The species was estimated to occur in 2005 at a mean density of 0.32 ± 0.11 birds/ha for the portion of the survey area coincident with its range in Ka`ū (Table 4). Given the above density and range, the current population in Ka`ū was estimated by Tweed *et al*. (In review) at 2,556 birds (95% CI = 1,340 – 4,876 birds; Table 5). However, the range extent, and thus population size, may be overestimated if the species no longer occurs in the northerly quarter of the projected range (i.e., only one detection was recorded in this area in 1976, but the area remains under-sampled). The population estimate may also be inaccurate if the estimated mean annual density does not closely approximate actual density. The mean density for 2002 was about 3 times greater that of the 2005 (1.07 versus 0.35 birds/ha, respectively; Table 4). It is possible, but unlikely, that the population declined 3-fold in a 3 year period. The differences among estimates may instead be a reflection of sampling error rather than changes in population size. In contrast to the population estimate above, an extrapolation of the mean annual density for 2002 yields a much higher estimate of 8,493 birds (95% CI = 4,995 – 14,441 birds).

The mean annual densities of Hawai`i `Ākepa observed above 1,500 m in 1976 and 2005 were not significantly different (presumed slope = 0.002; 95% CI = -0.010 to 0.010; *P* = 0.966; Figure 29; Tables 4 and 6); however, intra- and inter-annual variability was high and the conclusion of “no change” may not be warranted. The densities detected below 1,500 m were significantly but negligibly different (presumed slope = -0.003; 95% CI = -0.006 to 0.000; *P* = 0.032). The negligible trend was the outcome of a very low density followed by the likely extirpation of Hawai`i `Ākepa from low elevation forest.

\`I\`iwi (*Vestiaria coccinea*)

A total of 1,655 \`I\`iwi was detected during surveys (Table 2). Detection distances ranged up to 167 m (mean = 32.1 ± 17.5 m [SD]; Appendix 1). The detectability models for trend analysis and density prediction yielded effective detection radii of 38.0 ± 0.4 and 36.5 ± 0.4 m (SE), respectively.

Poisson regression was initially used to identify a suite of habitat variables correlated to \`I\`iwi density. The variables canopy cover, stature, elevation (squared), matted-fern, precipitation and survey date accounted for 27% of the total (null) deviance in \`I\`iwi density (Table 3). The factor "year 2005" was used as a fixed effect in the hierarchical species-habitat model for predicting densities (Appendix 2). \`I\`iwi counts exhibited a moderately strong seasonal pattern that peaked in mid-May (i.e., survey date 125; Figure 30). The seasonal effect was incorporated in the predictive model with sine and cosine values equal to 0.836 and -0.549, respectively.

The abundance predicted by the hierarchical model moderately approximated that of the validation dataset (Figure 31). The Wilcoxon test of the difference in means between the count distributions was not significant ($Z = -1.799$, $P = 0.072$; Table 3) and indicated that the correspondence of model predictions and observed counts was adequate. The regression slope was 0.44 (Figure 31) and revealed that the model was, to a small extent, under-predicting the abundance of \`I\`iwi. However, the correlation among observed and predicted counts was 0.73 ($P < 0.001$) and showed that the model was fairly precise.

\`I\`iwi was the fourth-most abundant native species in Ka\`ū, and birds were widespread in mid- and upper-elevation forest habitat (Figure 32). Encouragingly, \`I\`iwi also occurred at moderate densities at lower elevations, particularly in the drier northeastern part of the study area. For example, in central Ka\`ū, the mean density in 2002 was 3.5 ± 0.3 and 1.5 ± 0.2 birds/ha in forest >1,500 m and <1,500 m, respectively (Table 4). The spatial distribution of the predicted counts corresponded well with that observed (Figure 33). The population of \`I\`iwi was estimated at 78,154 birds (SD = 9,242; 95% CI = 64,349 – 93,382; Table 5). Of this total, about 47,042 individuals or 60% were predicted to occur ≥1,500 m.

\`I\`iwi density appears to have decreased in many parts of its range across the islands since the HFBS (Camp *et al*. In review, Gorresen *et al*. 2005, Gorresen *et al*. In prep.). In some cases the differences in abundance over time may simply reflect wide-ranging movement in response to nectar availability (Ralph and Fancy 1995). However, in Ka\`ū both the lower and upper elevation densities exhibited a parallel pattern in downward trends and suggest that seasonal movement into one area was not offset by diminished numbers in the other. The densities of \`I\`iwi observed both above and below 1,500 m were significantly less in 2005 compared to 1976 (presumed slope above 1,500 m = -0.067; 95% CI = -0.090 to -0.044; $P < 0.001$; presumed slope below 1,500 m = -0.017; 95% CI = -0.032 to -0.002; $P = 0.029$; Figure 34; Tables 4 and 6). Given that the amount of intra- and inter-annual variability was fairly modest, it is likely that projected negative trends are correct.

\`Apapane (*Himatione sanguinea*)

A total of 9,895 \`Apapane was detected during surveys (Table 2). Detection distances ranged up to 304 m (mean = 32.8 ± 18.3 m [SD]; Appendix 1). The detectability models for trend analysis and density prediction both yielded an effective detection radius of 38.4 ± 0.2 m (SE).

Poisson regression was initially used to identify a suite of habitat variables correlated to `Apapane density. The variables temperature, canopy cover, stature, koa, elevation (squared) and survey date accounted for 42% of the total (null) deviance in `Apapane density (Table 3). The factor "year 2005" was used as a fixed effect in the hierarchical species-habitat model for predicting densities (Appendix 2). `Apapane counts exhibited a fairly strong seasonal pattern that peaked at the end of April (i.e., survey date 110; Figure 35). The seasonal effect was incorporated in the predictive model with sine and cosine values equal to 0.948 and -0.317, respectively.

The abundance predicted by the hierarchical model closely approximated that of the validation dataset (Figure 36). The Wilcoxon test of the difference in means between the count distributions was not significant (Z = -1.220; *P* = 0.222; Table 3) and indicated that the correspondence of model predictions and observed counts was adequate. The regression slope was 0.60 (Figure 36) and revealed that the model was, to a small extent, under-predicting the abundance of `Apapane. However, the correlation among observed and predicted counts was 0.78 (*P* < 0.001) and showed that the model was precise.

`Apapane was the most abundant native species in Ka`ū. Birds were widespread throughout forest habitat and present in the degraded forest and pasture in the southern-most portion of the study area (Figure 37). The species also occurred at relatively high densities at lower elevations, particularly in the northern half of the study area. For example, in central Ka`ū, the mean density in 2002 was 17.8 $\pm$ 0.8 and 10.6 $\pm$ 0.6 birds/ha in forest >1,500 m and <1,500 m, respectively (Table 4). The spatial distribution of the predicted counts corresponded well with that observed (Figure 38). The population of `Apapane was estimated at 491,928 birds (SD = 23,966; 95% CI =454,673 – 535,593; Table 5). About 292,682 individuals or 59% of the predicted total `Apapane were predicted to occur $\geq$1,500 m.

Unlike most of the native species, `Apapane density appears to have increased in many parts of its range since the HFBS (Camp *et al*. In review, Gorresen *et al*. 2005, Gorresen *et al*. In prep.). However, the difference in the `Apapane density observed in the central part of the Ka`ū study area above 1,500 m in 1976 and 2005 was not conclusive because of high inter-annual variability (presumed slope = 0.040 95% CI = -0.015 to 0.095; *P* = 0.156; Figure 39; Tables 4 and 6), and to some extent, this may be attributable to foraging movements. In contrast, the density of `Apapane below 1,500 m was significantly greater in 2002 than that observed in 1976 (presumed slope = 0.213; 95% CI = -0.164 to 0.261; *P* < 0.001).

Non-native Birds

Red-billed Leiothrix (*Leiothrix lutea*)

A total of 1,347 Red-billed Leiothrix was detected during surveys (Table 2). Detection distances ranged up to 152 m (mean = 44.7 ± 21.4 m [SD]; Appendix 1). The detectability models for trend analysis and density prediction yielded effective detection radii of 53.4 ± 0.6 and 53.3 ± 0.6 m (SE), respectively.

Poisson regression was initially used to identify a suite of habitat variables correlated to Red-billed Leiothrix density. The variables canopy stature, koa, grass cover, matted-fern, precipitation, elevation (squared), and survey date accounted for 33%

of the total (null) deviance in Red-billed Leiothrix density (Table 3). The factor "year 2005" was used as a fixed effect in the hierarchical species-habitat model for predicting densities (Appendix 2). Red-billed Leiothrix counts showed a strong seasonal pattern that peaked in mid-May (i.e., survey date 127; Figure 40). The seasonal effect was incorporated in the predictive model with sine and cosine values equal to 0.817 and -0.577, respectively.

The abundance predicted by the hierarchical model closely approximated that of the validation dataset (Figure 41). The Wilcoxon test of the difference in means between the count distributions was not significant (Z = -0.425; *P* = 0.671; Table 3) and indicated that the correspondence of model predictions and observed counts was adequate. However, although the correlation among observed and predicted counts was 0.68 (*P* < 0.001) and showed that the model was fairly precise, the regression slope was only 0.41 (Figure 41) and indicated that the model was under-predicting the abundance of Red-billed Leiothrix.

Red-billed Leiothrix was the second-most abundant non-native species in Ka\`ū, and were widespread throughout forest habitat (Figure 42). Leiothrix were most abundant at lower elevations, but also occurred in modest numbers at higher elevations. For example, in central Ka\`ū, the mean density in 2002 was 0.6 ± 0.1 and 2.1 ± 0.2 birds/ha in forest above and below 1,500 m, respectively (Table 4). The spatial distribution of the predicted counts corresponded well with that observed (Figure 43). The population of Red-billed Leiothrix was estimated at 39,237 birds (SD = 4,784; 95% CI = 31,711 – 47,164; Table 5). Of this total, about 7,981 individuals or 20% were predicted to occur ≥1,500 m.

Red-billed Leiothrix density appears to have decreased in parts of its range (e.g., Kūlani-Keauhou and \`Ōla\`a) since the HFBS (Gorresen *et al*. 2005). However, in Ka\`ū the density of Red-billed Leiothrix below 1,500 m was significantly greater in 2002 than that observed in 1976 (presumed slope = 0.048; 95% CI = 0.034 to 0.062; *P* < 0.001; Figure 44; Tables 4 and 6). The densities observed above 1,500 m was not significantly different (presumed slope = -0.005; 95% CI = -0.012 to 0.002; *P* = 0.147).

Japanese White-eye (*Zosterops japonicus*)

A total of 2,457 Japanese White-eye was detected during surveys (Table 2). Detection distances ranged up to 122 m (mean = 26.4 ± 14.9 m [SD]; Appendix 1). The detectability models for trend analysis and density prediction yielded effective detection radii of 30.2 ± 0.3 and 30.1 ± 0.3 m (SE), respectively.

Poisson regression was initially used to identify a suite of habitat variables correlated to Japanese White-eye density. The variables temperature, precipitation, elevation (squared) and survey date accounted for 22% of the total (null) deviance in Japanese White-eye density (Table 3). The factor "year 2005" was used as a fixed effect in the hierarchical species-habitat model for predicting densities (Appendix 2). Japanese White-eye counts showed a weak seasonal pattern that peaked in mid-June (i.e., survey date 155; Figure 45). The seasonal effect was incorporated in the predictive model with sine and cosine values equal to 0.456 and -0.890, respectively.

A visual comparison of the predictions of the hierarchical model with that of the validation dataset (i.e., reserved observations) appeared to show a moderately close approximation of observed and predicted counts (Figure 46). However, the Wilcoxon test of the difference in means between the count distributions was significant (Z = -

3.916; *P* < 0.001; Table 3) and the regression slope was only 0.36 (Figure 46). These results indicate that the model under-predicted Japanese White-eye abundance. The correlation among observed and predicted counts was 0.57 (*P* < 0.001), a moderately accurate level of precision.

Japanese White-eye was the most abundant non-native species in Ka`ū. It was widespread throughout forest habitat and occurred at moderately high densities in open habitats (e.g., pasture with forest remnants and native woodland; Figure 47). Although Japanese White-eye was most abundant at lower elevations, the species also occurred in modest densities at higher elevations. For example, in central Ka`ū, the mean density in 2002 was 1.1 + 0.2 and 6.4 + 0.5 birds/ha in forest above and below 1,500 m, respectively (Table 4). The spatial distribution of the predicted counts corresponded well with that observed (Figure 48). The population of Japanese White-eye was estimated at 245,232 birds (SD = 32,618; 95% CI = 195,266 – 302,889; Table 5). About 34,107 individuals or 14% of the predicted total Japanese White-eye were predicted to occur >1,500 m.

Japanese White-eye density appears to have increased in many parts of its range since the HFBS (e.g., `Ōla`a and East rift; Gorresen *et al*. 2005). In Ka`ū, the density of Japanese White-eye above 1,500 m was greater in 2002 than that observed in 1976 (presumed slope = 0.067; 95% CI = 0.040 to 0.094; *P* < 0.001; Figure 49; Tables 4 and 6). However, the difference in density below 1,500 m was not conclusive because of moderately high intra-annual variability (presumed slope = 0.040; 95% CI = -0.016 to 0.095; *P* = 0.158).

Northern Cardinal (*Cardinalis cardinalis*)

A total of 235 Northern Cardinal was detected during surveys (Table 2). Detection distances ranged up to 304 m (mean = 32.8 ± 18.3 m [SD]), and the detectability model for trend analysis yielded an effective detection radius of 38.4 ± 0.2 m (SE; Appendix 1). Northern Cardinal counts exhibited a weak seasonal effect which peaked in early March (Figure 50).

Hierarchical models of species-habitat associations were not developed for Northern Cardinal because of the species' low incidence of occurrence. Population size was calculated by extrapolating the mean densities observed in 2002 above and below 1,500 m to the extent of these areas (19,145 and 28,263 ha, respectively). This approach yielded an estimate of 997 birds above 1,500 m (95% CI = 314 to 3,170) and 9,988 birds below 1,500 m (95% CI = 5,895 to 16,922), for a combined total of 10,985 birds (95% CI = 6,209 to 20,092) in the Ka`ū study area.

Although found at low abundances, Northern Cardinal occurred throughout the forest and pasture and degraded forest habitats (Figure 51). For example, in central Ka`ū, the mean density in 2002 was 0.05 + 0.03 and 0.35 + 0.10 birds/ha in forest above and below 1,500 m, respectively (Table 4).

Trends in Northern Cardinal density were either negligible or absent (presumed slope above 1,500 m = 0.001; 95% CI = 0.000 to 0.002; *P* = 0.097; presumed slope below 1,500 m = 0.013; 95% CI = 0.006 to 0.021; *P* < 0.001; Figure 52; Tables 4 and 6).

Discussion

The analyses presented in this report are the latest synthesis of bird survey data and habitat information for Ka`ū, and they constitute an update of the landmark study by Scott *et al.* (1986). Species-habitat models were developed to relate bird counts to a variety of habitat variables, seasonal and year effects and other factors affecting bird detectability. The models were applied to the prediction of densities into unsurveyed areas, the generation of distribution maps and the estimation of population size. Four years of surveys (1976, 1993, 2002 and 2005) were examined to assess trends in densities. Monitoring recommendations are provided based on the results of these analyses.

Species-Habitat Models

The species-habitat models developed for this study generally overestimated abundance at sites known to have low densities and under-predicted abundance in areas with high densities. This is a common drawback of Poisson models applied to count data with numerous zeros (e.g., Jones *et al*. 2002; Thogmartin *et al*. 2004). This problem may be caused by the inclusion of counts from habitats unsuitable to a species, the limited ability of a species to disperse into and occupy all available suitable habitat, or failure to detect birds that are present (Kuhnert *et al*. 2005). Alternative models that employ a zero-inflated Poisson or negative binomial approach (e.g., Agarwal *et al*. 2002) may result in less skewed predictions, but do so at the cost of increased model complexity. Such an approach typically involves a mixture of models in which one distribution models specifies the probability of obtaining zero counts and a second distribution models non-zero counts.

The degree to which the species-habitat models under- or over-predicted counts roughly depended on species abundance and the ubiquity of observed zero counts in the data analyzed. Attempts to model rare or very uncommon species were not productive, and a population estimate for each of these species was handled with a simple extrapolation of observed mean density onto the estimated range size. Hawai`i `Elepaio, the least common of the species modeled, ranked lowest in the assessment of model performance (Table 3). Although the spatial distribution of observed and predicted counts corresponded well with one another, the model yielded lower than expected densities and likely underestimated the population size of `elepaio. Surprisingly, the models for Hawai`i `Amakihi and Japanese White-eye, both common species, also tended to underpredict counts and the means of the observed and predicted distributions were not equivalent (Table 2). Japanese White-eye density may have been underestimated because habitat and other factors may not have been able to account for aggregations of large numbers of birds. In general, however, observed abundance was well approximated by the spatial distribution of predicted densities, and the models were fairly precise for both species (Table 3). Although the species-habitat models for Ōma`o, `Apapane, `I`iwi and Red-billed Leiothrix also moderately underestimated bird numbers, the models accounted for a reasonable to good amount of the variability in abundance and the mapped predictions corresponded well with that observed.

Species Distribution

Despite the predictive difficulties in a number of the species-habitat models, there was broad agreement in the distributions and population sizes predicted by this study and that of Scott *et al*. (1986). The observed and predicted distributions of native species demonstrates three general patterns: (1) small range and restricted to forest habitat; (2) large range but primarily limited to forest habitat; and (3) widespread and found in a variety of vegetation types. The three endangered species - `Akiapōlā`au, Hawai`i Creeper, Hawai`i `Ākepa - and to a lesser extent, Hawai`i `Elepaio, exhibit the most restricted distribution. The endangered species' populations are entirely limited to a narrow (3 – 4 km) band of forest and adjacent woodland above 1,500 m. In contrast, the range of Hawai`i `Elepaio extends across the entire elevation gradient of forest in Ka`ū, but is mostly concentrated towards the northern third of the study area. Encouragingly, about two-thirds of its population occurs below 1,500 m, and individuals have been detected down to lower reaches of forest habitat (about 700 to 800 m). Despite the apparent eastward contraction of the species' range, the low elevation distribution may indicate that Hawai`i `Elepaio are to some degree resistant to avian malaria, or the disease may not be as prevalent in this area as it is in other windward regions.

`I`iwi and Red-billed Leiothrix both occur in nearly all forest habitat in the study area. Predicted `I`iwi occurrence includes the upper portion of degraded forest and pasture habitat in the Kahuku parcel of the Hawai`i Volcanoes National Park, and birds have been observed foraging in this area during the late summer (i.e., after the survey period; T. Pratt, pers. obs.). The particularly high vulnerability of `I`iwi to malaria infection (Atkinson *et al*. 2005) suggests that the species' occurrence in forest at elevations as low as 800 – 900 m reflects seasonal foraging movements rather than residency by breeding individuals. However, based on the number of observed detections and the predicted distribution, as much as 40% of the population may be seasonally present below 1,500 m.

Ōma`o, Hawai`i `Amakihi and `Apapane are widely distributed in the study area and found throughout forest, relict forest stands within pasture, and upper elevation woodland habitats. Remarkably, the proportion of these species' populations observed and predicted to occur below 1,500 m ranged from 34% (Hawai`i `Amakihi) and 41% (`Apapane) up to 64% (Ōma`o). Their occurrence, in places down to 700 m, indicates that these birds may be survivors of prior malaria infections. It is possible that resistance to malaria is evolving in these individuals as a result of the relatively high transmission rates and selective pressures at lower elevations (Atkinson *et al*. 2001, 2005).

Japanese White-eye and Northern Cardinal are widespread in the study area and found in all vegetation types. Although most abundant in forest at low elevations, the Japanese White-eye was also found as high as 2,100 m in `ōhi`a shrubland. The fairly uncommon Northern Cardinal occupied both closed native forest and open degraded forest in pasture settings.

Region-wide Density Trends

Trends derived from infrequent or short-term datasets should be evaluated with caution. Short-term programs may not be able to detect trends, especially for species for which abundances fluctuate widely (Hatfield *et al*. 1996). This problem was particularly acute in the Ka`ū data analyses for which only four year's worth of comparable data were available. Preliminary investigation revealed that the sample size afforded by four annual density estimates was not sufficient to apply regression methods to the assessment of trend. Although the trend conclusions were tempered by using all annual density estimates in the assessment of trend, the actual analyses were limited to a two-sample comparison of the 1976 HFBS with the last year of survey (either 2002 [area <1,500 m] or 2005 [area >1,500 m]).

Native Birds

Native forest bird trends were mixed. Despite their extirpation below 1,500 m, no trends in density were evident for the three endangered species - `Akiapōlā`au, Hawai`i Creeper and Hawai`i `Ākepa. However, high inter- and intra-annual variability and the small number of years available for analysis may have precluded drawing significant trend results for these species. Although the densities of the relatively uncommon Hawai`i `Elepaio did not statistically differ, the hint of a decline at higher elevations coupled to an apparent range contraction warrants that closer attention be paid to the species' regional status. The high variability exhibited by `Ōma`o and Hawai`i `Amakihi makes it difficult to accept the statistical conclusion of a decline in densities at this time. These species show a moderate to highly cyclic pattern in annual densities (Camp *et al*. 2003), and the chance sampling of two points along such population cycles could yield opposite results. The downward trend of `I`iwi at upper elevations and the increase in `Apapane numbers at lower elevations are less equivocal results. Both conclusions are consistent with patterns observed elsewhere in their range (Camp *et al*. In review, Gorresen *et al*. In prep.).

Non-native Birds

In general, the densities of non-native birds have remained stable and relatively low at upper elevations. This result is comparable with that observed elsewhere on windward Hawai`i Island (specifically, Hakalau Forest National Wildlife Refuge [Camp *et al*. 2003], Kūlani-Keauhou and `Ōla`a [Gorresen *et al*. 2005]). Although Japanese White-eye density above 1,500 m in 2005 was greater than in 1976, consideration of the 1993 and 2002 survey data suggests that there is little to no overall increase in density.

The Red-billed Leiothrix is the only non-native species to demonstrate a marked upward trend below 1,500 m. This trend contrasts with the declines in leiothrix density in the Kūlani-Keauhou, `Ōla`a, and possibly Mauna Loa Strip survey areas (Gorresen *et al*. 2005).

Recommendations

The large populations of endangered species within forest habitat above 1,500 m, and the occurrence of sizable populations of common species below 1,500 m, highlights the importance of the Ka`ū region to the native forest bird fauna of Hawai`i Island. These facts impart particular urgency to the need for a comprehensive and effective monitoring of bird abundance and distribution. We provide for the reader's consideration several general and specific recommendations on survey and analytical design aimed at improving the current monitoring program.

Conduct both extensive and intensive bird surveys.

We propose the establishment of a monitoring framework that *intensively* samples select areas and *extensively* samples a larger region to provide both the “close-ups” and the “big picture” needed to anticipate and follow population changes. The type of information derived from intensive and extensive surveys are complementary but differ in their applicability (Camp *et al*. In prep.). Information gathered a both scales are critical factors in assessing extinction risk and species status (e.g., see BirdLife International 2004).

Intensive surveys would target specific areas based on management objectives and the “local” status of forest birds within the Ka`ū region. For example, low- to mid-elevation concentrations of native birds in the northeastern part of the study area may call for more focused surveys in that area. Likewise, intensive surveys may be directed at high elevations areas harboring endangered species. Such surveys may also be used to provide the baseline conditions for assessing the effects of planned ungulate exclosures on bird abundance. Intensive surveys may be comprised of more samples within an area, more frequent surveys, or both.

Extensive surveys, for logistical reasons, are limited in the frequency at which they are conducted and can only effectively track population trends over long periods of time. However, broad-scale, if infrequent, surveys can determine the extent of a species’ range, changes in its coverage over time (e.g., apparent range contraction of Hawai`i `Elepaio; Figure 9), and population connectivity and size (from extrapolated or modeled densities). Presently, only the central third of the Ka`ū study area has been surveyed consistently enough to infer population trends. A few additional well-spaced transects to the north and south of the central area that span the elevational gradient would permit the comparison of densities to that recorded during the 1976 HFBS, as well as provide a more complete picture of changes in species’ range. Current surveys have not adequately sampled about a third of the regional range of `Akiapōlā`au, Hawai`i Creeper, Hawai`i `Ākepa. Expanded coverage is particularly important for assessing the distribution of the endangered species and estimating range size (important, in turn, to the extrapolation of density to population size; e.g., see above Hawai`i `Ākepa account). The logistical cost of broadening survey coverage may be offset by reducing the number of transects within the area currently sampled.

Design bird surveys sampling to better address modeling uncertainty.

The relative uncertainty associated with densities predicted by species-habitat models is greatest in under-sampled habitats and where observed density is low and variable (Figure 53). Surveys should be designed to provide a broader coverage of sampled habitats (i.e., a habitat-directed approach). Such an approach may only require that minimal additional sampling be allocated to a variety of habitat “strata” to achieve adequate coverage (e.g., upper elevation woodland and shrubland where many species-habitat models exhibit high predictive uncertainty). Alternatively, greater sampling effort may be targeted where predictive uncertainty is high for certain species (e.g., endangered birds; i.e., a species-directed approach). A species-directed approach may require more concentrated sampling in specific areas (e.g., near the margins of a species’ range).

Maintain a consistent sampling schedule.

Bird surveys in mid-spring appear to coincide with the period when the majority of species are most vocal in Ka`ū (Figure 54). For trend analyses, it is important to maintain as consistent a sampling schedule as logistically feasible to minimize the year-to-year differences of seasonal effects on bird detections.

Conduct demographic studies to better assess the status of rare and endangered species.

Variable-circular plot methods and other count data are relatively ineffective at tracking changes in species that occur at very low densities (Buckland *et al*. 2001), particularly over short time periods or with datasets comprised of a few years of survey. Consequently, VCP has been of limited use to date in determining the status of rare species such as `Akiapōlā`au, Hawai`i Creeper and Hawai`i `Ākepa in Ka`ū. Monitoring the demographic parameters (e.g., survival, reproduction, health, movements, predation, etc.) that regulate population growth can provide substantially better information on species status than do surveys of occurrence and abundance (Steidl 2001). Demographic studies for these species should be considered for the Ka`ū study area.

Habitat restoration is critical to recovery of endangered bird populations in Ka`ū.

The Ka`ū region has long been recognized as one of the largest native forest bird communities in Hawai`i (Scott et al. 1986), and our study confirms that this is still the case. Numerous studies and management plans have emphasized the importance of habitat restoration for Hawaiian forest bird recovery in the high elevation forest and woodland habitat that now serves as the main refuge for most species (e.g., Scott and Conant 2001, U.S. Fish and Wildlife Service 2006). The analyses and models in this report support those conclusions. Some of the more obvious and generally recognized actions that might be considered include programs to reestablish forest cover, reduce rat depredation, control weeds, and fence and remove ungulates.

Areas of bird habitat in Ka`ū that are particularly important candidates for restoration include the upper elevation forest and woodland that harbor populations of the endangered `Akiapōlā`au, Hawai`i Creeper and Hawai`i `Ākepa (Figures 22, 25 and 28). In addition, forest habitat in the northern third of the Ka`ū study area may support much of the seasonal or year-round populations of Hawai`i `Elepaio and `I`iwi that reside below 1,500 m (about 70% and 40%, respectively; Table 5; Figures 8 and 33). This habitat lies entirely within the Ka`ū Forest Reserve, the Kapāpala Forest Reserve and the Kapāpala Cooperative Game Management Area, and should be prioritized for restoration given its importance to Hawai`i `Elepaio and `I`iwi, both species that are known or suspected of being in decline in many parts of their range (Gorresen *et al*. In prep.). Reforestation of adjacent upper elevation habitat in the Kapāpala Forest Reserve may also promote reestablishment of endangered and non-endangered bird populations and their connectivity to those in the Central Windward regions to the north-east. On-going and planned restoration of forest and woodland habitat in the Ka`ū and adjacent regions (e.g., Kahuku Unit of the Hawai`i Volcanoes National Park) should result in improved prospects for all native forest birds in the region.

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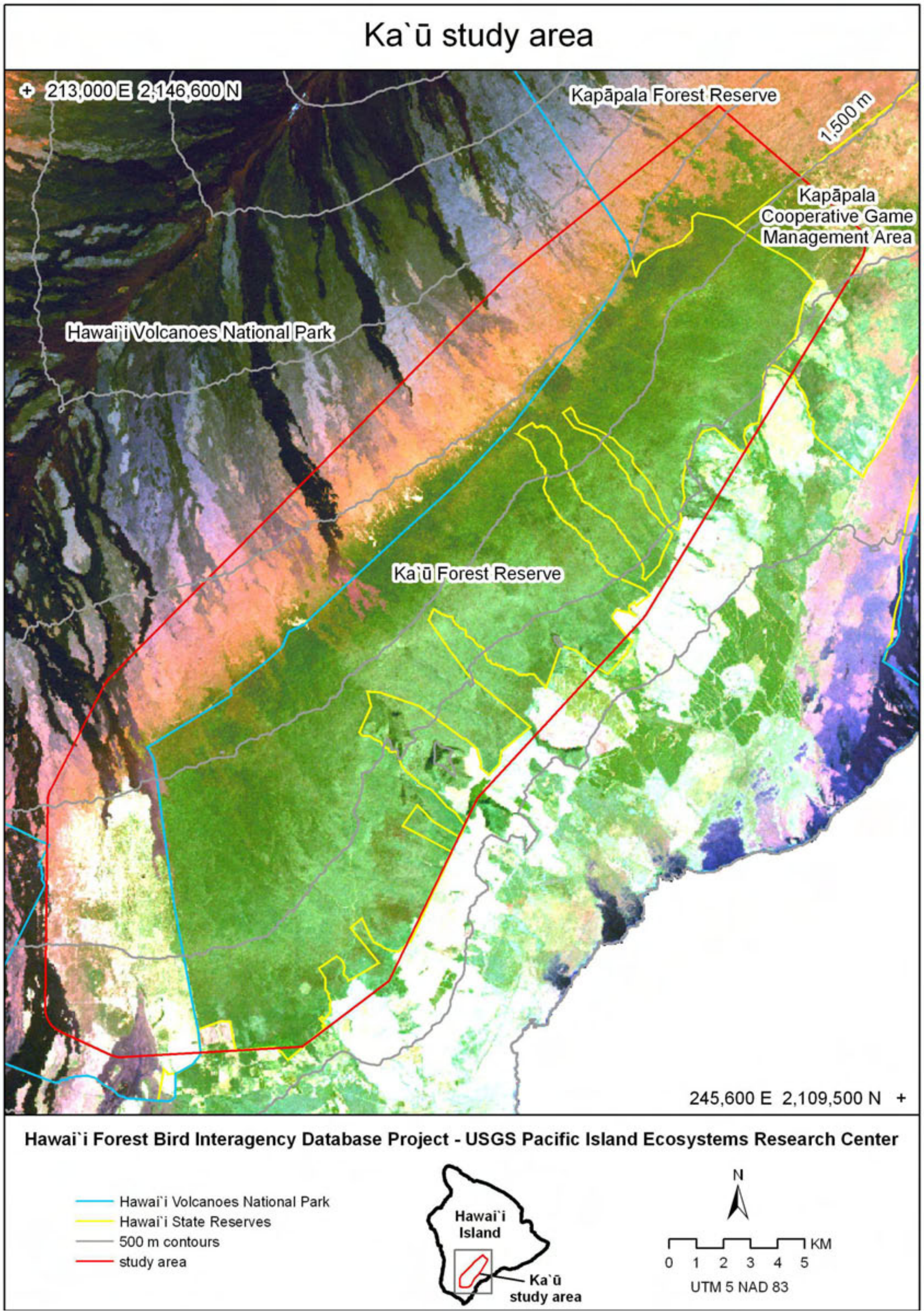


Figure 1. Study area and administrative boundaries overlaid on a natural color Landsat ETM satellite image (path/row 62/47; dated January 31, 2001). Elevation contours are shown in 500 meter intervals.

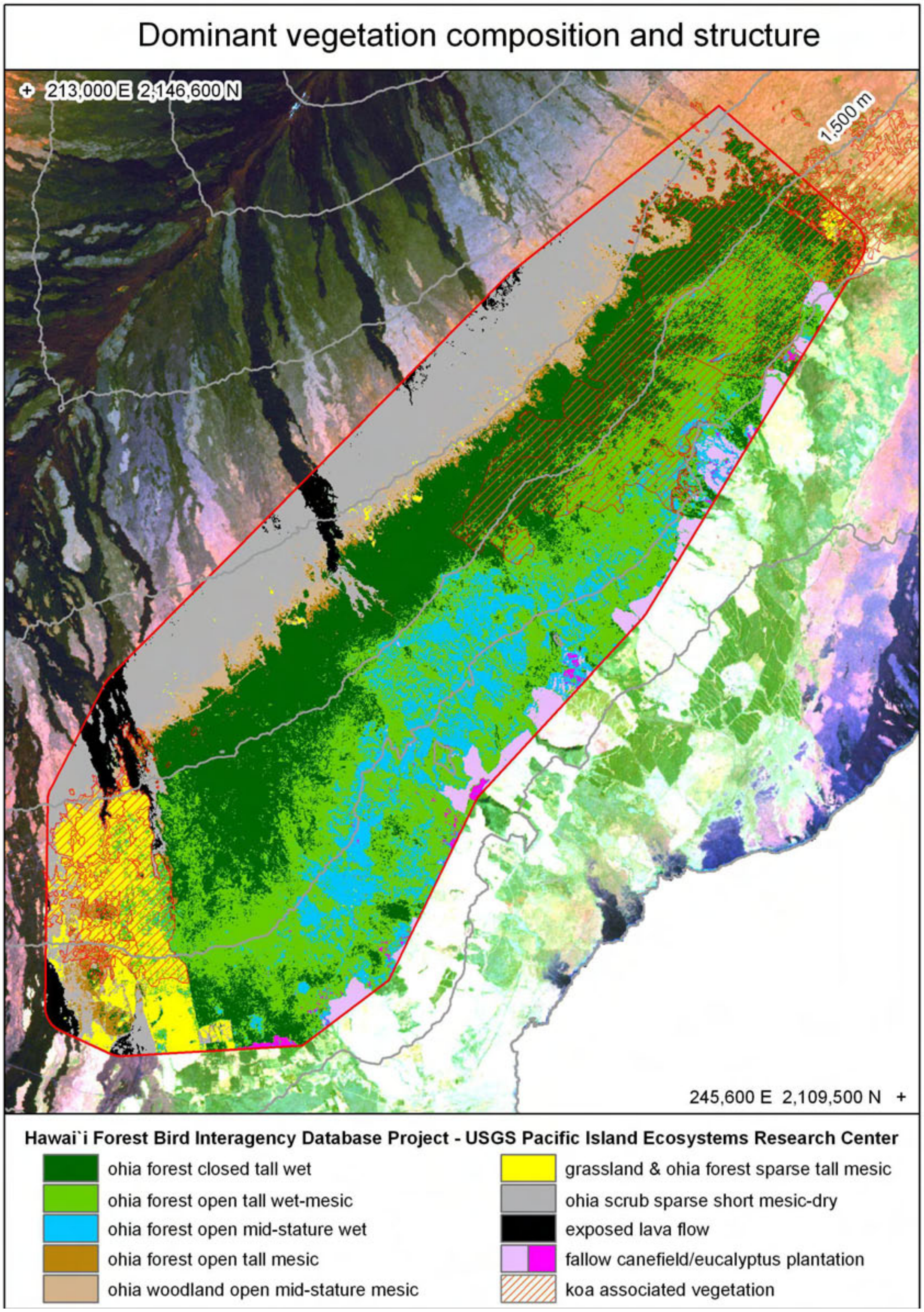


Figure 2. Land-cover types. Elevation contours are shown in 500 meter intervals.

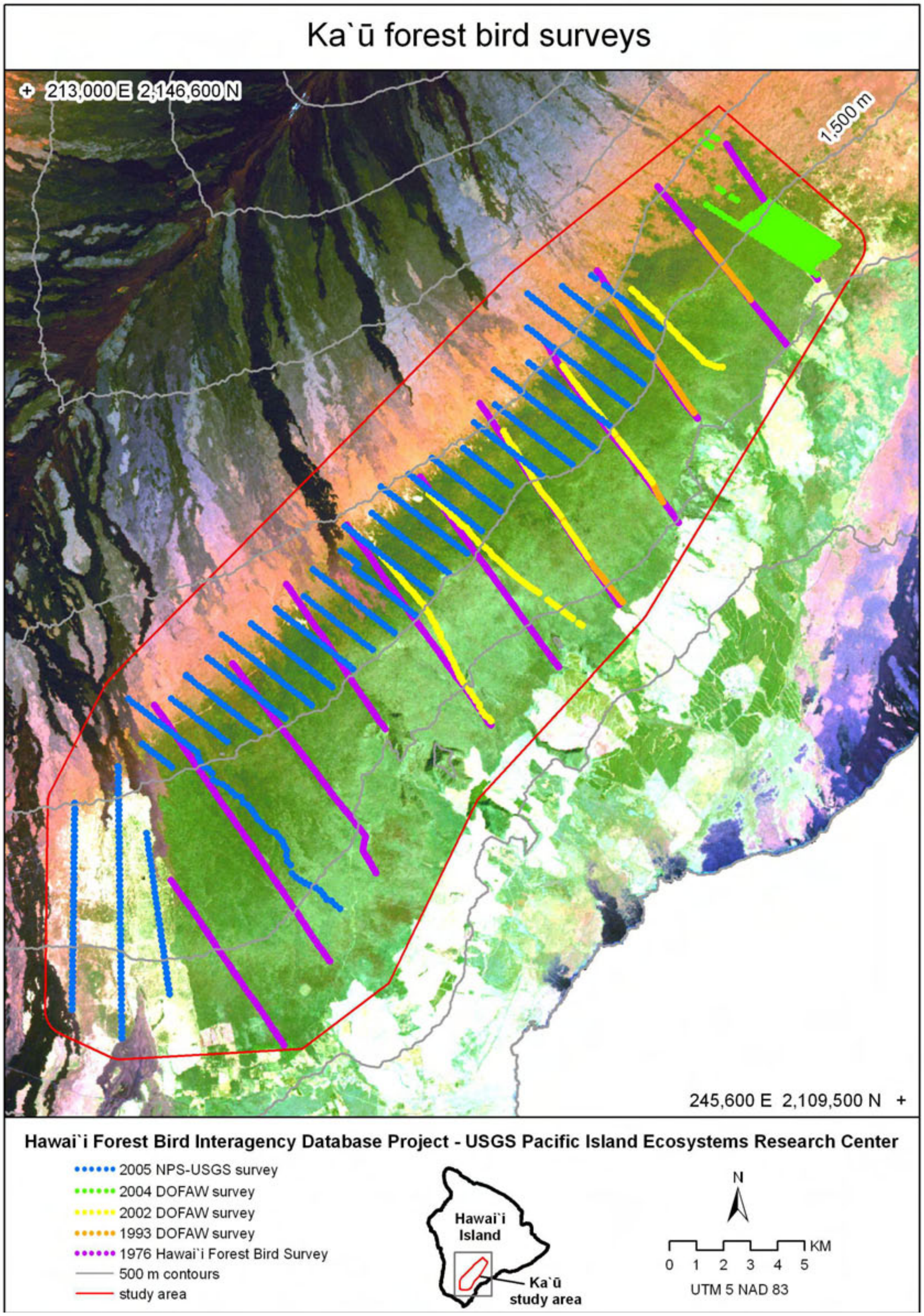


Figure 3. Survey coverage by year and agency (i.e, DOFAW, NPS-USGS). Elevation contours are shown in 500 meter intervals.

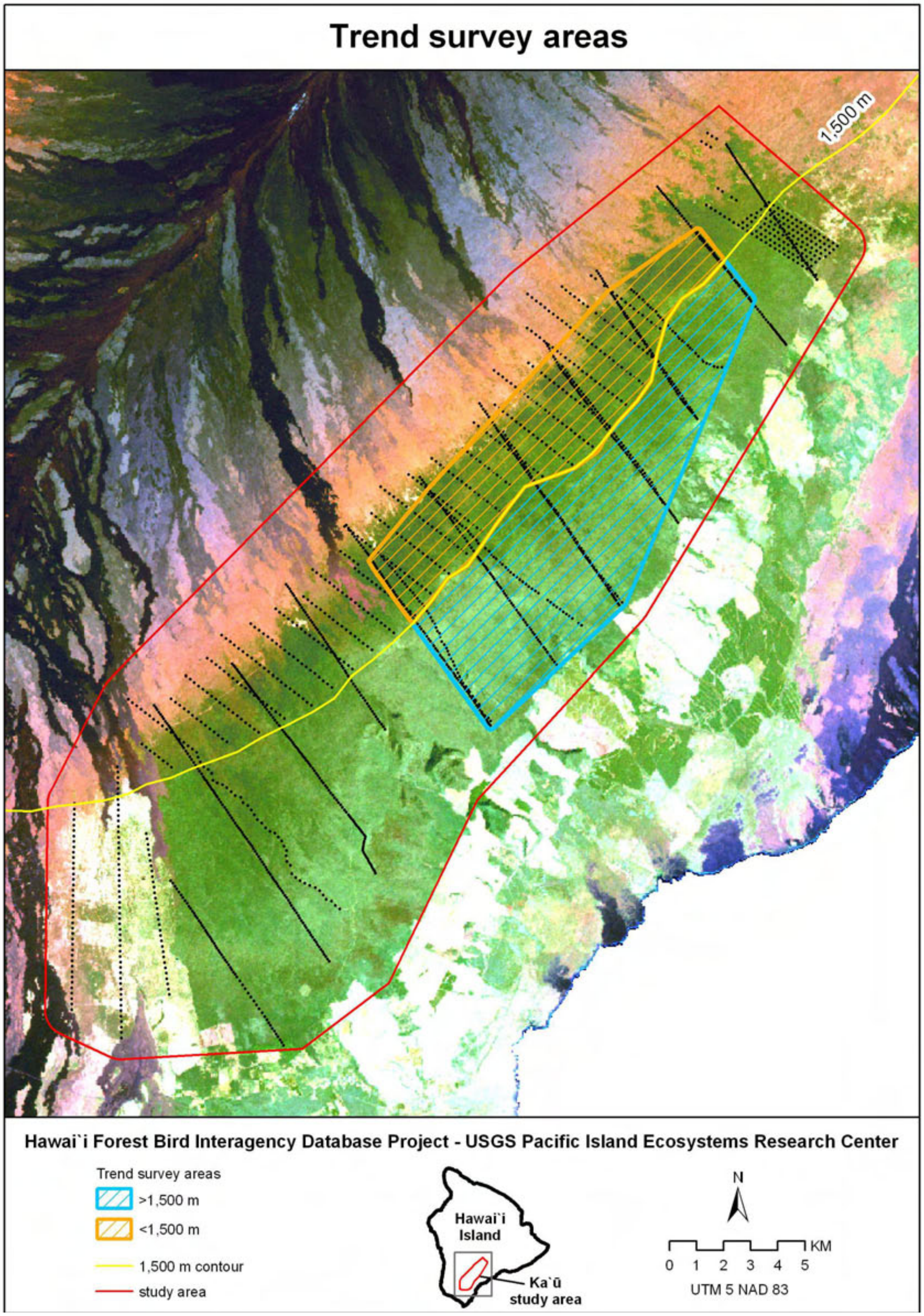


Figure 4. Trend analyses were limited to a subset of the study area with a relatively long series of surveys (orange and blue hatched areas). Analyses were separately conducted for the areas above and below the 1,500 m contour (yellow line), a threshold delineating the upper reach of the “mosquito zone”.

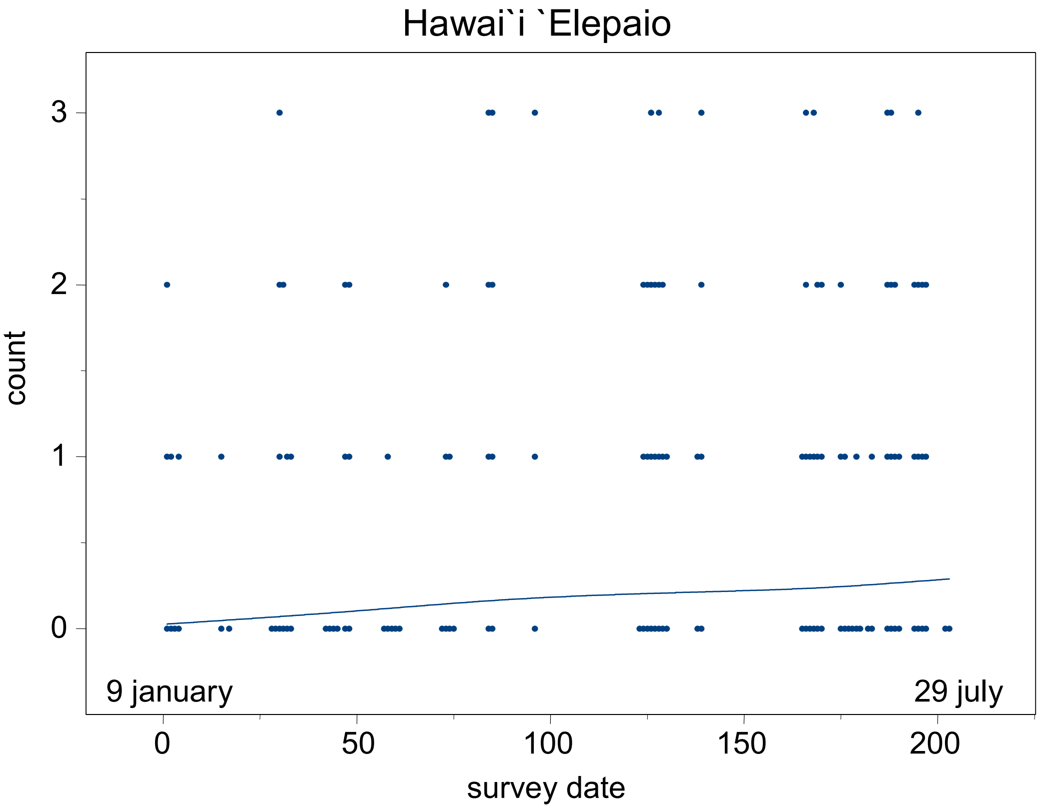
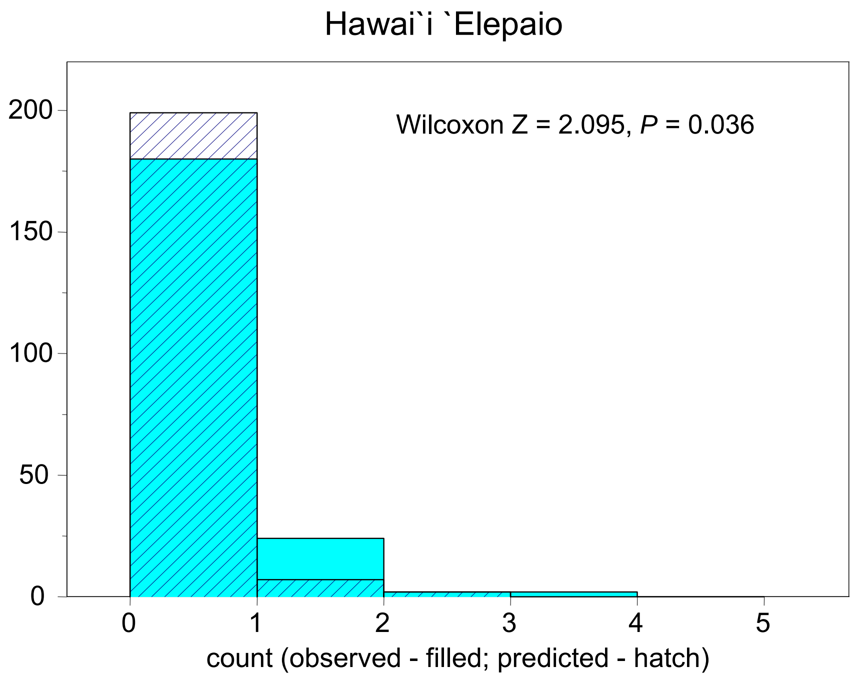


Figure 5. Seasonal effect as indicated by count and survey date (beginning on January 9 and ending on July 29). The smoothing spline fit to observed count data identified the peak seasonal effect used to predict counts.



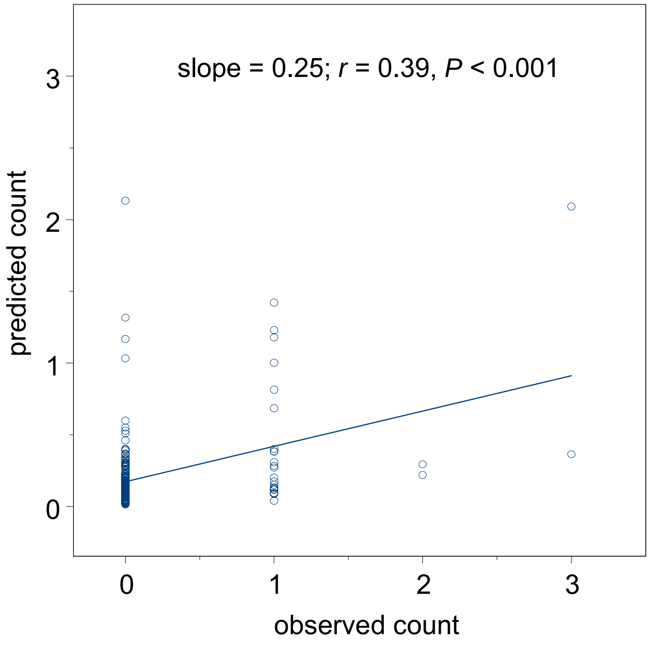


Figure 6. Accuracy assessment of predicted Hawai`i `Elepaio counts. The fit between observed (filled) and predicted (hatch) counts were examined with the Wilcoxon rank sum test. A significant *P*-value indicates that the means are different (i.e., not well fit). The slope of the trendline illustrates the degree to which observed and predicted counts approximate a 1-to-1 correspondence. A slope near 1 indicates the predictions are unbiased (i.e., do not under-predict abundance). The correlation coefficient (r) and *P*-value represents the precision of the model. Predictive models with a correlation near 1 are highly precise.

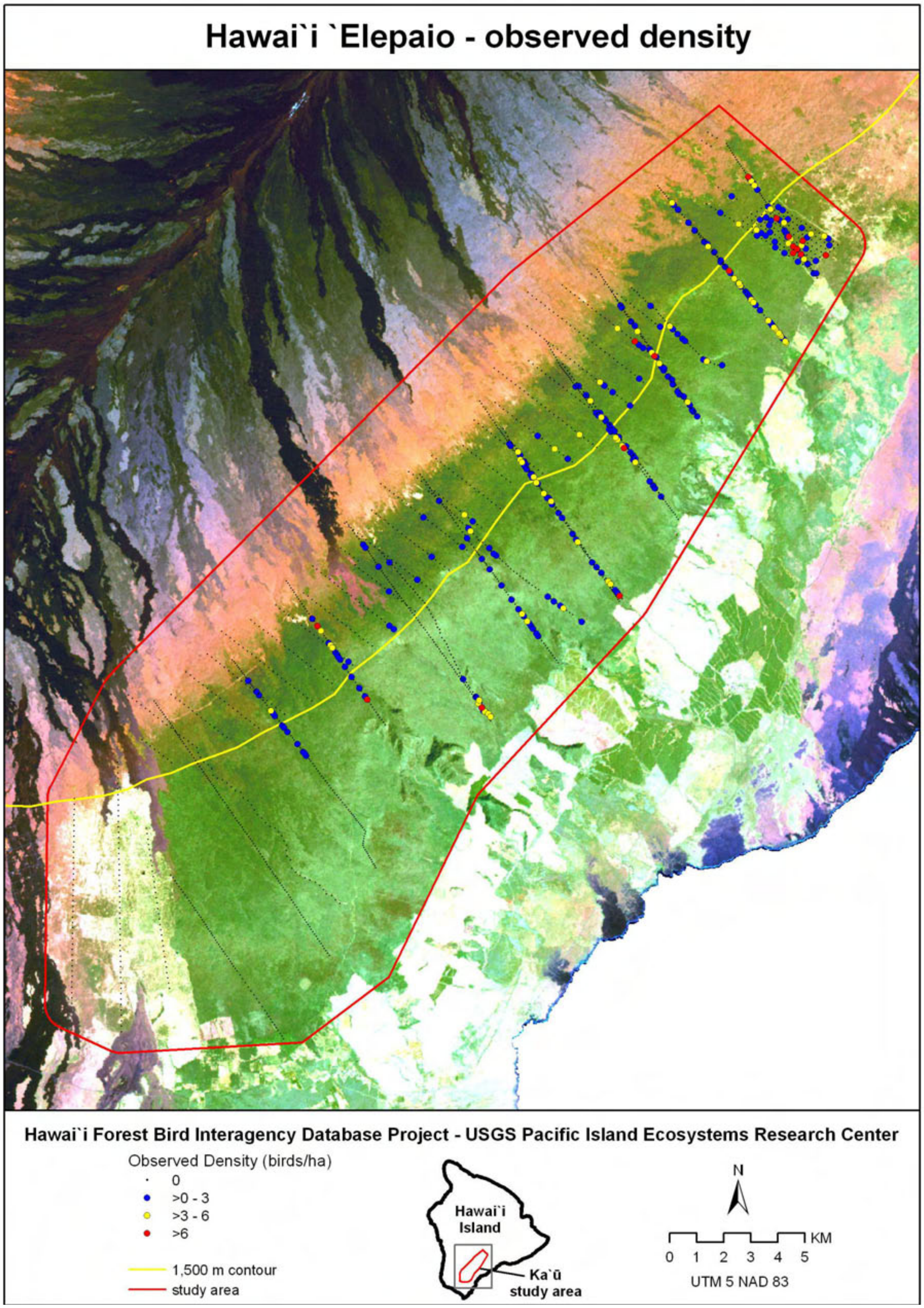


Figure 7. Observed distribution of Hawai`i `Elepaio density in Ka`ū.

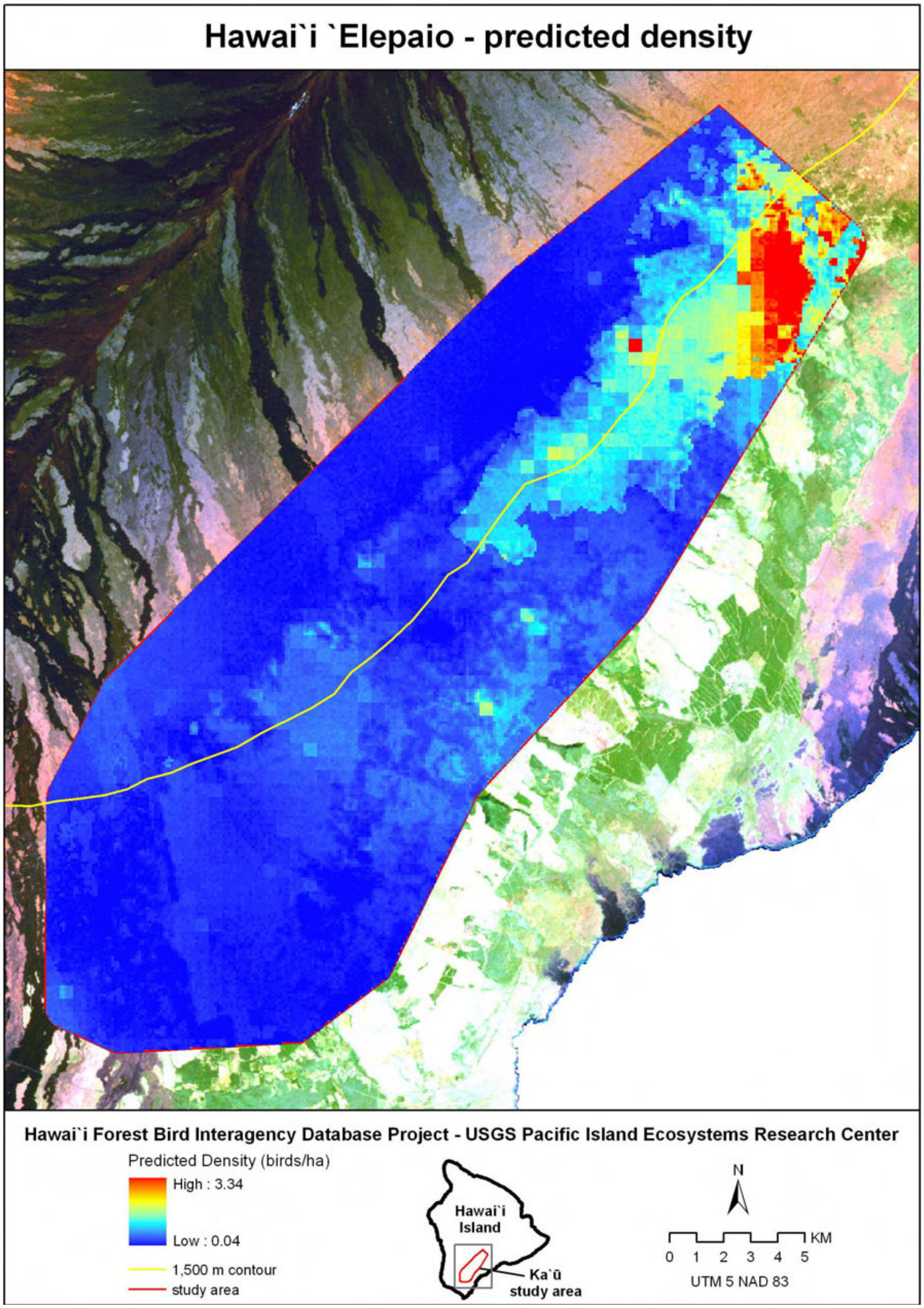


Figure 8. Predicted distribution of Hawai`i `Elepaio density in Ka`ū.

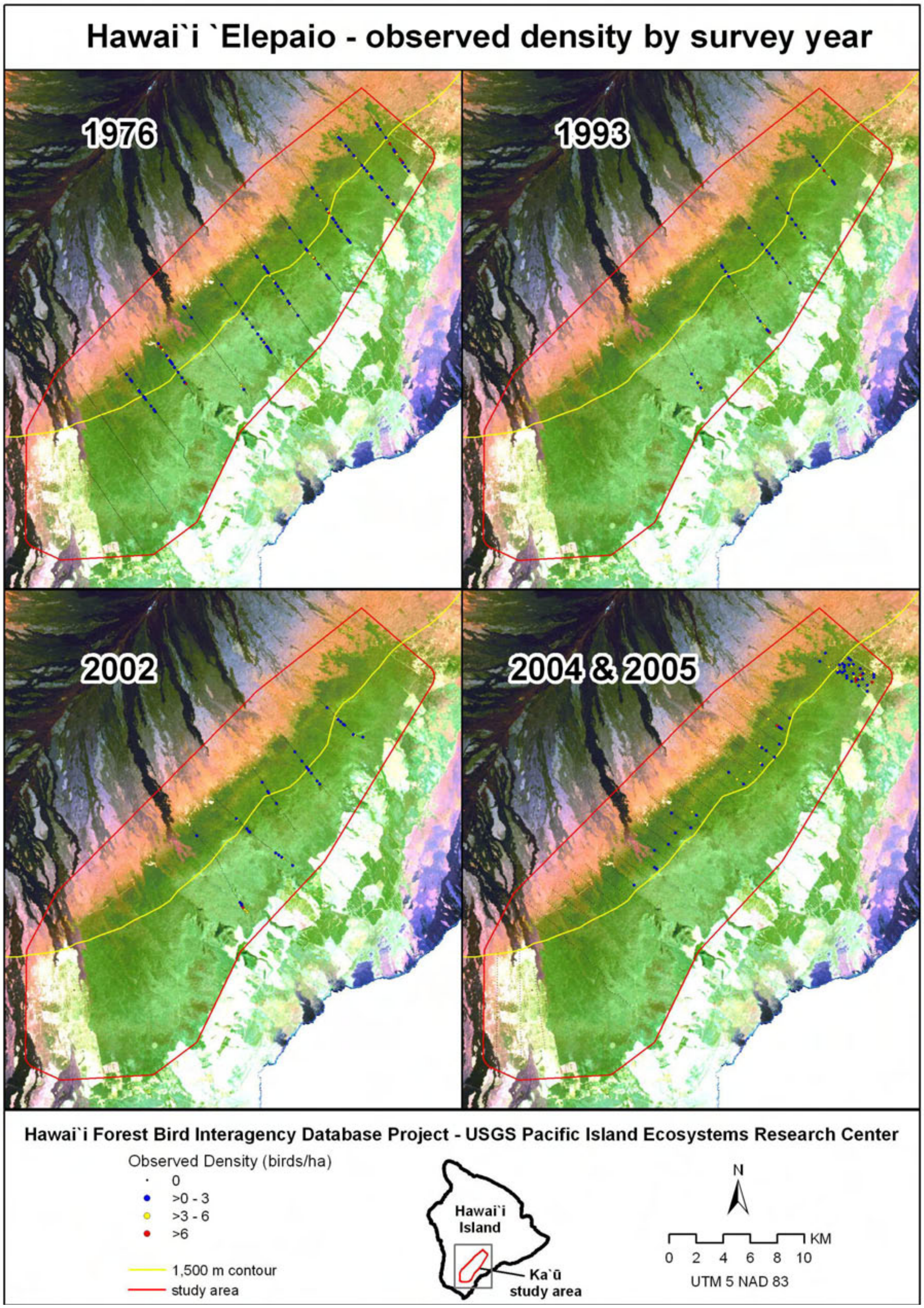


Figure 9. Observed distribution of Hawai`i `Elepaio density in Ka`ū by survey year.

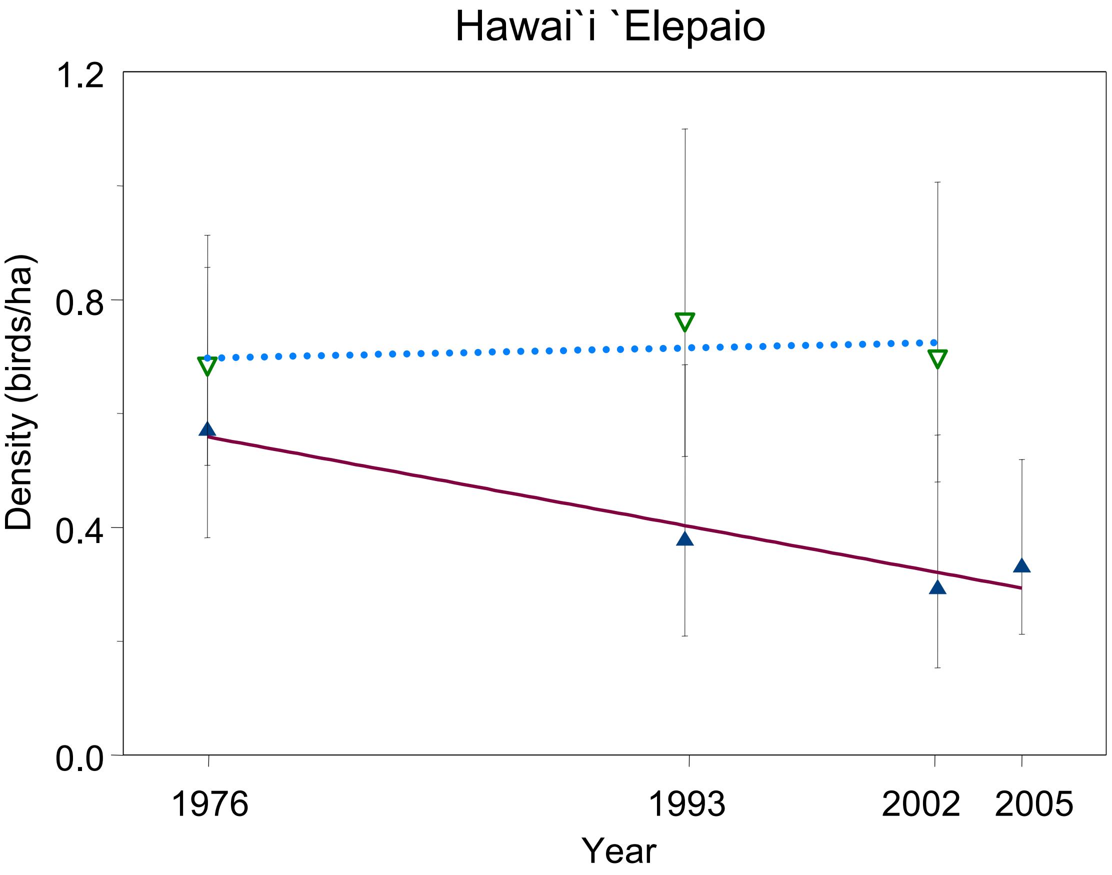


Figure 10. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. Equivalence tests of the densities observed above and below 1,500 m concluded that there were no trends evident (presumed slope above 1,500 m = -0.008; 95% CI = -0.018 to 0.001; *P* = 0.089; presumed slope below 1,500 m = 0.001; 95% CI = -0.012 to 0.013; *P* = 0.936).

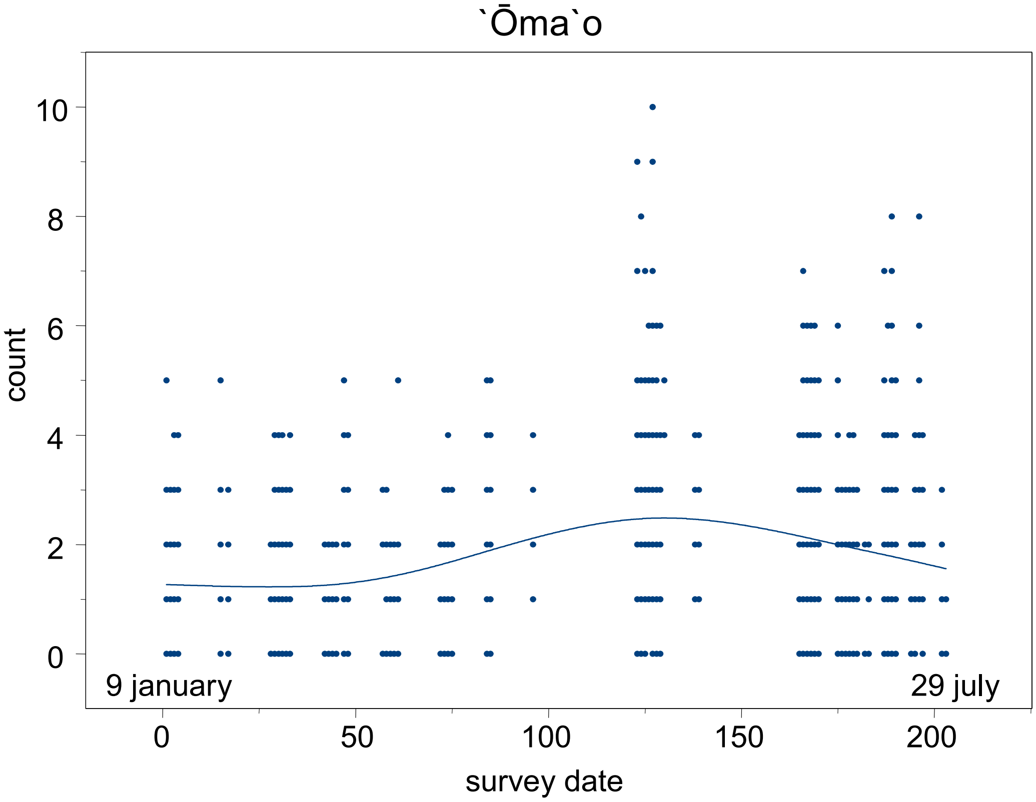


Figure 11. Seasonal effect as indicated by count and survey date (beginning on January 9 and ending on July 29). The smoothing spline fit to observed count data identified the peak seasonal effect used to predict counts.

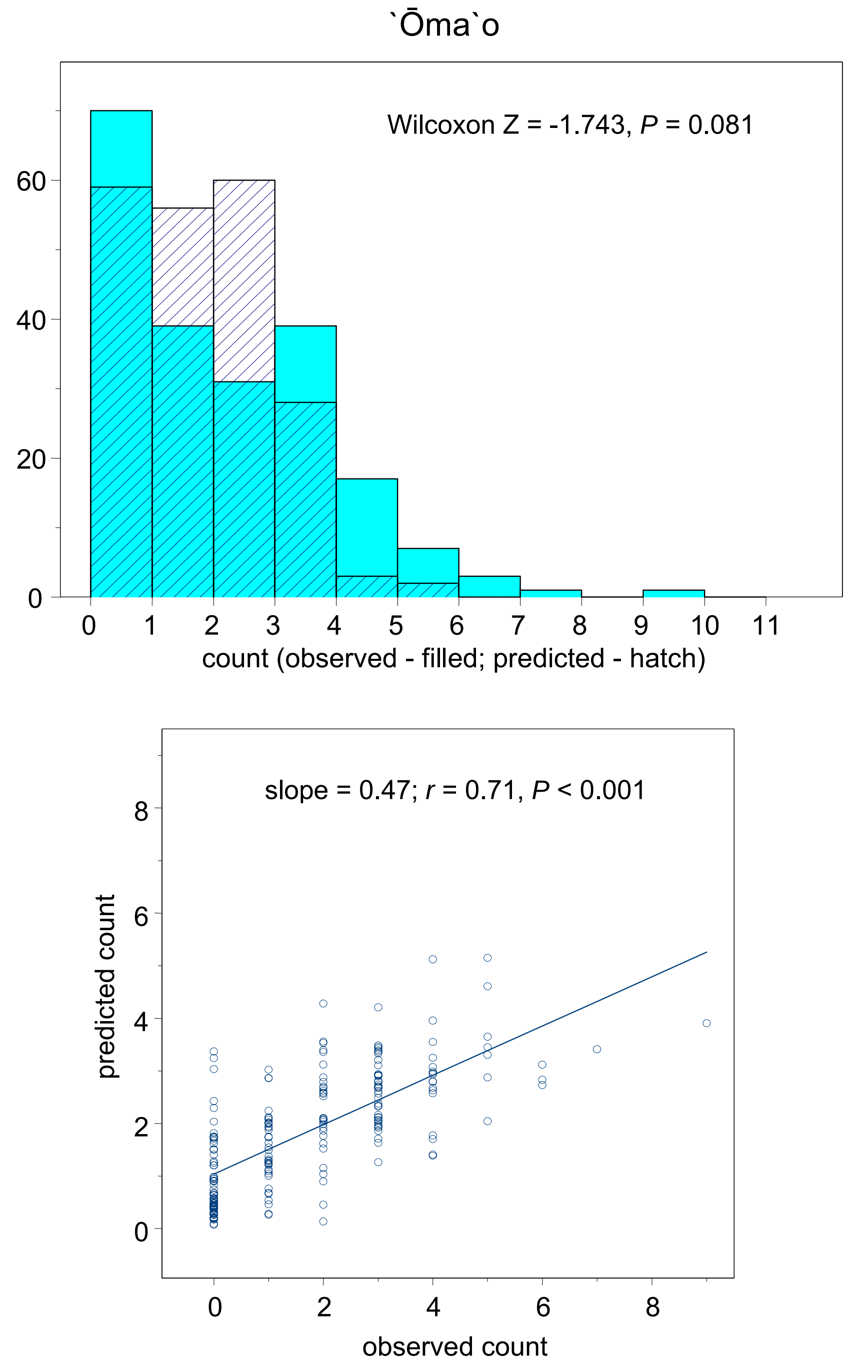


Figure 12. Accuracy assessment of predicted `Ōma`o counts. The fit between observed (filled) and predicted (hatch) counts were examined with the Wilcoxon rank sum test. A significant *P*-value indicates that the means are different (i.e., not well fit). The slope of the trendline illustrates the degree to which observed and predicted counts approximate a 1-to-1 correspondence. A slope near 1 indicates the predictions are unbiased (i.e., do not under-predict abundance). The correlation coefficient (r) and *P*-value represents the precision of the model. Predictive models with a correlation near 1 are highly precise.

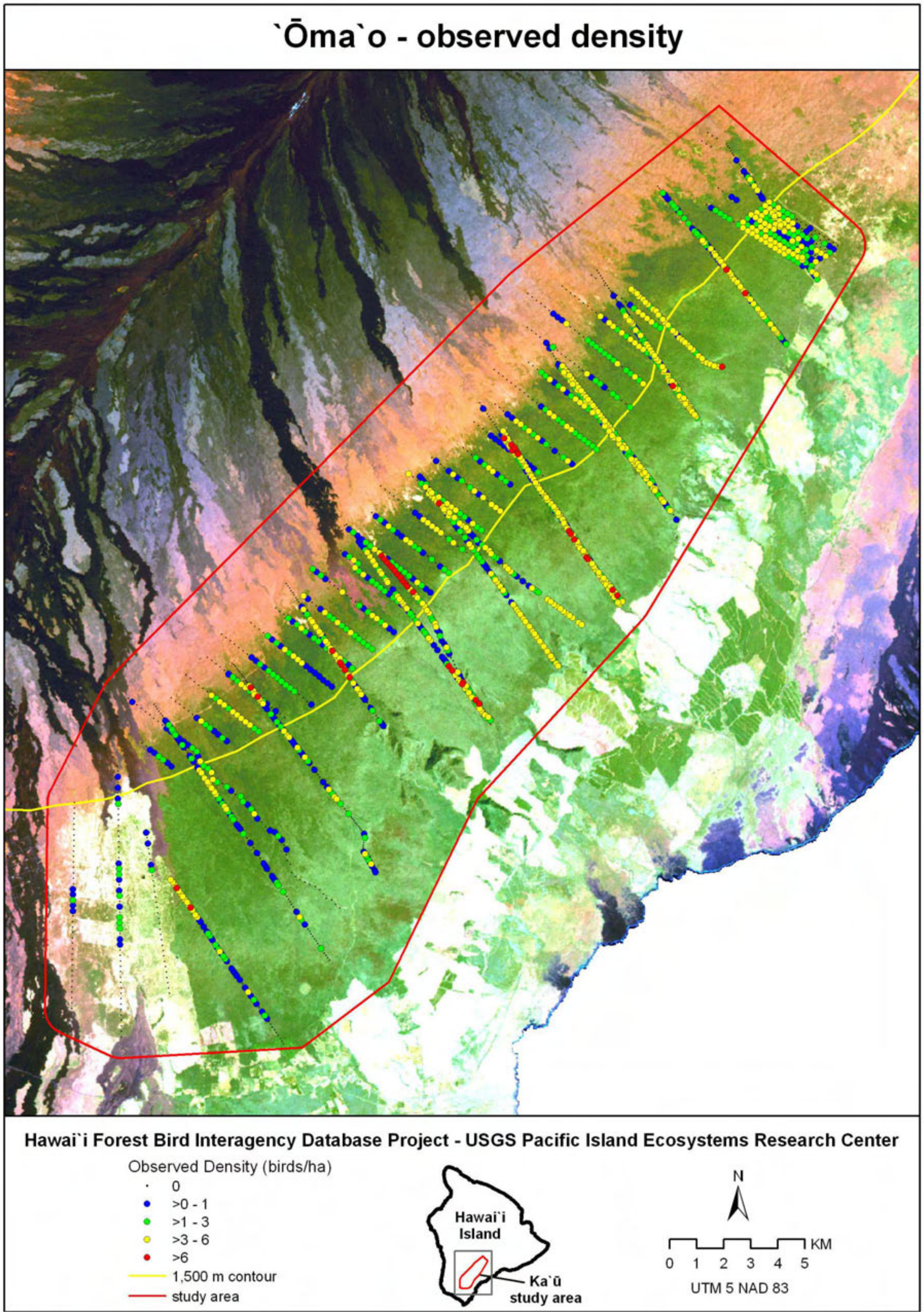


Figure 13. Observed distribution of `Ōma`o density in Ka`ū.

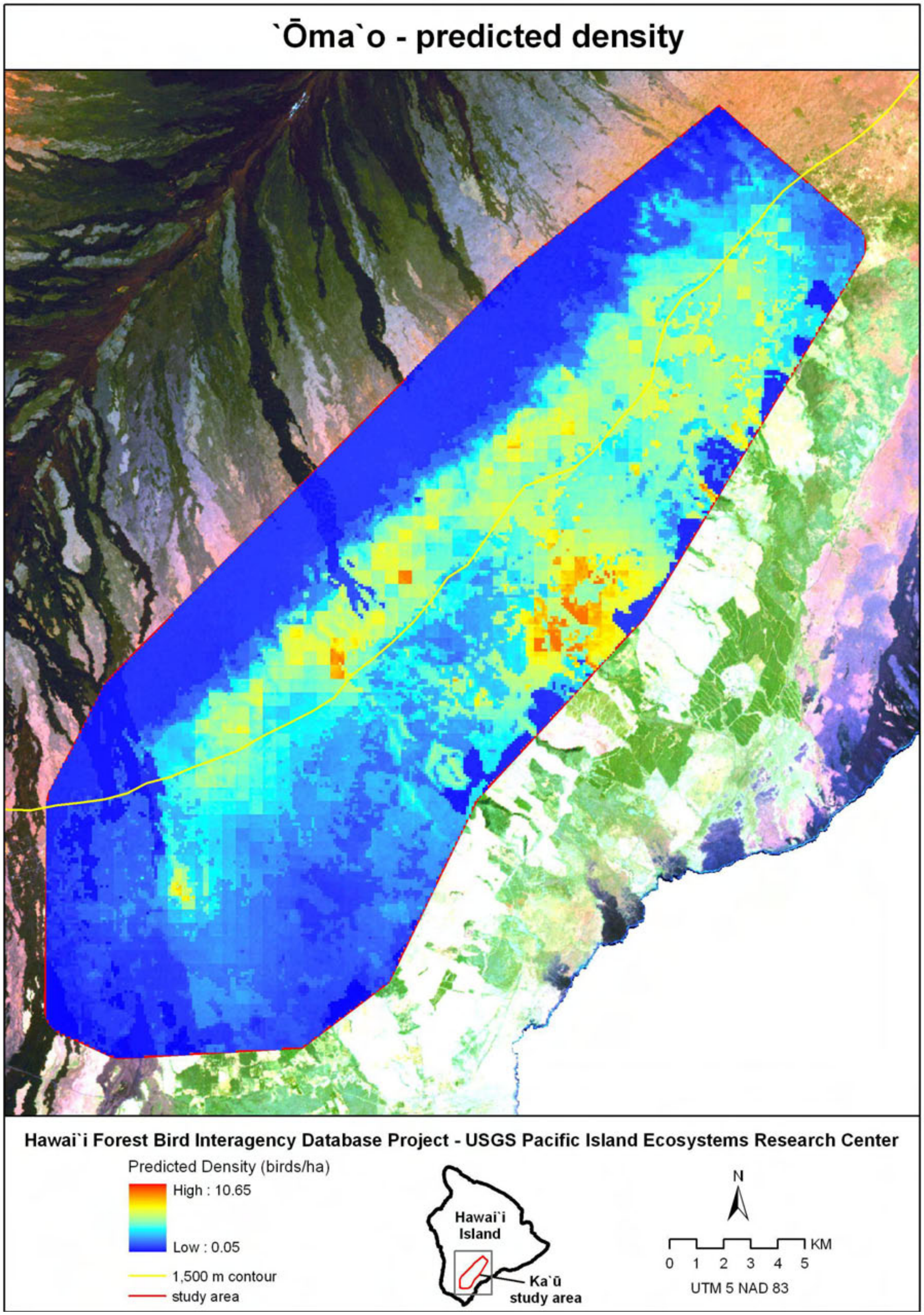


Figure 14. Predicted distribution of `Ōma`o density in Ka`ū.

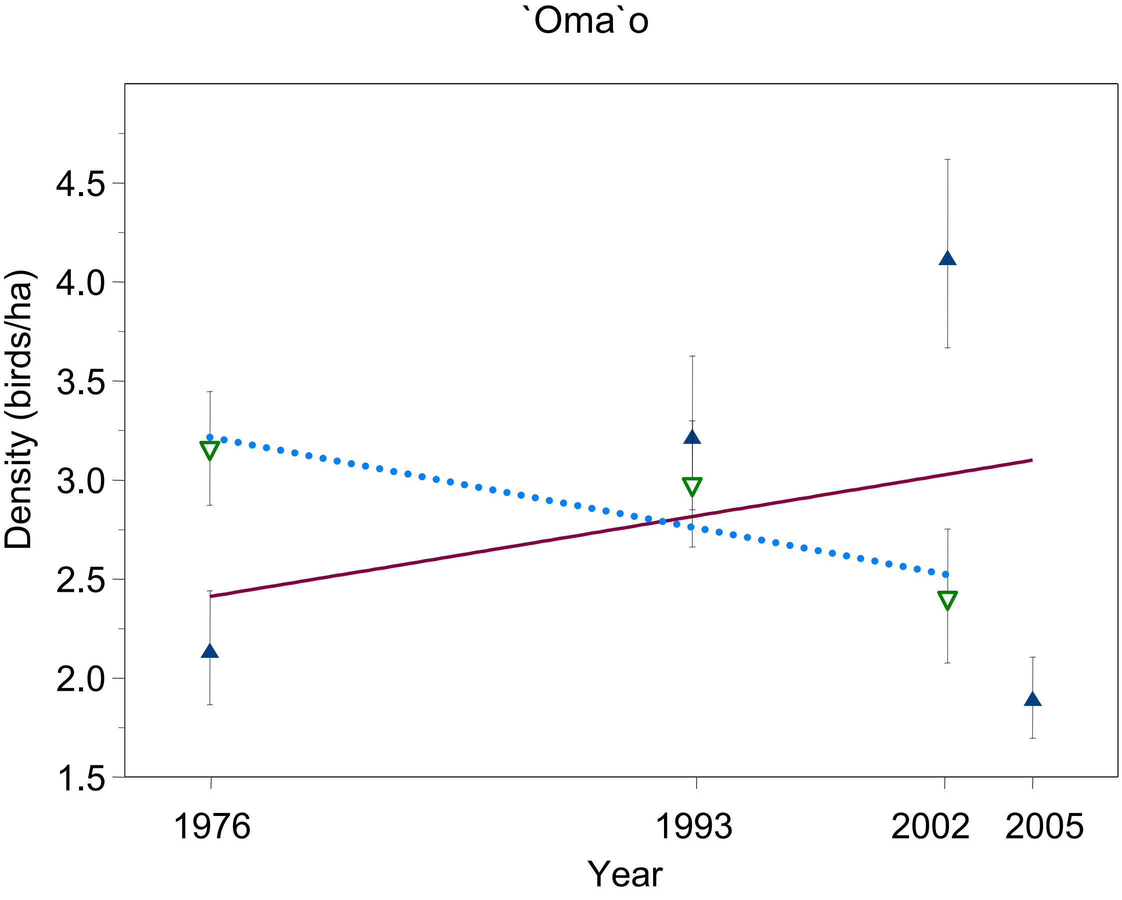


Figure 15. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. The equivalence test of the densities observed >1,500 m in 1976 and 2005 concluded that there were no trends evident (but see species account; presumed slope = -0.008; 95% CI = -0.020 to 0.004; *P* = 0.174). The equivalence test of the difference in densities observed <1,500 m in 1976 and 2002 revealed a significant decrease in density (presumed slope = -0.029; 95% CI = -0.046 to -0.012; *P* < 0.001).

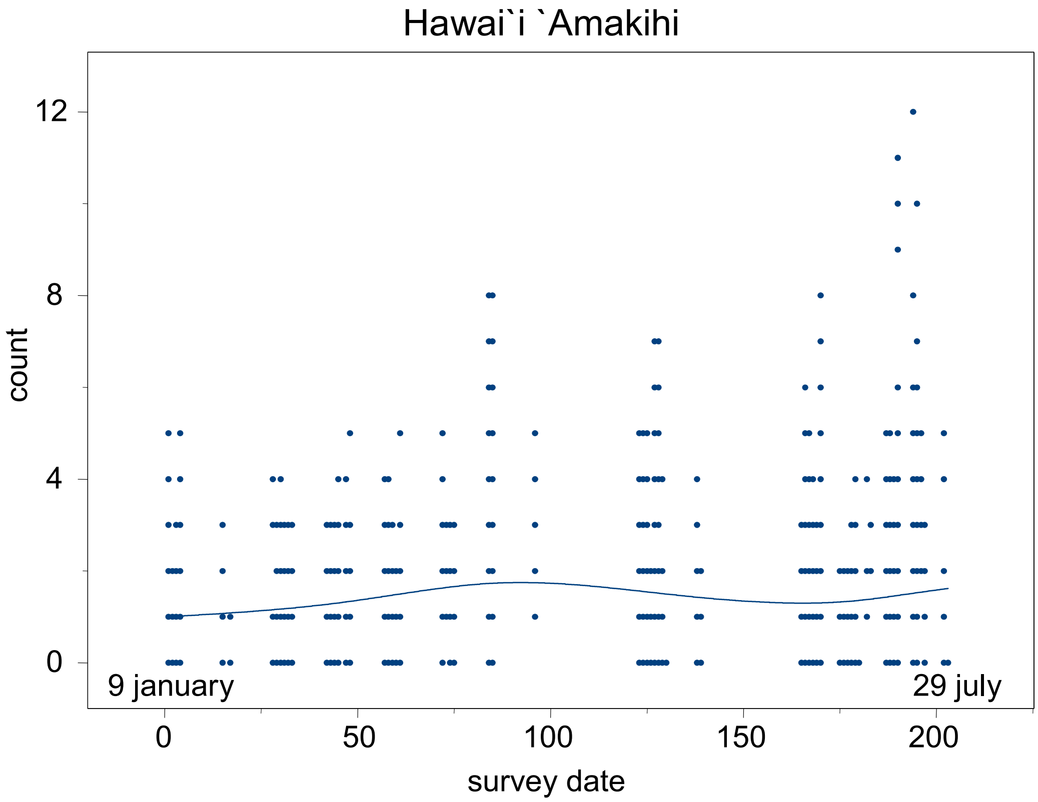


Figure 16. Seasonal effect as indicated by count and survey date (beginning on January 9 and ending on July 29). The smoothing spline fit to observed count data identified the peak seasonal effect used to predict counts.

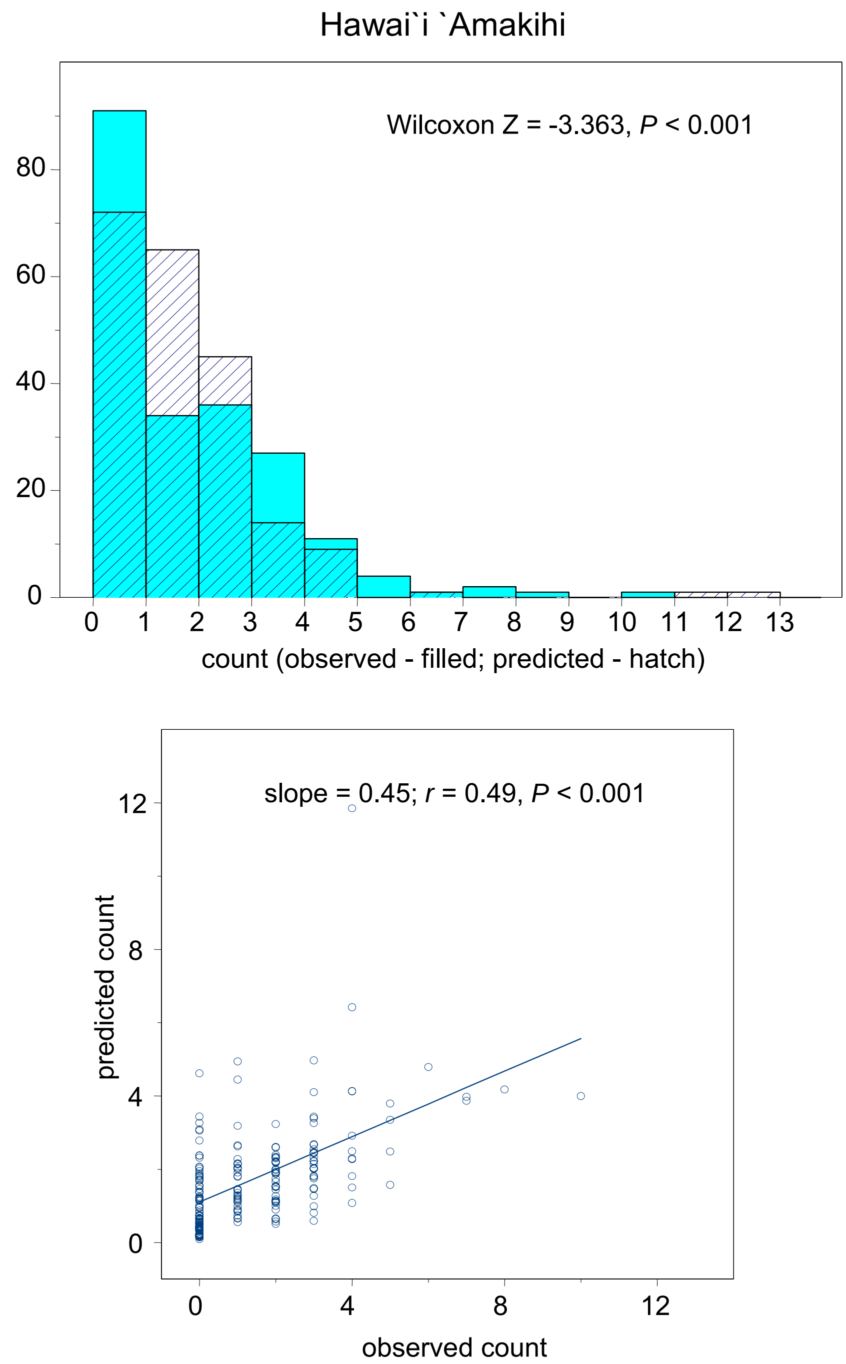


Figure 17. Accuracy assessment of predicted Hawai`i `Amakihi counts. The fit between observed (filled) and predicted (hatch) counts were examined with the Wilcoxon rank sum test. A significant *P*-value indicates that the means are different (i.e., not well fit). The slope of the trendline illustrates the degree to which observed and predicted counts approximate a 1-to-1 correspondence. A slope near 1 indicates the predictions are unbiased (i.e., do not under-predict abundance). The correlation coefficient (r) and *P*-value represents the precision of the model. Predictive models with a correlation near 1 are highly precise.

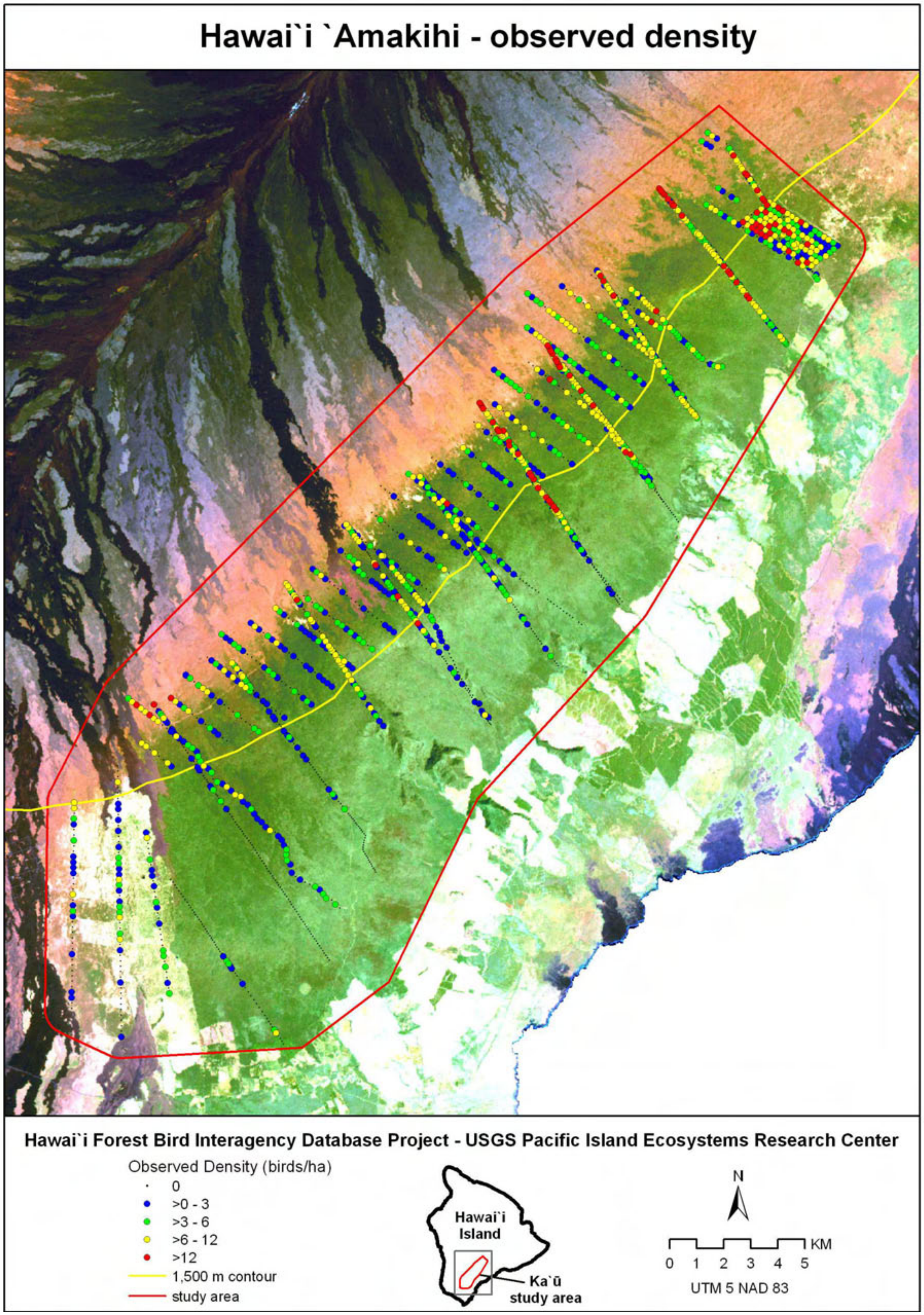


Figure 18. Observed distribution of Hawai`i `Amakihi density in Ka`ū.

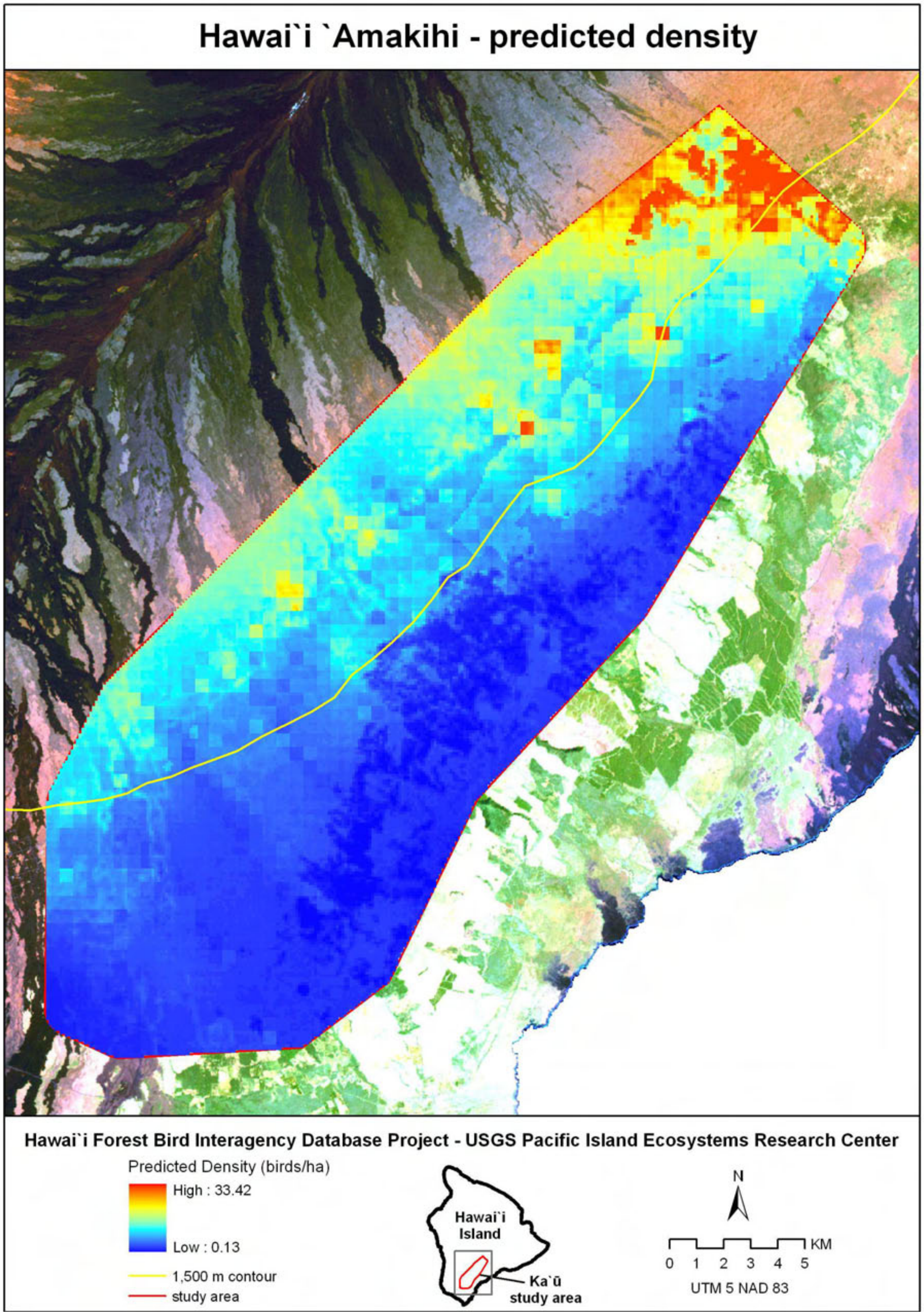


Figure 19. Predicted distribution of Hawai`i `Amakihi density in Ka`ū.

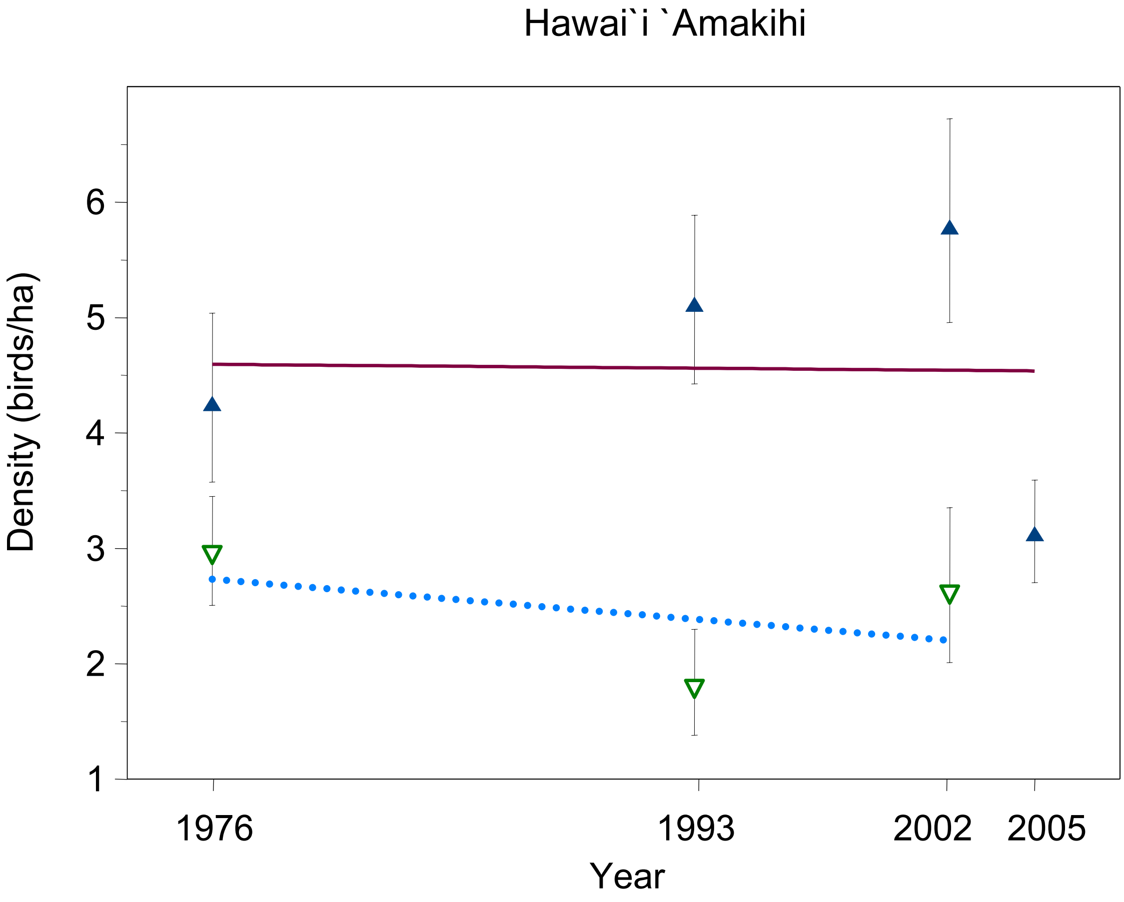


Figure 20. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. The equivalence test of the difference in densities observed >1,500 m in 1976 and 2005 yielded negative trend (but see species account; presumed slope = -0.039; 95% CI = -0.068 to -0.010; *P* = 0.009). The equivalence test of the difference in densities observed <1,500 m in 1976 and 2002 was inconclusive (presumed slope = -0.013; 95% CI = -0.044 to 0.018; *P* = 0.404).

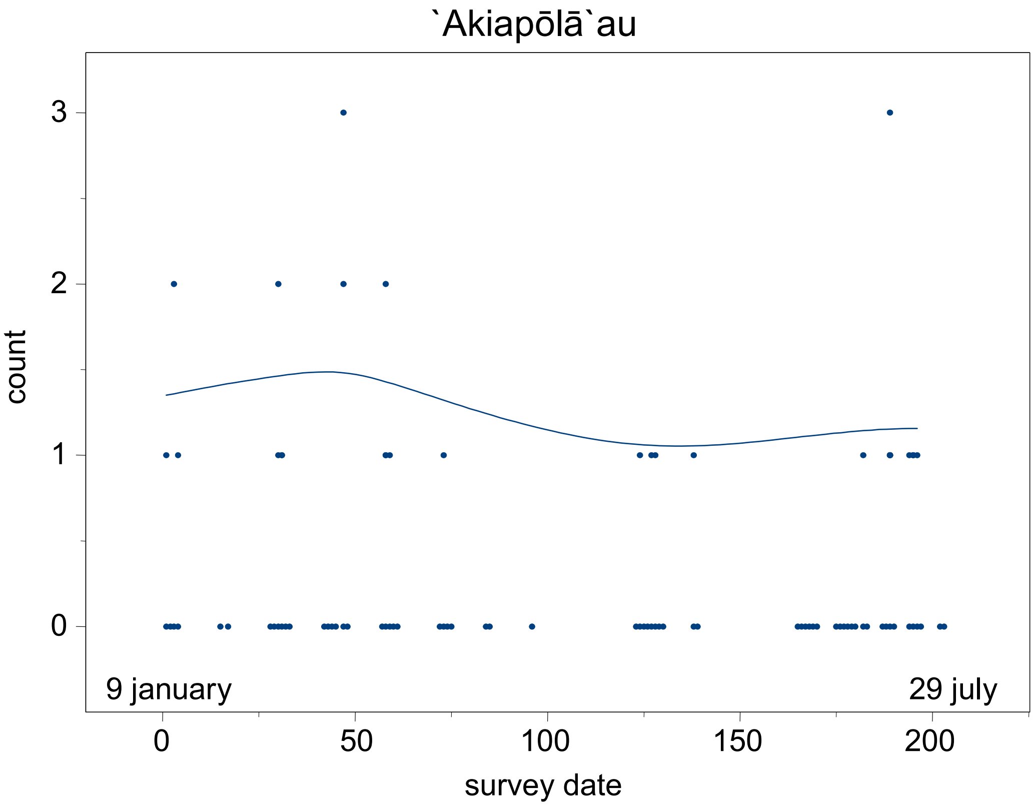


Figure 21. Seasonal effect as indicated by count, survey date (beginning on January 9 and ending on July 29) and smoothing spline. The smoothing spline excludes zero counts to reduce its overwhelming effect on discerning peak counts.

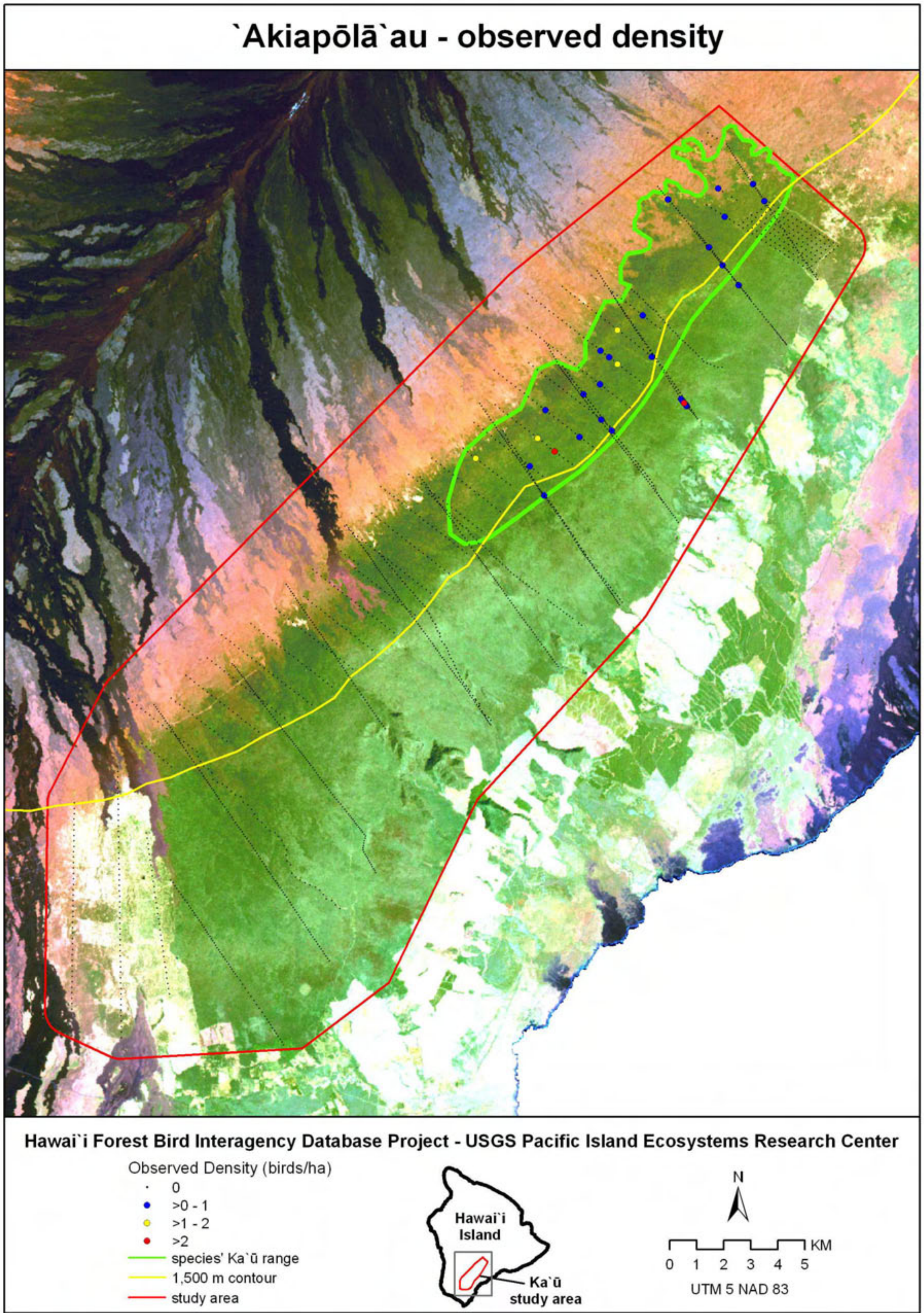


Figure 22. Observed distribution of `Akiapōlā`au density in Ka`ū.

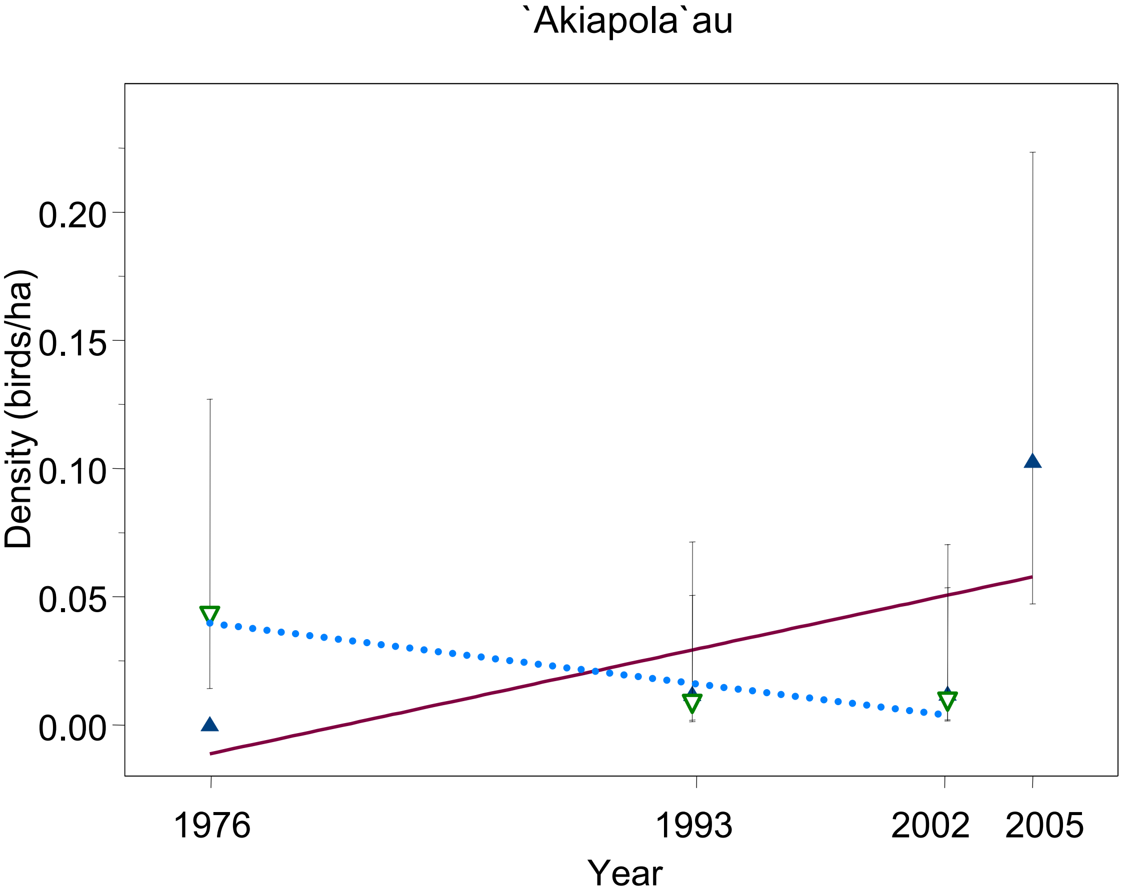


Figure 23. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. Equivalence tests of the densities observed above and below 1,500 m concluded that there were no trends evident (but see species account; presumed slope above 1,500 m = 0.004; 95% CI = 0.001 to 0.006; *P* = 0.015; presumed slope below 1,500 m = -0.001; 95% CI = -0.003 to 0.001; *P* = 0.224).

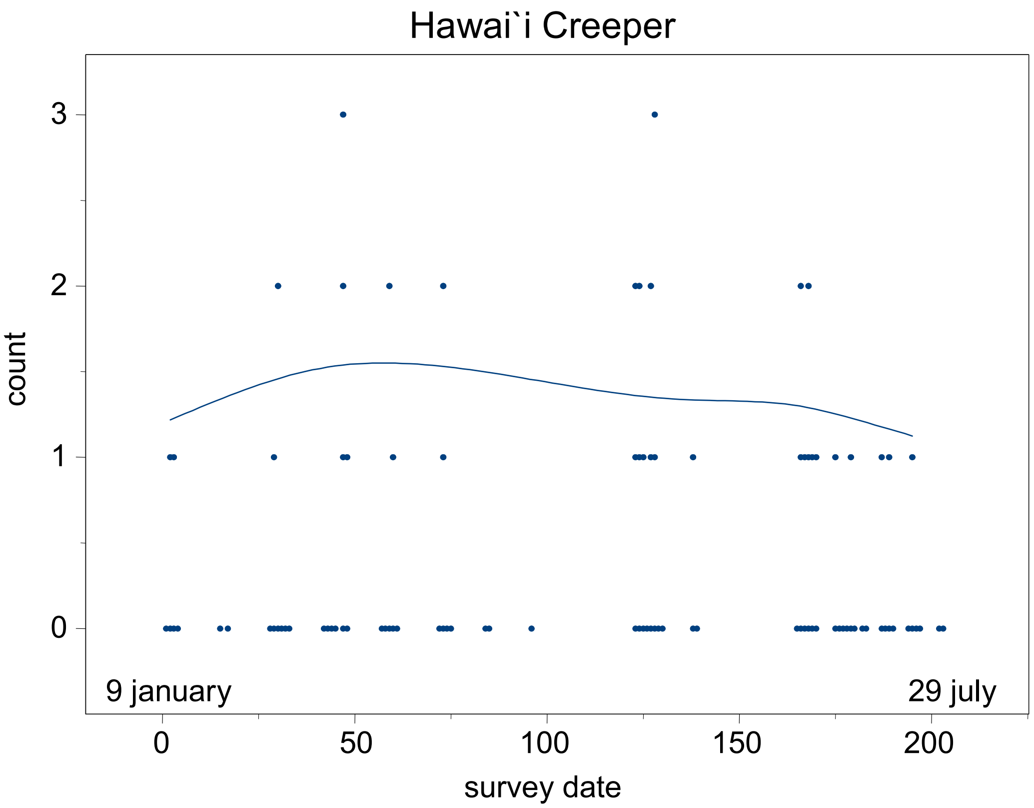


Figure 24. Seasonal effect as indicated by count, survey date (beginning on January 9 and ending on July 29) and smoothing spline. The smoothing spline excludes zero counts to reduce its overwhelming effect on discerning peak counts.

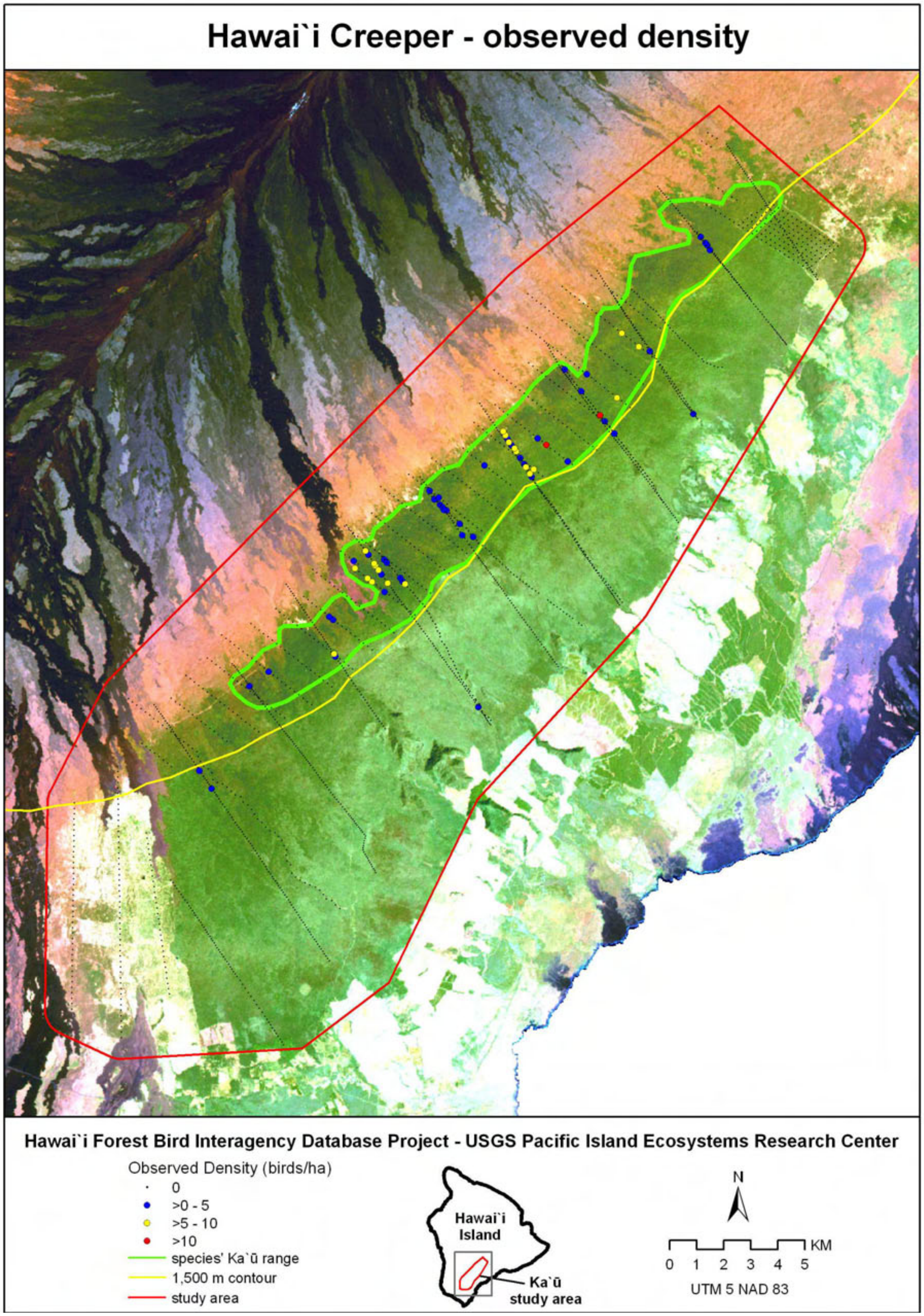


Figure 25. Observed distribution of Hawai`i Creeper density in Ka`ū.

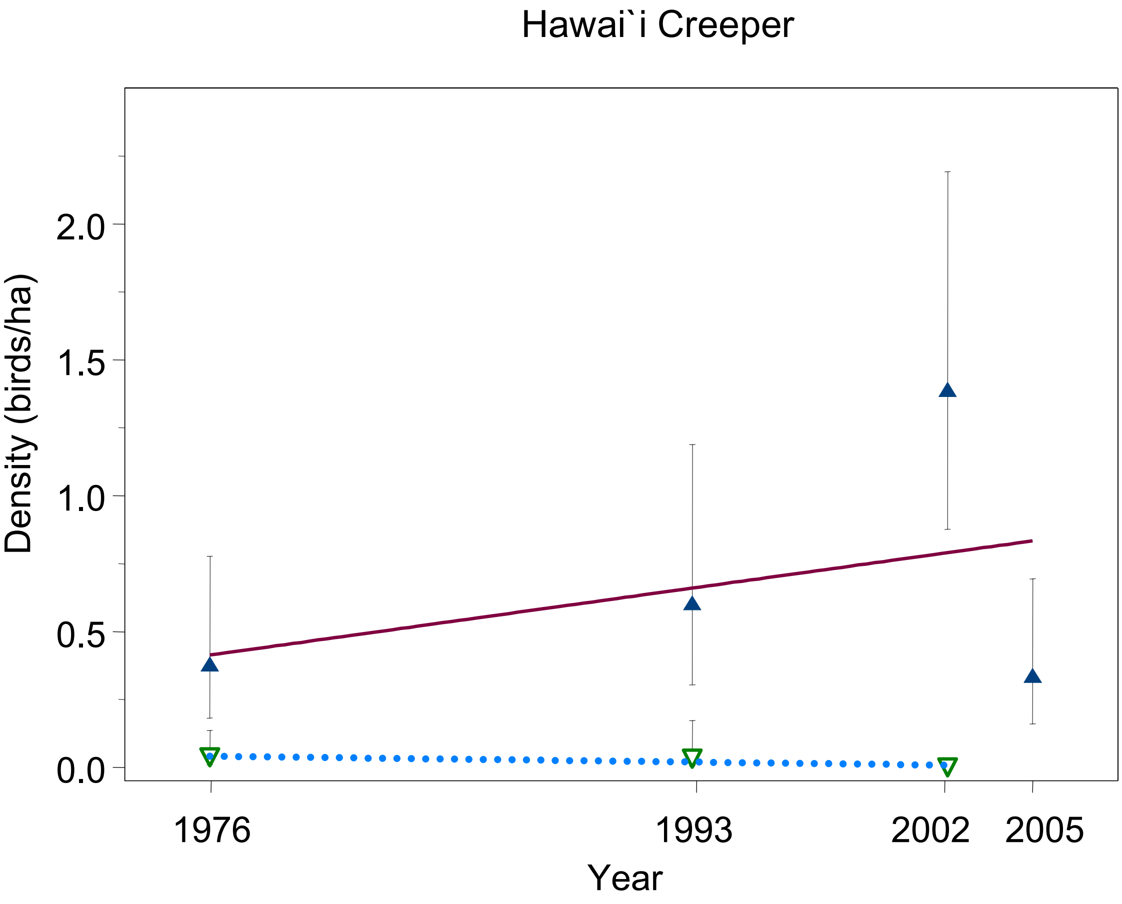


Figure 26. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. Equivalence tests of the densities observed above and below 1,500 m concluded that there were no trends evident (but see species account; presumed slope above 1,500 m = -0.001; 95% CI = -0.014 to 0.012; *P* = 0.827; presumed slope below 1,500 m = -0.001; 95% CI = -0.004 to 0.001; *P* = 0.175).

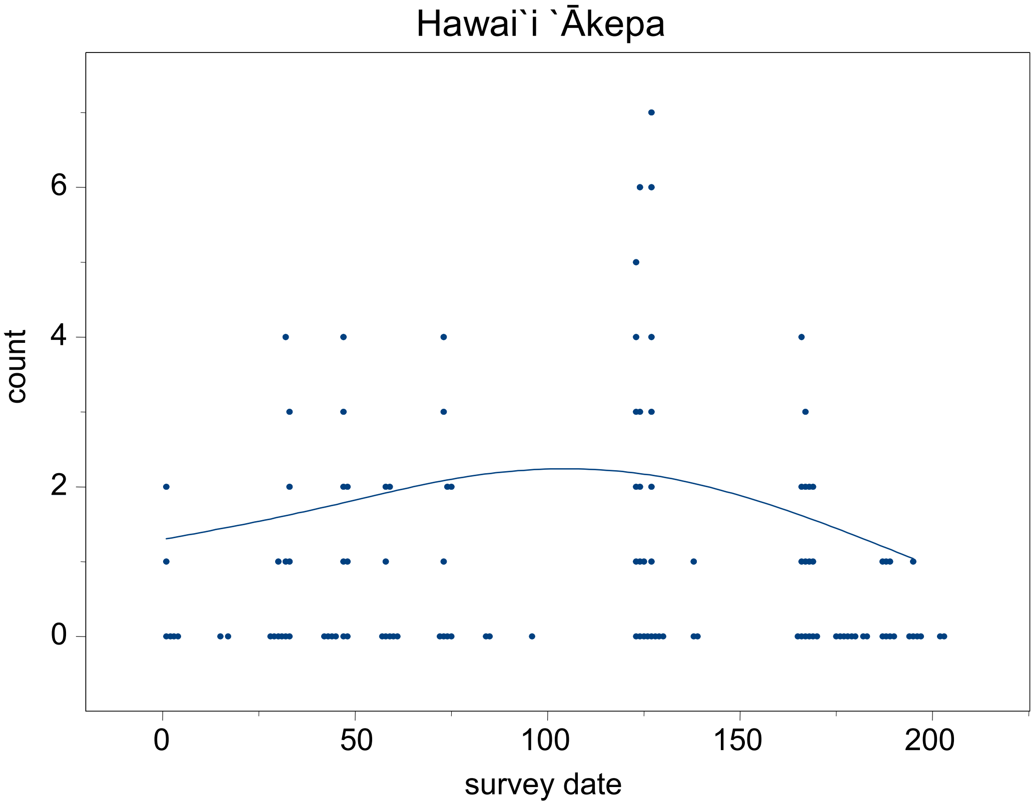


Figure 27. Seasonal effect as indicated by count, survey date (beginning on January 9 and ending on July 29) and smoothing spline. The smoothing spline excludes zero counts to reduce its overwhelming effect on discerning peak counts.

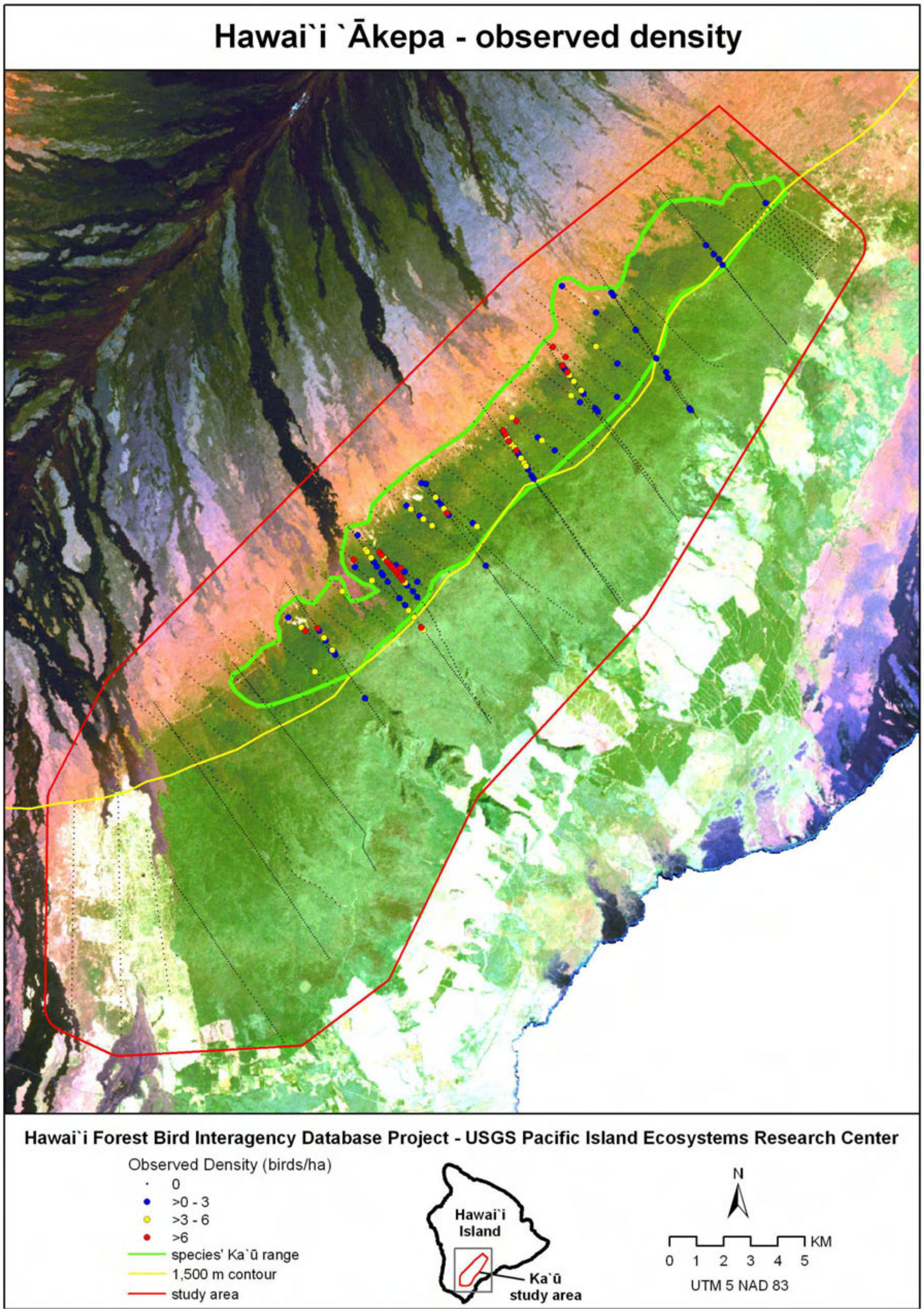


Figure 28. Observed distribution of Hawai`i `Ākepa density in Ka`ū.

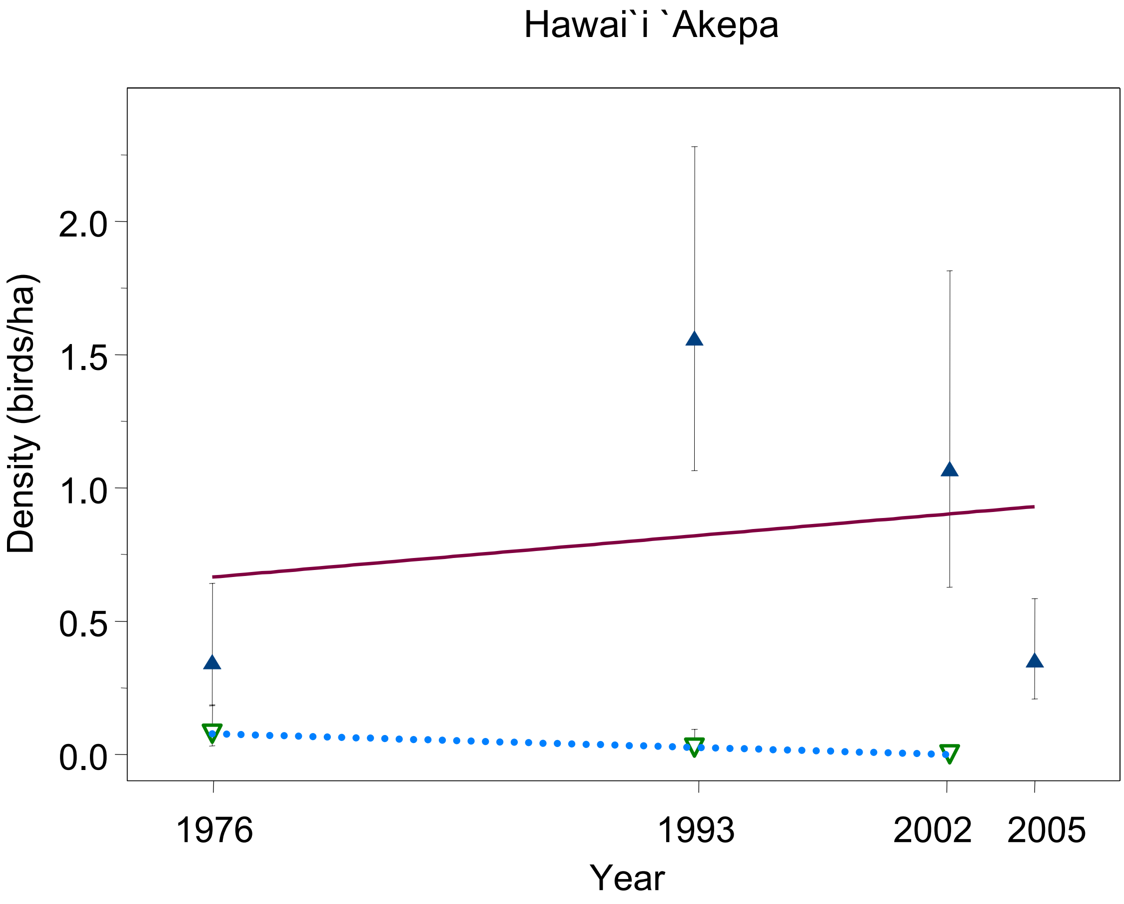


Figure 29. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. Equivalence tests of the densities observed above and below 1,500 m concluded that there were no trends evident (but see species account; presumed slope above 1,500 m = 0.000; 95% CI = -0.010 to 0.010; *P* = 0.966; presumed slope below 1,500 m = -0.003; 95% CI = -0.006 to 0.000; *P* = 0.032).

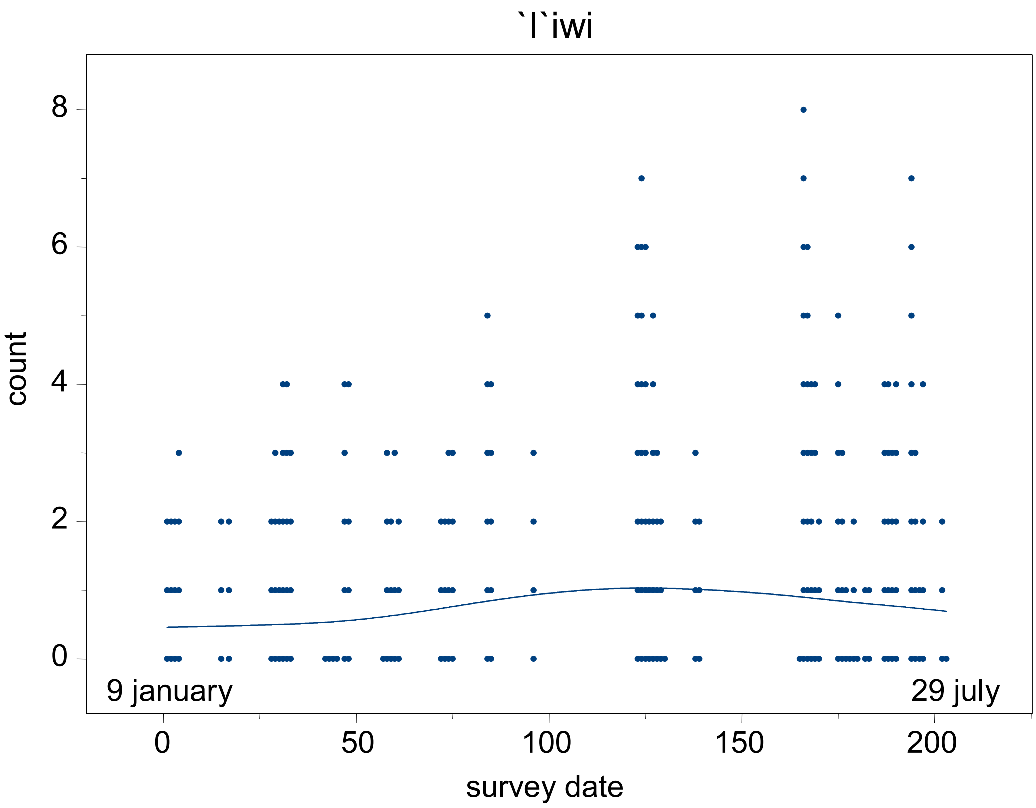


Figure 30. Seasonal effect as indicated by count and survey date (beginning on January 9 and ending on July 29). The smoothing spline fit to observed count data identified the peak seasonal effect used to predict counts.

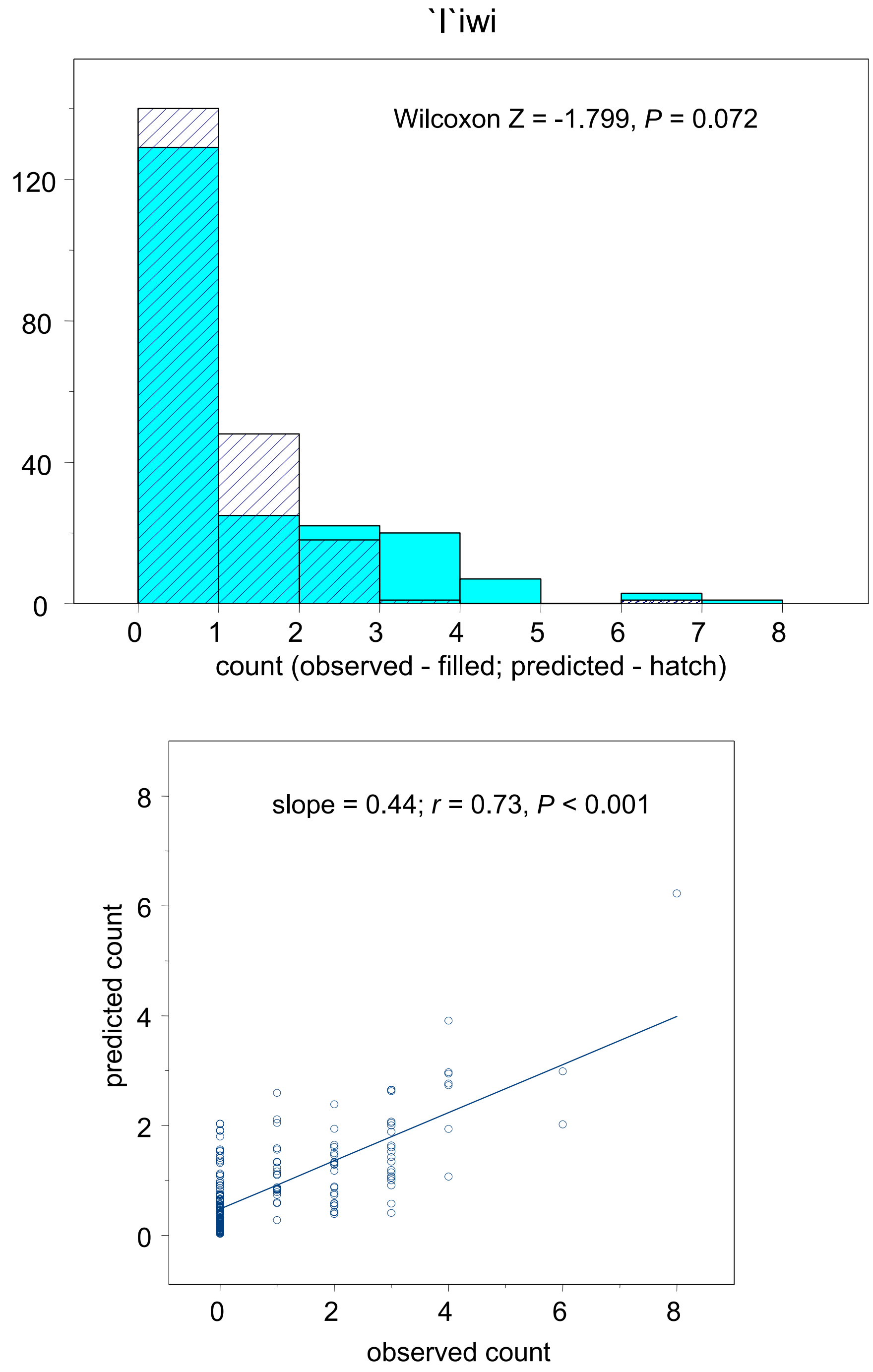


Figure 31. Accuracy assessment of predicted `I`iwi counts. The fit between observed (filled) and predicted (hatch) counts were examined with the Wilcoxon rank sum test. A significant *P*-value indicates that the means are different (i.e., not well fit). The slope of the trendline illustrates the degree to which observed and predicted counts approximate a 1-to-1 correspondence. A slope near 1 indicates the predictions are unbiased (i.e., do not under-predict abundance). The correlation coefficient (r) and *P*-value represents the precision of the model. Predictive models with a correlation near 1 are highly precise.

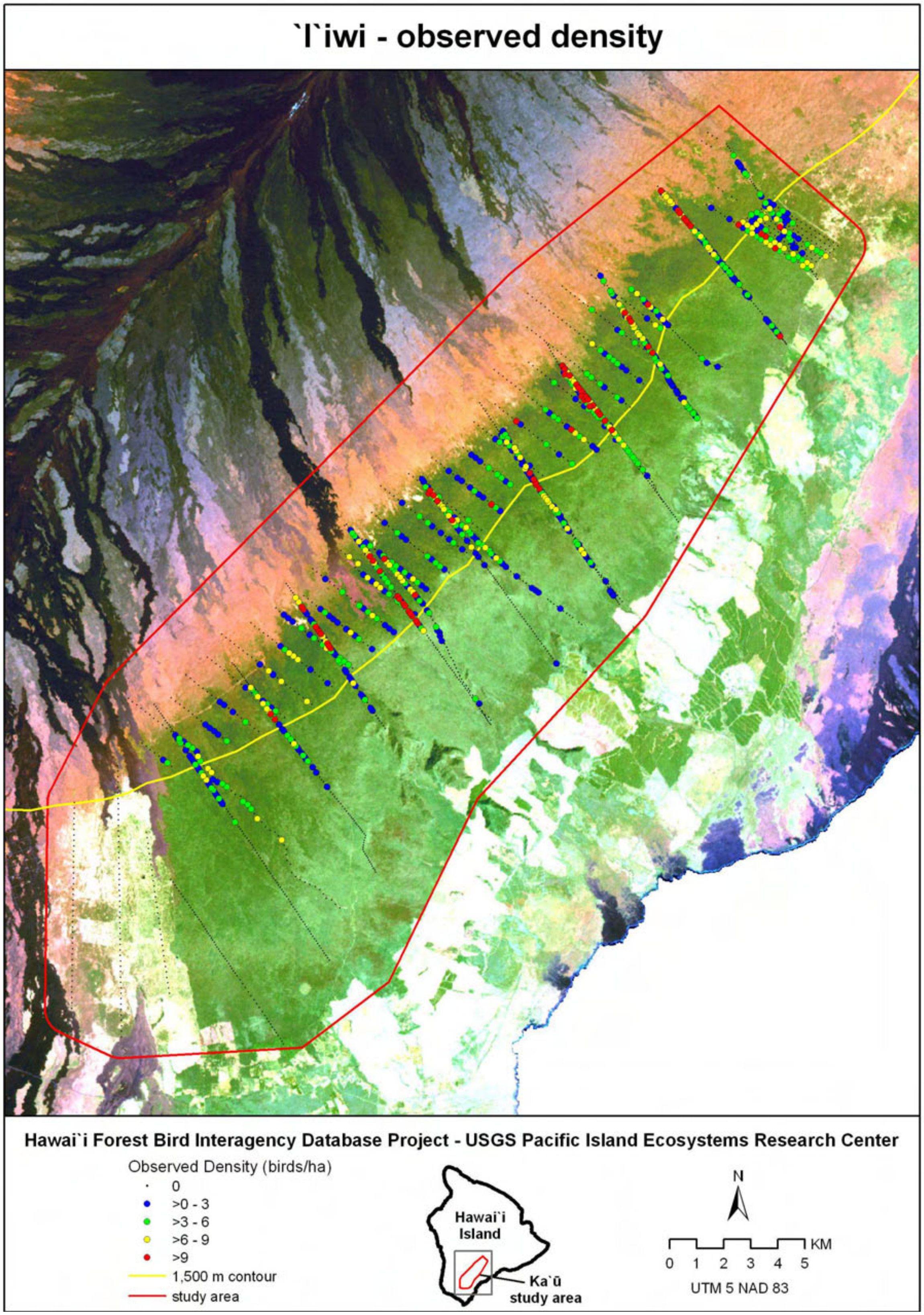


Figure 32. Observed distribution of `I`iwi density in Ka`ū.

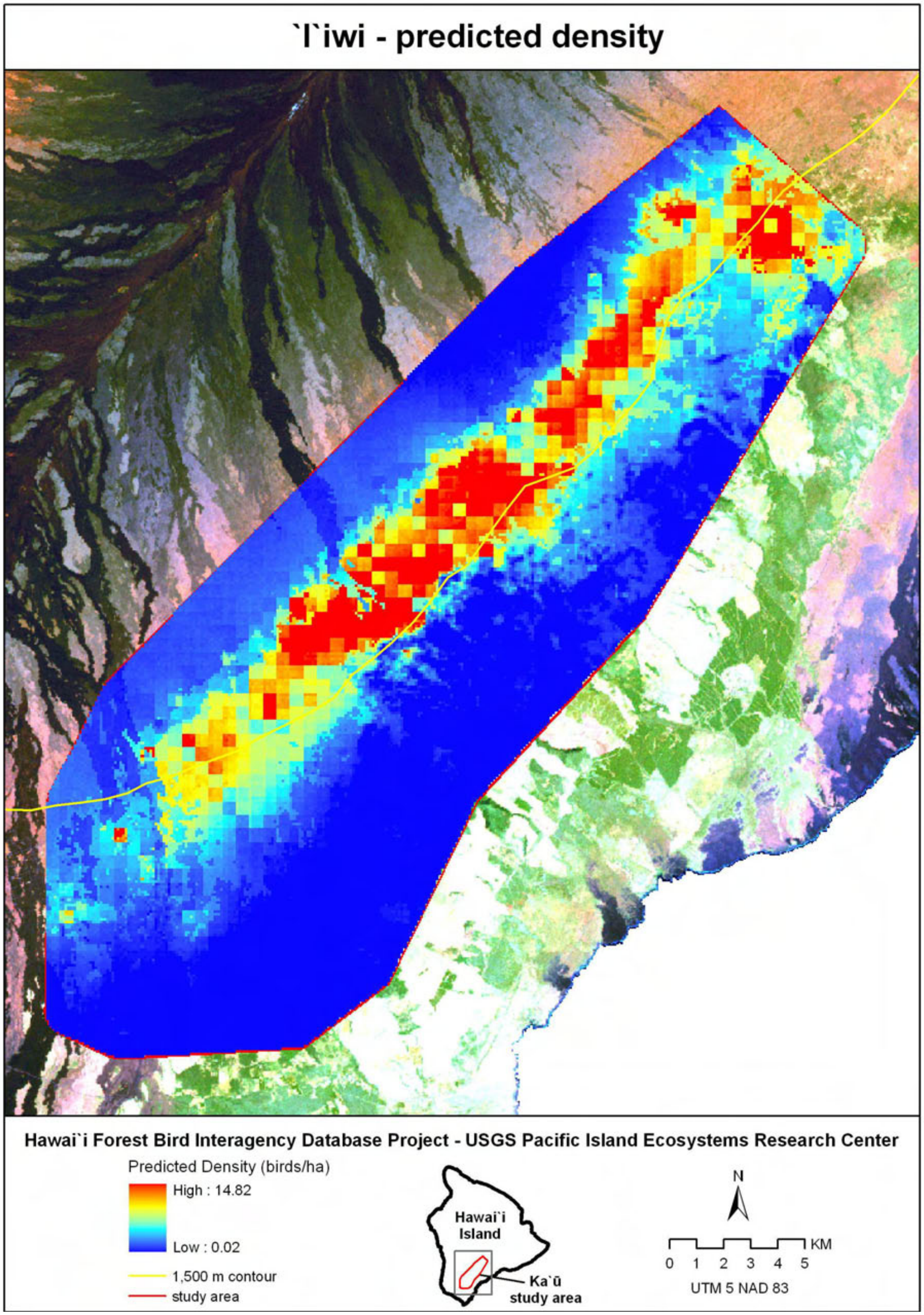


Figure 33. Predicted distribution of `I`iwi density in Ka`ū.

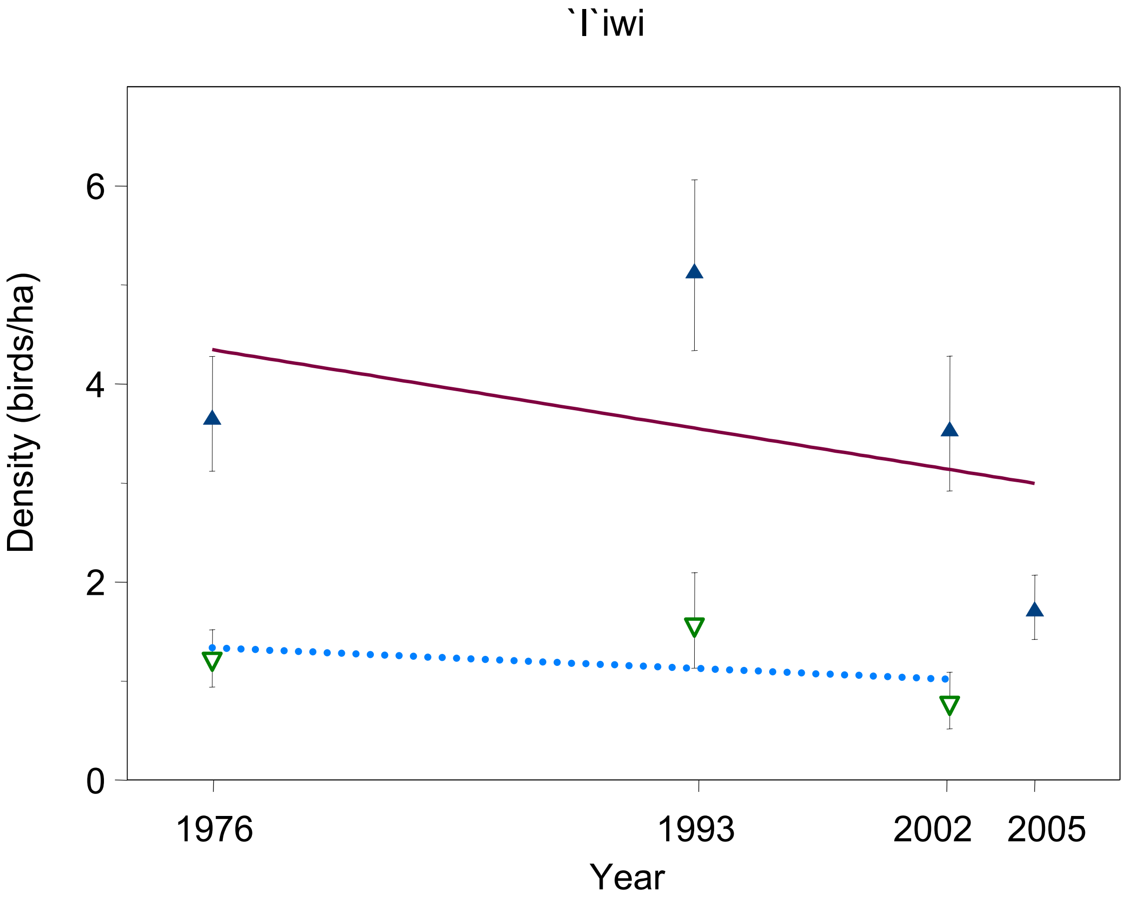


Figure 34. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. Equivalence tests revealed significant decreases in the densities observed >1,500 m in 1976 and 2005 (presumed slope = -0.067; 95% CI = -0.090 to -0.044; P < 0.001) and <1,500 m in 1976 and 2002 (presumed slope = -0.017; 95% CI = -0.032 to -0.002; P = 0.029).

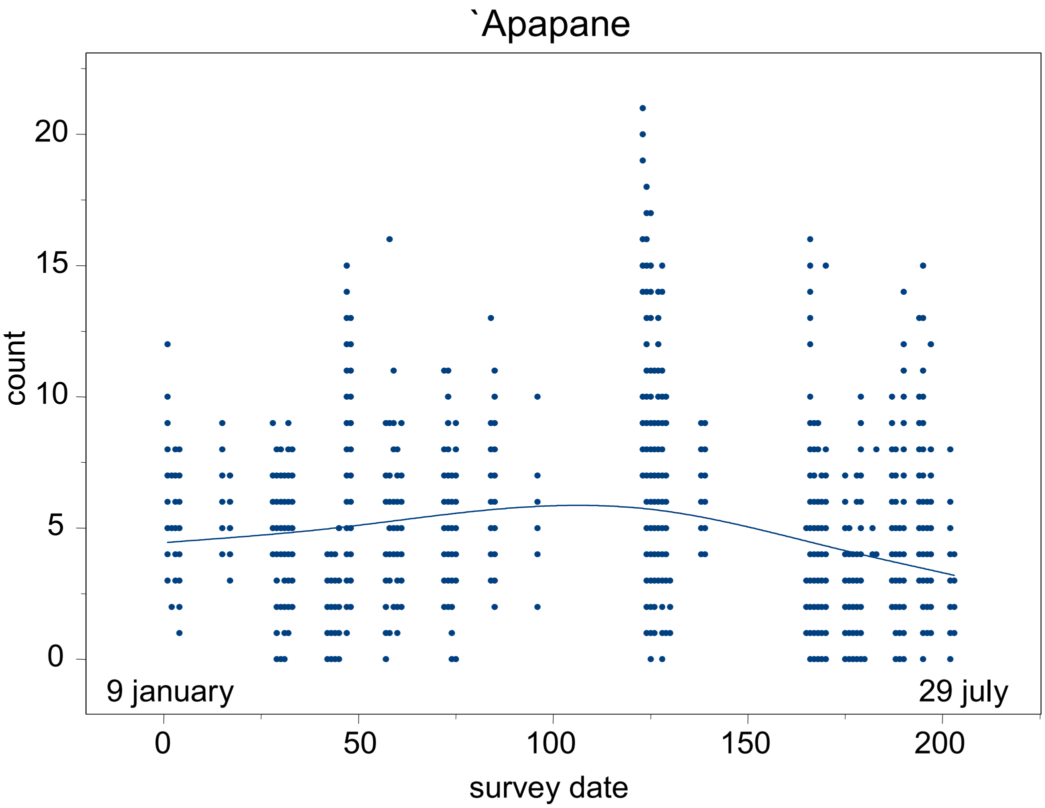


Figure 35. Seasonal effect as indicated by count and survey date (beginning on January 9 and ending on July 29). The smoothing spline fit to observed count data identified the peak seasonal effect used to predict counts.

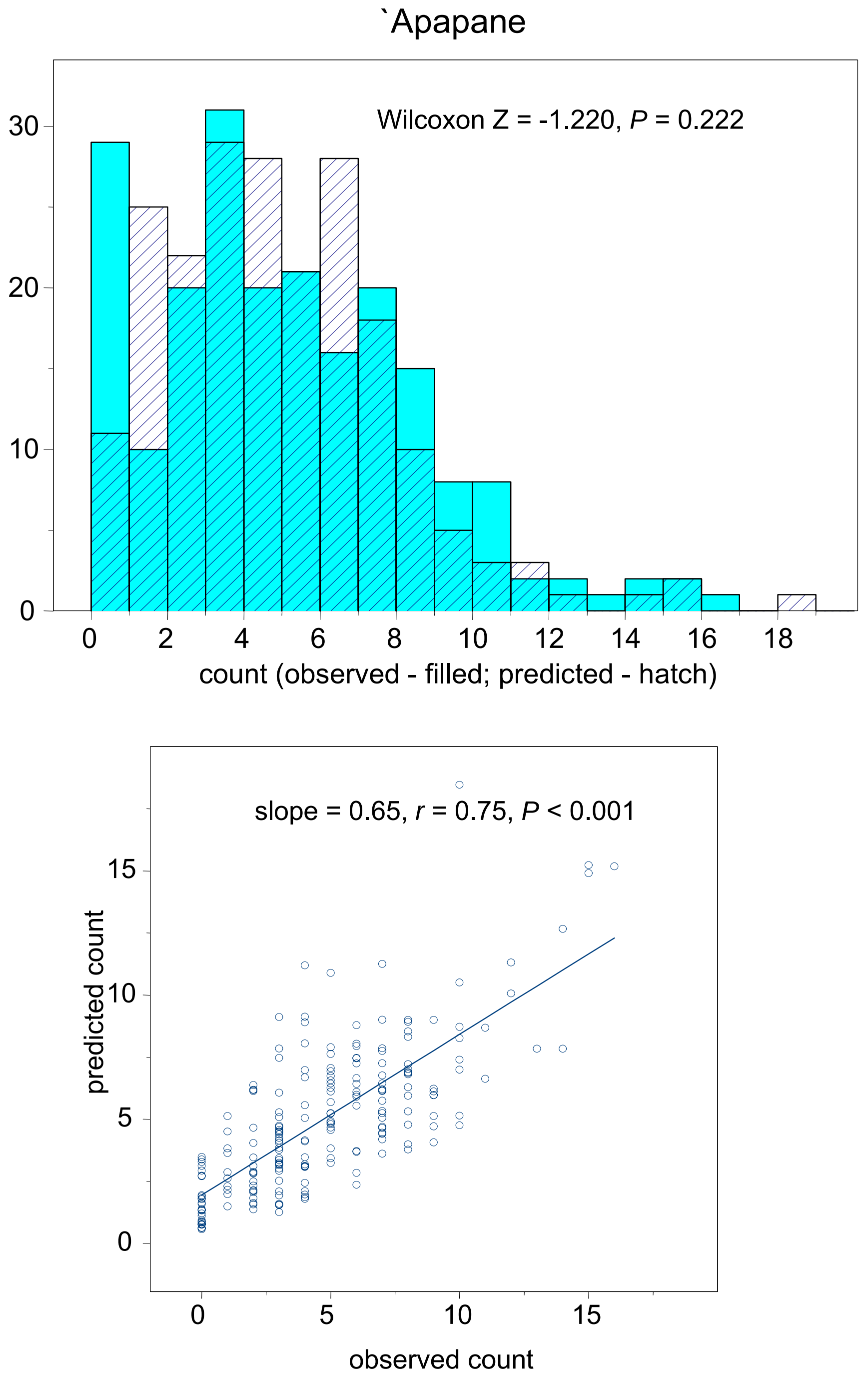


Figure 36. Accuracy assessment of predicted `Apapane counts. The fit between observed (filled) and predicted (hatch) counts were examined with the Wilcoxon rank sum test. A significant *P*-value indicates that the means are different (i.e., not well fit). The slope of the trendline illustrates the degree to which observed and predicted counts approximate a 1-to-1 correspondence. A slope near 1 indicates the predictions are unbiased (i.e., do not under-predict abundance). The correlation coefficient (r) and *P*-value represents the precision of the model. Predictive models with a correlation near 1 are highly precise.

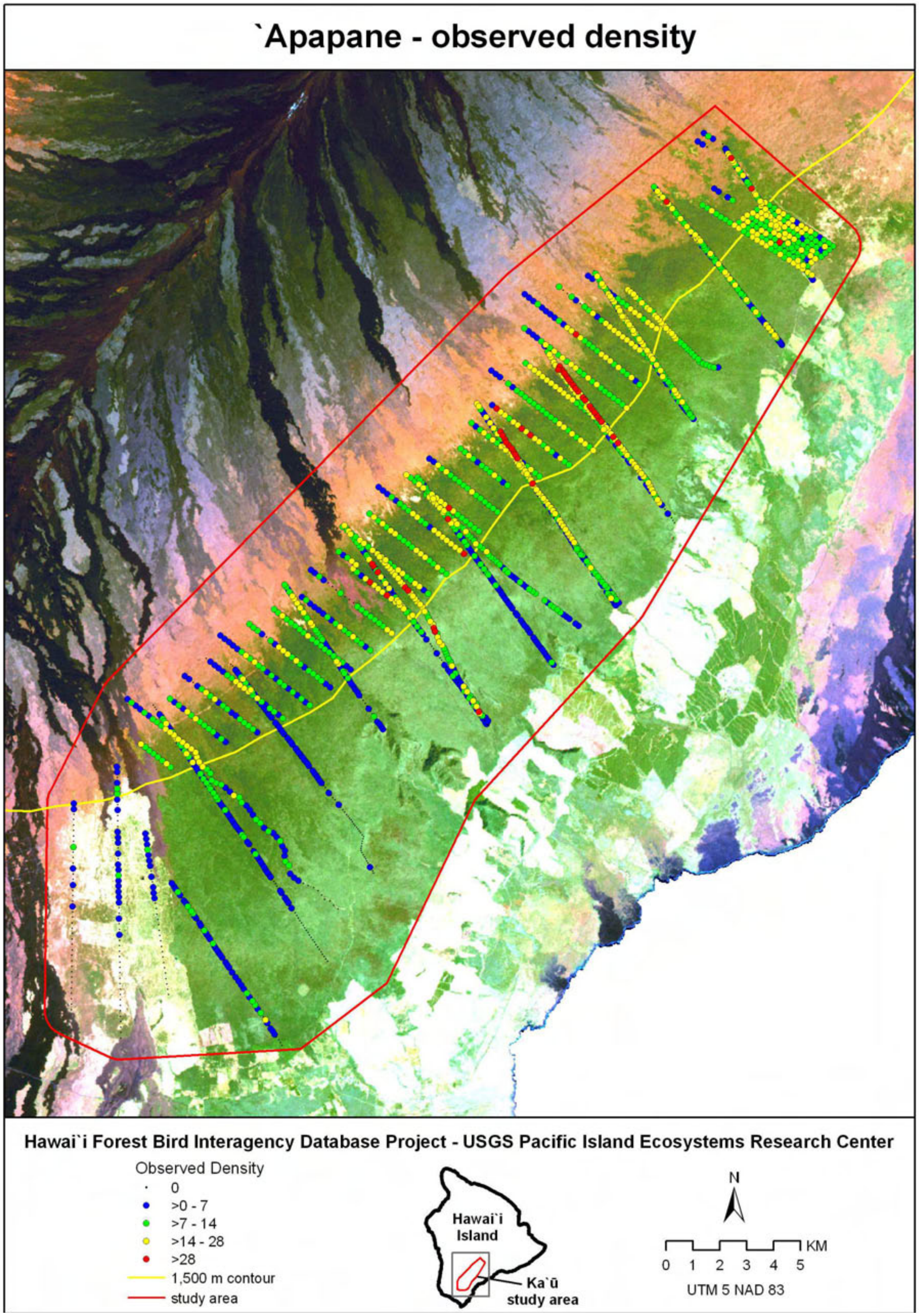


Figure 37. Observed distribution of `Apapane density in Ka`ū.

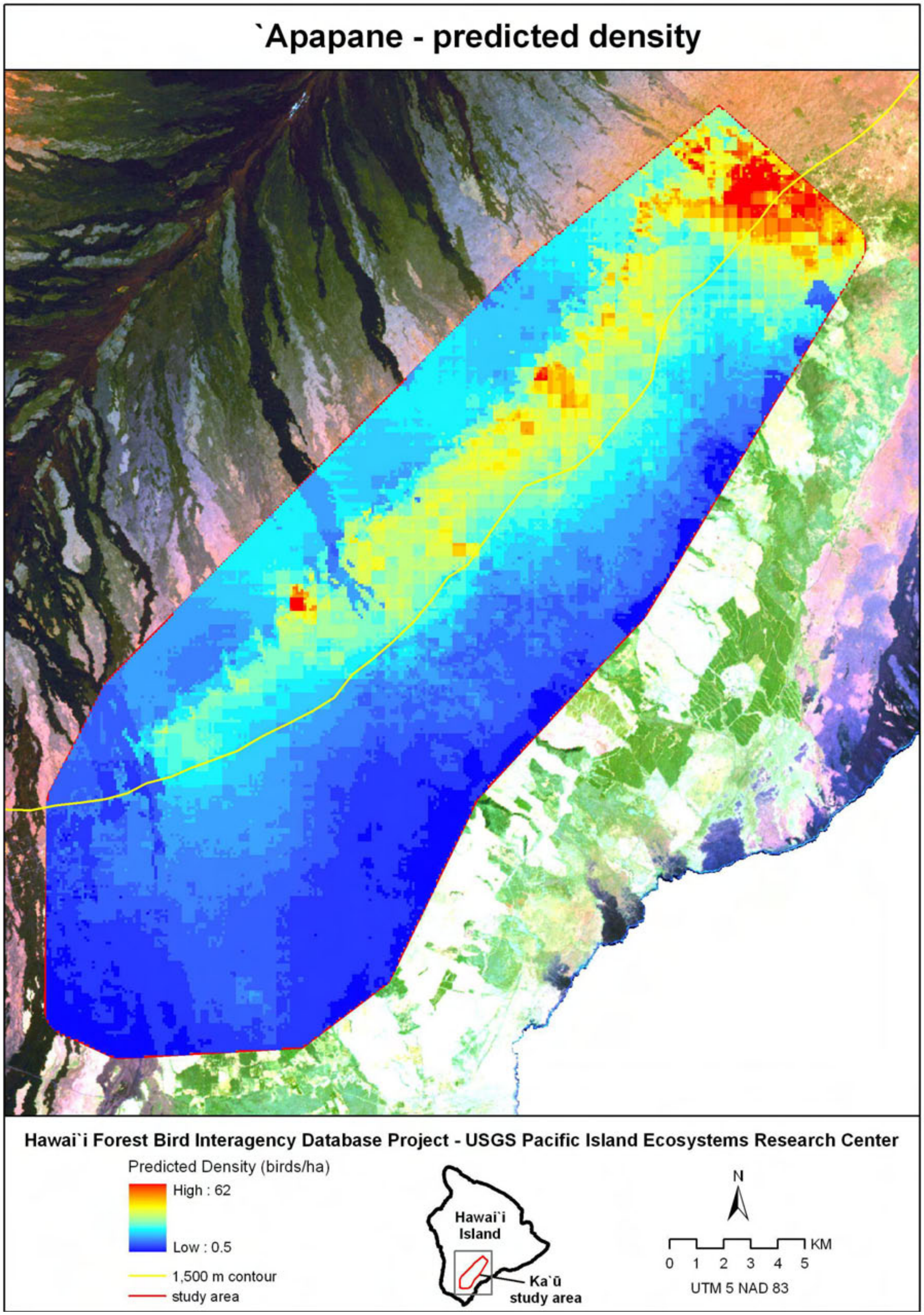


Figure 38. Predicted distribution of `Apapane density in Ka`ū.

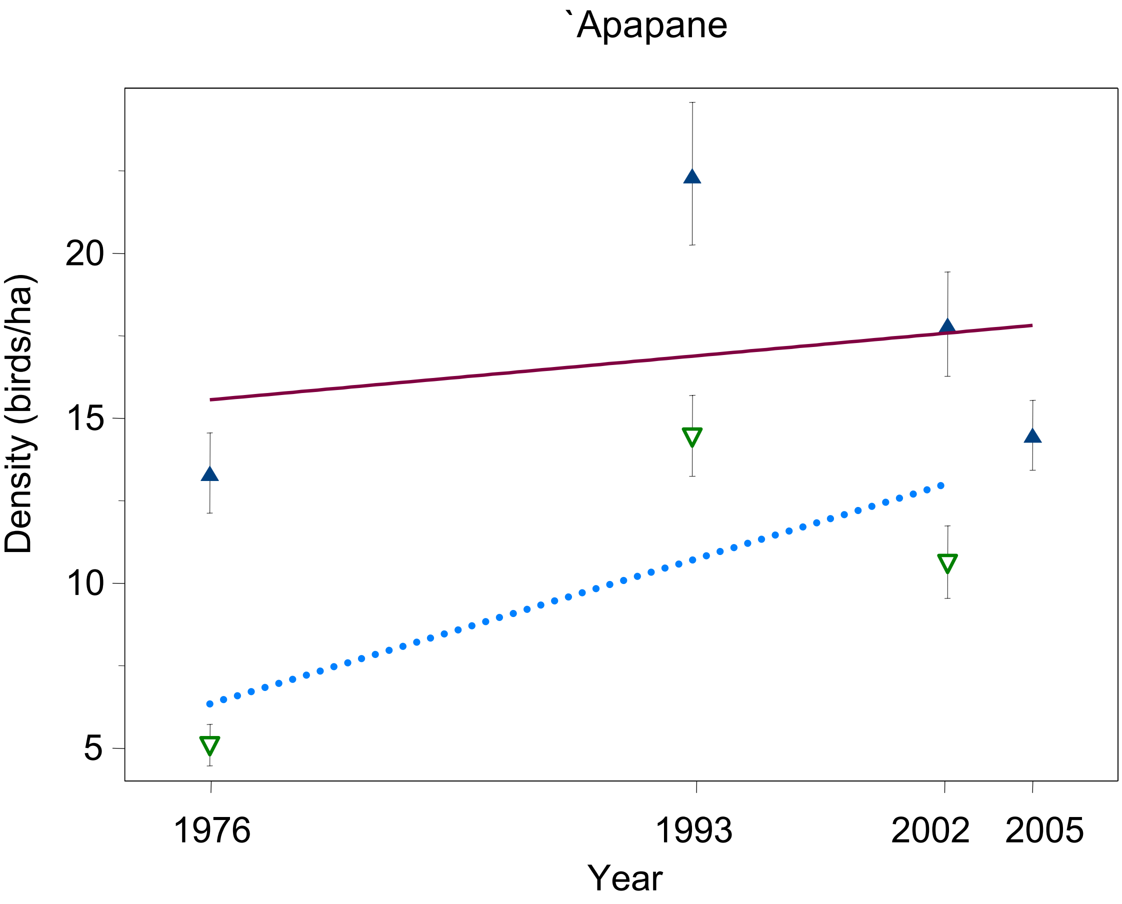


Figure 39. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. The equivalence test of the trend in densities observed >1,500 m in 1976 and 2005 was inconclusive (presumed slope = 0.040; 95% CI = -0.015 to 0.095; *P* = 0.156). The equivalence test revealed a significant increase in the densities observed <1,500 m in 1976 and 2002 (presumed slope = 0.213; 95% CI = 0.164 to 0.261; *P* < 0.001).

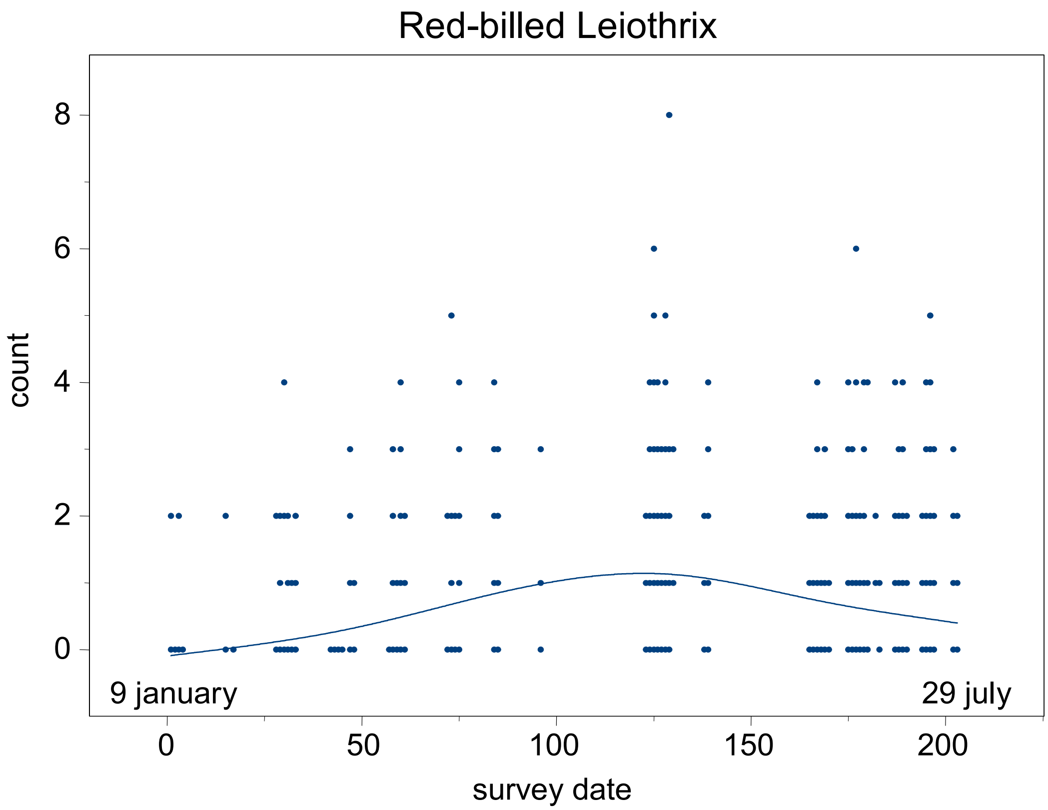


Figure 40. Seasonal effect as indicated by count and survey date (beginning on January 9 and ending on July 29). The smoothing spline fit to observed count data identified the peak seasonal effect used to predict counts.

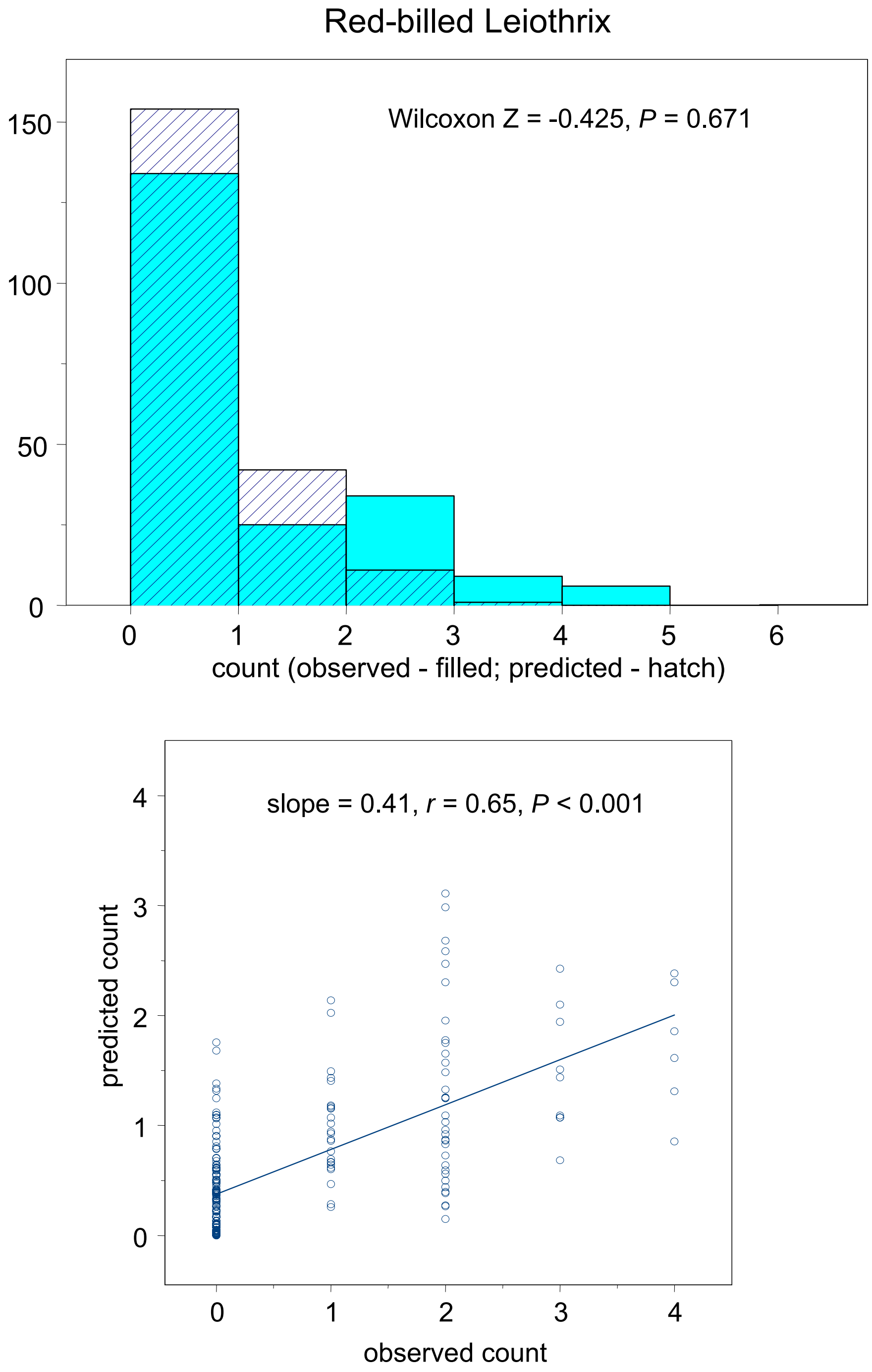


Figure 41. Accuracy assessment of predicted Red-billed Leiothrix counts. The fit between observed (filled) and predicted (hatch) counts were examined with the Wilcoxon rank sum test. A significant *P*-value indicates that the means are different (i.e., not well fit). The slope of the trendline illustrates the degree to which observed and predicted counts approximate a 1-to-1 correspondence. A slope near 1 indicates the predictions are unbiased (i.e., do not under-predict abundance). The correlation coefficient (r) and *P*-value represents the precision of the model. Predictive models with a correlation near 1 are highly precise.

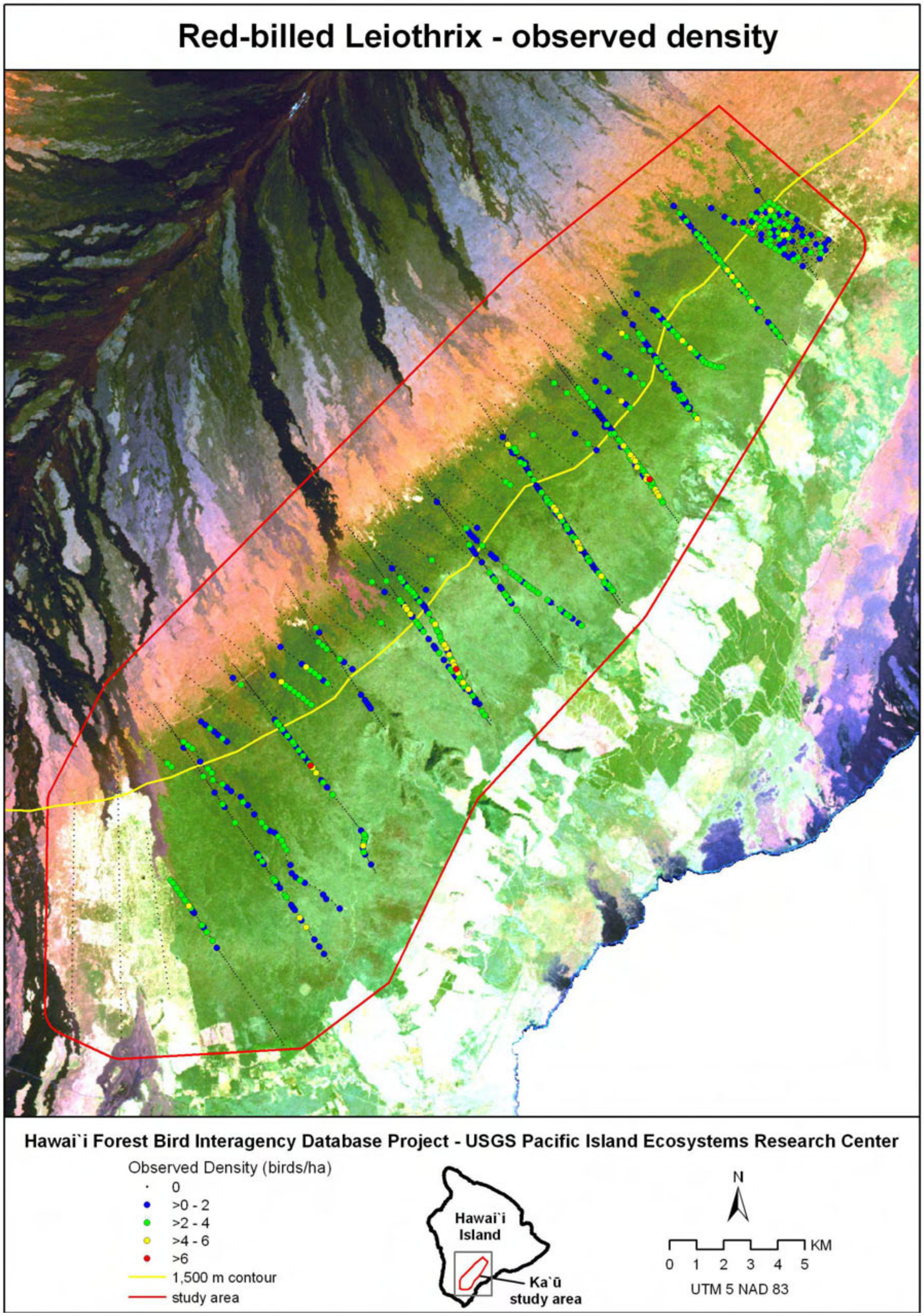


Figure 42. Observed distribution of Red-billed Leiothrix density in Ka`ū.

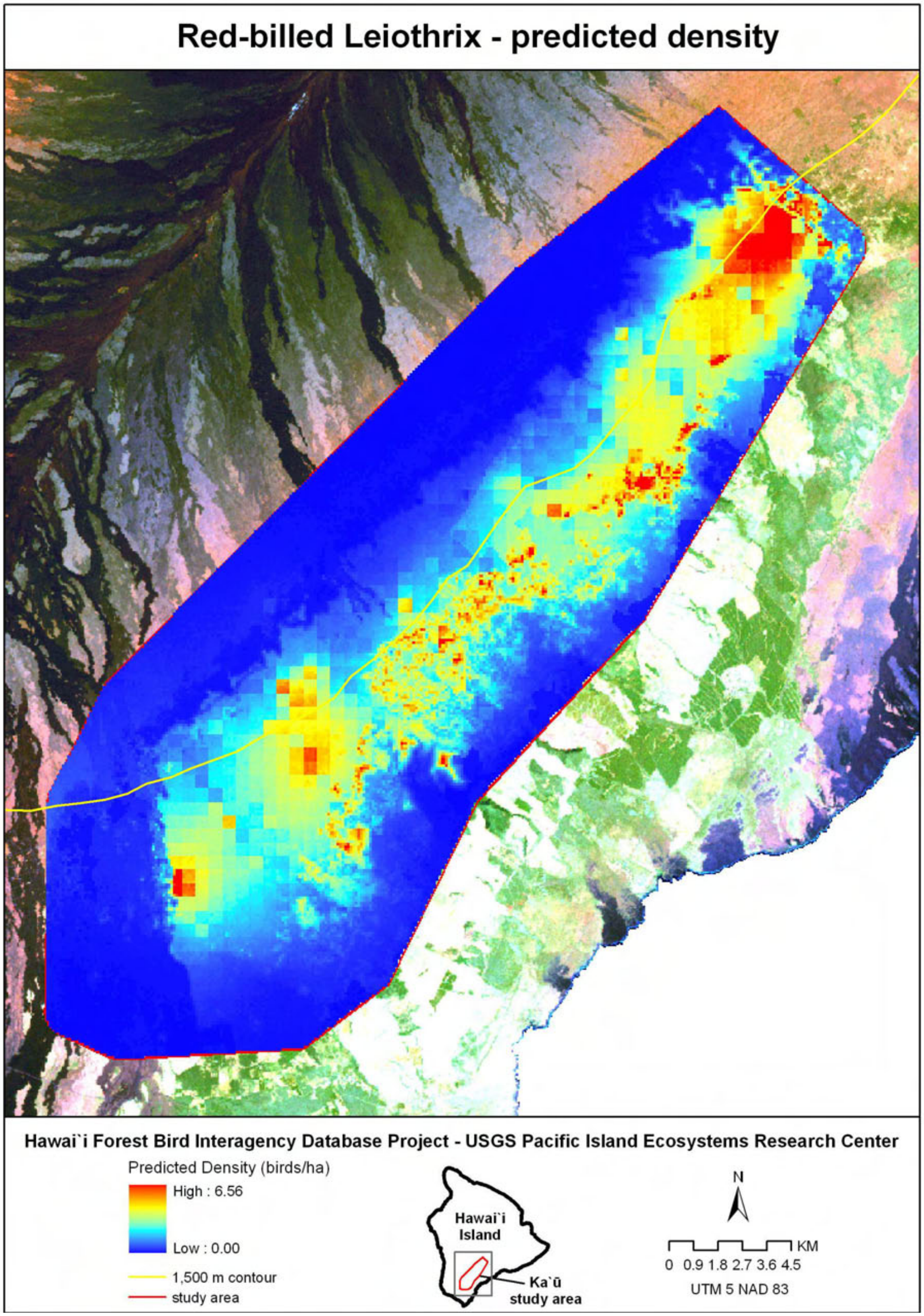


Figure 43. Predicted distribution of Red-billed Leiothrix density in Ka`ū.

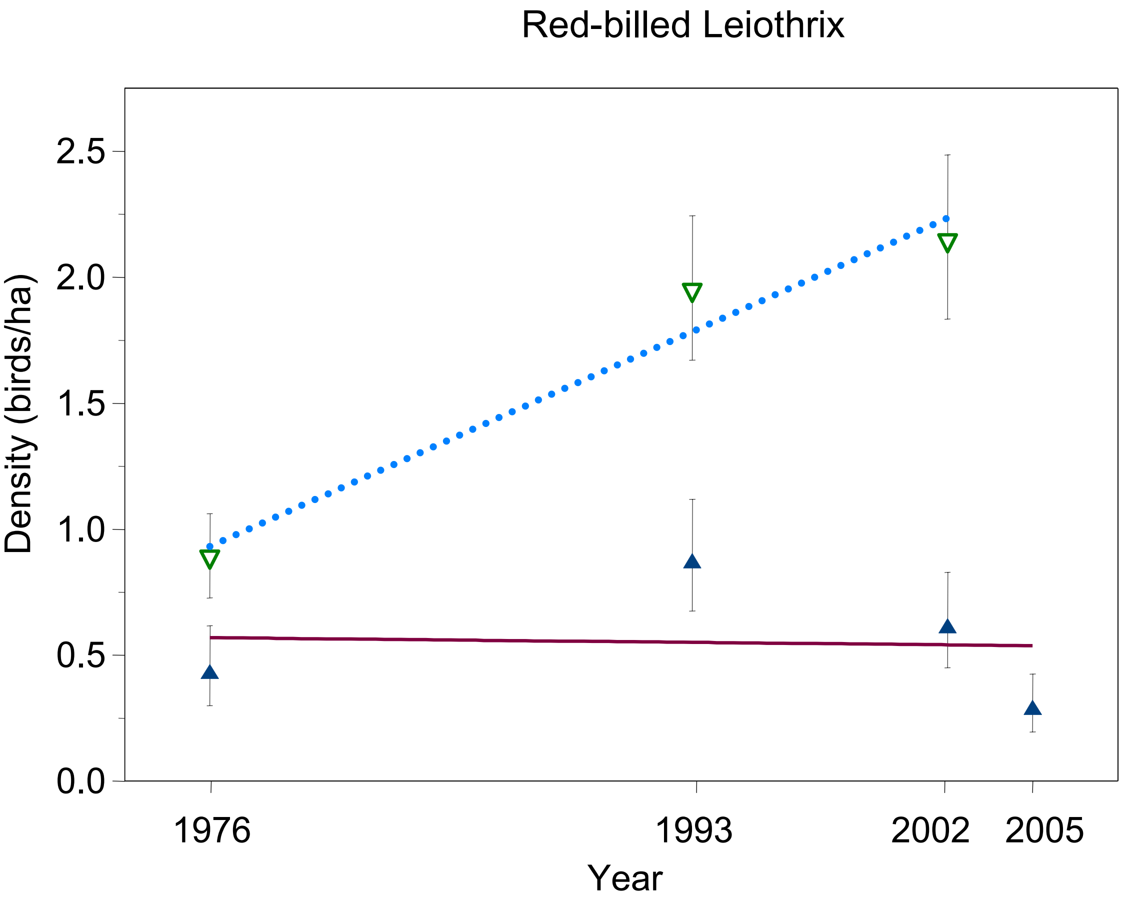


Figure 44. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. The equivalence test of the densities observed >1,500 m in 1976 and 2005 concluded that there were no trends evident (presumed slope = -0.005; 95% CI = -0.012 to 0.002; *P* = 0.147). The equivalence test revealed a significant increase in the densities observed <1,500 m in 1976 and 2002 (presumed slope = 0.048; 95% CI = 0.034 to 0.062; *P* < 0.001).

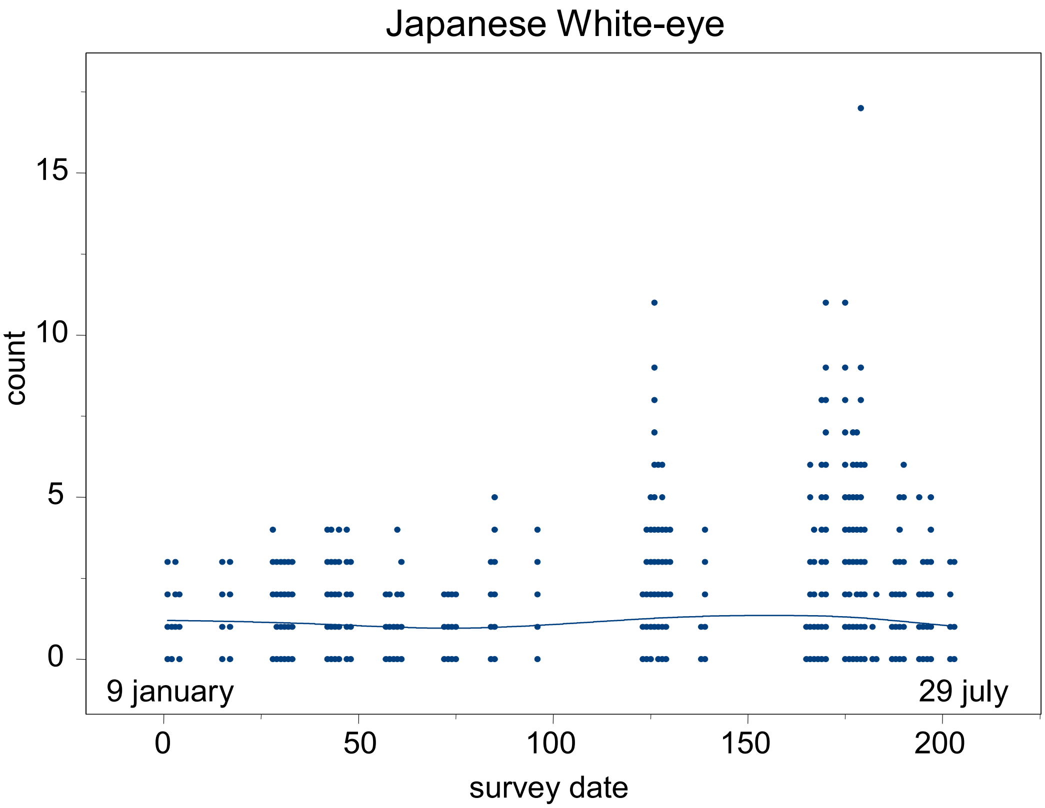


Figure 45. Seasonal effect as indicated by count and survey date (beginning on January 9 and ending on July 29). The smoothing spline fit to observed count data identified the peak seasonal effect used to predict counts.

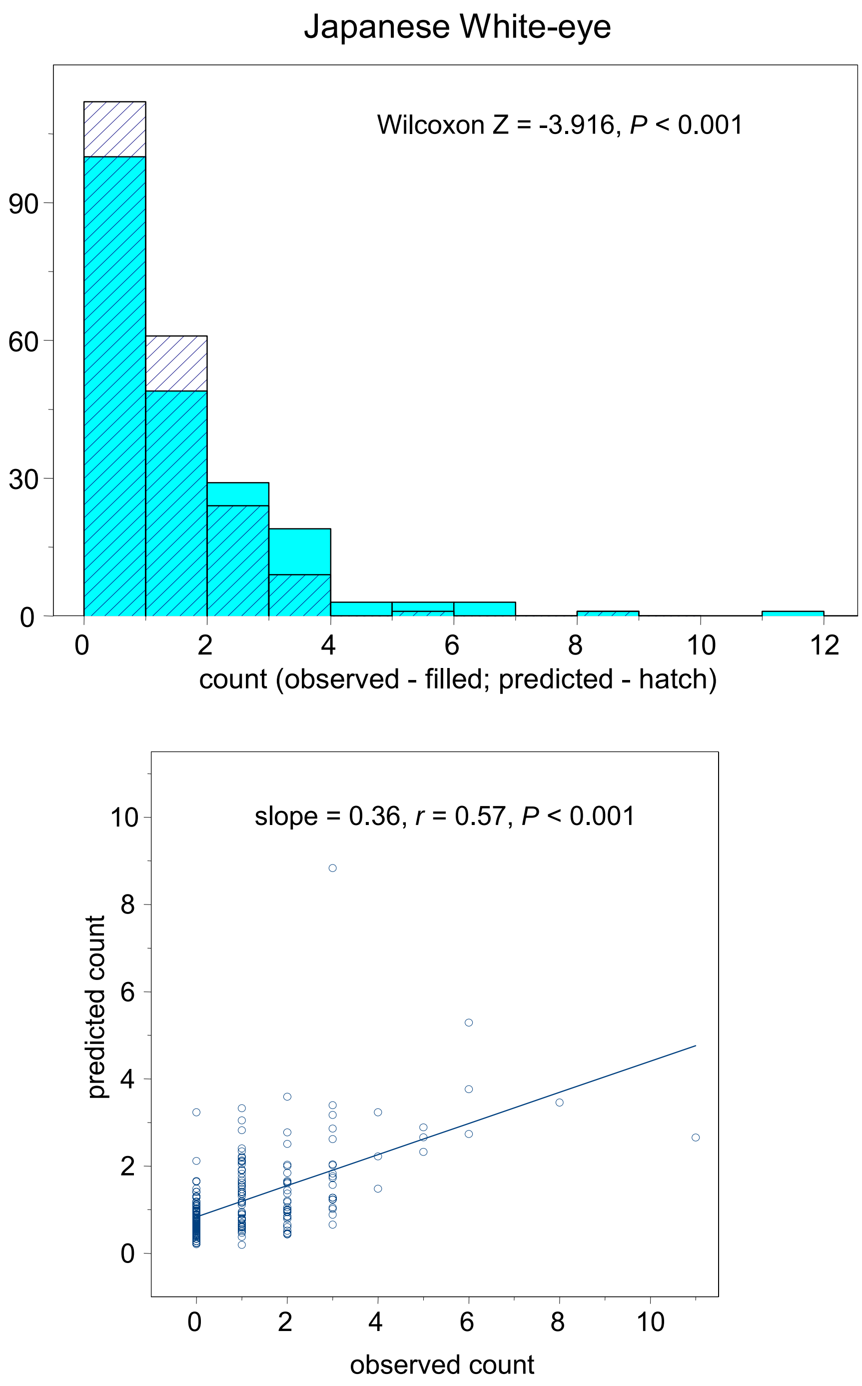


Figure 46. Accuracy assessment of predicted Japanese White-eye counts. The fit between observed (filled) and predicted (hatch) counts were examined with the Wilcoxon rank sum test. A significant *P*-value indicates that the means are different (i.e., not well fit). The slope of the trendline illustrates the degree to which observed and predicted counts approximate a 1-to-1 correspondence. A slope near 1 indicates the predictions are unbiased (i.e., do not under-predict abundance). The correlation coefficient (r) and *P*-value represents the precision of the model. Predictive models with a correlation near 1 are highly precise.

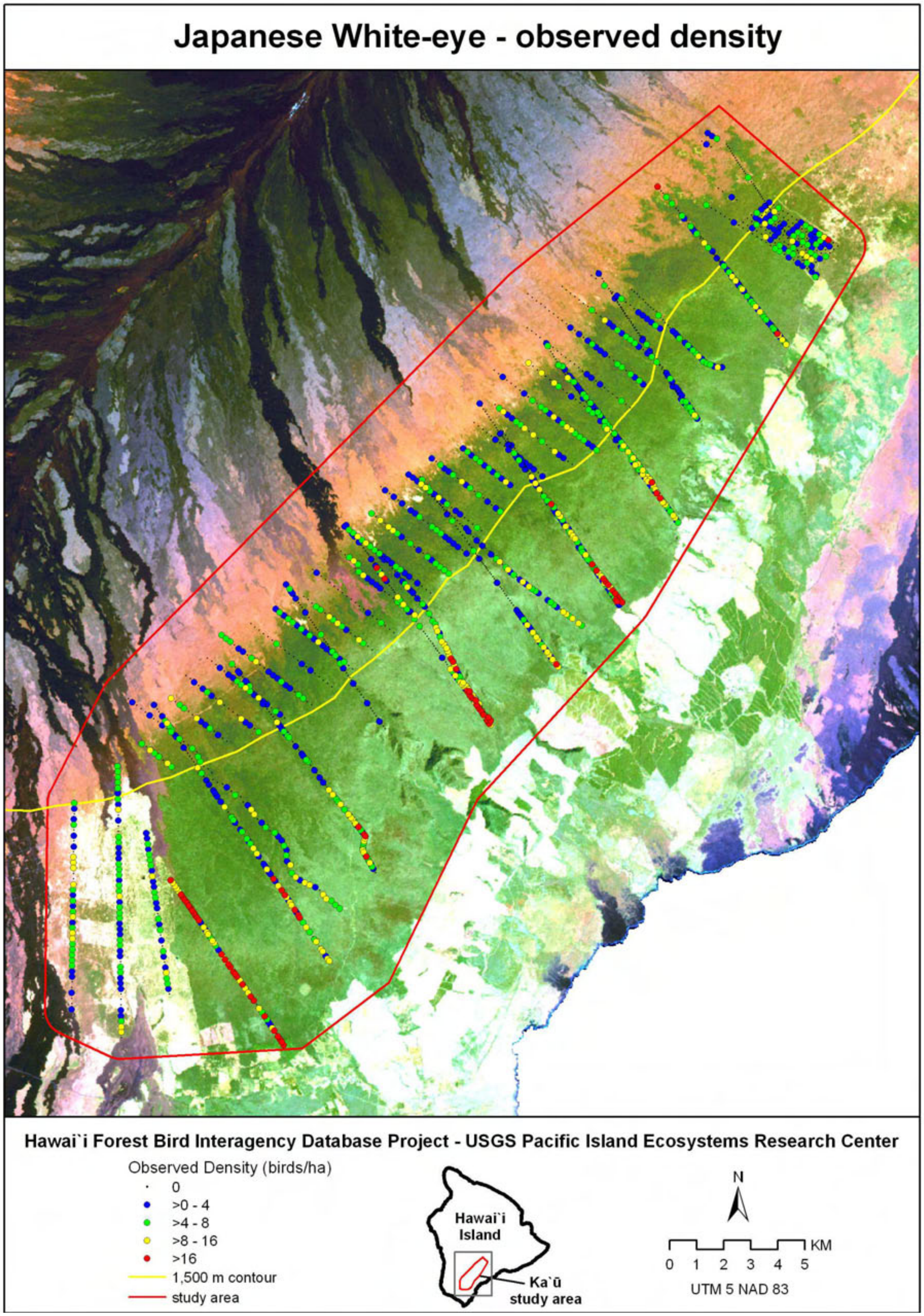


Figure 47. Observed distribution of Japanese White-eye density in Ka`ū.

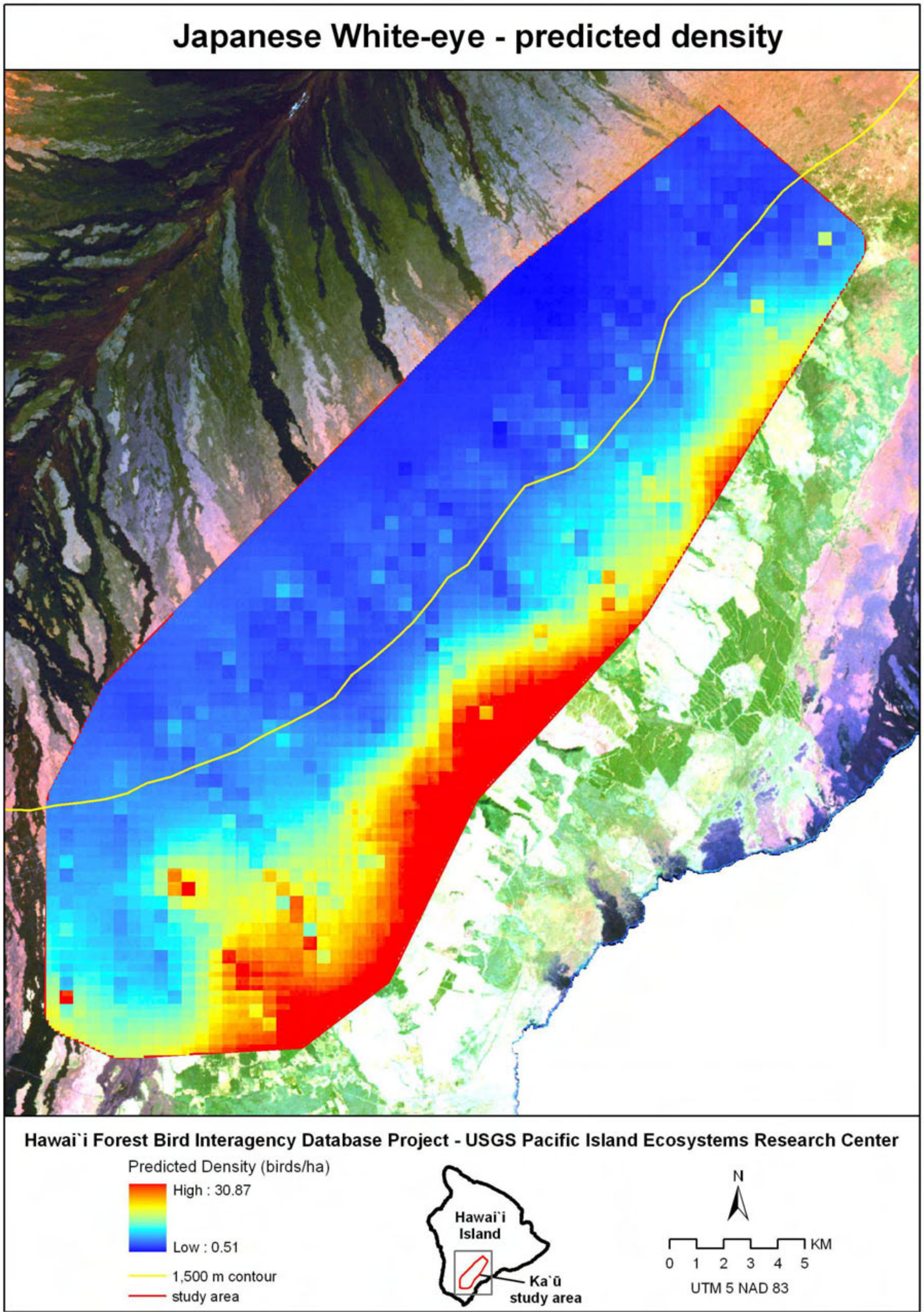


Figure 48. Predicted distribution of Japanese White-eye density in Ka`ū.

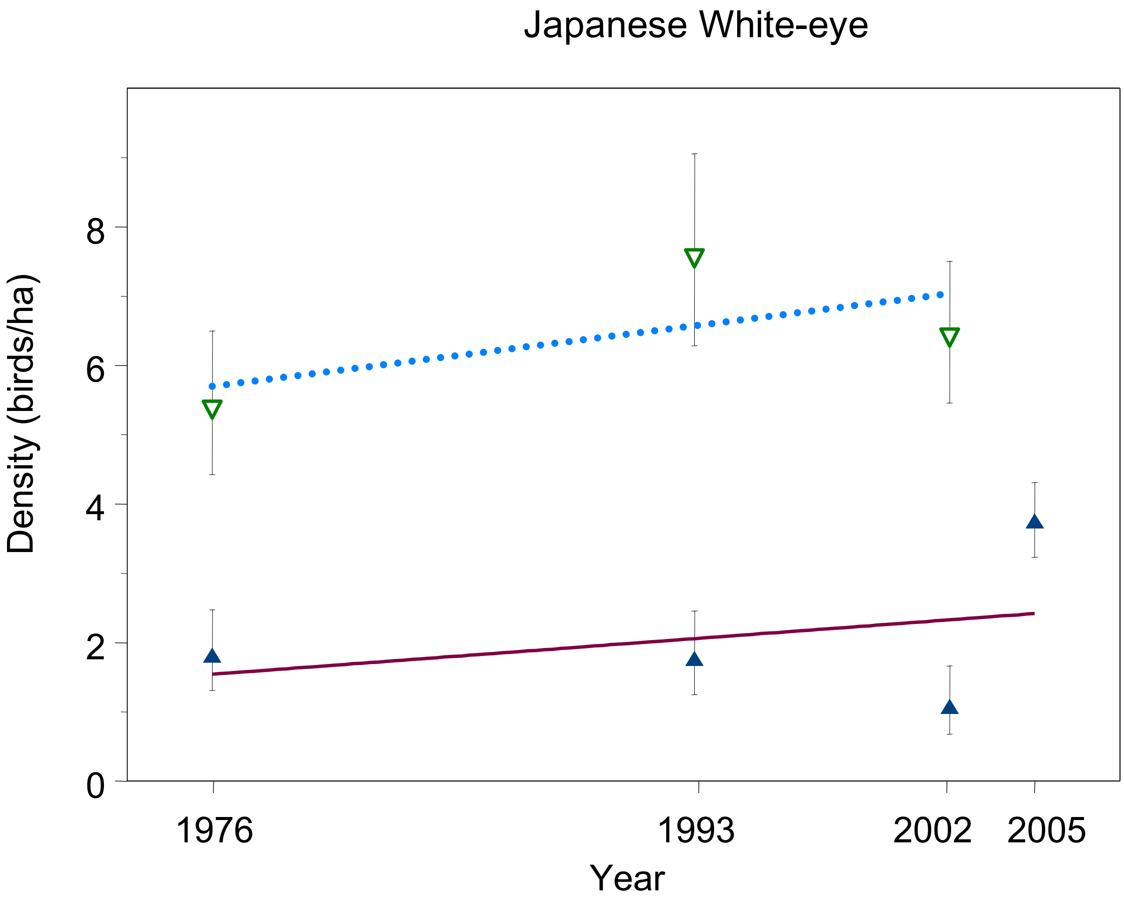


Figure 49. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. The equivalence test revealed a significant increase in the densities observed >1,500 m in 1976 and 2005 (presumed slope = 0.067; 95% CI = 0.040 to 0.094; $P < 0.001$). The equivalence test of the difference in densities observed <1,500 m in 1976 and 2002 was inconclusive (presumed slope = 0.040; 95% CI = -0.016 to 0.095; $P = 0.158$).

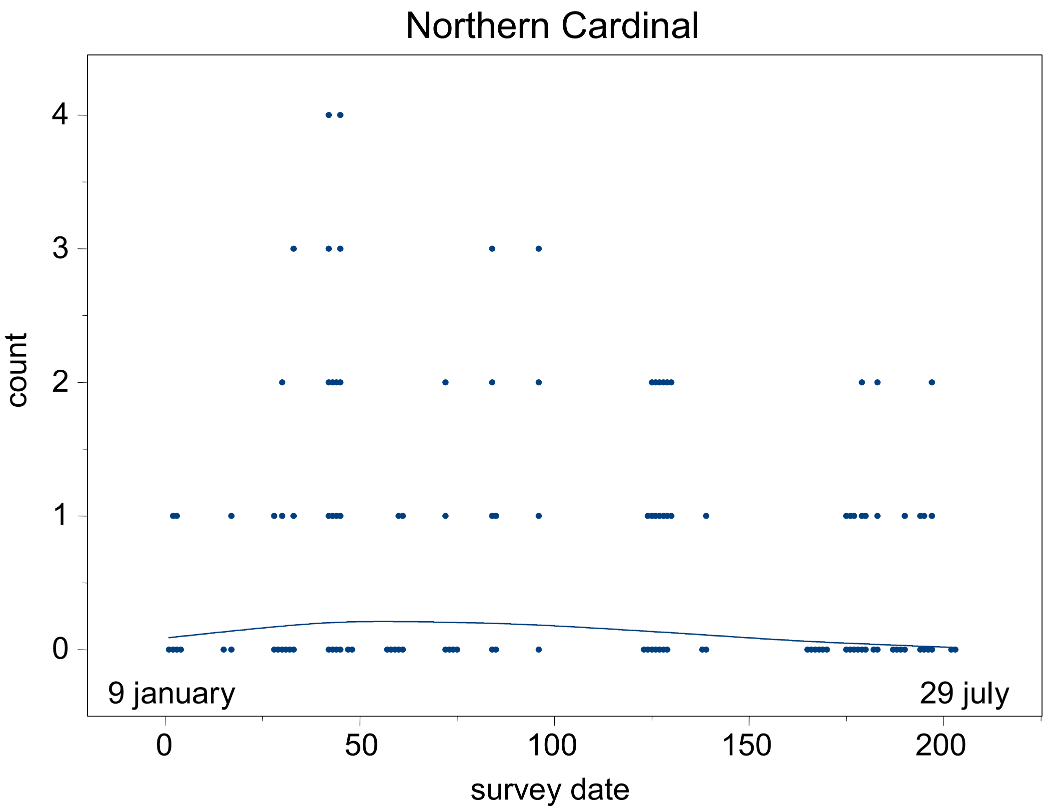


Figure 50. Seasonal effect as indicated by count, survey date (beginning on January 9 and ending on July 29) and smoothing spline.

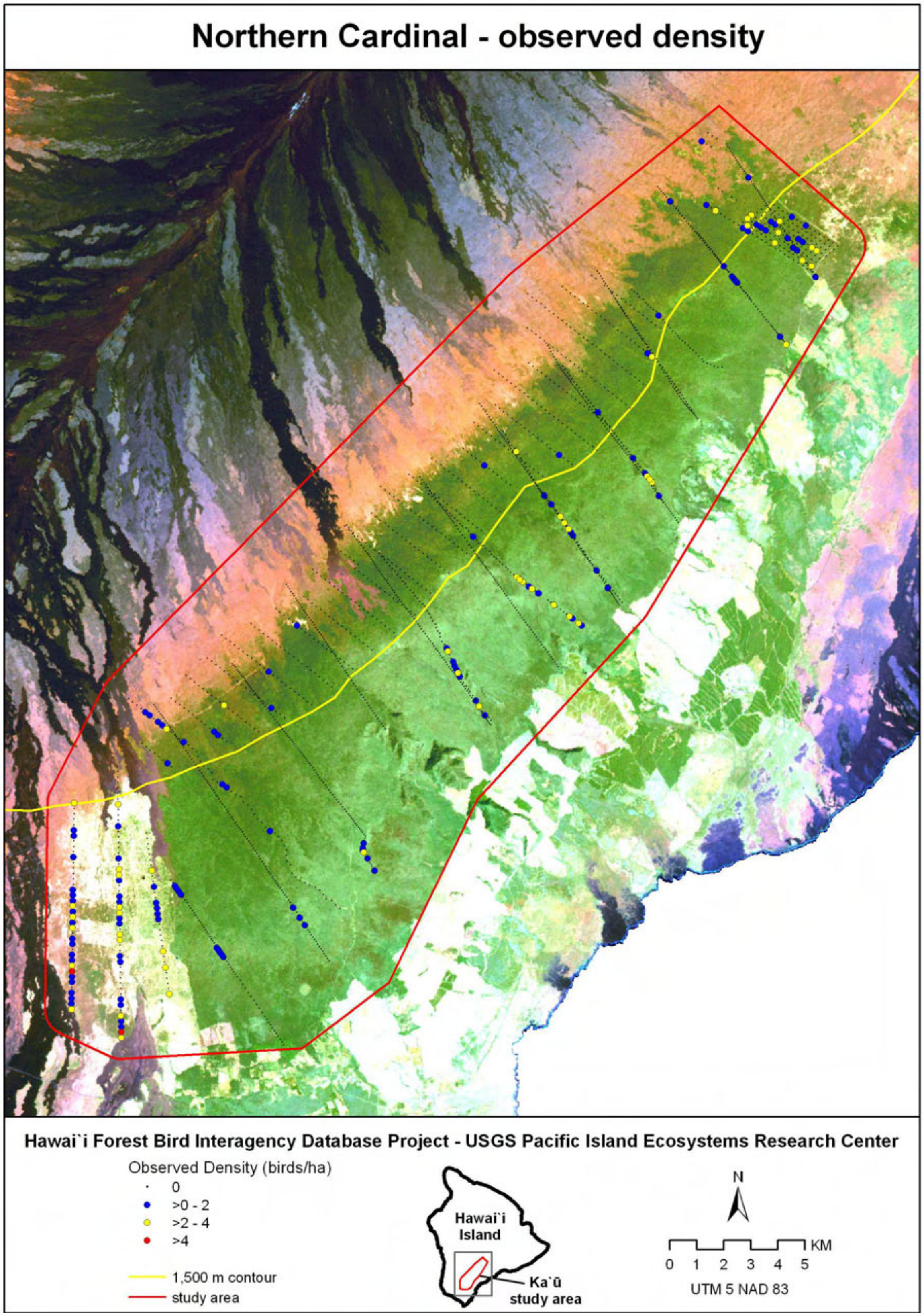


Figure 51. Observed distribution of Northern Cardinal density in Ka`ū.

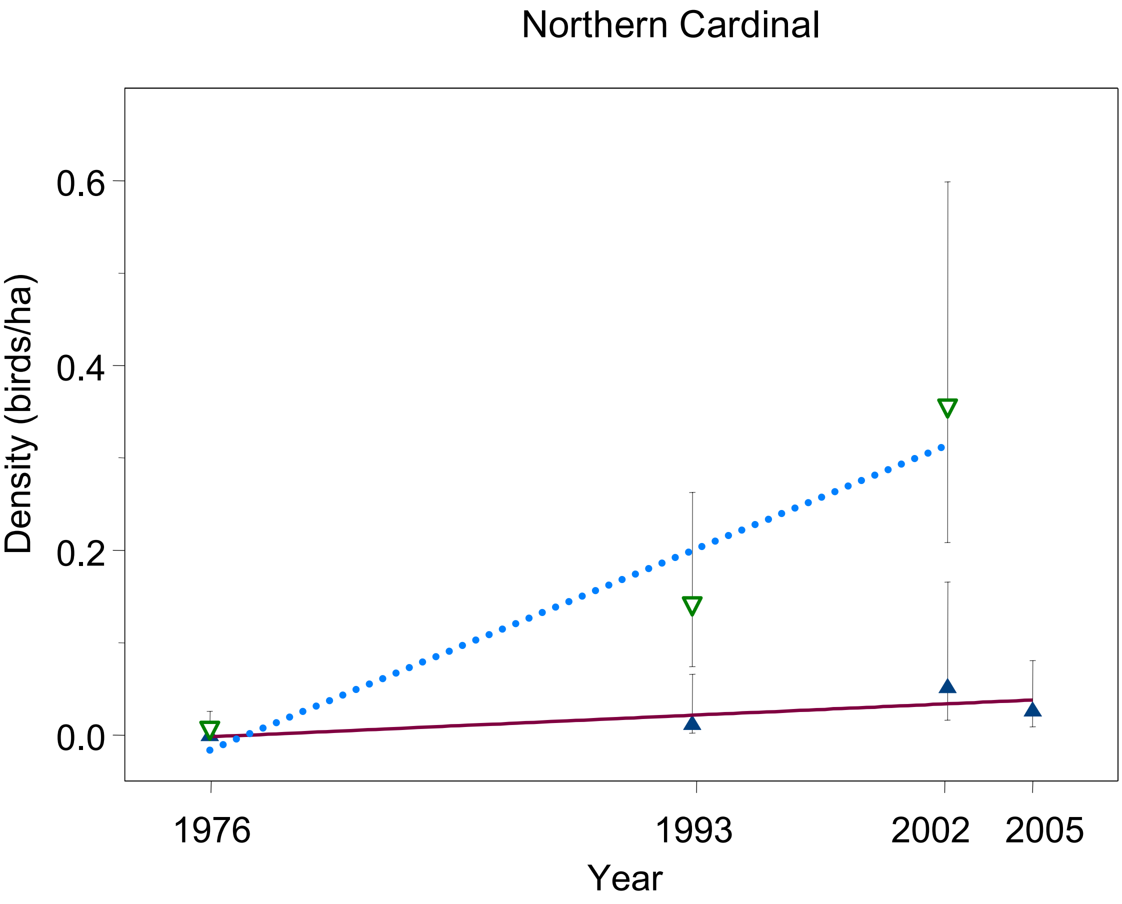


Figure 52. Bird density (mean birds/hectare + 95% CI) from 1976 (HFBS) to 2005 for areas above (closed triangles) and below 1,500 m (open triangles) in the central portion of the Ka`ū study area. Trendlines show the general linear relationship between untransformed density and survey year, and are included for illustrative purposes only. Equivalence tests of densities observed above and below 1,500 m concluded that there were no trends evident (presumed slope above 1,500 m = 0.001; 95% CI = 0.000 to 0.002; $P = 0.097$; presumed slope below 1,500 m = 0.013; 95% CI = 0.006 to 0.021; $P < 0.001$).

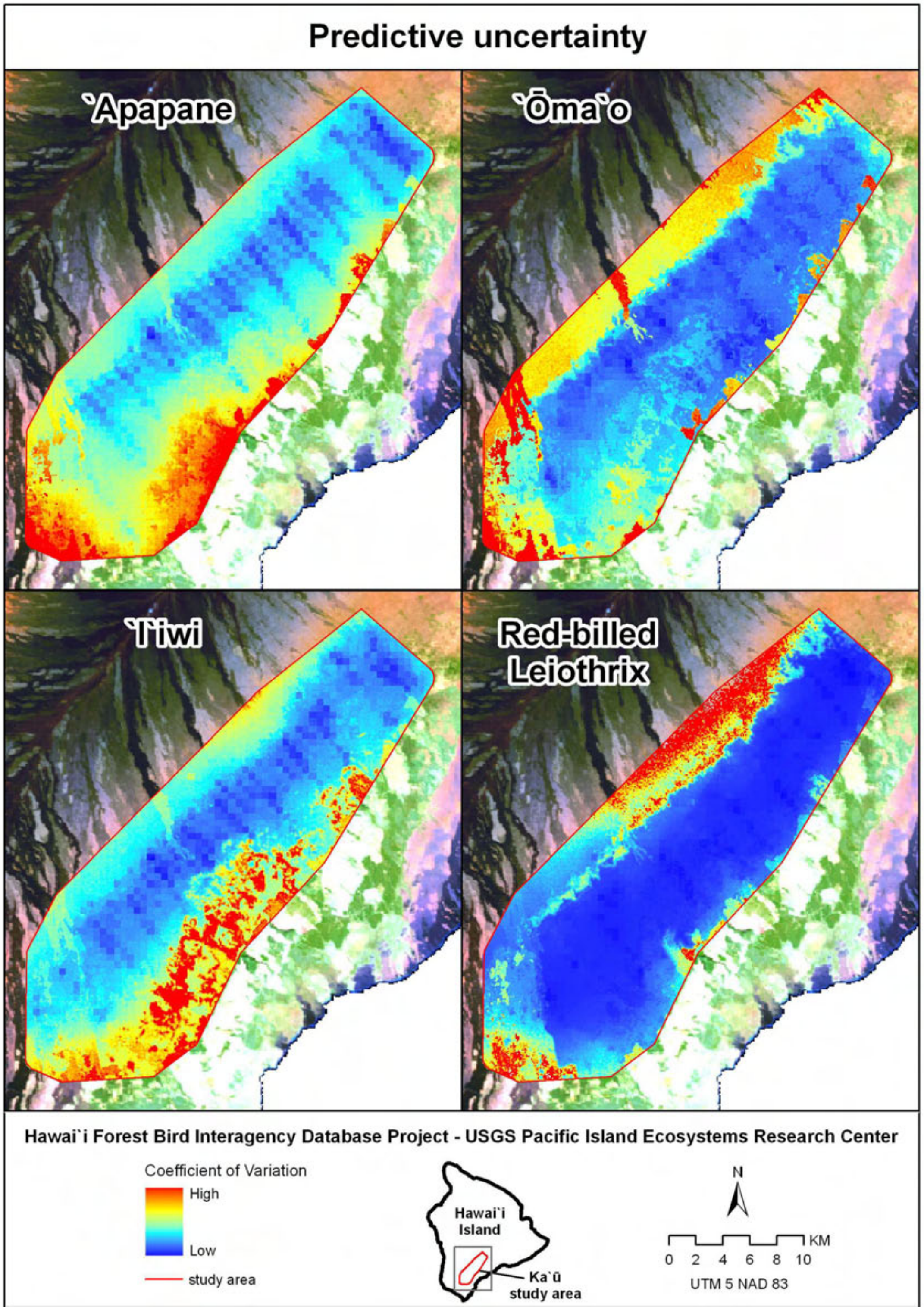


Figure 53. Illustrative examples of the relative uncertainty of densities predicted by species-habitat models. Uncertainty as measured by the coefficient of variation of the predictions is greatest in under-sampled habitats and where observed density is low and variable.

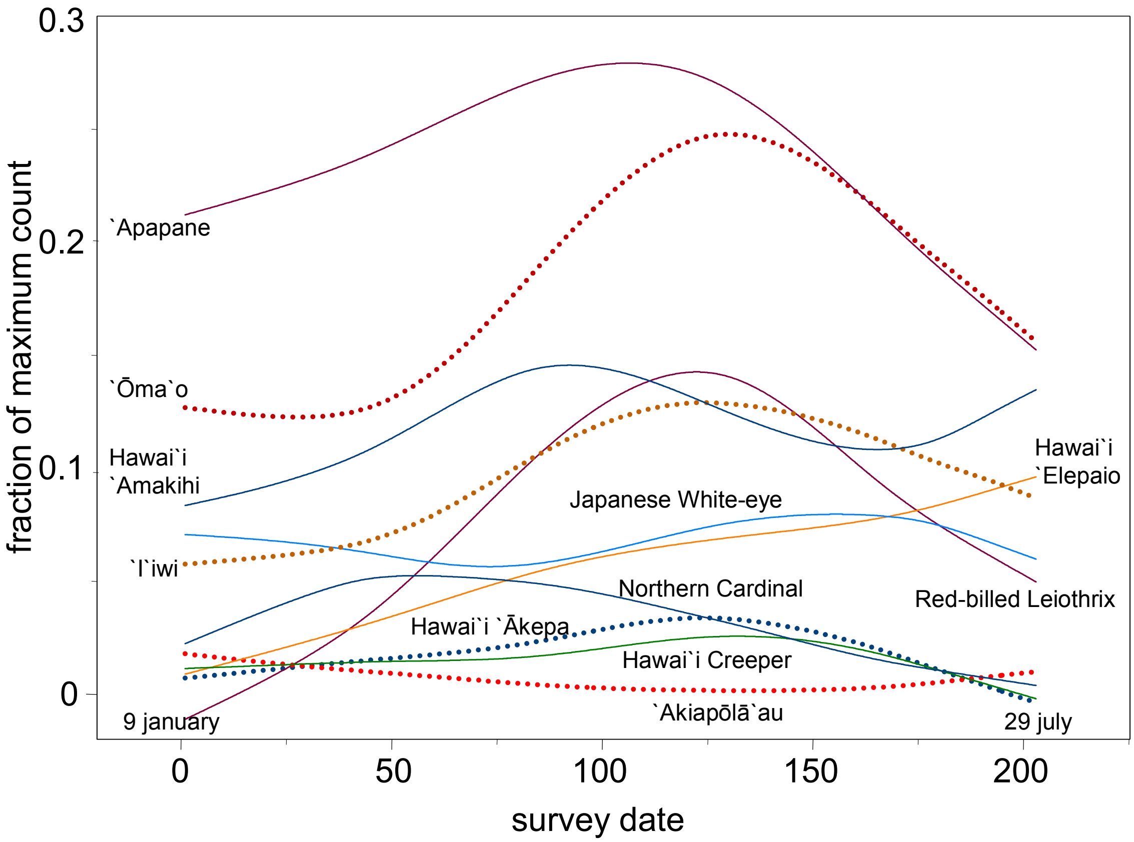


Figure 54. Seasonal effects as indicated by the peak count by survey date (beginning on January 9 and ending on July 29). The smoothing splines of count data shown previously for each species were standardized and superimposed to determine "optimal" periods for multiple species surveys. Data were standardized for between-species comparison by expressing count as a fraction of the maximum count observed.

Table 1. Descriptive statistics of habitat variables at survey stations in the Ka`ū study area. Habitat variable abbreviations are interpreted below. Methods used to derive habitat values are described in the section "Measures of Bird Habitat Attributes".

	Habitat Variable															
	koa	mf	grass	shrub	tf	div	closed	open	sparse	low	mid	high	precip	temp	elev	slope
Mean	0.31	0.04	0.21	0.88	0.53	3.04	0.54	0.30	0.14	0.08	0.13	0.77	1,704	15.0	1,542	7
Standard Deviation	0.46	0.19	0.41	0.33	0.50	1.50	0.44	0.36	0.28	0.23	0.26	0.36	323	1.7	311	3
Minimum	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	1,232	11.0	721	2
Maximum	1.00	1.00	1.00	1.00	1.00	11.00	1.00	1.00	1.00	1.00	1.00	1.00	2,843	19.7	2,257	24

Variable abbreviations
koa - occurrence of koa as a canopy dominant or co-dominant.
mf - occurrence of matted-fern as a sub-canopy component
grass - occurrence of grassland as major vegetation type
shrub - occurrence of native shrubland as major vegetation type
tf - occurrence of tree-fern as a sub-canopy component
div – diversity of vegetation types
closed – proportion of area in closed canopy
open - proportion of area in closed canopy
sparse - proportion of area in sparse or no canopy
low - proportion of area with low stature vegetation
mid - proportion of area with mid-stature vegetation
high - proportion of area with high stature vegetation
precip – mean annual precipitation (mm)
temp – mean annual temperature (degrees Celsius)
elev – average elevation (m)
slope – average slope (degrees)

Table 2. Descriptive statistics of the observed and predicted counts (panel a) and densities (panel b) for the set of species modeled in Distance. Predictive models were not developed for rare species (indicated with a dash). The sum of all detections for each species is based on the full dataset of survey observations. For comparative purposes, all other statistics are based on the validation (i.e., reserved) dataset.

a) bird counts

Species	Data	Sum	Minimum	1st Quartile	Mean	Median	3rd Quartile	Maximum	Standard Deviation
Hawai`i `Elepaio	observed	398	0	0	0.163	0	0	3	0.463
	predicted		0.013	0.065	0.212	0.127	0.232	2.132	0.296
`Ōma`o	observed	3,893	0	0	1.707	1	3	9	1.693
	predicted		0.072	0.899	1.838	1.838	2.713	5.149	1.122
Hawai`i `Amakihi	observed	2,961	0	0	1.374	1	2	10	1.691
	predicted		0.093	0.660	1.620	1.454	2.218	6.420	1.141
`Akiapōlā`au	observed	38	0	0	0.010	0	0	1	0.098
	predicted		-	-	-	-	-	-	-
Hawai`i Creeper	observed	94	0	0	0.043	0	0	3	0.283
	predicted		-	-	-	-	-	-	-
Hawai`i `Ākepa	observed	256	0	0	0.149	0	0	6	0.607
	predicted		-	-	-	-	-	-	-
`I`iwi	observed	1,655	0	0	0.859	0	2	8	1.377
	predicted		0.028	0.256	0.856	0.587	1.293	6.227	0.829
`Apapane	observed	9,895	0	2	4.659	4	7	16	3.448
	predicted		0.579	2.836	4.964	4.659	6.661	18.47	2.991
Red-billed Leiothrix	observed	1,347	0	0	0.692	0	1	4	1.073
	predicted		0	0.096	0.657	0.457	1.021	3.11	0.671
Japanese White-eye	observed	2,457	0	0	1.039	1	2	8	1.396
	predicted		0.194	0.609	1.183	0.933	1.522	5.29	0.823
Northern Cardinal	observed	235	0	0	0.091	0	0	3	0.335
	predicted		-	-	-	-	-	-	-

Table 2 (continued).

b) bird densities

Species	Data	Minimum	1st Quartile	Mean	Median	3rd Quartile	Maximum	Standard Deviation
Hawai`i `Elepaio	observed	0	0	0.371	0	0	6.807	1.051
	predicted	0.029	0.147	0.481	0.288	0.525	4.837	0.671
`Ōma`o	observed	0	0	1.858	1.088	3.265	9.796	1.843
	predicted	0.078	0.978	2.001	2.000	2.953	5.605	1.221
Hawai`i `Amakihi	observed	0	0	3.279	2.387	4.774	23.868	4.036
	predicted	0.222	1.576	3.866	3.469	5.293	15.323	2.724
`Akiapōlā`au	observed	0	0	0.010	0	0	1.072	0.105
	predicted	-	-	-	-	-	-	-
Hawai`i Creeper	observed	0	0	0.322	0	0	12.970	1.313
	predicted	-	-	-	-	-	-	-
Hawai`i `Ākepa	observed	0	0	0.188	0	0	13.043	1.232
	predicted	-	-	-	-	-	-	-
`I`iwi	observed	0	0	2.053	0	4.182	19.119	3.292
	predicted	0.066	0.611	2.047	1.403	3.090	14.882	1.982
`Apapane	observed	0	4.314	10.048	8.628	15.098	34.510	7.437
	predicted	1.250	6.117	10.706	10.048	14.367	39.838	6.451
Red-billed Leiothrix	observed	0	0	0.775	0	1.120	4.479	1.201
	predicted	0	0.107	0.735	0.512	1.144	3.482	0.752
Japanese White-eye	observed	0	0	3.646	3.510	7.020	28.079	4.901
	predicted	0.681	2.136	4.151	3.275	5.342	18.567	2.889
Northern Cardinal	observed	0	0	0.105	0	0	3.441	0.384
	predicted	-	-	-	-	-	-	-

Table 3. Assessment of the predictive performance of the hierarchical species-habitat models. “Proportion of deviance” refers to the amount of variability in bird counts accounted for by habitat variables and season. The correspondence between the means of observed and predicted count distributions is measured with the Z statistic and associated *P*-value of the Wilcoxon rank sum test. A significant *P*-value indicates that the means of the Poisson distributed data are different (i.e., not well fit). “Slope” refers to the regression coefficient that measures the degree to which the observed and predicted counts approximate a 1-to-1 correspondence. A slope near 1 indicates the predictions are unbiased (i.e., do not under-predict abundance). The correlation coefficient and associated *P*-value represents the relative precision of the model. Predictive models with a correlation near 1 are highly precise.

Species	Proportion Deviance	Wilcoxon Z	*P*-value	Slope	Correlation	*P*-value
Hawai\`i \`Elepaio	18%	2.095	0.036	0.25	0.48	<0.001
\`Ōma\`o	24%	-1.743	0.081	0.46	0.70	<0.001
Hawai\`i \`Amakihi	27%	-3.363	0.001	0.40	0.59	<0.001
\`I\`iwi	27%	-1.799	0.072	0.44	0.73	<0.001
\`Apapane	42%	-1.220	0.222	0.60	0.78	<0.001
Red-billed Leiothrix	33%	-0.425	0.671	0.41	0.68	<0.001
Japanese White-eye	22%	-3.916	<0.001	0.38	0.64	<0.001

Table 4. Estimated annual bird density in the Ka`ū study area. Summary for each year includes the mean density (#/ha), standard error (SE), annual sampling effort (# Stations), and number of individuals detected (# Birds). Species are ordered taxonomically within native and alien groups.

Species	Year	Density	SE	# Stations	# Birds
Hawai`i `Elepaio					
>1,500m	1976	0.572	0.118	162	39
	1993	0.379	0.116	94	15
	2002	0.294	0.099	88	11
	2005	0.332	0.076	213	30
<1,500m	1976	0.682	0.102	234	67
	1993	0.760	0.144	138	44
	2002	0.695	0.131	126	37
`Ōma`o					
>1,500m	1976	2.134	0.146	162	314
	1993	3.215	0.196	94	276
	2002	4.117	0.239	88	331
	2005	1.891	0.104	213	367
<1,500m	1976	3.147	0.146	234	673
	1993	2.964	0.161	138	373
	2002	2.391	0.170	126	275
Hawai`i `Amakihi					
>1,500m	1976	4.244	0.370	162	291
	1993	5.106	0.368	94	203
	2002	5.774	0.444	88	215
	2005	3.116	0.225	213	280
<1,500m	1976	2.942	0.238	234	291
	1993	1.783	0.230	138	104
	2002	2.599	0.336	126	138
`Akiapōlā`au					
>1,500m	1976	0.000	0.000	162	0
	1993	0.012	0.013	94	1
	2002	0.012	0.013	88	1
	2005	0.103	0.042	213	20
<1,500m	1976	0.043	0.026	234	9
	1993	0.008	0.009	138	1
	2002	0.009	0.010	126	1
Hawai`i Creeper					
>1,500m	1976	0.376	0.143	162	14
	1993	0.601	0.213	94	13
	2002	1.387	0.326	88	28
	2005	0.334	0.128	213	16
<1,500m	1976	0.037	0.028	234	2
	1993	0.033	0.033	138	1
	2002	0.000	0.000	126	0
Hawai`i `Ākepa					
>1,500m	1976	0.343	0.112	162	30

Species	Year	Density	SE	# Stations	# Birds
	1993	1.558	0.303	94	81
	2002	1.067	0.291	88	50
	2005	0.349	0.093	213	40
<1,500m	1976	0.078	0.036	234	10
	1993	0.026	0.019	138	2
	2002	0.000	0.000	126	0
`I`iwi					
>1,500m	1976	3.654	0.293	162	260
	1993	5.129	0.433	94	212
	2002	3.537	0.341	88	137
	2005	1.716	0.164	213	161
<1,500m	1976	1.196	0.146	234	123
	1993	1.539	0.242	138	93
	2002	0.751	0.143	126	42
`Apapane					
>1,500m	1976	13.290	0.617	162	993
	1993	22.310	1.089	94	967
	2002	17.784	0.797	88	721
	2005	14.450	0.536	213	1417
<1,500m	1976	5.058	0.321	234	545
	1993	14.419	0.620	138	918
	2002	10.589	0.556	126	614
Red-billed Leiothrix					
>1,500m	1976	0.431	0.079	162	62
	1993	0.870	0.111	94	72
	2002	0.611	0.095	88	48
	2005	0.289	0.057	213	54
<1,500m	1976	0.879	0.084	234	183
	1993	1.937	0.145	138	237
	2002	2.135	0.165	126	239
Japanese White-eye					
>1,500m	1976	1.802	0.292	162	82
	1993	1.753	0.301	94	46
	2002	1.063	0.243	88	26
	2005	3.736	0.273	213	222
<1,500m	1976	5.363	0.526	234	351
	1993	7.545	0.699	138	290
	2002	6.401	0.515	126	226
Northern Cardinal					
>1,500m	1976	0.000	0.000	162	0
	1993	0.012	0.013	94	1
	2002	0.052	0.033	88	4
	2005	0.027	0.016	213	5
<1,500m	1976	0.005	0.005	234	1
	1993	0.139	0.046	138	17
	2002	0.353	0.096	126	39

Table 5. Estimated population size of bird species in the Ka`ū study area. With the exception of species indicated with shading, population estimates were derived from hierarchical species-habitat models and variance is reported as standard deviation (SD). Population estimates for shaded entries were calculated by extrapolating mean density by area occupied and variance is reported as standard error (SE). The coefficient of variation (CV) is a standardized measure of the relative variability of the population estimates. Estimates include the size and proportion of the total population that occurs above 1,500 m.

Species	Population Size	SD/SE	CV	5th Percentile	95th Percentile	Population >1,500 m	Proportion >1,500 m
Hawai`i `Elepaio	14,621	4,279	0.29	8,388	22,711	4,677	32%
`Ōma`o	82,378	7,493	0.09	70,519	94,578	29,781	36%
Hawai`i `Amakihi	154,749	9,393	0.06	140,463	170,416	102,475	66%
`Akiapōlā`au	1,073	307	0.29	616	1,869	1,073	~100%
Hawai`i Creeper	2,268	797	0.35	1,159	4,438	2,268	~100%
Hawai`i `Ākepa	2,556	863	0.34	1,340	4,876	2,556	~100%
`I`iwi	78,154	9,242	0.12	64,349	93,382	47,042	60%
`Apapane	491,928	23,966	0.05	454,673	535,593	292,682	59%
Red-billed Leiothrix	39,237	4,784	0.12	31,711	47,164	7,981	20%
Japanese White-eye	245,232	32,618	0.13	195,266	302,889	34,107	14%
Northern Cardinal	10,985	2,416	0.22	6,209	20,092	997	9%

Table 6. Trends in bird density above and below 1,500 m in the Ka`ū study area. Analytical conclusions under the heading “Trend” consist either of a positive or negative trend (“+” or “–“), a negligible or no trend (“none”) or inconclusive outcome (“?”). The summary also includes the presumed slope based on the two-sample comparison of mean densities for two years, standard error (SE), the significance of the trend slope (“Trend P”), the significance of the upper and lower equivalence tests (“Lower Equiv. P” and “Upper Equiv. P”), and the lower and upper 95% confidence interval of the slope.

Species	Trend	Slope	SE	Trend *P*	Lower Equiv. *P*	Upper Equiv. *P*	Lower CI	Upper CI
Hawai`i `Elepaio								
>1,500m	None	-0.008	0.005	0.089	0.001	<0.001	-0.018	0.001
<1,500m	None	0.001	0.006	0.936	<0.001	<0.001	-0.012	0.013
`Ōma`o								
>1,500m	None	-0.008	0.006	0.174	0.001	<0.001	-0.020	0.004
<1,500m	-	-0.029	0.009	0.001	0.596	<0.001	-0.046	-0.012
Hawai`i `Amakihi								
>1,500m	-	-0.039	0.015	0.009	0.787	<0.001	-0.068	-0.010
<1,500m	?	-0.013	0.016	0.404	0.192	0.006	-0.044	0.018
`Akiapōlā`au								
>1,500m	None	0.004	0.001	0.015	<0.001	<0.001	0.001	0.006
<1,500m	None	-0.001	0.001	0.224	<0.001	<0.001	-0.003	0.001
Hawai`i Creeper								
>1,500m	None	-0.001	0.007	0.827	0.001	<0.001	-0.014	0.012
<1,500m	None	-0.001	0.001	0.175	<0.001	<0.001	-0.004	0.001
Hawai`i `Ākepa								
>1,500m	None	0.000	0.005	0.966	<0.001	<0.001	-0.010	0.010
<1,500m	None	-0.003	0.001	0.032	<0.001	<0.001	-0.006	0.000
`I`iwi								
>1,500m	-	-0.067	0.012	<0.001	1.000	<0.001	-0.090	-0.044

Species	**Trend**	**Slope**	**SE**	**Trend *P***	**Lower Equiv. *P***	**Upper Equiv. *P***	**Lower CI**	**Upper CI**
<1,500m	-	-0.017	0.008	0.029	0.103	<0.001	-0.032	-0.002
\`Apapane								
>1,500m	?	0.040	0.028	0.156	0.009	0.678	-0.015	0.095
<1,500m	+	0.213	0.025	<0.001	<0.001	1.000	0.164	0.261
Red-billed Leiothrix								
>1,500m	None	-0.005	0.003	0.147	<0.001	<0.001	-0.012	0.002
<1,500m	+	0.048	0.007	<0.001	<0.001	0.999	0.034	0.062
Japanese White-eye								
>1,500m	+	0.067	0.014	<0.001	<0.001	0.998	0.040	0.094
<1,500m	?	0.040	0.028	0.158	0.009	0.676	-0.016	0.095
Northern Cardinal								
>1,500m	None	0.001	0.001	0.097	<0.001	<0.001	0.000	0.002
<1,500m	None	0.013	0.004	0.000	<0.001	0.001	0.006	0.021

Appendix 1. Bird detectability and model parameters from the program Distance used to calculate density in the trends and density surface models. Data includes the mean and maximum distance (meters) at which birds were detected, distance at which data were truncated (“Trunc”), detection model functions (H-rate K = hazard rate key; H-norm K = half normal key), covariates, and detection radius (i.e., effective area sampled). Species are ordered taxonomically within native and alien categories.

					Trend models		**Density surface models**	
Species	**Distance Mean (± SD)**	**Distanc eMax.**	**Trunc**	**Model Function**	**Covariates**	**Detection Radius (± SE)**	**Covariates**	**Detection Radius (± SE)**
Hawai`i `Elepaio	28.5 (13.5)	79	57.9	H-rate K	Observer, Gust & Month	37.4 (0.74)	Observer & Gust	37.5 (0.73)
`Ōma`o	43.8 (20.2)	213	79.1	H-rate K	Observer, Month, Cloud & Gust	54.1 (0.36)	Observer, Cloud & Gust	54.1 (0.36)
Hawai`i `Amakihi	30.5 (16.2)	157	59.9	H-rate K	Observer, Month, Gust, Wind, Time, Cloud & Rain	36.6 (0.30)	Observer, Gust, Wind, Time, Cloud & Rain	36.5 (0.30)
`Akiapōlā`au	47.2 (29.9)	122	86.0	H-norm K	None	54.5 (4.26)	None	54.5 (4.26)
Hawai`i Creeper	27.8 (17.8)	100	48.5	H-norm K	None	27.1 (1.49)	None	27.1 (1.49)

					Trend models		Density surface model	
Species	**Distance Mean (± SD)**	**Distanc eMax.**	**Trunc**	**Model Function**	**Covariates**	**Detection Radius (± SE)**	**Covariates**	**Detection Radius (± SE)**
Hawai`i `Ākepa	33.2 (16.7)	111	50.0	H-rate K	None	41.6 (1.67)	Gust, Wind & Observer	38.4 (0.92)
`I`iwi	32.1 (17.5)	167	55.8	H-rate K	Observer	38.0 (0.39)	Observer & Gust	36.5 (0.39)
`Apapane	32.8 (18.3)	304	59.7	H-rate K	Observer, Month, Time, Gust, Cloud, Wind & Rain	38.4 (0.16)	Observer, Time, Gust, Cloud, Wind & Rain	38.4 (0.16)
Red-billed Leiothrix	44.7 (21.4)	152	73.6	H-rate K	Observer, Month & Wind	53.4 (0.56)	Observer & Wind	53.3 (0.56)
Japanese White-eye	26.4 (14.9)	122	44.5	H-rate K	Observer & Month	30.2 (0.25)	Observer, Gust, Time, Cloud & Wind	30.1 (0.25)
Northern Cardinal	58.3 (27.5)	122	74.7	H-rate K	None	52.7 (4.18)	None	52.7 (4.18)

Appendix 2. Posterior distributions of mean standardized parameters from the hierarchical species-habitat models. Variable parameters include the mean, standard deviation (SD), median, Monte Carlo (MC) error, and 95% credibility intervals from 1,000 samples. Species are ordered taxonomically within native and alien categories.

Hawai`i `Elepaio

Variable	**mean**	**SD**	**median**	**MC error**	**2.50%**	**97.50%**
intercept	-2.914	0.218	-2.917	0.030	-3.306	-2.485
koa	0.874	0.297	0.848	0.046	0.331	1.463
tree-fern	0.393	0.117	0.396	0.010	0.156	0.616
canopy stature	-0.114	0.185	-0.128	0.018	-0.456	0.272
precipitation	0.168	0.152	0.163	0.021	-0.126	0.471
sine	0.458	0.231	0.465	0.025	-0.005	0.881
cosine	-0.791	0.156	-0.797	0.017	-1.085	-0.487
year effect - 1993	-0.444	0.236	-0.431	0.018	-0.917	-0.003
year effect - 2002	-0.503	0.254	-0.495	0.016	-1.027	-0.042
year effect - 2004	-0.665	0.279	-0.663	0.024	-1.277	-0.137
year effect - 2005	-0.044	0.223	-0.042	0.020	-0.464	0.393

`Ōma`o

Variable	**mean**	**SD**	**median**	**MC error**	**2.50%**	**97.50%**
intercept	-0.137	0.073	-0.138	0.003	-0.274	0.010
canopy stature	0.400	0.085	0.398	0.003	0.236	0.568
tree-fern	0.106	0.043	0.107	0.001	0.022	0.190
canopy closure	0.315	0.051	0.315	0.002	0.217	0.416
koa	0.098	0.105	0.094	0.006	-0.099	0.309
precipitation	0.070	0.085	0.070	0.006	-0.099	0.238
slope	0.038	0.034	0.038	0.001	-0.029	0.104
sine	0.020	0.072	0.020	0.003	-0.120	0.163
cosine	0.018	0.044	0.017	0.001	-0.070	0.103
year effect – 1993	0.101	0.071	0.100	0.002	-0.040	0.241
year effect – 2002	0.111	0.075	0.111	0.002	-0.036	0.258
year effect – 2004	0.265	0.153	0.271	0.006	-0.038	0.552
year effect – 2005	-0.362	0.079	-0.362	0.003	-0.517	-0.208

Hawai`i `Amakihi

Variable	mean	SD	median	MC error	2.50%	97.50%
intercept	-0.513	0.075	-0.513	0.009	-0.668	-0.376
temperature	-0.689	0.049	-0.688	0.004	-0.784	-0.598
koa	0.341	0.095	0.338	0.013	0.162	0.548
matted-fern	-0.352	0.061	-0.351	0.004	-0.468	-0.230
precipitation	-0.029	0.080	-0.025	0.012	-0.208	0.124
diversity	0.107	0.024	0.107	0.001	0.056	0.153
sine	0.358	0.077	0.355	0.008	0.206	0.513
cosine	-0.436	0.051	-0.436	0.005	-0.528	-0.331
year effect - 1993	-0.287	0.087	-0.291	0.006	-0.454	-0.112
year effect - 2002	0.073	0.093	0.073	0.007	-0.092	0.257
year effect - 2004	-0.347	0.129	-0.345	0.012	-0.593	-0.095
year effect - 2005	0.180	0.085	0.178	0.009	0.014	0.341

`I`iwi

Variable	mean	SD	median	MC error	2.50%	97.50%
intercept	-1.371	0.135	-1.380	0.019	-1.611	-1.101
canopy closure	0.317	0.076	0.313	0.008	0.173	0.468
canopy stature	0.071	0.131	0.073	0.017	-0.195	0.330
elevation^2	-0.472	0.083	-0.471	0.008	-0.640	-0.311
matted-fern	-0.463	0.091	-0.463	0.006	-0.646	-0.289
precipitation	-0.382	0.068	-0.386	0.006	-0.510	-0.243
sine	0.286	0.122	0.282	0.014	0.055	0.550
cosine	-0.700	0.077	-0.705	0.009	-0.842	-0.539
year effect – 1993	0.349	0.126	0.351	0.011	0.100	0.594
year effect – 2002	-0.234	0.136	-0.237	0.012	-0.499	0.020
year effect – 2004	-0.092	0.216	-0.095	0.024	-0.528	0.311
year effect – 2005	0.159	0.111	0.164	0.011	-0.068	0.371

`Apapane

Variable	mean	SD	median	MC error	2.50%	97.50%
intercept	0.799	0.055	0.800	0.008	0.688	0.922
temperature	-0.729	0.033	-0.729	0.003	-0.792	-0.665
canopy closure	0.102	0.027	0.101	0.003	0.050	0.156
koa	0.011	0.061	0.008	0.008	-0.106	0.135
canopy stature	0.251	0.042	0.251	0.004	0.170	0.331
elevation^2	-0.167	0.037	-0.167	0.004	-0.236	-0.094

sine	0.484	0.049	0.483	0.006	0.392	0.574
cosine	-0.169	0.027	-0.168	0.003	-0.226	-0.119
year effect - 1993	0.308	0.049	0.310	0.004	0.207	0.396
year effect - 2002	0.037	0.052	0.037	0.004	-0.064	0.139
year effect - 2004	-0.597	0.093	-0.597	0.010	-0.779	-0.422
year effect - 2005	0.093	0.052	0.086	0.006	0.003	0.198

Red-billed Leiothrix

Variable	mean	SD	median	MC error	2.50%	97.50%
intercept	-1.347	0.155	-1.354	0.021	-1.656	-1.044
$elevation^2$	-1.564	0.147	-1.563	0.014	-1.856	-1.281
grass	-0.758	0.145	-0.751	0.014	-1.079	-0.491
precipitation	0.105	0.067	0.106	0.006	-0.022	0.233
koa	0.333	0.202	0.348	0.032	-0.084	0.724
matted-fern	0.312	0.066	0.312	0.009	0.181	0.442
canopy stature	0.465	0.183	0.466	0.027	0.111	0.847
sine	0.654	0.124	0.650	0.013	0.433	0.902
cosine	-0.472	0.090	-0.475	0.010	-0.628	-0.276
year effect – 1993	0.260	0.128	0.260	0.011	0.012	0.490
year effect – 2002	0.346	0.136	0.351	0.013	0.075	0.603
year effect – 2004	-0.635	0.219	-0.637	0.022	-1.042	-0.174
year effect – 2005	0.267	0.131	0.268	0.010	0.011	0.508

Japanese White-eye

Variable	mean	SD	median	MC error	2.50%	97.50%
intercept	0.204	0.084	0.203	0.011	0.050	0.372
temperature	0.751	0.051	0.751	0.004	0.656	0.851
precipitation	0.054	0.089	0.068	0.014	-0.140	0.195
$elevation^2$	0.064	0.060	0.068	0.007	-0.055	0.169
sine	-0.086	0.091	-0.087	0.009	-0.265	0.100
cosine	0.308	0.051	0.307	0.005	0.217	0.415
year effect - 1993	0.167	0.095	0.167	0.009	-0.028	0.351
year effect - 2002	0.001	0.108	0.007	0.008	-0.227	0.207
year effect - 2004	0.227	0.219	0.226	0.025	-0.172	0.672
year effect - 2005	-0.083	0.098	-0.084	0.010	-0.271	0.101