

Habitat suitability through time: using time series and habitat models to understand changes in bird density

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Abstract. Confronted with a rapidly changing world and limited resources for conservation, ecologists are increasingly challenged with predicting the impact of climate and land-use change on wildlife. A common approach is to use habitat-suitability models (HSMs) to explain aspects of species' occurrence, such as presence, abundance, and distribution, utilizing physical habitat characteristics. Although HSMs are useful, they are limited because they are typically created using spatial rather than temporal data, which omits temporal dynamics. We explored the value of combining spatial and temporal approaches by comparing HSMs with autoregressive population models. We investigated a 28-year period of bird community dynamics at a field site in northern California during which time the plant community has been transitioning from scrub to conifer forest. We used the two model frameworks to quantify the contribution of vegetation change, weather, and population processes (autoregressive models only) to variation in density of seven bird species over the first 23 years. Model predictive ability was then tested using the subsequent five years of population density data. HSMs explained 58% to 90% of the deviance in species' density. However, models that included density dependence in addition to vegetation covariates provided a better fit to the data for three of the seven species, Song Sparrow (*Melospiza melodia*), White-crowned Sparrow (*Zonotrichia leucophrys*), and Wrentit (*Chamaea fasciata*). These three species have more localized dispersal compared to the other four species, suggesting that dispersal tendency may be an important life-history trait to consider when predicting the impact of climate and land-use change on population levels. Our results suggest that HSMs can effectively explain and predict variation in species' densities through time, however for species with localized dispersal, it may be especially informative to include population processes.

Key words: climate change; habitat suitability model; population density; Ricker; species distribution model; succession; time series.

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INTRODUCTION

Habitat suitability models (HSMs) are an integral component of most species distribution

models, and are thus a cornerstone of predicting species' response to climate and land-use change (Guisan and Thuiller 2005, Elith and Leathwick 2009). However, certain assumptions may limit

their applicability, particularly for predicting species responses to future conditions (Pearson and Dawson 2003, Araujo and Guisan 2006). Because HSMs are usually created using population data collected across space rather than through time, any temporal dynamics in species-environment interactions are not captured (Elith and Leathwick 2009, Wiens et al. 2009). Furthermore, most of these models ignore population-dynamic processes, such as dispersal, biologically realistic growth rates, and density dependence. If the ability of a species to colonize and persist in areas with high habitat suitability is not limited by temporal population dynamics, then these simple spatial models may be adequate. However, if the abundance of a species is strongly influenced by local reproductive rates, density dependence, or other temporally varying factors, then HSMs may fail to provide an accurate prediction of habitat suitability, or misrepresent the true uncertainty associated with the process (Pearson and Dawson 2003, Rotenberry and Wiens 2009).

To move conservation forward in increasingly dynamic ecological systems, the focus needs to transition from using temporally static habitat models when predicting species response to future conditions toward explicitly incorporating temporal processes. For a given environmental stressor, the rate of change in part determines the extent of ecological impact (Huntley et al. 2010); for example, rapidly changing conditions can result in a mismatch between habitat use and habitat quality resulting in non-ideal habitat selection and ecological traps (Battin 2004, Arlt and Pärt 2007). The importance of incorporating time-dependent processes into HSMs to improve understanding has been acknowledged (Bissonette and Storch 2007). However, challenges remain in dealing with the complexity of both spatial and temporal variation, and most efforts to predict species response to climate and land-use change in recent years have been based on temporally static models (Wiens et al. 2009).

Efforts to overcome the temporally static nature of HSMs are diverse and increasing. One strategy has been to focus on identifying the source of errors and improving statistical methods (Barry and Elith 2006, Elith and Graham 2009). Other strategies include indentifying strengths and limitations of HSMs in different

scenarios by comparing different modeling techniques (Moisen and Frescino 2002, Elith and Graham 2009), or by physiological and mechanistic modeling based on relationships between energetics and environmental conditions (Kearney and Porter 2009, Buckley et al. 2010). Finally, efforts are increasingly applied to validate the temporal applicability of HSMs by comparing models constructed from climate conditions with species distributions from earlier time periods (Tingley et al. 2009, Veloz et al. 2011).

These approaches each assume that distribution and abundance of species are determined by extrinsic factors, ignoring processes that are intrinsic to population processes such as biologically realistic growth rates and density dependence. How might we more formally address intrinsic population processes? One way is to look beyond the HSM framework and use common analytical tools that incorporate temporally dynamic processes. Population models based on time series of population density have long been a foundation of ecological research (Moran 1953, Dennis and Taper 1994, Herrando-Pérez et al. 2012). Logistic population models are widely used to fit population growth and density dependence parameters to time series data. These models can be modified to include environmental factors, such as weather or habitat characteristics (Dennis and Otten 2000, Boggs and Inouye 2012), and can be further modified to accommodate linear and non-linear trends in carrying capacity (Holyoak and Baillie 1996, Lima et al. 2008, Fowler and Pease 2010).

Recently, there has been growing interest in integrating the HSM framework with a population model framework to incorporate population processes and improve projections (Franklin 2010, Huntley et al. 2010). Keith and colleagues (2008) combined HSMs with spatially explicit population models to understand factors affecting persistence of plant species in future climate scenarios. Anderson and colleagues (2009) incorporated dispersal to understand extinction risk at the range margins of two lagomorphs under contrasting future climate scenarios. While combining PVA and HSM approaches provides a promising way forward, an explicit comparison of the two approaches would inform our understanding of the value in incorporating temporal population processes into HSMs. Such

a comparison offers the possibility that there are complementary uses of these two kinds of models.

Studying long-term population responses of animals to successional changes in plant communities provides an opportunity to compare these two modeling frameworks. It has long been understood that vegetation succession can affect the distribution and abundance of animals, although most studies have substituted space for time and few have followed the response of a community through time (e.g., Johnston and Odum 1956, Venier and Pearce 2005; but see Holmes and Sherry 2001, Drever and Martin 2007). Furthermore, attempts to predict future response to vegetation change using models generated with spatial variability have often been unsuccessful (Fielding and Haworth 1995, Rotenberry and Wiens 2009, Vallecillo et al. 2009), indicating that the complexity of habitat suitability is frequently not captured by using cross-sectional data. Studying the response of populations to successional vegetation dynamics through time as opposed to across space provides an opportunity to evaluate the role of temporal processes in affecting habitat suitability.

Here, we compare the utility of HSMs and population (logistic) models both retrospectively and prospectively using a 28-year dataset detailing changes in density of seven passerines and near-passerines in a landscape undergoing rapid secondary vegetation succession. We developed both HSM and population models for these species to evaluate the influence of population processes, vegetation change, and variation in rainfall on species density from 1983 to 2005. We then compared and contrasted the utility of each approach in predicting changes in density in the subsequent 5 years. Our objectives were (1) to evaluate the ability of a HSM and a population model to retrospectively explain variation in species densities over time, and (2) to compare the ability of HSMs and population models to prospectively predict changes in bird density.

METHODS

Data collection

Study site and system.—Our 36 hectare study area at the Palomarin Field Station (“Palomarin”) of Point Blue Conservation Science (formerly the

Point Reyes Bird Observatory) is located at the southern end of the Point Reyes National Seashore, Marin County, California (see Porzig et al. 2011 for details). Prior to incorporation into the National Park in 1965, much of the study area and surrounding landscape was cultivated for agriculture or grazing (Mewaldt and King 1977). Since incorporation into the park, the only substantial disturbance to the study area has been the annual maintenance of a dirt road through the study plot. Since territory data collection began in 1980, the remnant grassland and cultivated fields have undergone rapid successional revegetation by coastal scrub dominated by coyote bush (*Baccharis pilularis*) and Douglas-fir (*Pseudotsuga menziesii*) (Figs. 1 and 2). Rainfall patterns are typical of a Mediterranean climate, with the vast majority of the rain accumulating from October to April (Fig. 3; Chase et al. 2005).

Bird density.—Annual breeding density of each species was quantified with intensive (>30 visits per season) spot-mapping (Ralph et al. 1993). Data collection began in 1980, but for the purposes of this study, we begin in 1982 when methods were fully standardized for all species. From 1982 to 2010, the study area was surveyed throughout the breeding season (15 March–31 July) by 3–5 biologists. Daily censuses lasted 4–6 hours and were typically conducted during the first 6 hours of daylight. Biologists systematically searched the study area, covering the entire study area at least once every two weeks. Locations of each bird encounter were mapped and territorial behaviors were described (Silkey et al. 1999). Mapping of territory boundaries was facilitated by grid stakes placed every 30 meters and color banded individuals of five of the species in this analysis, Wrentit (*Chamaea fasciata*), Song Sparrow (*Melospiza melodia*), White-crowned Sparrow (*Zonotrichia leucophrys*), Spotted Towhee (*Pipilo maculatus*), and Bewick’s Wren (*Thryomanes bewickii*). Territory boundaries were determined by a combination of criteria, including counter-singing, breeding observations, and clustering and timing of singing locations. Throughout the study, the final territory maps for each season were vetted by G. R. Geupel.

This extremely intensive spot-mapping effort, on a gridded study area ensures very low or negligible rates of measurement error, an impor-



Fig. 1. Palomarin study area in Marin County, California, USA circa 1970 (top) and 2008 (bottom).

tant consideration with the application of autoregressive models to time series (Dennis and Taper 1994). Territories were included in the analysis if they were at least 50% within the study area. The time series for each species was constructed from the number of territories within the 36 hectare study area each year.

For the purposes of this analysis, we focus on territory densities of seven species representing a

range of life-history strategies: Anna's Hummingbird (*Calypte anna*), Bewick's Wren, Wrentit, Orange-crowned Warbler (*Oreothlypis celata*), Spotted Towhee, Song Sparrow, and White-crowned Sparrow. These species vary in their foraging strategies, nesting microhabitat preferences, dispersal tendencies, and migratory strategies. Foraging strategies range from nectivore (Anna's Hummingbird), to primarily insectivore

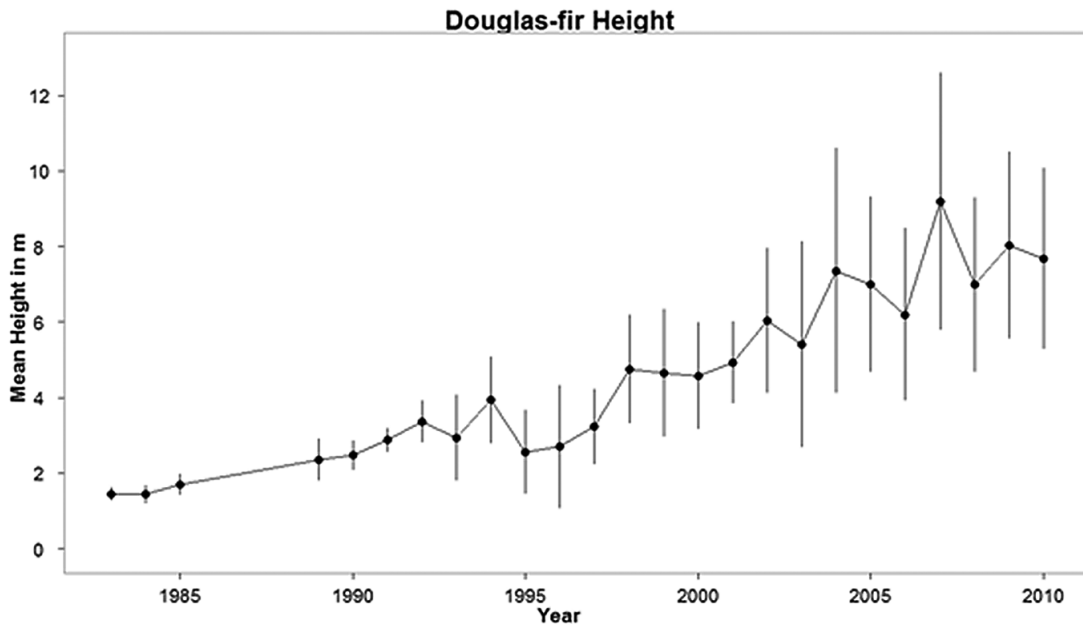


Fig. 2. Changes in mean Douglas-fir height at eight locations in the study area at Palomarin Field Station, Marin County, California, USA.

(Orange-crowned Warbler, Bewick’s Wren), to mixed insectivore/gramnivore (White-crowned Sparrow, Song Sparrow). Nesting microhabitat preferences range from lower canopy (Anna’s

Hummingbird) to shrub (Wrentit, Song Sparrow, White-crowned Sparrow), ground (Spotted Towhee, Orange-crowned Warbler), and cavity/crevice (Bewick’s Wren). Six of the seven species are

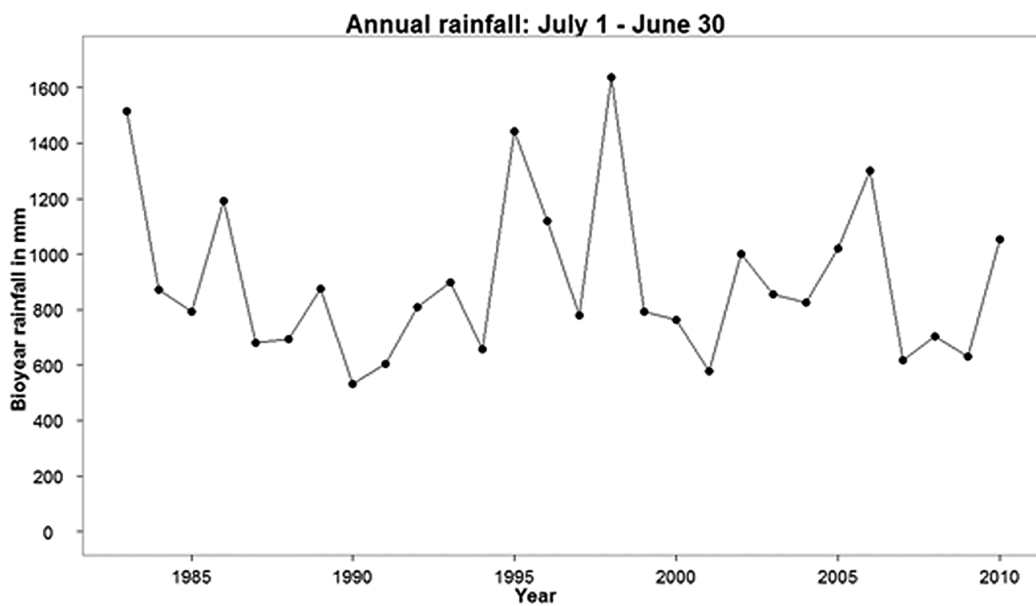


Fig. 3. Annual biyear (July 1–June 30) rainfall at Palomarin Field Station, Marin County, California, USA.

year-round residents; Orange-crowned Warbler is a migrant. Dispersal strategy ranges from strong natal philopatry (e.g., Wrentit; Baker et al. 1995) to weak natal philopatry (e.g., Orange-crowned Warbler; Point Blue, unpublished data).

Vegetation.—Vegetation was measured annually at eight locations. Each location consists of four 10-meter transects. Height and length of all shrub and tree species intersecting each 10-meter transect were measured. We summarized transect data by summing the total length (a measure of percent cover) and averaging the height of the seven dominant woody species at the eight survey locations each year. Vegetation measurements were not taken in 1986, 1987, or 1988; we interpolated values of each vegetation variable in these years using local polynomial regression. We focused on cover and height of the dominant woody plant species because they represent the dominant successional changes in the plant community at our study site.

Rainfall.—Rainfall was measured daily. Annual rainfall was totaled from 1 July to 30 June; this ‘bioyear’ rainfall is equivalent to the ‘water year’ used by hydrologists summarizing precipitation in California (Chase et al. 2005). Summarizing rainfall in this way provides a description of the annual rainfall in the wet season immediately preceding the breeding season.

Model descriptions

Habitat suitability models.—We used generalized additive models (GAMs) because they are among the most commonly used statistical models among species distribution models and can accommodate nonlinear relationships (Guisan and Thuiller 2005, Zuur et al. 2009). GAMs can also accommodate abundance data and are likelihood-based so that, unlike other algorithms, they are easily compared to other likelihood models via an information criterion. The GAM is of the following form:

$$Y_i = \alpha + f(X_i) + \varepsilon_i \tag{1}$$

where Y_i is abundance, and $f(X_i)$ is a smoothing function fit with penalized cubic regression splines (Zuur et al. 2009) and ε_i is the unexplained variance.

Population models.—The basic form of the logistic family of population models describes trends in density in terms of an annual popula-

tion growth rate, or r , and a density dependent rate. We used a discrete-time stochastic logistic model, also known as a stochastic Ricker (1954) model, because it is widely used with vertebrate species and is more robust than other logistic-types models such as the theta-logistic (Clark et al. 2010). The basic structure of model is

$$N_{t+1} = N_t e^{r(1-\alpha N_t) + \varepsilon} \tag{2}$$

where N_t is the population in the current year, N_{t-1} is the population in the previous year, r is the intrinsic population growth rate, α is the density-dependent term, and ε is random variation. We considered the model in its basic form (above) as well as two modified forms that allow incorporation of environmental covariates. The first alternative structure is of the following form:

$$N_{t+1} = N_t e^{r(1-\alpha N_t) + x + \varepsilon} \tag{3}$$

where x is an exogenous covariate (Dennis and Otten 2000).

The second alternative structure also allows for the incorporation of environmental covariates, but does so such that the covariates contribute to a trend in carrying capacity (Holyoak and Baillie 1996). This structure is of the form:

$$N_{t+1} = N_t e^{r(1-\alpha_t N_t) + \varepsilon} \tag{4}$$

Environmental covariates can be included into the carrying capacity with the following function:

$$\alpha_t = e^{\ln(\alpha) - dx} \tag{5}$$

Biological justification of candidate models.—The GAMs (Eq. 1) represent a situation in which carrying capacity varies and is entirely determined by the explanatory variables, variables extrinsic to the population processes. The biological interpretation of this is that carrying capacity can vary by year. The Ricker models represent hypotheses in which annual densities are based on the previous year’s population as well as rates of growth and density dependence. The Ricker model with environmental covariates (Eq. 3) describes a situation in which the long-term average carrying capacity is constant but fluctuations can be created by covariates. The Ricker model with environmental covariates in the density-dependent term allows for a linear trend in carrying capacity.

We built HSMs using vegetation and rainfall data as predictor variables. While habitat is made up of more components than these two variables, prior work leads us to believe they represent major components of bird habitat in our system (MacArthur et al. 1962, Rotenberry 1985). The structure and species composition of the vegetation community affects nest cover, food availability and the predator community (Felix et al. 2007, Johnson 2007). Rainfall is also an important contributor to habitat because it affects insect and seed availability as well as cover for nests from predators via annual plant growth vigor (Dybala et al. 2013). Rainfall fluctuates on a shorter time scale than successional changes in vegetation and thus captures short-term variability in habitat.

In using the Ricker model structure, we chose to focus on population level patterns. Population models based on time series of density do not have information on reproduction, survival, or age structure that are necessary to understand the underlying demographic mechanisms of population change. However, because of the frequent mismatch between single demographic processes and population level patterns, evaluating the effect of environmental variation on overall population size and the combined or 'ensemble' growth rate is equally important in informing conservation and management (Herando-Pérez et al. 2012).

Data analysis

For vegetation, we considered variables independently and via ordination. Because many of the vegetation variables are correlated, we used Principal Components Analysis (PCA) to reduce the dimensionality of the data. We chose PCA over other ordination techniques (e.g., non-metric multidimensional scaling) to preserve the non-ranked relationships among the data. We used PCA for the 14 vegetation variables (height and length of each of the seven dominant plant species) and retained the first two axes of the PCA scores. For rainfall, we used biyear rainfall and previous biyear rainfall. We considered previous biyear rainfall because prior work at Palomarin has shown that biyear rainfall is positively correlated with reproductive success in the same summer and that reproductive success is positively correlated with density in the subsequent year, thus demonstrating a 1 year

time lag effect of biyear rainfall on density (Chase et al. 2005).

We created candidate HSMs using a two-step process. The first step identified the vegetation variables that consistently explained the most variation in species abundance. We fit 16 single-variable GAMs to the time series of densities for each species; the candidate models included the two PC-axis scores and the height and length of each of the seven dominant plant species. The three vegetation variables that consistently explained the most variation in each species were the first principal component, height of Douglas-fir and height of coyote bush. In the second step, we combined each of these three best vegetation variables with rainfall and lag rainfall. Because Douglas-fir and coyote bush show strong and significant correlation with each other (Pearson's correlation coefficient = 0.79, $p < 0.001$), we did not include them in the same model, nor did we include either variable in a model with PC1. To avoid overfitting (given 23 years of data), candidate models were limited to a maximum of two-predictor variables. The final model set is listed in Table 1.

We intentionally did not address the temporal autocorrelation in fitting the GAMs. Habitat suitability models that use spatial variation in habitat and animal abundance do not typically incorporate time and thus any variability in density that is due to temporal autocorrelation is not accounted for. This reflects that a goal of our analysis was to compare the results from typical habitat suitability modeling approach (ignoring time) to a more explicitly temporal model that incorporates both a population process and habitat and weather covariates.

We built Ricker models from the time series of territory densities. Candidate models included models without covariates as well as models with vegetation and rainfall variables as covariates and models with vegetation covariates contributing to a trend in carrying capacity. The covariates that were considered were biyear rainfall, previous biyear rainfall, Douglas-fir height, coyote bush height and the first principal component of vegetation change. All predictor variables were scaled and centered to facilitate model convergence. The complete set of candidate models is listed in Table 1. All analyses were conducted using R (R Development Core Team

Table 1. Description of the set of candidate models, including the type of model (GAM or Ricker), the assumed behavior of the carrying capacity, and the predictor variables.

Model	Type	Behavior of carrying capacity	Variables
gam_veg1	GAM	varying	Baccharis (BAPI) height
gam_veg2	GAM	varying	Douglas-Fir (PSME) height
gam_rain1	GAM	varying	rain
gam_rain2	GAM	varying	lag rain
gam_veg1 + rain2	GAM	varying	BAPI height; lag rain
gam_veg1 + rain1	GAM	varying	BAPI height; rain
gam_veg2 + rain2	GAM	varying	PSME height; lag rain
gam_veg2 + rain1	GAM	varying	PSME height; rain
gam_rain1 + rain2	GAM	varying	rain, lag rain
gam_PC1	GAM	varying	PC1
gam_PC1 + rain1	GAM	varying	PC1, rain
gam_PC1 + rain2	GAM	varying	PC1, lag rain
density_indep	Ricker	fixed	Dens. Indep. growth
ricker	Ricker	fixed	Dens Dep growth
ricker_veg2	Ricker	varying, constant average	Dens Dep, PSME height
ricker_veg1	Ricker	varying, constant average	Dens Dep, BAPI height
ricker_rain1	Ricker	varying, constant average	Dens Dep, rain
ricker_rain2	Ricker	varying, constant average	Dens Dep, lag rain
ricker_veg2 + rain1	Ricker	varying, constant average	Dens Dep, PSME height, rain
ricker_veg2 + rain2	Ricker	varying, constant average	Dens Dep, PSME height, lag rain
ricker_veg1 + rain1	Ricker	varying, constant average	Dens Dep, BAPI height, rain
ricker_veg1 + rain2	Ricker	varying, constant average	Dens Dep, BAPI height, lag rain
ricker_rain1 + rain2	Ricker	varying, constant average	Dens Dep, rain, lag rain
ricker_veg1_trend	Ricker	trend	Dens Dep, BAPI height
ricker_veg2_trend	Ricker	trend	Dens Dep, PSME height
ricker_PC1	Ricker	varying, constant average	Dens Dep, PC1
ricker_PC1_rain1	Ricker	varying, constant average	Dens Dep, PC1, rain
ricker_PC1_rain2	Ricker	varying, constant average	Dens Dep, PC1, lag rain
ricker_PC1_trend	Ricker	trend	Dens Dep, PC1

2012); GAMs were fitted using library mgcv (Wood 2004).

Comparing models.—We identified the best HSM, the best population model, and the best overall model between the two model types using AICc scores (Burnham and Anderson 2002) and considered models within a Δ AIC of 2 to be similarly supported as the top model. Because both GAMs and the nonlinear Ricker models are likelihood based and were fitted using the exact same dataset, their penalized likelihoods can be compared using an information criterion (Burnham and Anderson 2002).

Evaluating predictive ability.—To test the predictive ability of the different models, we fit the above models to data from 1983 to 2005 and predicted abundance for each species from 2006 to 2010 using the best population model (with or without vegetation and rainfall covariates) and the best habitat model (containing one of the three vegetation variables, with or without rainfall covariates). Although our time series starts in 1982, we fit models to the data starting in 1983 because Ricker models use density in the

previous time step. We calculated the 95% prediction intervals via posterior simulation. For the GAMs, we generated replicate predictions from the covariance matrix of parameter estimates. For the Ricker models, we bootstrapped replicate time series using the parameter estimates. We then compared predictions and associated prediction intervals to observed values by plotting the predicted vs. observed values and visually assessing the differences from a 1:1 line.

RESULTS

Temporal changes in physical and habitat variables

Substantial change in the physical environment during our study resulted in a wide range of variation on which to base our modeling of species' densities. Vegetation structure changed dramatically (Fig. 1). Average height of Douglas-fir increased from 1.4 m in 1983 to 7.6 m in 2010 (Fig. 2). Average height of coyote bush increased from 0.7 m in 1983 to 1.3 m in 2010. Length of woody plants along transects (cover) also in-

creased, Douglas-fir by 3000% and coyote bush by 180%. Bioyear rainfall was highly variable, with no linear trend ($p = 0.71$, Fig. 3). Rainfall totals ranged from a low of 533 mm in 1990 to a high of 1639 mm in 1998.

Habitat suitability models

The HSMs performed well for all species. The best habitat-suitability model explained 58% of deviance for Wrentit, 58% for Bewick's Wren, 76% for Song Sparrow, 77% for Anna's Hummingbird, 81% for Spotted Towhee, 81% for White-crowned Sparrow, and 90% for Orange-crowned Warbler (Fig. 4). Douglas fir was the most common vegetation variable with predictive ability, appearing among the top models for all but two species. For these two species, Wrentit and White-crowned Sparrow, the first principal component was the vegetation variable in the top model. Including rainfall as a covariate was supported among the top models ($\Delta\text{AICc} \leq 2$) for four out of the seven species: Anna's Hummingbird, Bewick's Wren, Orange-crowned Warbler, and Spotted Towhee. Despite the simplicity of the candidate models, the GAMs explained a high proportion of the deviance with relatively simple smoothing functions, ranging from linear smoothers (e.g., Spotted Towhee) to a cubic smoother (e.g., Orange-crowned Warbler).

Population models

Deviance explained by the best stochastic Ricker model was 30% for Orange-crowned Warbler, 49% for Bewick's Wren, 60% for Anna's Hummingbird, 64% for Wrentit, 74% for Song Sparrow, 78% for Spotted Towhee, and 82% for White-crowned Sparrow. The model with the most support for six out of seven species included vegetation and/or rainfall covariates in the model structure (Fig. 5; Appendix: Table A1). A model with only a trend in carrying capacity was supported as the top model for two species, Song Sparrow and White-crowned Sparrow, and among the top models for Bewick's Wren, Orange-crowned Warbler and Spotted Towhee (Fig. 5; Appendix: Table A1). Only Wrentit was best supported by a population model with no environmental covariates; both a density dependent and independent model had a comparable amount of support ($\Delta\text{AICc} = 0.8$ for the difference between these two models). For White-

crowned Sparrow, 9 out of 17 Ricker models had a $\Delta\text{AICc} \leq 2$, including a density dependent model without covariates and a density independent model. Douglas-fir height was the most commonly included covariate. Two of the seven species (Anna's Hummingbird and Spotted Towhee) had rainfall included in the top model, and rainfall was included among the top models for Wrentit and White-crowned Sparrow.

Comparing the two kinds of models

Species varied in whether habitat suitability or population models had more support based on AICc values. For three species (Anna's Hummingbird, Orange-crowned Warbler, and Spotted Towhee), HSMs were clearly better supported, with the best population model having a $\Delta\text{AICc} > 2$. For three species (Wrentit, Song Sparrow, and White-crowned Sparrow), population models had greater support than the HSMs. For one species, Bewick's Wren, the support for a HSM and population model was approximately equal (Fig. 5; Appendix: Table A1).

Predicting abundance in 2006–2010 with the best HSM and the best population model for each species showed that neither model made notably more accurate predictions (Figs. 4 and 6). The 95% confidence envelope of the HSMs failed to encompass the observed values more often than the confidence envelope for the Ricker model. In these cases, the Ricker models gave a more accurate view of model uncertainty (Fig. 4).

DISCUSSION

Our results suggest that even in the absence of demographic information, species-environment HSMs can effectively explain and predict variation in species' densities through time. Overall, a simple HSM without temporal processes explained over half of the deviance in trends for all seven species examined. Our results also illustrate that while environmental variables alone are generally adequate, there is potential for improvement. By combining population growth rates and density dependent feedbacks with environmental variables, our ability to explain trends was improved for three of the seven species. This result suggests that in some cases incorporating demographic patterns into HSMs can improve projections and hence con-

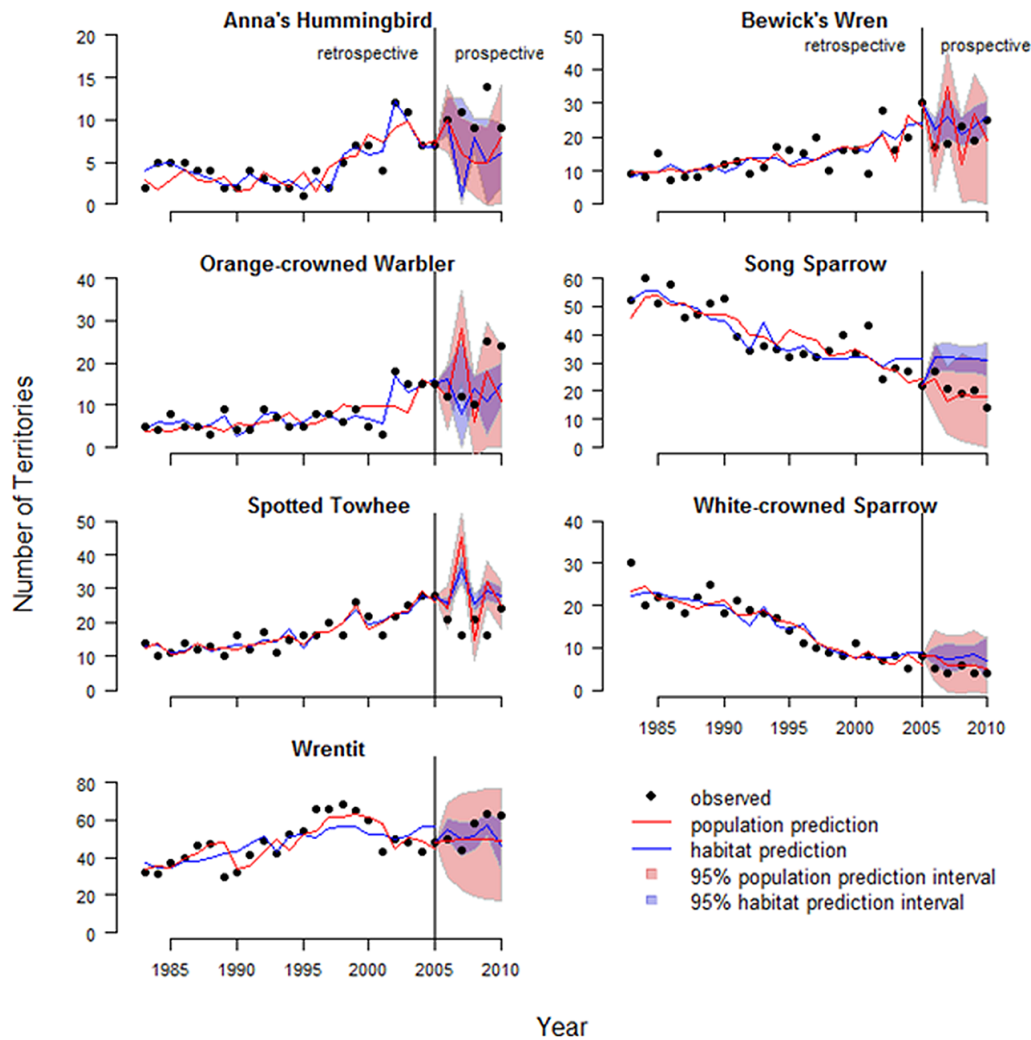


Fig. 4. Number of territories of each of the seven focal species per 36 hectares, model estimates and predictions.

servation planning. While it is known that density dependence can alter predictions of population viability models (Ginzburg et al. 1990), this has not, to our knowledge, been examined in the context of predicting population densities in comparison with HSMs. Here, we compare the retrospective and prospective applications of these models, focusing on the inferences about the intrinsic population processes and extrinsic environmental influences in the context of life-history variation to provide insight into the relative benefits of the two approaches.

The retrospective application

Fitting candidate models to the period 1983–

2005 provided insight into the relative contribution of intrinsic population processes and extrinsic environmental influences. Overall, our results strongly support the influence of vegetation change on the density of these species. Although successional changes in plant structure and composition are due to the lack of human disturbance and suppression of natural disturbances (e.g., fire) since the early 1960s, our results support the conclusions of other studies that the indirect impact of climate change on bird abundance through changes in plant communities that provide bird habitat will be an important predictor of future climate-change impacts (Seoane et al. 2004, Stralberg et al. 2009, Boggs

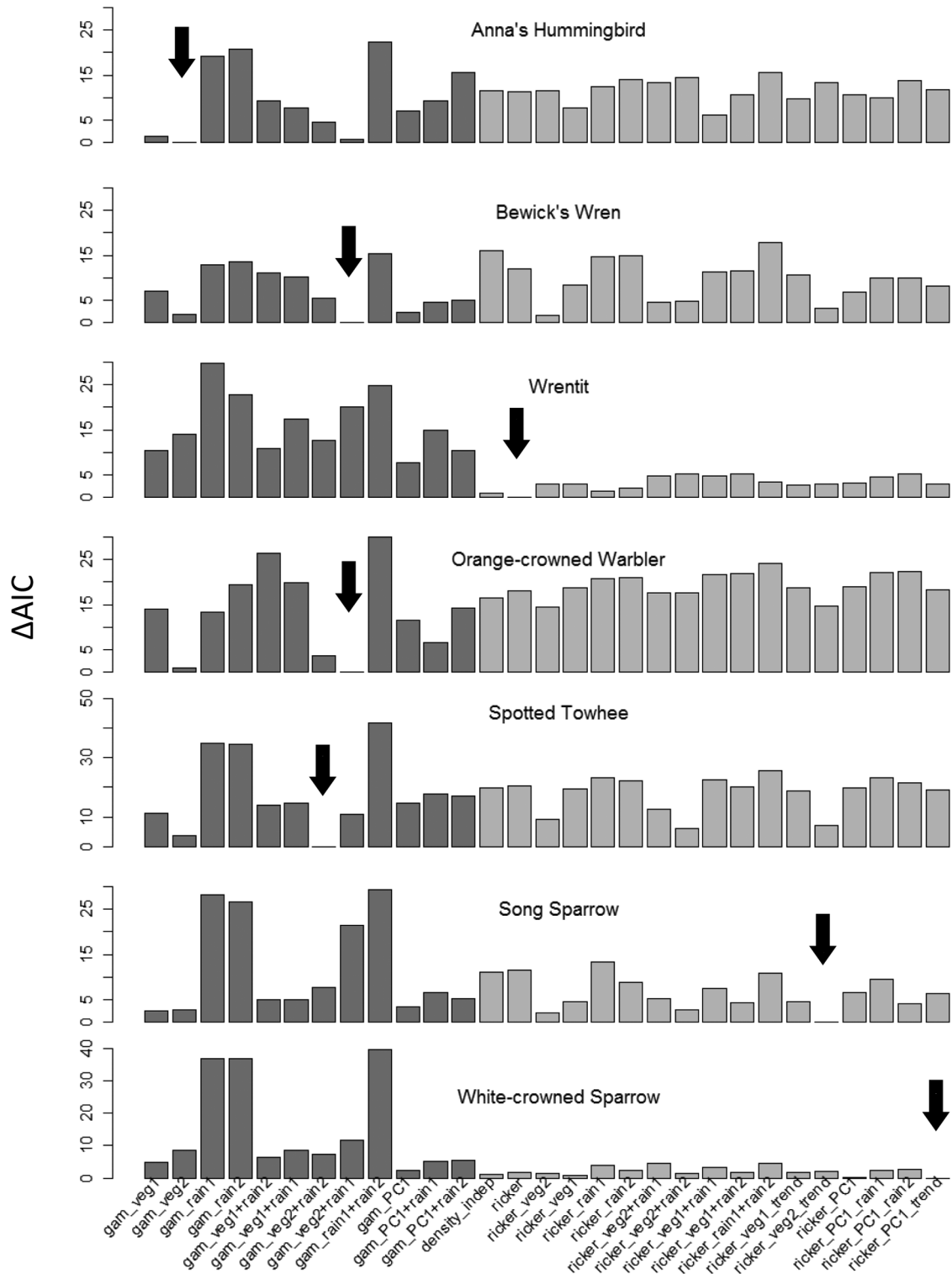


Fig. 5. Chart of $\Delta AICc$ values for each model. Dark gray bars are GAMs, light gray bars are logistic models. Black arrows point to the best model ($\Delta AICc = 0$). Table 1 describes the models.

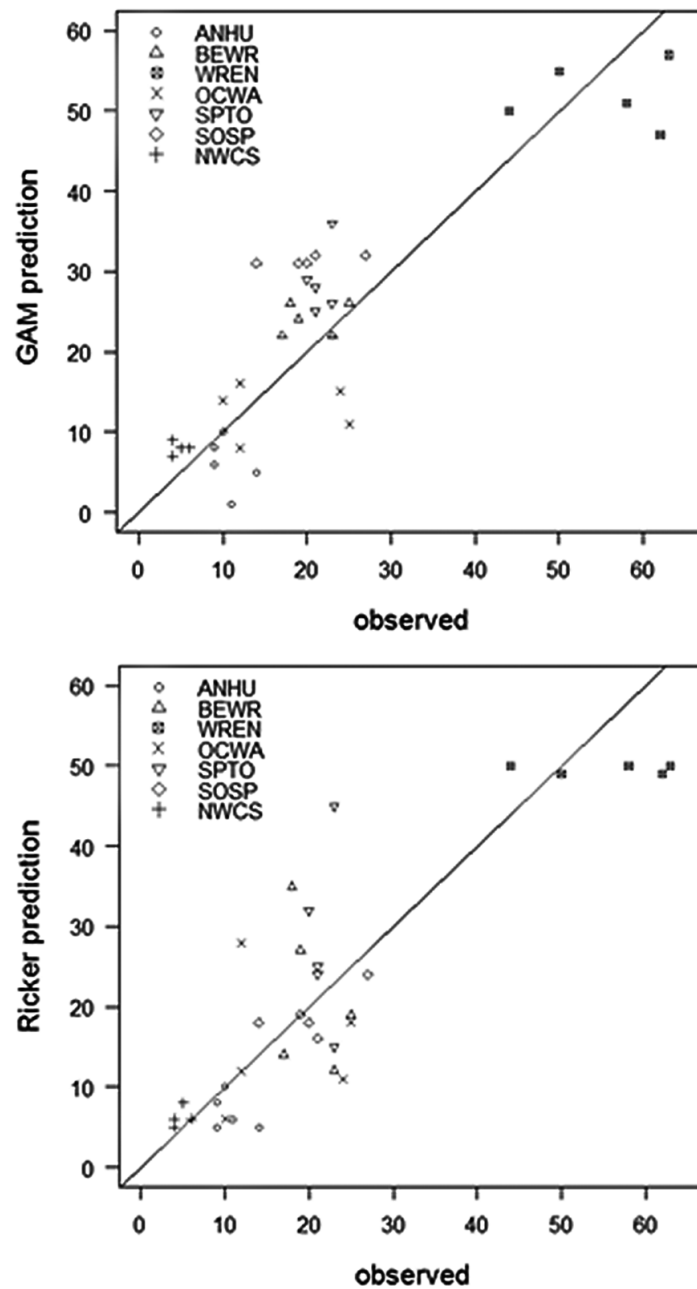


Fig. 6. Model predictions plotted against observed values for GAMs and Ricker models with a 1:1 line for all seven species: Anna’s Hummingbird (ANHU), Bewick’s Wren (BEWR), Wrentit (WREN), Orange-crowned Warbler (OCWA), Spotted Towhee (SPTO), Song Sparrow (SOSP) and White-crowned Sparrow (NWCS). Species are distinguished by type of point.

and Inouye 2012). While rainfall did not explain a large percentage of the variance in densities, our results support previous work that show that annual weather rainfall patterns can contribute to

vital rates (Chase et al. 2005, Dybala et al. 2013) and ultimately density (Silkey et al. 1999, Dennis and Otten 2000).

Despite the success in modeling densities using

environmental factors, the HSM assumption that population density changes around the carrying capacity are entirely determined by factors extrinsic to population processes was not supported in all cases. This indicates that intrinsic population processes account for some of the variation in abundance and the fact that our modified Ricker models did not fit perfectly indicates that carrying capacity does not vary perfectly with environmental changes. A possible explanation is that temporal lags are involved in species-habitat relationships, as has been shown in other studies (Knick and Rotenberry 2000, Ambrosini et al. 2002).

Despite the many attempts to identify types of biological processes that should be incorporated into HSMs, their prioritization remains elusive (Wiens et al. 2009). Comparing multiple species allows us to evaluate the effects of life-history traits in modulating the response of species to changes in vegetation. We found that three species (Wrentit, Song Sparrow, and White-crowned Sparrow) whose trends were best explained by a population model all have relatively high rates of local recruitment and small localized dispersal kernels (Halliburton and Mewaldt 1976, Petrinovich and Patterson 1982; Point Blue, *unpublished data*), with Wrentits being the most extreme case (Baker et al. 1995). This is consistent with the idea that dispersal and recruitment rates are relevant demographic processes to incorporate into HSMs. Just as future extinction risk is sensitive to dispersal ability in mammals (Schloss et al. 2012), other birds (Barbet-Massin et al. 2011), and plants (Martínez et al. 2012), the projections of HSMs of birds are also likely sensitive to dispersal ability.

The prospective application

HSMs were originally developed to predict spatial distribution of abundance and are increasingly applied to project patterns of spatial distribution into the future (Elith and Leathwick 2009). Logistic population models were developed to estimate rates of growth and density dependence and are commonly used to evaluate temporal patterns in abundance (Clark et al. 2010). Our results show that, at least over the five year period that we evaluated predictive ability, neither model was clearly more accurate in predicting species abundances. However, the

confidence envelope around the Ricker predictions encompassed the observed values more often. Fig. 4 indicates that as the prediction interval increases, demographic uncertainty plays an increasingly important role.

Ultimately, the appropriate approach to take when modelling species response to future climate and land-use scenarios will depend on the temporal and spatial scale of the question, and the life history characteristics of the species. Our investigation shows that HSMs perform well when explaining and predicting variation in density through time, but in some cases, particularly for species with small natal dispersal distances, an approach that incorporates intrinsic population processes can better explain and predict temporal variation in density. While these results validate the common usage of HSMs for predicting species response to climate and land use change, they also indicate that incorporating population processes can improve models, particularly for some life histories.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. ΔAIC values for each model. Models within ΔAIC of 2 are in boldface. The best model for each class (Ricker or GAM) is in italics.

Model name	Model type	Anna's Hummingbird	Bewick's Wren	Wrentit	Orange-crowned Warbler	Spotted Towhee	Song Sparrow	White-crowned Sparrow
gam_veg1	GAM	1.3	7	10.4	13.9	11.3	2.5	5
gam_veg2	GAM	0	1.7	13.9	0.9	3.8	2.6	8.7
gam_rain1	GAM	19.3	12.8	29.9	13.3	34.9	28.2	36.9
gam_rain2	GAM	20.7	13.6	22.9	19.4	34.7	26.7	36.9
gam_veg1 + rain2	GAM	9.1	11.1	10.9	26.4	13.8	4.9	6.3
gam_veg1 + rain1	GAM	7.6	10.1	17.4	19.9	14.7	5	8.6
gam_veg2 + rain2	GAM	4.5	5.4	12.7	3.6	0	7.7	7.5
gam_veg2 + rain1	GAM	0.5	0	20.1	0	10.7	21.5	11.8
gam_rain1 + rain2	GAM	22.4	15.3	24.8	30.2	41.9	29.5	39.9
gam_PC1	GAM	7	2.2	7.6	11.4	14.5	3.4	2.3
gam_PC1 + rain1	GAM	9.3	4.5	14.9	6.6	17.8	6.5	5.2
gam_PC1 + rain2	GAM	15.5	5	10.3	14.3	17.1	5.1	5.5
density_indep	Ricker	11.5	16.1	0.8	16.5	19.8	11.1	1
ricker	Ricker	11.3	12	0	18	20.5	11.5	1.7
ricker_veg2	Ricker	11.4	1.4	2.9	14.4	9.2	1.9	1.4
ricker_veg1	Ricker	7.6	8.2	2.9	18.7	19.4	4.4	0.8
ricker_rain1	Ricker	12.4	14.6	1.3	20.8	23.4	13.3	3.9
ricker_rain2	Ricker	14	14.9	1.9	21	22.2	8.8	2.5
ricker_veg2 + rain1	Ricker	13.4	4.4	4.6	17.6	12.5	5.2	4.5
ricker_veg2 + rain2	Ricker	14.5	4.7	5.2	17.7	6.1	2.7	1.4
ricker_veg1 + rain1	Ricker	6.1	11.3	4.6	21.7	22.7	7.5	3.2
ricker_veg1 + rain2	Ricker	10.6	11.5	5.2	22	20.1	4.3	1.7
ricker_rain1 + rain2	Ricker	15.5	17.9	3.2	24.1	25.5	10.9	4.4
ricker_veg1_trend	Ricker	9.7	10.5	2.7	18.8	18.8	4.4	1.7
ricker_veg2_trend	Ricker	13.2	3	2.8	14.6	7	0	2.2
ricker_PC1	Ricker	10.6	6.8	3	19	19.8	6.4	0.1
ricker_PC1_rain1	Ricker	10	9.9	4.5	22.1	23.1	9.4	2.4
ricker_PC1_rain2	Ricker	13.7	10	5.2	22.3	21.6	4.1	2.6
ricker_PC1_trend	Ricker	11.7	8	2.9	18.4	19.2	6.2	0