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Using density surface models to estimate spatio-temporal changes in population densities and trend

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Precise measures of population abundance and trend are needed for species conservation; these are most difficult to obtain for rare and rapidly changing populations. We compare uncertainty in densities estimated from spatio-temporal models with that from standard design-based methods. Spatio-temporal models allow us to target priority areas where, and at times when, a population may most benefit. Generalised additive models were fitted to a 31-year time series of point-transect surveys of an endangered Hawaiian forest bird, the Hawai'i 'ākepa *Loxops coccineus*. This allowed us to estimate bird densities over space and time. We used two methods to quantify uncertainty in density estimates from the spatio-temporal model: the delta method (which assumes independence between detection and distribution parameters) and a variance propagation method. With the delta method we observed a 52% decrease in the width of the design-based 95% confidence interval (CI), while we observed a 37% decrease in CI width when propagating the variance. We mapped bird densities as they changed across space and time, allowing managers to evaluate management actions. Integrating detection function modelling with spatio-temporal modelling exploits survey data more efficiently by producing finer-grained abundance estimates than are possible with design-based methods as well as producing more precise abundance estimates. Model-based approaches require switching from making assumptions about the survey design to assumptions about bird distribution. Such a switch warrants carefully considered. In this case the model-based approach benefits conservation planning through improved management efficiency and reduced costs by taking into account both spatial shifts and temporal changes in population abundance and distribution.

Keywords: density estimation, distance sampling, point-transect sampling, spatio-temporal smoother, variance propagation



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Introduction

Species management, particularly the conservation of rare species, is costly requiring increasingly limited funding, personnel and time. Conservation planning focuses on

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the proposed benefits returned from management actions, the costs of implementing actions, and the likely outcome of actions (Walls 2018). Traditionally, management actions are based on the spatial distribution of a species under the simplifying assumption of uniform benefits across the spatial extent of the area where the effort is prescribed. Identifying the location and timing of greatest population change, such as fluctuations in a population as it expands into an area or contracts reversing species recovery and threatening species persistence, could deliver greater benefits through maximising the type and cost-effectiveness of management actions (Cattarino et al. 2016, Tulloch et al. 2016). We propose using spatio-temporal modelling to identify priority areas and times where a species may most benefit from management actions as it responds spatially and temporally to changing demographic parameters and environmental conditions.

The Hawai'i 'ākepa *Loxops coccineus* (hereafter 'ākepa) is an internationally and federally endangered Hawaiian honeycreeper (Fringillidae; Pratt 1994, BirdLife International 2016) endemic to Hawai'i Island, USA. 'Ākepa declined dramatically during the 20th century due to mosquito transmitted avian diseases (Pratt 1994), habitat modification (Scott et al. 1986, Pratt 1994), introduced predators (Lepson and Freed 1997), and food resources competitors (Lepson and Freed 1997). 'Ākepa are now restricted to five spatially distinct populations with an estimated global abundance in 2016 of 16 248 (95% confidence interval (CI) 10 074–25 198) birds (Judge et al. 2018). The largest population, estimated to contain more than 11 000 birds in 2012 (Camp et al. 2016), is on the eastern side of Mauna Kea volcano in Hakalau Forest National Wildlife Refuge (Judge et al. 2018).

Refuge-wide distance sampling monitoring reveals that 'ākepa are stable to increasing (Camp et al. 2016, Rozek et al. 2017), and that the population is expanding into the adjacent reforested pasture (Paxton et al. 2018). 'Ākepa densities, however, vary locally (Reding et al. 2010) and localised populations may be declining despite widespread increases (Freed and Cann 2010). Spatial differences in 'ākepa densities may be due to the species' biology. 'Ākepa are strongly philopatric, have relatively small home ranges and there is scant evidence of movement among populations (Lepson and Freed 1997). Modelling the spatio-temporal distribution in the 'ākepa population can help reveal patterns in its distribution and abundance.

Conventional distance sampling methods are a hybrid between model-based methods for estimating detectability and design-based methods to estimate density in the survey region (Buckland et al. 2001). Borchers et al. (2002) proposed a fully model-based approach to distance sampling, and Royle and Dorazio (2008) proposed an equivalent model specifically for line transect sampling. Royle et al. (2004) proposed modelling of plot counts, including a component in the likelihood corresponding to imperfect detection, but did not consider spatial models for distance sampling.

Spatial distance sampling models based on point process models were first proposed by Stoyan (1982) and Högmänder (1991). Hedley (2000) and Hedley and Buckland (2004) developed models based on aggregating detections within small segments of transects and modelling the number of detected objects or groups, offering a simpler analysis method, leading to what is now termed density surface modelling. Miller et al. (2013) provided software for fitting density surface models, using the two-stage approach proposed by Hedley and Buckland (2004), in which the detection function is modelled in the first stage, and the counts modelled in the second, with an estimated offset to account for detectability. Buckland et al. (2016) provided a more general framework for model-based distance sampling, and reviewed the above approaches. We adopt the density surface modelling approach here. We estimated detection probabilities using standard multiple-covariate distance sampling methods (Buckland et al. 2015). We model spatial and temporal correlation using penalized spline-based smoothing within a generalized additive modelling framework. We used methods developed in Williams et al. (2011) and described more fully in Bravington et al. (2018) to propagate variances between model stages.

There is a rich variety of possible smooth functions to model spatial and temporal correlation (Cressie and Wikle 2015). Wood (2017) recommends using regression splines to fit a smooth curve to model the relationship between the predictor and response variables where the amount of smoothing is controlled by a penalty term (from a frequentist viewpoint) or prior of the space of functions (from a Bayesian viewpoint). We take this generalized additive model (GAM) approach here for several reasons. First, densities of 'ākepa vary relatively smoothly throughout Hakalau. The flexible nature of GAMs allows for modelling smooth patterns across space and over time. Second, the amount of smoothing is controlled within the GAM framework that prevents over-fitting. Finally, the well-developed software package mgcv (Wood 2016) facilitates modelling smoothers including model selection and model checking.

Spatio-temporal models attempt to capture the relationship between the response (in our case density) and covariates (in our case space and time). We used a 2-stage model to assess spatio-temporal patterns in bird densities across a 31-year time series. Using uncertainty in densities estimated from conventional design-based methods as a baseline, we compared the uncertainty derived from spatio-temporal models to conventional design-based methods where the change in uncertainty was calculated as the ratio in CI widths. Our methods can increase the cost-effectiveness of species conservation through more precise allocation of management actions, improve our understanding of species response to management actions, and facilitate conservation planning elsewhere in the species range.

Material and methods

Study area and sampling design

Hakalau Forest National Wildlife Refuge, Hawai'i (hereafter Hakalau; 19°51'N, 155°18'W) was established in 1985 and is actively managed to preserve native forest birds, rainforest plants and their habitats. The 15 390-ha montane forest is dominated by native 'ōhi'a *Metrosideros polymorpha* and koa *Acacia koa* with a mixture of native and non-native understory plants. Temperature averages 15°C with annual variation <5°C, and precipitation averages 2500 mm with a maximum of 6100 mm (Juvik and Juvik 1998). Regeneration in the study area has proceeded naturally since the removal of cattle in 1988 (Maxfield 1998).

A systematic, random design spanning the upper elevation (1400–1920 m) forest of Hakalau was established, consisting of 350 point samplers (hereafter, points) on 14 transects (Fig. 1). Points were spaced approximately 150 m apart along the transects. The study area was divided into two strata, with the south stratum (918 ha) having generally higher densities of 'ākepa than the north stratum (2143 ha). To increase survey efficiency, transect lines were closer together in the south stratum (approximately 500 m) than the north stratum

(approximately 1000 m). For more information on the region and study area see Scott et al. (1986) and Camp et al. (2010).

Bird sampling

Point-transect distance sampling methods were used at Hakalau to sample forest birds in 1987–2017 (excluding 2009). Trained and calibrated observers recorded the horizontal distance from the centre of each point to birds detected during an 8-min count (Camp et al. 2010, 2016). Individual birds were detected and their locations recorded as exact distances. Cloud cover, rain, wind strength, gust strength and time of day each point was surveyed were also recorded. Sampling commenced at dawn and continued until 11:00, and occurred only during favourable weather conditions (halting when conditions exceeded light rain and Beaufort 3 winds).

Stage 1. Detection probability estimation

We estimated the 'ākepa detection probability from the point transect data using program *Distance*, ver. 7.1, release 1 (Thomas et al. 2010). Candidate detection function models were restricted to the half-normal and hazard-rate key

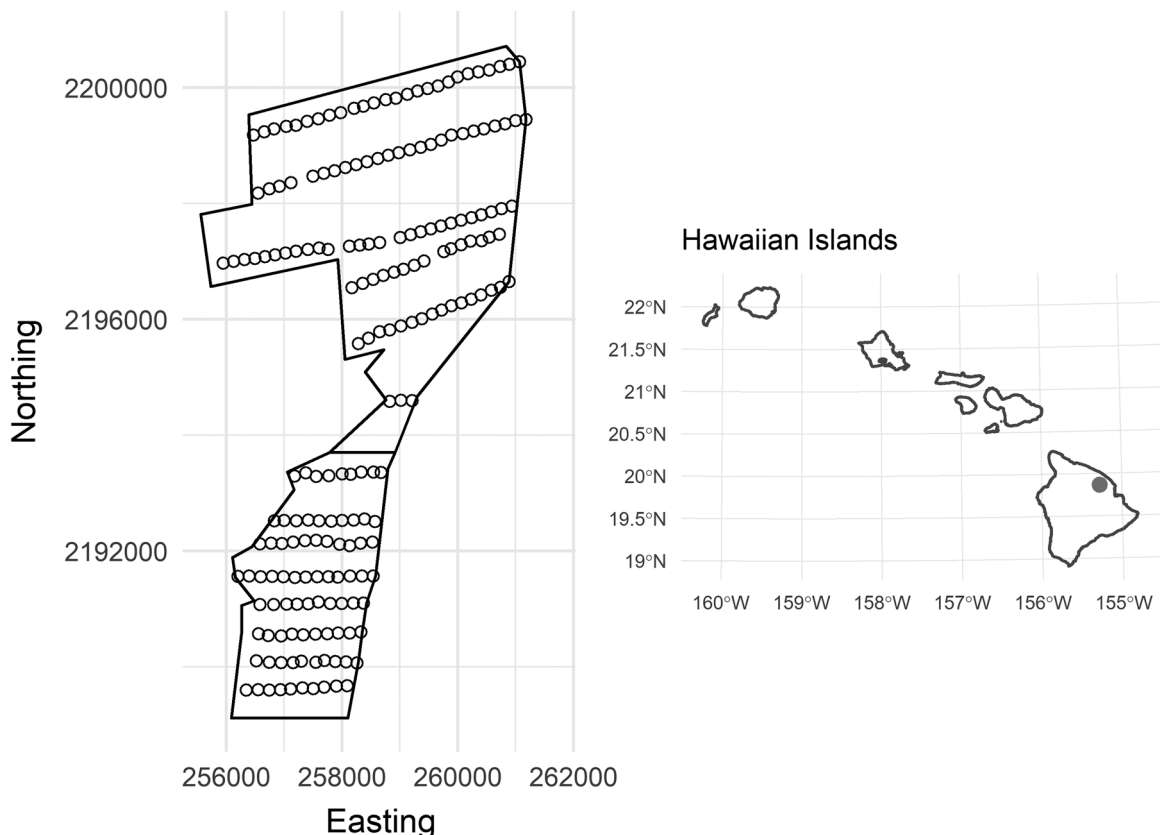


Figure 1. Study area showing survey points (open circles) separated into north and south strata (polygons). The location (black dot) of Hakalau Forest National Wildlife Refuge is shown on Hawai'i Island, Hawaiian Islands. Base map from World Geodetic System 1984 (WGS84) zone 5; coastline from U.S. Geological Survey's National Elevation Dataset (USGS, U.S. Geological Survey 2014).

functions with at most two adjustment terms (Buckland et al. 2001). We considered covariates such as observer, weather conditions and year (see list of covariates in Supplementary material Appendix 3 Table A1). We used a forward selection algorithm to add covariates, at each step adding the covariate that produced the greatest reduction in Akaike’s information criterion (AIC); we stopped when no additional covariate produced a decrease in AIC. Interactions between covariates were not considered. Correlation, confounding effects and combinations of covariates are presented in Supplementary material Appendix 3. Data were truncated at a distance w where the estimated detection probability (using a preliminary detection function model) was about 0.1 to facilitate detection function modelling and to avoid over-fitting to distant detections. AIC was used to select models and candidate models were evaluated with a Kolmogorov–Smirnov goodness-of-fit test (Buckland et al. 2015). We selected a hazard-rate key detection function with only year as a covariate model for estimating ‘ākepa detection probability, \hat{p}_i . We incorporated the year i , for $i = 1, 2, 3, \dots, 31$, detection probabilities in Stage 2 as the effective area searched, computed as $\hat{v}_i = \pi w^2 \hat{p}_i$.

Stage 2. Design-based density estimation

We used the year-specific estimated detection probabilities to estimate year and strata-specific densities in `Distance` (Thomas et al. 2010). Using post-stratification procedures we generated annual stratum-specific densities, \hat{D}_{ij} , and standard errors, $SE(\hat{D}_{ij})$, where i represents year and j stratum (north and south). Subscript notation is dropped for clarity. Annual mean densities within the study area were computed from area-weighted estimates (Thomas et al. 2010). Following the method by Burnham et al. (1987; as cited in Buckland et al. 2001, pp. 76–77) we computed the log-normally distributed confidence interval as $(\hat{D} / C, \hat{D}C)$ where $C = \exp\left[z_\alpha \sqrt{\widehat{\text{var}}(\ln\{\hat{D}\})}\right]$ for the design-based method. z_α was the upper $\alpha\%$ from the $N(0, 1)$ distribution, 1.96 in this case, and $\widehat{\text{var}}(\ln\{\hat{D}\}) = \ln\left[1 + \frac{\widehat{\text{var}}(\hat{D})}{\hat{D}^2}\right]$.

We used the delta method (Seber 1973) to compute annual $\widehat{\text{var}}(\hat{D})$ as

$$\widehat{\text{var}}(\hat{D}_i) = \hat{D}_i^2 \left[\frac{\widehat{\text{var}}(\hat{p}_i)}{\hat{p}_i^2} + \frac{\sum \left[\left(\frac{A_j}{A} \right)^2 \text{var} \left(\frac{n_{ij}}{k_{ij}} \right) \right]}{\sum \left(\frac{A_j n_{ij}}{A k_{ij}} \right)^2} \right]$$

where A_j is the area of the j -th stratum and A is the total area. The annual \hat{p}_i and $\widehat{\text{var}}(\hat{p}_i)$, and annual, stratum-specific

encounter rate $\frac{n_{ij}}{k_{ij}}$ and encounter rate variance $\text{var} \left(\frac{n_{ij}}{k_{ij}} \right)$ values were computed using `Distance`. The encounter rate variance was calculated using the empirical between-sample variation method (Thomas et al. 2010, `Distance for Windows User’s Guide`).

Stage 2. Model-based density estimation

Progressing from west to east traverses from the pasture–forest edge into progressively more suitable habitat. The substratum underlying Hakalau transitions from relatively fertile, old lava flows (11 000–64 000 years old) in the south to nutrient-limited, new lava flows (5000–11 000 years old) in the north (Vitousek et al. 2009, USFWS, U.S. Fish and Wildlife Service 2010). The interaction between the spatial variables could have dramatic influence on ‘ākepa distribution because vegetation in the northeastern portion has a more complex and denser structure in the canopy, understory and ground cover than in the southwestern portion (Jacobi 2018, Hart et al. 2020). Therefore, spatial smooths of location (UTM variables `east` and `north`) were used in the model.

Previous analyses demonstrated that ‘ākepa densities and abundances across Hakalau were stable to increasing over time (Camp et al. 2010, 2016). These overall trends likely missed smaller-scale temporal heterogeneity in the population, which can be captured by including a smooth of year. Such heterogeneity can be observed in spatio–temporal maps that depict local trends in bird densities (Camp et al. 2016). We summarised trends in densities at two spatial scales: 1) broad-scale trends across Hakalau, and 2) regional-scale trends coinciding with the northern and southern stratum of Hakalau.

We fitted a GAM with smooths of location (`east` and `north`), time (`year`), their interactions and offset ($\log(\hat{v}_i)$). This model has the form

$$\begin{aligned} \log\{\mathbb{E}(n_{ik})\} = & f_1(\text{east}_k) + f_2(\text{north}_k) + f_3(\text{year}_i) \\ & + f_4(\text{east}_k, \text{north}_k) + f_5(\text{east}_k, \text{year}_i) + f_6(\text{north}_k, \text{year}_i) \\ & + f_7(\text{east}_k, \text{north}_k, \text{year}_i) + \log(\hat{v}_i) \end{aligned}$$

where n_{ik} was the bird count in the i -th year at the k -th point. Smooths (f_{1-7}) were modelled as thin plate regression splines (TPRS; Wood 2003). The advantage of the TPRS approach is that knot positions were selected automatically from the data, eliminating knot placement subjectivity. The TPRS is isotropic (i.e. rotationally invariant), which was appropriate as projected UTM coordinates are isotropic. The space–time interactions in f_{5-7} were anisotropic as space and time measurements were on different scales, so interactions with time were generated via tensor products (Wood et al. 2013). For each term, the maximum basis complexity was set and the penalty controlling the degree of smoothing was selected using restricted maximum likelihood (REML; Wood 2017, p. 185). The model was built in R (www.r-project.org) using the `mgcv` package (Wood 2016).

We modelled the counts with three response distributions: Poisson, negative binomial and Tweedie distributions, all with a log link function. Sensitivity in our choice of response distribution and model assumptions were checked through inspection of the deviance residuals following approaches suggested by Wood (2017). We refitted the model with intercept to the residuals to determine if any residual variance remained (Wood 2017, p. 243).

Judge et al. (2018) showed that ‘ākepa density varies by habitat type. Spatial models are particularly useful for exploring how densities relate to habitat types, and other variables such as climate and elevation. We identified point-specific habitat type based on the terrestrial ecosystems data from the LANDFIRE classification (USGS, U.S. Geological Survey 2013). Habitat was classified at the formation level describing plant communities of the U.S. National Vegetation Classification (Jennings et al. 2009, and <<http://usnvc.org>>), and defined by broad combinations of growth forms (e.g. forest trees) with moisture (e.g. wet or mesic) and temperature (e.g. montane) conditions.

Exploratory analysis indicated that within our study area there were two habitat types: 1) montane mesic forest; and 2) montane wet forest. Thus, habitat was categorical with two levels. Generally there was greater coverage in montane wet forest than montane mesic forest (148 points in wet forest and 52 points in mesic forest; Supplementary material Appendix 6 Fig. A18). We included the categorical variable `habitat` in the spatio-temporal smoother model of the form

$$\begin{aligned} \log\{\mathbb{E}(n_{ik})\} = & f_1(\text{east}_k) + f_2(\text{north}_k) + f_3(\text{year}_i) \\ & + f_4(\text{east}_k, \text{north}_k) + f_5(\text{east}_k, \text{year}_i) + f_6(\text{north}_k, \text{year}_i) \\ & + f_7(\text{east}_k, \text{north}_k, \text{year}_i) + \text{habitat}_b + \log(\hat{\nu}_i) \end{aligned}$$

where `Habitat` was a two-level variable taking values ‘wet’ or ‘mesic’, and the other variables were as above. AIC was used to select between the smoother-only and the smoother-with-habitat models.

Propagating variance

Variance was propagated in the spatio-temporal models using two methods: one that assumes independence between detection probability estimates at the point level and one that does not. The delta method (Seber 1973) may be used to combine variances among models, assuming independence of parameters between models. Using the delta method the `Distance`-derived detection probability variances were combined with the GAM density estimate variances to produce total uncertainty in the GAM derived density estimates per year.

We propagated detection probability uncertainty through to the spatio-temporal model using the variance propagation method of Williams et al. (2011) and Bravington et al. (2018). This allowed us to capture uncertainty from both the detection and spatial models without assuming independence among parameters. The approach effectively fits a one-stage

model in two stages, by correcting the detection stage during refitting of the spatial model, adjusting the estimated detection probabilities via a random effect with covariance matrix given by that of the detection function model (and zero mean). This covariance ensures that the uncertainty in the detection function is propagated through to estimates for the spatial model. We expect that the correction would lead to no effect on point estimates of the detection probability on average, conditional on the detection model being correct. If there is systematic deviation (reflected as an increase or decrease in the detection probability of (say) greater than two standard deviations), this may indicate an inadequate detection model (e.g. missing detection covariate or imperfect detection at zero distance). Refitting the spatio-temporal model with a correction to include detection function uncertainty was performed using the `dsm_varprop` function in the R package `dsm` (Miller et al. 2018) (R code provided in Supplementary material Appendix 1). We then used posterior simulation (Wood 2017, sect. 7.2.7) to generate possible predictions from the model, taking appropriate summaries to give uncertainty estimated.

Differences in the widths of CIs generated using the design-based log-normal confidence intervals computed with parameter estimates from `Distance` (DB; $CIW_{DB,i}$) and the two variance propagated methods (delta method [DM; $CIW_{DM,i}$] and variance propagated [VP; $CIW_{VP,i}$]) were calculated. The change in uncertainty was calculated as the ratio $\frac{CIW_{m,i}}{CIW_{DB,i}} \times 100\%$ for each year i by variance calculation method m , where m can be DM or VP.

Spatio-temporal maps

We predicted density over the study area on a 200×200 m grid across Hakalau. Using predictions we produced broad-scale trends across Hakalau, as well as uncertainty in the form of coefficient of variation maps.

Data deposition

The data are available from USGS <<https://doi.org/10.5066/P98IO297>> (Camp 2019).

Results

Survey implementation

Generally the same points were surveyed between 1987 and 2017 providing relatively equal coverage of the refuge over years (mean number of points = 175.2, SD = 26.8, range 136–199 points; Supplementary material Appendix 2 Fig. A5). Changes in ‘ākepa counts, and subsequently densities, were therefore not due to changes in the sampling frame. Total numbers of ‘ākepa detected varied by year (mean = 94.7, SD = 33.8, range 41–182 birds) but counts generally followed a similar pattern of many points with no birds detected

and several points with one to rarely 5–9 birds detected (Supplementary material Appendix 2 Fig. A6).

Stage 1. Detection probability estimation

A hazard-rate detection function model with *year* as a factor covariate was selected by AIC (having improved fit over the no-covariate model by >153 AIC points; Supplementary material Appendix 3 Fig. A7, Table A1). The Kolmogorov–Smirnov goodness-of-fit test was not significant at the $\alpha = 0.05$ level ($D_n = 0.02$, $p = 0.17$). Truncation distance was $w = 58$ m yielding 3953 observations from 6850 points. The effective area surveyed for ‘ākepa was $\hat{\nu} = 0.516$ ha, which was derived from the effective detection radius of $EDR = 40.546$ m ($SE = 0.243$, 95% CI 40.072–41.025) and the detection probability of $\hat{p} = 0.489$ ($SE = 0.006$, 95% CI 0.477–0.500).

Stage 2. Design-based density estimation

Design-based densities from distance sampling ranged from 0.29 to 1.47 birds ha^{-1} over the 31-year time series (Fig. 2, top panel; Supplementary material Appendix 4 Table A3). Densities were much more variable in the northern stratum than in the southern stratum (Fig. 2, bottom panels left and right, respectively, Supplementary material Appendix 4 Table A4, A5).

Stage 2. Model-based density estimation

We evaluated Poisson, negative binomial and Tweedie distributions for the spatio-temporal model. We used the

default basis complexity after checking that the basis size had sufficient flexibility for the smooth terms in the model. Inspection of residual quantile–quantile (QQ) plots and AIC scores showed that the negative binomial distribution gave the best fit to the data (Supplementary material Appendix 5 Table A6, A7). The estimated negative binomial over-dispersion parameter was 1.944 and the deviance explained was 52.7%. The effective degrees of freedom (EDF) values were approximately zero for the model refitted to the residuals (Supplementary material Appendix 5 Table A8) suggesting that there was little un-modelled residual structure. Plots of the smooth terms involving *east*, *north*, *year* and their interactions are shown in Supplementary material Appendix 5 Fig. A15, A16.

Spatial model including habitat

Results indicated that including *habitat* minimally improved the spatio-temporal model. Residual plots (Supplementary material Appendix 6 Fig. A19) appeared reasonable. The effect of *habitat* was positive but only weakly significant ($\chi^2 = 4.814$, $df = 1$, $p = 0.028$). The EDFs for the smoother terms were similar to those from the smoother-only model (compare Supplementary material Appendix 6 Table A9 to Supplementary material Appendix 5 Table A7). The deviance explained was 53%, providing only a small increase in modelling residual variance. Compared to the smoother-only model the AIC value for the smoother with *habitat* model was larger by >16 units. Therefore, *habitat* was dropped and spatio-temporal inference was based on the smoother-only model.

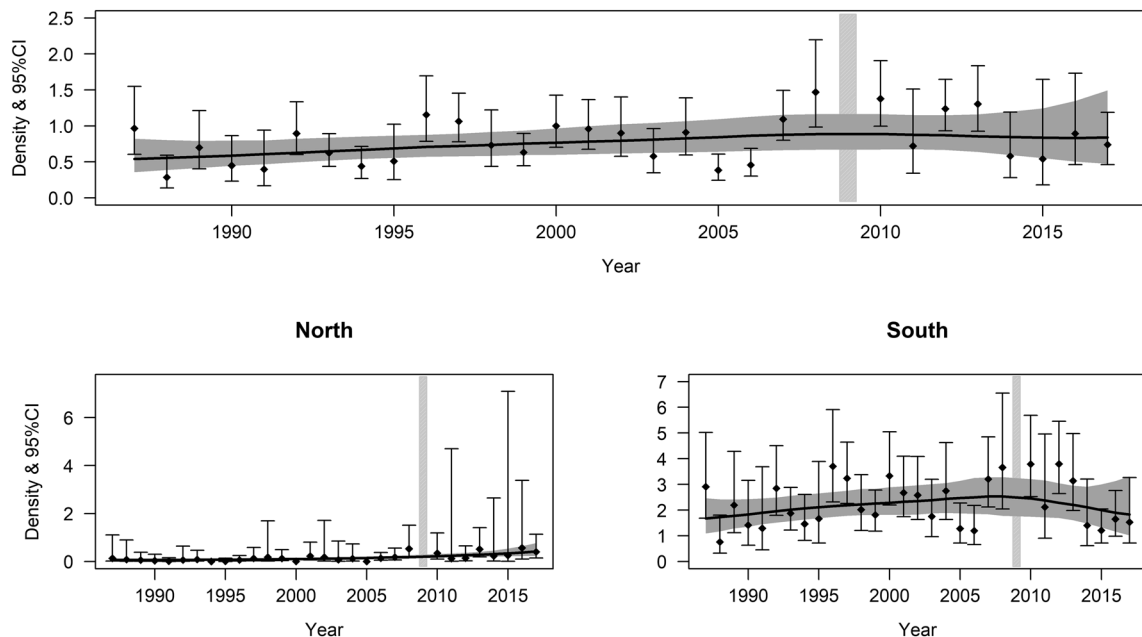


Figure 2. Predicted trends derived from the spatio-temporal GAM for the ‘ākepa population across Hakalau (top panel), north (bottom left panel) and south (bottom right panel) strata of Hakalau. GAM generated density (birds ha^{-1}) estimates (black line) with detection probability variance propagated uncertainty (95% CI gray ribbon). Density estimate with 95% CI from the design-based method (diamond and whisker bar). Surveys were not conducted in 2009 (vertical bar).

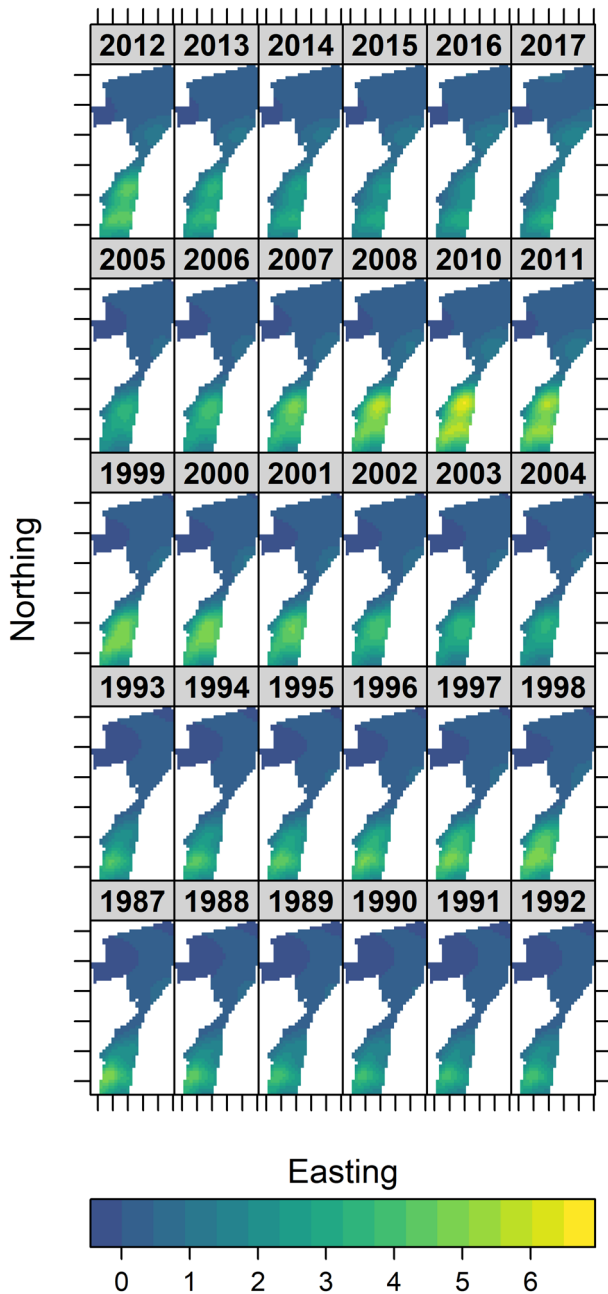


Figure 3. Predicted spatio-temporal surfaces of 'ākepa densities in Hakalau between 1987 and 2017. Densities range from 0 (dark blue) to 6.5 birds ha^{-1} (yellow) within the study area.

Spatio-temporal patterns

Densities of Hawai'i 'ākepa varied both spatially and temporally (Fig. 3). Across the time series, densities remained low in the northern portion of the refuge, but densities were much more dynamic in the central and southern parts of the refuge. Starting in 1987 an area of high density occurred in the south-west that diminished over several years before increasing and persisting into the mid-1990s. The high density area then appeared to diffuse into the central portion of the refuge through the early 2000s before a high density area reformed

to the north-east of its original location, and by the late 2000s had reached densities of 6 birds ha^{-1} . The high density area subsequently diffused again to moderate numbers of birds by the end of the time series, 2–3 birds ha^{-1} .

Overshadowed by the dynamics in the southern half of Hakalau, subtle changes occurred throughout the north. Early in the time series the northern portion was roughly split between an area devoid of 'ākepa and an area with <0.25 birds ha^{-1} . The pattern persisted into the mid-1990s before 'ākepa started increasing and expanding so that by 2017 the area devoid of 'ākepa was restricted to a small patch in the north-west portion of Hakalau.

Uncertainty in densities are shown in maps of coefficient of variation (CV; Supplementary material Appendix 5 Fig. A17). The per cell uncertainty ranged widely with CVs from 0.09 to 2.02, and varied spatially. Densities were most precise in the southern portion and most variable in the north-west portion of the study area, which was consistent with the amount of effort that was put into those areas. These patterns persisted across the entire time series. Thus, areas where change was most rapid, the northern half of the study area particularly the northwest portion, were locations where the drivers of the population may have been most influential.

Temporal patterns

Initially estimated at 0.54 birds ha^{-1} , the 'ākepa density increased between 1987 and the late 2000s to a maximum of 0.90 birds ha^{-1} , and subsequently declined to 0.84 birds ha^{-1} in 2017 (Fig. 2, top panel; Supplementary material Appendix 4 Table A3). However, the trends in the two regions of the study area are substantially different. Trends in the north stratum were generally upward throughout the time series while trends in the south stratum oscillated (Fig. 2, bottom panels left and right, respectively). Average densities also differed between the two strata. Densities in the north stratum are a fraction of the densities observed in the south stratum (means of 0.16 birds ha^{-1} compared to 2.16 birds ha^{-1} , respectively; Supplementary material Appendix 4 Table A4, A5). These patterns are reflected in the spatio-temporal maps (Fig. 3).

Uncertainty comparison between methods

In addition to producing coefficient of variation maps depicting where the population is changing most rapidly, we observed improvements in annual density precision using model-based methods (Fig. 2; Supplementary material Appendix 4 Table A3). This increased precision is a result of accounting for the correlation structure in space and time. That is, the expectation of the variance estimate at one point was a function of the state at the previous time point. Although the pooled detection probability was very precise (CV=0.012), we incorporated uncertainty from the detection probability because there was substantial variation between years. The delta method gives on average a CI width that was 52.4% shorter than the CI width of the design-based method (SD=18.5%; Supplementary material Appendix 4 Table A3). This pattern was more prominent in the north

stratum where design-based CI widths were wider than in the south stratum. There was an average 90.6% reduction in the length of the CI widths (SD=6.4%; Supplementary material Appendix 4 Table A4) in the north stratum, while the average CI width was 59.7% shorter in the south stratum (SD=13.7%; Supplementary material Appendix 4 Table A5).

The average CI width using the variance propagation method was 37.2% shorter than the design-based CI width (SD=26.1%; Supplementary material Appendix 4 Fig. A9, left panel; Supplementary material Appendix 4 Table A3). In the north stratum there was an average 83.4% reduction in the length of the CI widths (SD=12.3%; Supplementary material Appendix 4 Fig. A9, middle panel; Supplementary material Appendix 4 Table A4). While in the south stratum the variance propagation method CI width was on average 45.7% shorter than the design-based method CI width (SD=24.5%; Supplementary material Appendix 4 Fig. A9, right panel; Supplementary material Appendix 4 Table A5).

Discussion

Our analysis shows that precision in animal abundance estimates can be improved through the application of spatio-temporal modelling using GAMs and underscores the need to account for estimator uncertainty through variance propagation. We observed large variation in counts among different points, as well as between years, which is typical of Hawaiian forest bird monitoring (Camp et al. 2009), and counts elsewhere (Link and Sauer 1998). Accounting for the various sources of variation is critical to assess management and conservation goals. Established approaches to compute total variance include: 1) delta method assuming independence (Seber 1973); 2) bootstrap methods (Hedley and Buckland 2004); 3) fully Bayesian approaches (Niemi and Fernández 2010, Sigourney et al. 2018); and the approach here 4) using random effects in the GAM (Bravington et al. 2018). The delta method assumption of independence is not appropriate here as the detection probabilities estimated in the first stage are included in the offset in the second stage GAM. Under our sampling design bootstrap resampling would be of lines instead of points (Buckland et al. 2015). It is then unclear exactly how the different units (lines for the detection probability domain and blocks for the spatio-temporal domains) are resampled (Lahiri 2003). Bayesian methods such as Niemi and Fernández (2010) and Sigourney et al. (2018) require writing custom code and checking priors and convergence, incurring a high computational cost. The variance propagation approach avoids the concerns of the above methods by accounting for possible interactions between detection and density models, non-independence between years and spatial correlation among points while still being computationally efficient.

Standard distance sampling, including the multiple covariate extension, is a hybrid of design- and model-based methods where inference comes from the design portion and

detection probability from the model-based portion. Design-based methods are most appropriate if the primary goal of the surveys is to estimate population size and track changes through time (Buckland et al. 2015). The random placement of points in a study area allows for extrapolating densities at the points to the wider study area, providing inference about total abundance. When the goal of the survey is to map species distribution or compare whether densities on sub-regions differ model-based methods can be more appropriate. A model-based approach is particularly useful to assess the effectiveness of management actions under a control-treatment design, or to account for spatio-temporal correlation in the counts as we have done. Switching from design- to model-based methods requires a substitution of assumptions about the survey design, where it is assumed that sample locations are chosen using a random sampling scheme, to assumptions about the animal distribution, where it is assumed that animal locations are a realisation of the spatial model. The survey team can assume that the design assumption is met, while they are not in control of the animal distribution. Assumption violation can lead to bias and hence the design-based approach is generally considered more robust. Thus, switching between the methods requires careful consideration of the survey goals, method-specific advantages and disadvantages, and available data. As long as the surveys are conducted following design-based methods the data can be analysed using either design- or model-based methods as appropriate (Buckland et al. 2015).

Sampling at Hakalau is based on a stratified, systematic random sampling design. Therefore, the design-based analysis required that we stratify the study area by sampling intensity to produce unbiased density estimates. Standard distance sampling methods, even incorporating model-based analysis procedures, do not fully account for the spatial structure of the sampling design (Buckland et al. 2015). Spatial distance sampling models, that integrate detection function modelling exploit our data more efficiently by avoiding the need to stratify the study area and can incorporate plot-level covariates that influence both bird detection probability and densities (Miller et al. 2013).

The covariate habitat we used classifies plant communities at the formation level of the U.S. National Vegetation Classification (Jennings et al. 2009, and <<http://usnvc.org>>). The formation level is defined by broad combinations of growth forms with moisture and temperature conditions, and is a classification level that is unlikely to change from management actions designed to enhance forest habitat. It is unlikely that ‘ākepa and other Hawaiian forest birds are responding to habitat at the coarse formation level, which was reflected in our analyses where there was no strong evidence that habitat influenced ‘ākepa densities. More likely, forest birds respond to changes in crown cover and canopy height, floristic community composition and understory components (Scott et al. 1986). Interestingly, Scott et al. (1986) found only limited response of native passerines to understory components; however, after the removal of ungulates

from portions of the refuge (Maxfield 1998, Hess 2016) it appears that the forest birds may have positively responded to the recovering understory as the forest canopy has changed very little since the 1970s (Jacobi 2018). Point-level description of the understory vegetation is available only for surveys conducted in 2016 and 2017, which will be useful for future studies that wish to incorporate understory variables to describe its relationship with bird density and potentially improve model residuals and deviance.

Biological conclusions

Estimating densities using smoothing methods eliminated biologically impossible changes in densities. While it is possible that a population can decrease by half or more from one year to the next, it is not possible for 'ākepa to double as they produce only one or two eggs per year yielding a 1.47 birth rate with hatch year survival ranging from 0.23 to 0.43 (Woodworth and Pratt 2009). The biologically realistic growth rate is then between 0.57 and 1.06 indicating that the population could halve between years but increase only slightly assuming that all adult birds survived (Newman et al. 2014). Estimates produced through standard distance sampling analyses changed substantially (and unrealistically) between years, while annual density estimates from the spatio-temporal model are more biologically plausible (Fig. 2) (though there is no constraint on survival or growth rate explicitly in the model). More advanced demographic modelling could be achieved by including the previous year estimate as an offset following Conn et al. (2015) and Swallow (2015), and/or through population dynamics modelling that combines bird abundance with priors on annual changes, which can be informed by demographic vital rates (Newman et al. 2014).

We used a simple spatial smoother that assumes that the bird population is continuous across the refuge including proximate areas outside the study area. This assumption may be realistic to the north, east and south of the study area that juxtaposes contiguous 'ōhi'a dominated forest. The 'ākepa population, however, does not extend west into the pasture, especially early in the time series when grass dominated that habitat and prior to afforestation management. Not detected until 2007, 'ākepa moved into the afforested pasture once the trees had sufficient time to provide suitable habitat (Paxton et al. 2018). From the initial Hawai'i forest bird survey (HFBS), Scott et al. (1986) noted that 'ākepa are absent from about a fifth of the northern Hamakua study area. Adjacent to the area devoid of 'ākepa is a relatively large area with very low densities of 1–10 birds km⁻², in which the northern portion of Hakalau occurs. At the start of our time series densities in the north region are comparable to HFBS densities. However, by the last survey densities are nearly three times greater and the GAM-generated CIs do not bracket the HFBS point estimates, despite relatively large CVs, but still densities are low at only 40 birds km⁻².

Management implications

A main goal of our spatio-temporal modelling was to unveil geographical and temporal patterns that can be used to identify population responses to management actions. Thus, our modelling attempted to elucidate short-term responses in population abundances to long-term management effects. Our analyses show where the 'ākepa population has changed, presumably in response to management actions and changes in environmental conditions. Accounting for both spatial shifts and temporal changes in population abundance and distribution in our analysis benefits conservation planning through improved management efficiency and reduced costs. Management actions can then be applied to priority areas where a species is most likely to respond or requires further intervention. Since 1985, management in the open-forest stratum at Hakalau has consisted of fencing, removing and controlling non-native ungulates, and controlling invasive non-native plants (USFWS, U.S. Fish and Wildlife Service 2010). Removal of feral cattle *Bos taurus* was achieved promptly (Maxfield 1998) but control of pigs *Sus scrofa* has been more difficult (Hess et al. 2010, Hess 2016). After the release from grazing and trampling, vegetation in the study area has responded with evidence of early seral regeneration (Hess et al. 2010).

Controlling pigs has been more challenging due to their prolific reproductive rates, difficulties of locating and removing the last individuals, and egress into the study area from the surrounding reservoir populations (Hess 2016). Feral pigs were removed from management units in the south stratum by 2002 (Hess et al. 2006). Over this period 'ākepa increased by nearly one bird ha⁻¹. Since 2008 though 'ākepa have decreased to densities that are similar to those at the start of the time series. These fluctuations occurred within the 95% CI, indicating that the south stratum 'ākepa population has fluctuated but that it has not increased or declined overall. The short-term declining trajectory since 2008 coincided with a pig reinvasion that has yet to be eradicated. Our data indicated that a response in 'ākepa densities lags pig eradication and habitat recovery by several years. Continued abundance monitoring, focusing on 'ākepa densities along the eastern edge of the south stratum, will provide information of 'ākepa trends and track the trajectory to inform management and conservation planning. Additional biological data, such as species' demographic data, may further improve decision making through prioritising management actions specific to improving species' productivity and mitigating threats. Detecting a response in demographic parameters, or derived demographic quantities of survival and reproduction, may be observed more quickly than detecting changes in just the abundance time series (Guillaumet et al. 2016).

It has been more difficult to remove pigs from the northern portion of the refuge. Our results show that 'ākepa remained at low densities in this region for an extended period before increasing relatively rapidly. This increase occurred some time after numbers of pigs had been suppressed and there

had been increases in native ferns and woody vegetation (Hess et al. 2010). By 2017, ‘ākepa densities remained near zero in only the north-west portion of the north stratum. This area coincides with an infestation of banana poka vine *Passiflora tarminiana*, a draping liana that can engulf the forest canopy layer. Loh and Tunison (1999) showed banana poka decreased by half after the removal of pigs in similarly managed rainforest habitat in Hawai’i Volcanoes National Park, Hawai’i Island. Refuge management includes controlling the vine and other invasive non-native plants. Eradicating this invasive vine on the refuge will be facilitated by removing it from adjacent reservoir populations. Given increases in ‘ākepa elsewhere in the north stratum it is reasonable to expect that ‘ākepa will continue to increase with the removal of non-native ungulates and plants. Our approach to identify and target priority areas assumes that there are positive responses between the level of management effort, spatial extent of the area managed and target species benefit, i.e. an immediate, proximate impact. Prioritised and efficient management will become more important as traditional approaches to conserving and managing species inadequately account for rapidly changing, uncertain environments and novel ecosystems (Hobbs et al. 2009).

Our approach provides a framework for understanding changes in bird populations, as well it can provide insight in anticipation of management that may facilitate conservation. A limitation of Camp et al. (2016) analysis of ‘ākepa abundance and trend is that they treated the entire study area as homogeneous, whereas we have shown that the distribution and density of ‘ākepa are heterogeneous varying over space and time. That is, our results provide insights into the distribution of ‘ākepa densities where our density surface maps illustrate the dynamics of the species through the study area, presumably in response to management. Extending the management that has improved habitat in the central portion of the open-forest stratum could benefit the adjacent population in the north region and where it extends east into lower elevations of the refuge (Camp et al. 2016). In addition, ‘ākepa occur in five spatially disjunct subpopulations with the Hakalau subpopulation being the largest (Judge et al. 2018). These subpopulations occur in comparable habitat, face similar threats, and hence the management at Hakalau may be beneficial. Management of these other subpopulations may benefit by coinciding with frequent monitoring and including spatio-temporal modelling similar to ours to maximise benefits from the management actions.

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Author contributions – RJC and LT conceived the ideas; SJK provided the data; RJC and DLM analysed the data; RJC lead the writing of the manuscript. All authors contributed critically to the manuscript and gave final approval for publication.

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Supplementary material (available online as Appendix ecog-04859 at <www.ecographyjournal.org/appendix/ecog-04859>). Appendix 1–6.