INFLUENCE OF SUBURBAN HABITAT ON A WINTERING BIRD COMMUNITY IN COASTAL NORTHERN CALIFORNIA

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Abstract. To evaluate factors influencing a suburban bird community in coastal northern California, we examined the abundance, richness, and diversity of wintering birds at 75 locations within the city of Arcata. For each location we used aerial imagery to determine the proportions of vegetation and impervious surfaces within 75 m and the distances to various landscape features. Human activity was measured and used as a covariate in model selection. Total bird abundance, species richness, and diversity declined with the proportion of road surface at a site, while the abundance of non-native species increased with the cover of roads and structures. The proportions of shrub and tree cover at a site predicted total abundance and richness positively. The effect of trees on species diversity was increasingly positive in more urban areas. Several species, such as Steller's Jay (*Cyanocitta stelleri*), Ruby-crowned Kinglet (*Regulus calendula*), Wrentit (*Chamaea fasciata*), Winter Wren (*Troglodytes troglodytes*), Yellow-rumped Warbler (*Dendroica coronata*), and Red-breasted Nuthatch (*Sitta canadensis*), were positively associated with tall vegetation and negatively associated with road and structure cover. The White-tailed Kite (*Elanus leucurus*) was positively correlated with grass and trees and negatively correlated with road and structure cover. These species may be the most vulnerable to the habitat changes associated with urbanization in this study area. We recommend maintaining/restoring native shrubs and or trees to enhance bird communities in developed areas or to improve planning where development is inevitable. Increasing shrub and tree cover may be especially valuable in newer neighborhoods and far from forest edges.

Key words: community, diversity, habitat, suburban, urbanization, wintering.

Influencia del Hábitat Suburbano sobre una Comunidad Invernal de Aves en la Costa del Norte de California

Resumen. Para evaluar los factores que influencian una comunidad suburbana de aves en la costa del norte de California, examinamos la abundancia, riqueza y diversidad de aves invernales en 75 localidades en la ciudad de Arcata. Para cada localidad utilizamos fotografías aéreas para determinar las proporciones de superficie de vegetación y zonas sin vegetación dentro de un radio de 75 m y las distancias a varios elementos del paisaje. La actividad humana fue medida y usada como una covariable en la selección del modelo. La abundancia total de las aves, la riqueza de especies y la diversidad disminuyeron con la proporción de superficie de caminos en un sitio, mientras que la abundancia de especies no nativas aumentó con la cobertura de caminos y estructuras. Las proporciones de cobertura de arbustos y árboles en un sitio predijeron positivamente la abundancia total y la riqueza. El efecto de los árboles sobre la diversidad de especies aumentó positivamente en las áreas más urbanas del pueblo. Varias especies, como *Cyanocitta stelleri*, *Regulus calendula*, *Chamaea fasciata*, *Troglodytes troglodytes*, *Dendroica coronata* y *Sitta canadensis* se asociaron positivamente con la vegetación alta y negativamente con la cobertura de caminos y estructuras. *Elanus leucurus* se correlacionó positivamente con los pastos y los árboles, y negativamente con la cobertura de caminos y estructuras. Estas especies pueden ser las más vulnerables a los cambios de hábitat asociados con la urbanización en esta área de estudio. Recomendamos mantener/restaurar los arbustos y/o árboles nativos para realzar las comunidades de aves en las áreas desarrolladas o mejorar la planificación donde el desarrollo es inevitable. El incremento de la cobertura de arbustos y árboles puede ser particularmente valioso en los vecindarios nuevos y en las áreas alejadas de los bordes del bosque.

INTRODUCTION

Of any human activity, the conversion of natural landscapes to urban environments produces some of the highest rates of local extinction (Wilcove et al. 1998, Marzluff 2001, McKinney 2002). Loss of species from urbanization can occur in a number of ways, including direct habitat loss, deleterious edge effects, direct human-caused mortality, and increased competition with non-native species (Czech et al. 1997, Brand and George 2001, Urban 2006). These factors often work simultaneously, magnifying the effect on local flora and fauna.

Development planners and residents need information about the factors influencing the distribution, abundance, and diversity of urban and suburban biota. In the U.S., 75% of

residents live in urban settings (U.S. Census Bureau 2002), and cities are spreading rapidly (U.S. Geological Survey 1999). Public decisions on national ecological issues are driven largely by perceptions of local natural environments (Michelson 1970, Middleton 1994). Therefore, management of urban and suburban habitats can affect biodiversity on a national scale (Owen 1978, Hadidian et al. 1997, Clergeau et al. 2001).

Within a developed area, the type and extent of urbanization can vary considerably (Jokimaki et al. 1996). Many cities in northern California, Oregon, and Washington consist of pastures with rural homes, blocklike neighborhoods, business districts, and city parks. Within and between these urbanized areas, the amount and type of vegetation surrounding developments vary extensively. The level of disturbance due to the number of humans and predatory pets also varies and may influence wildlife populations (Miller et al. 2003). Differences in vegetation, human activity, and proximity to various landscape features have been found to affect urban biotic communities significantly (Jokimaki et al. 1996, Clergeau et al. 2001). Some species are favored by the structural change and resource alteration associated with urbanization, while others are sensitive and often avoid developed areas (Blair 1996, Gering and Blair 1999, Brand and George 2001).

Studies of the effects of urbanization have rarely addressed small cities surrounded by agricultural and forested landscapes. These suburban ecotones provide a habitat complex that is structurally and ecologically different from large urban centers where most studies have been conducted. As a result, habitat use in small suburban areas may differ from previously studied relationships between urban wildlife and vegetation. For example, because of nearby natural habitat, species may respond differently to vegetation cover in a suburb–forest ecotone than in an urban center. In addition, because of nearby nonurbanized habitat, more species may inhabit suburb–forest ecotones.

Most investigations of urban bird communities, including that of Blair (1996), have categorized areas, ranked them in order of urbanization, and then compared various aspects of the communities. This method often ignores habitat features within a category that may influence community patterns. Therefore, it is important that habitat within an urbanized area be analyzed by nonranked multivariate methods so that smaller-scale variation in habitat and its effect on communities can be identified.

In coastal northern California, the factors that influence suburban bird communities in winter have not been clearly assessed. Winter habitat relationships are often overlooked but may be necessary for interpreting the effects of urbanization and understanding the source of conservation dilemmas. Recent data also suggest that nonbreeding habitat use can strongly influence subsequent reproductive success and demographics (Norris and Marra 2007). The objective of this study was to clarify the relationships between suburban vegetation, proximity to certain landscape features, human activity and the bird community wintering within the city of Arcata in northwestern California.

On the basis of previous research indicating that most bird species respond positively to vegetation volume and foliage height diversity (MacArthur and MacArthur 1961, Hohtola 1978), we hypothesized that overall bird use should increase with vegetation cover and complexity. We evaluated this hypothesis by examining the prediction that bird diversity, richness, and abundance increase with the proportion of shrub and tree cover at a site. We assessed whether vegetation complexity influences diversity, richness, and abundance by analyzing interactions with shrub and tree cover.

Blair (1996) found that use by non-native species increases with urbanization. In addition, in heavily urbanized areas bird communities are dominated by a few abundant species (Bezzel 1985, Clergeau et al. 2001). We hypothesized that use by non-native species, as well as the American Crow (see Figure 3 for all scientific names), Common Raven, and gulls should increase with the extent of urbanization. Concurrently, we expected use by most native species to decrease with urbanization. From this hypothesis we predicted that non-natives, gulls, crows, and ravens should increase in abundance with human activity and the proportion of impervious surface cover at a site, while most native species' abundance should decrease.

Last, we hypothesized that the distance to certain landscape features should influence the number of birds present at a site. We evaluated this hypothesis by testing the prediction that bird abundance, richness, and diversity vary with the distance to streams, forests, and fields or pastures.

METHODS

STUDY AREA

This study took place within the city of Arcata (40.9° N, 124.1° W), Humboldt County, coastal northern California. The city of Arcata is home to approximately 17 000 residents and approximately 7500 students of Humboldt State University. The city is positioned on an ecotone, with extensive coastal redwood (*Sequoia sempervirens*) forest to the east and a relatively narrow band of pastureland (~1–4.25 km) to the west, with the Pacific Ocean beyond. Southwestern Arcata includes the Arcata Marsh and Humboldt Bay. The study area included nearly all residential areas, business districts, schools, and other developed areas within the city limits but did not extend to the Arcata Marsh, Humboldt Bay, or the ocean.

SAMPLING DISTRIBUTION

Field observations were made by Kalinowski 4 days per week between 29 January and 11 March 2008 (except the first week in February when three surveys took place). Seventy-five sampling points were distributed randomly (with the constraint of being ≥150 m apart and ≥75 m from the urban edge) within the urbanized areas of Arcata by ArcGIS (version 9.2). Random points that were inaccessible (e.g., backyards) were adjusted

to the closest publicly accessible location. The study area was divided into six sections, each containing 12 or 13 points (i.e., one day's worth of points). For each survey, we randomly selected one of the six sections to visit. Within each section, we developed a set route prior to entering the field. We then randomly selected a starting point and direction along the route every time we visited that area. Each area was visited four times during the study, with data from all four visits used to minimize effects of imperfect probabilities of detection (MacKenzie et al. 2006).

DATA COLLECTION

We used point counts to estimate the number of birds within 75 m of each survey point. Distances to auditory and visual detections were estimated primarily with a rangefinder. When awkward angles made the rangefinder inappropriate, distances were estimated visually. Each point count lasted 10 min, initiated 1 min after arrival to accommodate a settling period (Blair 1996). Observations began 10 min after sunrise and concluded no later than 11:30 Pacific Standard Time. For each detection we recorded the species, the number of birds (if more than one at the same distance), and the activity (e.g., perched, flying, etc.). At each point, we recorded all of the following within 75 m: the number of people, cats, and dogs (summed for an index of human-related activity), and the number of visible bird feeders. People, cats, and dogs were summed to reduce the number of covariates in the models and because all are human-related factors. Weather was recorded as presence or absence of rain for each day of sampling. Three nonwintering species, Allen's Hummingbird (*Selasphorus sasin*), Rufous Hummingbird (*S. rufus*), and Violet-green Swallow (*Tachycineta thalassina*), were encountered during the last two weeks of surveys but were not considered in the analysis.

Abundance, richness, and diversity data included observations of flying birds for hummingbirds, gulls, hawks, falcons, American Crow, Common Raven, and Turkey Vulture only. These birds regularly search for food while flying, so we considered them to be using a site while in flight.

When we could not identify a bird to species, we assigned it to a more general category. In these cases, the general category, for example, chickadee, counted as a species for the total richness only if no species of chickadee was identified. For diversity, we accommodated unidentified species as follows: when zero species constituting the category were identified, we used the abundance from the general category in the calculation. When one species was identified, we added the abundance from the general category to that of the species that was identified. When two or more species were identified and there were observations assigned to the general category, we added the abundance from the general category to the species identified so that the ratios remained the same. For example, if there were two Black-capped Chickadees, eight Chestnut-backed Chickadees, and five unidentified chickadees, we distributed the five unidentified to the other two species. In this case, the

Black-capped would receive one (for a total of three) and the Chestnut-backed would receive four (for a total of 12), so the ratio of Black-capped to Chestnut-backed remains 1:4.

For each sampling point, we used ArcGIS to calculate the proportions of vegetation and impervious surfaces (i.e., roads and man-made structures) within a 75-m circle. We used two satellite images for analysis: (1) color orthophotography at a pixel resolution of 0.5′ (2003) and (2) true-color images from the National Agriculture Imagery at a resolution of 1 m (2005). We used a 10-m by 10-m grid layer on top of the images to identify what vegetation lay beneath each intersection point. At each intersection we identified the following categories: grass, trees, shrubs, structures, and roads. Grass was mostly lawns but also included fields and pastures of mixed grasses. Shrubs included dense hedges (<3 m tall) and low-growing vegetation that was not grass (i.e., herbaceous and woody bushes). Trees were considered any woody vegetation that arose from one to a few main stems (as opposed to many stems in a hedge). Trees and shrubs that were difficult to discern from the satellite images were identified in the field. Structures included houses and buildings. The category of roads included asphalt, sidewalks, and unvegetated dirt lots. Unvegetated dirt lots were rare, so we included them with roads to reduce the number of covariates in the models. For each of the 75 sampling points, we took the number in each category within the 75-m radius and divided it by the total number of intersection points to get a proportion for the individual categories. We also used ArcGIS to assess the distance (m) from each point to the closest field or pasture, stream, and the redwood forest. Two sites had been developed since the area had been photographed by the satellites, so we photographed them and digitized the cover types from our images.

STATISTICAL ANALYSES

We calculated the total abundance of birds for a site as the sum of all species' mean abundance from the four visits to that site. Richness was the total number of species detected at a site during the study. We used the Shannon index (Shannon and Weaver 1963) to calculate diversity.

Prior to modeling, we used NCSS (Number Cruncher Statistical Systems, Kaysville, UT) to analyze all habitat variables in a correlation matrix. We removed variables from analysis if they were strongly correlated with others ($r > 0.6$). Using NCSS, we incorporated all variables (both GIS and on-the-ground measurements) in a multinomial linear-regression model. The linear-regression model was our basis for selecting the variables that best predicted the abundance, richness, and diversity of wintering birds. Before modeling, we selected combinations and interactions of variables on the basis of relevance to our hypotheses described above and factors determined in previous research to influence the abundance, richness, and diversity of birds. To select combinations of the best-fitting and most parsimonious models, we ranked candidate models by Akaike's information criterion adjusted for

small samples (AIC_c). For multi-model inference, we averaged the coefficients and standard errors from competitive models ($\Delta_i < 2$) and used these averaged coefficients (model-averaged $\beta \pm 1$ SE) in figures of modeled relationships (Burnham and Anderson 2002). Significance was determined at $\alpha = 0.05$.

We used canonical correlation analysis in NCSS to analyze the abundance data. Canonical correlation analysis is a multivariate technique that correlates the abundance of each species with environmental variables by least-squares procedures (Muller 1982). Changes to community composition can be understood through differences in each species' abundance relative to habitat variables. The data consisted of each species' average abundance at each site. Gull species were lumped because of difficulty in identification. The environmental data included all habitat variables recorded at each site except weather. Analysis was restricted to species present at more than one site.

RESULTS

SPECIES RICHNESS

We observed 54 species of birds from 29 January to 11 March 2008. All coefficients of correlation among variables were <0.6, indicating little multicollinearity, so all were used for analyses. Three of 56 candidate models to predict species richness were competitive ($\Delta_i < 2$; Table 1), so we averaged the coefficients and standard errors. According to model-averaged coefficients, avian richness was predicted best by a negative relationship with road cover ($\beta = -13.16 \pm 2.69$), positive relationship with shrub cover ($\beta = 39.99 \pm 13.75$), negative relationship with distance to closest stream (higher richness near a stream; $\beta = -0.003 \pm 0.001$), positive relationship with tree cover ($\beta = 6.65 \pm 5.75$), negative interaction between tree and shrub cover ($\beta = -153.81 \pm 63.69$; Fig. 1),

TABLE 1.   Top three candidate models based on AIC_c model-selection procedures to predict bird species richness in Arcata, California. AIC_c difference (Δ_i) is the difference between the AIC_c of the model specified and the model with the lowest AIC_c. AIC_c weight (w_i) indicates the probability that the current model is the best predictive model within the set of candidates (Burnham and Anderson 2002).

Model	Coefficient	SE	P
Model 1[a]			
Intercept	15.05	1.74	0.00
Roads	−12.93	2.67	0.00
Shrubs	42.20	13.49	0.00
Distance to stream	−0.003	0.001	0.01
Trees	7.92	5.30	0.14
Trees × shrubs	−160.71	62.56	0.01
Model 2[b]			
Intercept	16.22	2.13	0.00
Roads	−13.24	2.69	0.00
Distance to stream	−0.003	0.001	0.01
Shrubs	33.03	14.50	0.03
Trees × shrubs	−122.72	65.84	0.07
Distance to redwoods × trees	0.02	0.01	0.09
Distance to redwoods	−0.001	0.001	0.25
Trees	1.70	6.87	0.81
Model 3[c]			
Intercept	15.53	1.82	0.00
Roads	−13.56	2.75	0.00
Shrubs	42.74	13.51	0.00
Trees × shrubs	−172.14	63.72	0.01
Distance to stream	−0.003	0.001	0.02
Trees	9.19	5.47	0.10
Weather	−0.45	0.47	0.34

[a] K (number of parameters) = 6, $AIC_c = 145.99$, $\Delta_i = 0.00$, $w_i = 0.33$, $R^2 = 0.45$.

[b] $K = 8$, $AIC_c = 147.32$, $\Delta_i = 1.33$, $w_i = 0.17$, $R^2 = 0.48$.

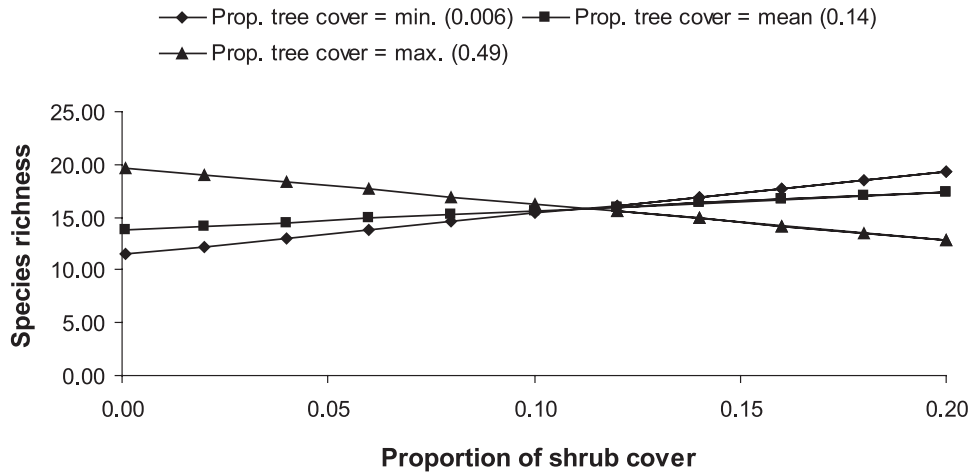[c] $K = 7$, $AIC_c = 147.40$, $\Delta_i = 1.41$, $w_i = 0.16$, $R^2 = 0.46$.

FIGURE 1.   Interaction of the changes to predicted species richness resulting from varying proportions of shrub and tree cover. Coefficients from the top three species-richness models were model-averaged. Observed minimum, mean, and maximum values for proportion of tree cover were used; proportion of shrub cover ranges from its minimum to its maximum. Observed mean values for all other variables were held constant to obtain predicted species richness from the models.

negative relationship with distance to redwood forest (higher richness near redwoods; $\beta = -0.001 \pm 0.001$), positive interaction between distance to redwood forest and tree cover ($\beta = 0.02 \pm 0.01$), and a negative relationship with rainy weather ($\beta = -0.45 \pm 0.47$). For all variables except weather, model-averaged coefficients ± 1 model-averaged standard error did not include zero. The top three models had R^2 values ranging from 0.45 to 0.48 and accounted for 0.66 cumulative AIC_c weight; all other candidate models had Δ_i values >2, indicating they were less competitive.

SPECIES DIVERSITY

Two of 57 candidate models had $\Delta_i < 2$ (Table 2), so we averaged their coefficients and standard errors. From model-averaged coefficients, species diversity was predicted best by a positive interaction between distance to redwood forest and tree cover ($\beta = 0.008 \pm 0.003$; Fig. 2), negative relationship with distance to redwood forest (higher diversity near redwoods; $\beta = -0.001 \pm 0.0004$), negative relationship with roads ($\beta = -1.92 \pm 0.89$), negative relationship with tree cover ($\beta = -3.14 \pm 1.47$), negative relationship with distance to closest stream (higher diversity near a stream; $\beta = -0.001 \pm 0.0004$), and a negative relationship with rain ($\beta = -0.27 \pm 0.16$). For all variables, model-averaged coefficients ± 1 model-averaged standard error did not include zero. These two models yielded R^2 values of 0.23 and 0.20 and accounted for 0.36 cumulative AIC_c weight; all other candidate models had Δ_i values >2.

TOTAL ABUNDANCE

Of 60 candidate models, two had $\Delta_i < 2$ (Table 3), so we averaged their coefficients and standard errors. According to model-averaged coefficients, total abundance was predicted best by a positive relationship with shrub cover ($\beta = 123.92 \pm 44.09$), positive relationship with distance to redwood forest (higher

TABLE 2. Top two candidate models based on AIC_c model-selection procedures to predict bird species diversity in Arcata, California. AIC_c difference (Δ_i) is the difference between the AIC_c of the current model and the model with the lowest AIC_c. AIC_c weight (w_i) indicates the probability that the model specified is the best predictive model within the set of candidates (Burnham and Anderson 2002).

Model	Coefficient	SE	P
Model 1[a]			
Intercept	3.78	0.61	0.00
Distance to redwoods × trees	0.008	0.003	0.00
Distance to redwoods	−0.001	0.000	0.01
Roads	−2.09	0.90	0.02
Trees	−3.20	1.46	0.03
Distance to stream	−0.001	0.000	0.10
Weather	−0.27	0.16	0.11
Model 2[b]			
Intercept	3.31	0.54	0.00
Distance to redwoods × trees	0.008	0.003	0.01
Distance to stream	−0.001	0.000	0.03
Distance to redwoods	−0.001	0.000	0.03
Trees	−3.06	1.47	0.04
Roads	−1.71	0.88	0.06

[a] K (number of parameters) = 7, $AIC_c = -17.81$, $\Delta_i = 0.00$, $w_i = 0.20$, $R^2 = 0.23$.
[b] $K = 6$, $AIC_c = -17.32$, $\Delta_i = 0.49$, $w_i = 0.16$, $R^2 = 0.20$.

abundance far from redwoods; $\beta = 0.008 \pm 0.003$), negative interaction between tree and shrub cover ($\beta = -563.83 \pm 239.43$), positive relationship with tree cover ($\beta = 43.05 \pm 21.04$), and a negative relationship with road cover ($\beta = -19.34 \pm 9.82$). For all variables, model-averaged coefficients ± 1 model-averaged standard error did not include zero. The top two models had R^2 values of 0.25 and 0.19 and accounted for 0.51 cumulative AIC_c weight; all other candidate models had Δ_i values >2.
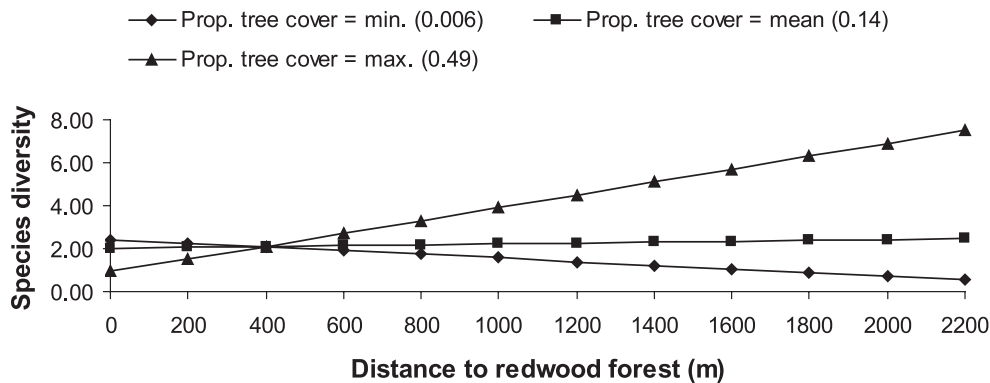

FIGURE 2. Interaction showing that the effect of tree-cover proportions on species diversity changes with distance to the redwoods. Coefficients from the top two species-diversity models were model-averaged. Observed minimum, mean, and maximum values for proportion of tree cover were used; distance to redwood forest ranges from its minimum to its maximum. Observed mean values for all other variables were held constant to obtain predicted species diversity from the models.

TABLE 3.   Top two candidate models based on AIC_c model-selection procedures to predict total bird abundance in Arcata, California. AIC_c difference (Δ_i) is the difference between the AIC_c of the model specified and the model with the lowest AIC_c. AIC_c weight (w_i) indicates the probability that the model specified is the best predictive model within the set of candidates (Burnham and Anderson 1998).

Model	Coefficient	SE	P
Model 1[a]			
Intercept	10.61	6.92	0.13
Shrubs	155.25	50.55	0.00
Distance to redwoods	0.008	0.003	0.00
Trees × shrubs	−563.83	239.43	0.02
Trees	43.05	21.04	0.04
Roads	−18.89	10.21	0.07
Model 2[b]			
Intercept	18.30	4.61	0.00
Distance to redwoods	0.007	0.002	0.00
Roads	−20.27	9.02	0.03
Shrubs	59.92	30.90	0.06

[a] K (number of parameters) = 6, AIC_c = 349.04, Δ_i = 0.00, w_i = 0.34, R^2 = 0.25.

[b] K = 4, AIC_c = 350.47, Δ_i = 1.43, w_i = 0.17, R^2 = 0.19.

COMMUNITY COMPOSITION

Average abundance in relation to habitat variables varied greatly by species. Canonical correlation analysis yielded insignificant correlations between the distribution of individual species and the habitat variables (df = 197, P = 0.15, R^2 = 0.93; Fig. 3), although some species–habitat correlations were strong. On the basis of loadings with individual variables, axis one (vertical in Fig. 3) described the distance from the redwood forest and separated more vegetated sites from sites more dominated by impervious surfaces. The sites closer to the city center and those with high proportions of impervious surfaces had high values; sites close to the redwoods and more vegetated sites had low values. Axis two (horizontal) separated sites with high proportions of roads (low values) from sites with high proportions of shrubs, human activity, and structures (high values). The four non-native species found during this study were House Sparrow, European Starling, Rock Pigeon, and Eurasian Collared-Dove. House Sparrows were negatively correlated with tree cover (r = −0.21), positively correlated with structure cover (r = 0.20), and positively correlated with distance from redwoods (higher abundance far from redwoods; r = 0.26). European Starlings were negatively correlated with tree cover (r = −0.32) and positively correlated with road cover (r = 0.32). Eurasian Collared-Doves were present at only two sites, Rock Pigeons at only one site. We excluded the Rock Pigeon from analysis (present at fewer than two sites), and the Eurasian Collared-Dove was not strongly correlated with any habitat variables.

Gulls were associated with the more urbanized regions of town represented by more structures, human activity, and being far from the redwood forest. The following species were positively correlated ($r \geq 0.15$) with tall vegetation (tree and or shrub cover) and negatively correlated ($r \leq -0.15$) with structures and roads: Steller's Jay, Ruby-crowned Kinglet, Wrentit, Winter Wren, Yellow-rumped Warbler, and Red-breasted Nuthatch. The White-tailed Kite was positively correlated with grass and trees and negatively correlated with structures and roads. Other species were positively correlated with shrubs and or trees but were not negatively correlated with both structures and roads. For example, the Song Sparrow was positively correlated with shrubs and negatively correlated with structures but not with roads.

DISCUSSION

Species richness, diversity, and overall abundance declined with the proportion of road surface at a site, suggesting that impervious ground cover affects suburban bird communities in coastal northern California negatively. In addition, non-native species increased in abundance with the proportion of roads (European Starling) or structures (House Sparrow). In other studies, non-native species have been shown to increase with impervious surfaces and often have a negative influence on populations of native birds (Case 1996, Hennings and Edge 2003). Factors that increase abundances of non-natives should be carefully considered in urban development and restoration projects.

The proportion of shrub cover at a site was positively correlated with species richness and overall bird abundance, revealing the importance of shrubs for maintaining abundances of many species. The proportion of tree cover was also a positive predictor for richness and overall abundance, though significantly for only one abundance model. Blair (1996) and Hennings and Edge (2003) also found the availability of trees and shrubs to be positively associated with the abundance of native birds. Hennings and Edge (2003) suggested that in urban areas increasing canopy cover is the most valuable means for conserving native birds; our results suggest that in our study area shrub and tree cover are important for bird conservation. We found that abundances of several species, the Steller's Jay, Ruby-crowned Kinglet, Wrentit, Winter Wren, Yellow-rumped Warbler, Red-breasted Nuthatch, and White-tailed Kite increased with the availability of shrubs and or trees and decreased with roads and structures. Among the species wintering in our study area, these may be the most vulnerable to the habitat changes associated with urbanization.

An interaction between tree and shrub cover showed that the effect of trees on richness and abundance depended on the amount of shrub cover present at a site, and vice versa. Where shrubs were scarce (<0.11 proportional cover for richness and <0.08 for abundance), extensive tree cover had a positive influence on species richness and abundance, but where
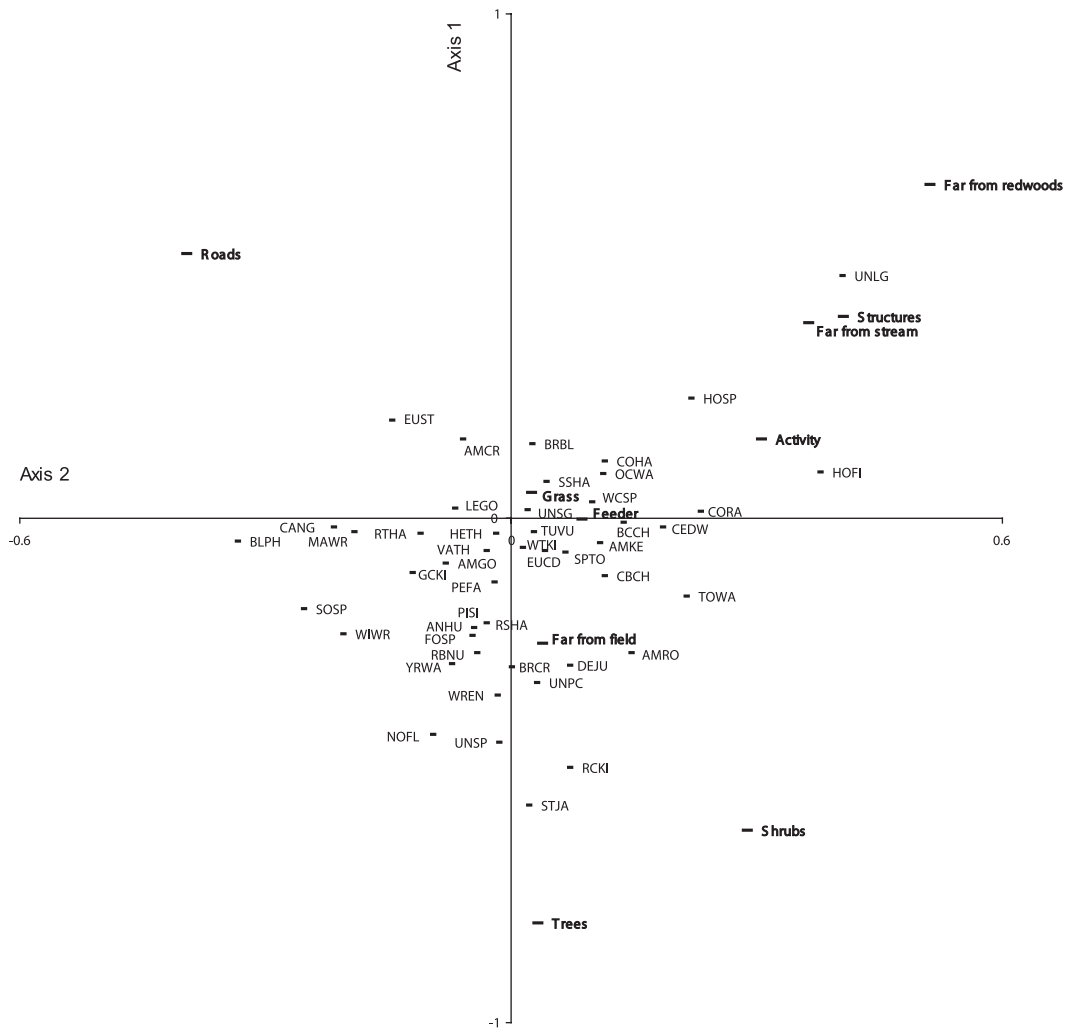
FIGURE 3.   Relationships of species abundances to habitat variables based on canonical correlation analysis. For habitat variables, the distance from the origin indicates the importance of the variable in the model. The location of a species relative to habitat variables indicates its correlation. AMCR, American Crow (*Corvus brachyrhynchos*); AMGO, American Goldfinch (*Spinus tristis*); AMKE, American Kestrel (*Falco sparverius*); AMRO, American Robin (*Turdus migratorius*); ANHU, Anna's Hummingbird (*Calypte anna*); BCCH, Black-capped Chickadee (*Poecile atricapillus*); BLPH, Black Phoebe (*Sayornis nigricans*); BRBL, Brewer's Blackbird (*Euphagus cyanocephalus*); BRCR, Brown Creeper (*Certhia americana*); CANG, Canada Goose (*Branta canadensis*); CBCH, Chestnut-backed Chickadee (*Poecile rufescens*); CEDW, Cedar Waxwing (*Bombycilla cedrorum*); COHA, Cooper's Hawk (*Accipiter cooperii*); CORA, Common Raven (*Corvus corax*); DEJU, Dark-eyed Junco (*Junco hyemalis*); EUCD, Eurasian Collared-Dove (*Streptopelia decaocto*); EUST, European Starling (*Sturnus vulgaris*); FOSP, Fox Sparrow (*Passerella iliaca*); GCKI, Golden-crowned Kinglet (*Regulus satrapa*); HETH, Hermit Thrush (*Catharus guttatus*); HOFI, House Finch (*Carpodacus mexicanus*); HOSP, House Sparrow (*Passer domesticus*); LEGO, Lesser Goldfinch (*Spinus psaltria*); MAWR, Marsh Wren (*Cistothorus palustris*); NOFL, Northern Flicker (*Colaptes auratus*); OCWA, Orange-crowned Warbler (*Vermivora celata*); PEFA, Peregrine Falcon (*Falco peregrinus*); PISI, Pine Siskin (*Spinus pinus*); RBNU, Red-breasted Nuthatch (*Sitta canadensis*); RCKI, Ruby-crowned Kinglet (*Regulus calendula*); RSHA, Red-shouldered Hawk (*Buteo lineatus*); RTHA, Red-tailed Hawk (*Buteo jamaicensis*); SOSP, Song Sparrow (*Melospiza melodia*); SPTO, Spotted Towhee (*Pipilo maculatus*); SSHA, Sharp-shinned Hawk (*Accipiter striatus*); STJA, Steller's Jay (*Cyanocitta stelleri*); TOWA, Townsend's Warbler (*Dendroica townsendi*); TUVU, Turkey Vulture (*Cathartes aura*); UNPC, unidentified chickadee (*Poecile* sp.); UNSG, unidentified goldfinch (*Spinus* sp.); UNLG, unidentified Gull (*Larus* sp.); UNSP, unidentified sparrow (Emberizidae); VATH, Varied Thrush (*Ixoreus naevius*); WCSP, White-crowned Sparrow (*Zonotrichia leucophrys*); WIWR, Winter Wren (*Troglodytes troglodytes*); WREN, Wrentit (*Chamaea fasciata*); WTKI, White-tailed Kite (*Elanus leucurus*); YRWA, Yellow-rumped Warbler (*Dendroica coronata*). The categories of unidentified arose from situations in which species could not be distinguished.

shrubs were more abundant (>0.11 for richness and >0.08 for abundance), increased tree cover did not increase richness or abundance. Conversely, where trees were relatively scarce (proportional cover <0.14), extensive shrub cover had a positive influence on richness and abundance, but where trees were abundant (>0.14), shrub cover did not increase richness (Fig. 1) or abundance. Therefore, at low proportions of either shrubs or trees, presence of the other was important for maintaining abundances of various bird species. This effect on species richness can be thought of as compensatory: the presence of many shrubs or trees is important but that of the two together is not additive. This result may have practical application for urban planners. For example, older neighborhoods tend to have smaller homes on lots with well-vegetated yards, while newer neighborhoods have larger homes with fewer and younger trees and shrubs (Whitney and Adams 1980, White et al. 2004). Because shrub cover may be more feasibly increased in less time than tree cover, city plantings could maximize their benefit to birds by planting shrubs in newer neighborhoods in which tree cover is minimal.

The interaction between tree cover and distance to redwood forest helps in interpreting the effect of tree cover on diversity. When close to the redwoods, a high proportion of trees at a site influences species diversity negatively. With increasing distance from the redwoods, the influence of trees on species diversity becomes increasingly positive (Fig. 2). Therefore, in the more heavily urbanized areas of Arcata (farther from the redwood forest), tree cover increases bird diversity. Nearer the redwoods, the area may be saturated with trees so that the addition of more trees does not enhance structural diversity and does not increase avian diversity.

Total abundance was higher farther from the redwoods, probably because of high numbers of gulls, crows, ravens, House Sparrows, and starlings, which exploit human-generated resources in cities and suburbs (Case 1996, Hennings and Edge 2003). In Arcata, however, species diversity was positively associated with proximity to the redwood forest, likely because of the juxtaposition of forest and suburban habitat. Here there is a mixing of species restricted primarily to forest, species associated with forest edge, and species able to endure more urbanized environments (Brand and George 2001). This relationship helps distinguish availability of raw resources (often high in more urban environments) and niche diversity, which may be high near forest ecotones (Hunter 1990). We did not address area sensitivity in this study, but the availability of nearby forest habitat may support more area-sensitive species than an urban center. The availability of habitat ecotones in suburban environments differs from that in heavily urbanized cities and may increase species diversity.

We found that species richness and diversity were positively correlated with close proximity to streams (though significantly so for species richness only). The importance of streamside vegetation has been demonstrated in other studies and can

probably be explained by the abundance of resources and structure of trees along riparian strips (Hennings and Edge 2003). In coastal northern California, riparian strips are dominated by deciduous trees that provide an abundance of insects, nectar, and new plant growth in early spring. Stands of deciduous trees tend to have a biota richer than that of conifers in part because of greater foliage height diversity, palatable leaves and litter, and nutrient-rich soil (Glenn-Lewin 1977, Hunter 1990). In our study area, the riparian understory is typically dominated by dense shrubs, which also had a positive effect on species richness and total abundance. Additionally, in coastal northern California deciduous trees are much less abundant than conifers and may therefore create localized "hotspots" for birds. Maintaining riparian vegetation is recommended for sustaining rich bird communities (Hennings and Edge 2003).

Other studies have found that different species respond differently to the resource changes associated with urbanization (Baschak and Brown 1995, Blair 1996, Marzluff 1998). At moderate levels of urbanization, as in spacious suburban residential areas, the diversity and abundance of birds may increase because of the availability of ornamental plants, perch locations (structures), and increased productivity from watering and fertilizing (Emlen 1974, Beissinger and Osborne 1982, Mooney and Gulmon 1983). Even at low levels of urbanization (e.g., golf courses and city parks), however, a large proportion of the native predevelopment community may be lost (Blair 1996). Furthermore, densities of non-native and nonterritorial birds increase with the volume of exotic plants, while native territorial birds increase with native plant species (Mills et al 1991). For maintaining predevelopment bird communities, landscaping with native plants may therefore be preferable to landscaping with non-native plants (Mills et al. 1991, Case 1996, Pavlik and Pavlik 2000).

In urban and suburban environments, trees and shrubs support a diversity of birds that may otherwise fail to subsist (Mills et al. 1991, Hennings and Edge 2003). Interactions among insects, birds, and plants help to sustain each other and a diverse array of other organisms (Herrera 1995, Jordano 1995, Cornelis and Hermy 2003). The aesthetics of vegetation also appeal to many people, and the demand for property with natural beauty is high (Lockwood et al. 2000). In addition, conservation easements are sometimes available to private landowners who preserve land as wildlife habitat. This is not a recommendation to build homes in naturally beautiful areas; instead, we emphasize that maintaining and restoring vegetation is an effective way to enhance areas that have already been developed or to improve planning in areas where development is inevitable (Rosenzweig 2003).

ACKNOWLEDGMENTS

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