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RESEARCH ARTICLE

Habitat quality and nest-box occupancy by five species of oak woodland birds

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ABSTRACT

Habitat quality can have important consequences for avian communities through impacts on survival and annual reproductive success. However, habitat quality is often hard to measure, leading to the use of occupancy as a proxy. We compared habitat use of 5 avian species that used nest boxes in the oak woodlands of central coastal California, USA, to determine which habitat characteristics best predicted box occupancy. We focused on the relationship between habitat characteristics and occupancy for five species—Ash-throated Flycatcher (*Myiarchus cinerascens*), House Wren (*Troglodytes aedon*), Oak Titmouse (*Baeolophus inornatus*), Violet-green Swallow (*Tachycineta thalassina*), and Western Bluebird (*Sialia mexicana*)—for which we had 12 consecutive years of data on nest boxes spread over a 700 ha study area. We also examined whether the physical habitat characteristics and box occupancy rates were good predictors of reproductive success, to infer whether they were useful indicators of habitat quality. The habitat characteristics influencing nest-box occupancy differed among the 5 species. Ash-throated Flycatchers were associated with fragmented habitats with less grassland. House Wrens were associated with riparian vegetation, as were Oak Titmice, which were also associated with chaparral. Violet-green Swallows were associated with chaparral but tended to nest farther from riparian corridors than Oak Titmice. Western Bluebirds nested away from riparian corridors and in areas with more grassland and oak woodland. Finally, occupancy rate was a better predictor than habitat characteristics of reproductive success, which suggests that occupancy can be a valuable proxy for habitat quality for these 5 species.

Keywords: habitat, habitat quality, habitat use, nest box, oak woodland, occupancy

Calidad de hábitat y ocupación de cajas nido por cinco especies de aves de bosques de roble

RESUMEN

La calidad de hábitat puede tener consecuencias importantes para las comunidades de aves a través de impactos en la supervivencia y en el éxito reproductivo anual. Sin embargo, la calidad de hábitat es usualmente difícil de medir, llevando a que se use la ocupación como una medida indirecta. Comparamos el uso del hábitat de cinco especies de aves que ocupan cajas nido en los bosques de roble en la costa central de California para determinar cuáles características del hábitat predicen mejor la ocupación de las cajas. Nos enfocamos en la relación entre las características del hábitat y la ocupación de *Myiarchus cinerascens*, *Troglodytes aedon*, *Baeolophus inornatus*, *Tachycineta thalassina* y *Sialia mexicana*, para las cuales tenemos 12 años consecutivos de datos provenientes de cajas distribuidas en un área de estudio de 700 ha. También examinamos si las características físicas del hábitat y las tasas de ocupación de las cajas fueron buenos predictores del éxito reproductivo, para inferir si fueron buenos indicadores de la calidad de hábitat. Las características del hábitat que influenciaron la ocupación de las cajas nido difirieron entre las cinco especies. *M. cinerascens* estuvo asociada con los fragmentos de hábitat con menos pastizales. *T. aedon* estuvo asociada con la vegetación ribereña, al igual que *B. inornatus*, que estuvo también asociada con el chaparral. *T. thalassina* estuvo asociada con el chaparral, pero tendió a anidar más lejos de los corredores ribereños que *B. inornatus*. *S. mexicana* anidó lejos de los corredores ribereños y en áreas con más pastizales y bosques de roble. Finalmente, la tasa de ocupación fue un mejor predictor del éxito reproductivo que las características del hábitat, sugiriendo que la ocupación puede ser una medida indirecta de la calidad del hábitat valiosa para estas cinco especies.

Palabras clave: bosques de roble, cajas nido, calidad del hábitat, hábitat, ocupación, uso del hábitat

INTRODUCTION

Habitat quality often determines individual survival and reproductive success (Johnson 2007). Consequently, individuals that occupy naturally heterogeneous landscapes should benefit from recognizing variation in habitat quality and choosing territories accordingly. Given the importance of habitat quality to reproductive success, it is important to understand what influences habitat quality and how habitat types influence choice of nest site. However, actual choice is difficult to establish, and critical features of habitat quality are often hard to assess (Jones et al. 2014). Habitat quality can either be evaluated directly by measuring features of the habitat itself, such as food abundance (Penteriani et al. 2002) and predation risk (Sergio and Newton 2003), or indirectly, using parameters like survival and reproductive success (Nilsson 1987, Johnson 2007). Compared to these measures, which are often expensive and difficult to estimate (Jones et al. 2014), historical occupation rates and physical habitat characteristics are valuable alternatives (Sergio and Newton 2003). Direct and indirect measures of habitat quality have been associated with occupancy in a variety of avian species (Sergio and Newton 2003, Doran and Holmes 2005, Dawson and Bortolotti 2006, Janiszewski et al. 2013, Jones et al. 2014).

Although observed patterns of occupancy are often inferred to reflect the results of habitat selection (Jones 2001), a simple examination of territory occupancy is of limited use unless the fitness consequences of variation in habitat use can be demonstrated. In heterogeneous habitats, high-quality individuals are likely to occupy the best habitats whereas less competitive individuals are forced to occupy less profitable habitats (Fretwell 1972). Given that competition for territories should vary according to profitability, high-quality territories should have a proportionally higher occupation rate than less attractive territories (Janiszewski et al. 2013). However, other factors associated with habitat, including intensity of competition within and among species, likelihood of nest predation, and food availability, can influence habitat selection (Jones 2001). Therefore, it is important to investigate both the physical habitat characteristics that influence occupancy and their relationship to reproductive success to determine the adaptive value of occupied habitat.

Secondary cavity-nesting birds can be limited by the availability of nest sites rather than by other habitat factors, such as food availability (Newton 1994). This limitation has led to the widespread use of nest boxes to conserve and study avian species that readily adopt boxes as nest sites. If nest boxes are widely available on the landscape, species that occupy the boxes should no longer be limited by the availability of nest sites. Nest-box characteristics such as size, age, and orientation can influence selection. For example, in site-faithful species, the oldest boxes on the landscape may appear to be more consistently occupied only because they have been available longer and, thus, are more likely to attract a high-quality occupant that will reuse them. However, when nest boxes are identical in size and shape, birds presumably choose nest sites on the basis of external criteria, which could include the surrounding habitat structure, proximity to competitors, food supply, and abundance of predators (Doran and Holmes 2005, Jones et al. 2014).

Understanding habitat use and the relationship between patterns of use (e.g., territory occupancy and habitat quality) can be important when managing species. Very little is known about the habitat preferences of many common species, including oak woodland inhabitants like Violet-green Swallows (*Tachycineta thalassina*) and Oak Titmice (*Baeolophus inornatus*). This can hinder management for species like the Oak Titmouse, which is in decline across much of its range (Cicero 2000). By examining a suite of species, it should be possible to detect whether any of the species' patterns of box occupancy are not positively associated with fitness. This would also be important to management if, for example, the association with habitat indicates that interspecific competition is preventing a species from nesting in better habitat (Bowers and Dooley 1991), and it could lead to management solutions that vary the size of nest-box entrances to exclude larger species from interfering with the nesting attempts of smaller species (Stanback et al. 2011).

We compared habitat use of 5 avian species that regularly use nest boxes in oak woodlands in California, USA. Because the boxes themselves were not limiting (occupation was $<$50%), it is reasonable to predict that use of a box would be guided primarily by habitat rather than by cavity availability. We first examined whether the 5 species were using nest boxes randomly. We then investigated which habitat characteristics were the best predictors of nest-box occupancy. We also examined whether including the migratory status of a species affected the habitat variables that predicted occupancy. Finally, we examined whether physical habitat characteristics and historical nest-box occupancy rates were good predictors of reproductive success, in order to infer whether they were useful indicators of habitat quality for both large and small species using nest boxes.

METHODS

Study Area

We studied a community of secondary cavity nesters breeding in nest boxes on Hastings Natural History Reservation and the adjoining Oak Ridge Ranch (hereafter "Hastings–Oak Ridge") in the upper Carmel Valley, Monterey County, California (Figure 1). The study area is

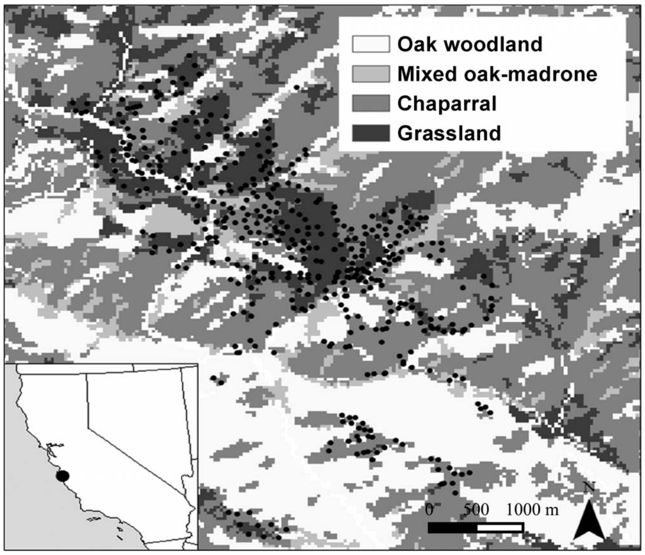

FIGURE 1. Distribution of the 4 major habitat types on our study area in the outer coast range of central California, USA, with nest box locations marked in black.

located in the outer coast range of central California and encompasses 700 ha. Habitat is composed of a mixture of oak woodland, mixed oak–madrone forest, open grassland, and chaparral. Nest boxes were checked a minimum of once per week from March through July during the study period, 1990–2001, with checks occurring more frequently as soon as any nesting activity was detected, to ensure that no nesting attempts were missed. All nesting activities were monitored so that the clutch size, number of eggs hatched, and number of young fledged were known for each nesting attempt of each species using the nest boxes. Nest boxes were made of 1.2 cm thick plywood and had approximate internal dimensions of 19.5 × 13 × 12.5 cm, with an entrance hole of 3.8 cm. Boxes were generally placed 1–1.5 m above the ground on a variety of support structures, including valley oaks (*Quercus lobata*), blue oaks (*Q. douglasii*), telephone poles, and fence posts. All boxes were randomly oriented, both over the entire study area and within each habitat type. A total of 360 boxes were placed at 380 different locations during the study period (Figure 1). Of those boxes, 17 were moved during the study period and thus occupied 2 or more locations in different years. To account for this change, nest-box location was included as a random effect in analyses. No more than 57% of boxes were used in any given year, with an average of 40% of boxes used, which suggests that the availability of nest boxes was not a limiting factor in this system. A box was considered occupied if a species laid one or more eggs during a given year. We did not count nests without eggs because some species will build auxiliary nests. Including only nests in which at least one egg was laid allowed us to measure nest-box use for reproduction. The occupancy rate (scored 0–12) for each box was calculated as the number of years that a given species used the box to breed.

Study Species

The 5 most common species using the nest boxes on Hastings–Oak Ridge were Ash-throated Flycatcher (*Myiarchus cinerascens*), House Wren (*Troglodytes aedon*), Oak Titmouse, Violet-green Swallow, and Western Bluebird (*Sialia mexicana*). All these species readily utilized man-made structures and artificial boxes for nesting, and they varied in whether they were migratory or resident. The resident species were Oak Titmouse and Western Bluebird (Cicero 2000, Guinan et al. 2008).

Ash-throated Flycatcher. The Ash-throated Flycatcher is a common migratory flycatcher that breeds in arid open woodlands across the western United States and northern Mexico. They are primarily insectivorous, hovering to capture prey on vegetation and the ground. A large portion of studies have focused on habitat selection in the desert scrub of the American Southwest, whereas few studies have been done in low- to mid-elevation semiarid oak woodlands, where Ash-throated Flycatchers are widespread breeders (Cardiff and Dittmann 2002). In central California, Ash-throated Flycatchers lay a mean of 4.2 eggs (range: 2–6; Cardiff and Dittmann 2002).

House Wren. The House Wren is a small passerine common in open shrubby woodlands throughout the Western Hemisphere. The House Wren is an insectivorous foliage gleaner and a partial migrant on Hastings–Oak Ridge, with at least some individuals present throughout the year. In the western United States, House Wrens are commonly found in wooded riparian areas, and oak woodlands are a preferred breeding habitat (Johnson 2014), with smaller forest fragments generally favored (Gutzwiller and Anderson 1987, Groom and Grubb 2002). Previous studies of microhabitat selection have found that House Wrens prefer to nest in habitat with sparse understory and low foliage density (DeGraaf 1987, Sedgwick and Knopf 1987, Finch 1989). In addition, reproductive success of House Wrens was higher in areas with sparse vegetation (Finch 1989). Despite these clear habitat preferences, in modeling habitat selection of House Wrens in the conterminous United States, Lawler et al. (2004) found that large-scale land-cover characteristics did not adequately capture habitat preferences. Throughout their range, clutch size for the House Wren usually varies between 3 and 10 eggs, with a mean of 6.46 in central California (Johnson 2014).

Oak Titmouse. The Oak Titmouse is an insectivorous foliage gleaner that is resident in dry oak woodlands along the western coast of North America (Cicero 2000). Little information is available on habitat selection in Oak Titmice. Previous work indicated a strong preference for dry oak and oak–pine woodlands (Cicero 2000), whereas a study of the "plain titmouse" (*Parus inornatus*), before it was split into the Oak Titmouse and the Juniper Titmouse (*B. ridgwayi*), found more nests in oak stands with moderate tree densities than in sparse or dense stands (Wilson 1992). The Oak Titmouse is in decline throughout much of its range (Cicero 2000), emphasizing the need for more information on its habitat use and reproductive success. Clutch size for the Oak Titmouse ranges from 3 to 9 eggs, with 6 to 7 being the most common (Cicero 2000).

Violet-green Swallow. Violet-green Swallows are migratory aerial insectivores that breed in woodlands throughout western North America, including open deciduous woodland (Brown et al. 2011). Almost no information is available on Violet-green Swallows' habitat selection, although they are known to nest in natural cavities, cliffs, and nest boxes and prefer nest sites in open areas such as in open groves or along woodland edges (Brown et al. 2011). Clutch size ranges from 4 to 6 eggs (Brown et al. 2011).

Western Bluebird. The Western Bluebird is a small thrush that primarily forages for insects by flycatching during the breeding season. They are found in a variety of habitats, including deciduous woodland, wooded riparian areas, grasslands, and areas with edge habitat (Guinan et al. 2008). In southern California, they breed in both open oak woodlands and coniferous forests, avoiding large agricultural areas and deserts during breeding (Garrett and Dunn 1981). Previous work for the North American Breeding Bird Survey found that Western Bluebirds showed a preference for areas with open overstory but did not favor large, open meadows (Guinan et al. 2008). At Hastings–Oak Ridge, where our study was conducted, male Western Bluebirds are philopatric and rely on mistletoe in the winter, with their degree of philopatry depending on the abundance of mistletoe on their parents' winter territories (Dickinson and McGowan 2005, Dickinson et al. 2014). Mistletoe grows primarily on the deciduous oaks at Hastings–Oak Ridge and is thus associated with blue oak–valley oak woodland, which comprises the open oak savanna. Clutch size is typically 5 eggs but ranges from 2 to 6 eggs (Guinan et al. 2008).

Habitat Data

Habitats were classified following the methods described by Wilson et al. (2014). The 4 major vegetation types surrounding nest-box locations and included in analyses were chaparral, blue oak–valley oak woodland, mixed oak–madrone forest, and open savanna grassland. The habitat around each nest-box location was defined as the area within a 100 m buffer, which is the size of an average territory for some of the study species (Wilson et al. 2014). Habitat metrics for the area surrounding each box were calculated using FRAGSTATS 4 (McGarigal et al. 2002). Calculated habitat metrics included edge density (m ha^{-1}) and the percentage of each of the 4 major habitat types within the buffer.

The stream layer for the study area was created with polylines outlining riparian corridors from a satellite image and previous approximations of riparian buffers. The distance from each nest-box location to the nearest stream was calculated in ArcGIS 10.0.

Analysis

We examined the influence of habitat variables on both nest-box occupancy and reproductive success for 5 species of secondary cavity nesters. We first examined whether each species was using nest boxes nonrandomly across the landscape. For each species, we examined the frequency of occupation of each nest box over the study period and compared it to a hypothetical Poisson distribution, using a goodness-of-fit test to determine whether the distribution of nest-box occupancy differed significantly from a random Poisson distribution (Goodenough et al. 2009). Results are reported as means ± SE.

We then analyzed the influence of habitat variables on box occupancy, which was a binary variable with "success" defined as a box in which one or more eggs were laid. To select the most important variables, we examined all habitat variables individually and included only those that decreased the corrected Akaike's Information Criterion (AIC_c) compared to the null model and had high R^2 values (calculated following the method outlined by Nakagawa and Schielzeth 2013). There was not enough prior research to test specific hypotheses for each species. Therefore, we examined all combinations of the retained habitat variables but did not include more than 2 habitat variables in a single model to determine the most important predictors of box occupancy. Based on their variance inflation factors, only percent chaparral and grassland were collinear and so were not included in the same model.

To determine the relative importance of the different habitat variables as predictors of either box occupancy or reproductive success, we used generalized linear mixed models in the lme4 package in R 3.1.2 (R Development Core Team 2015). We ran separate analyses for each species, with nest-box location and year included as random effects. Because only Western Bluebirds were individually color banded, we could not use individual ID as a random effect. We used the AIC_c values and examined Akaike weights (w_i) and model-averaged 95% confidence intervals (CIs) to assess which variables were important. Variables were considered significant if the model-averaged 95% CIs did not include zero. We assessed model fit by computing both marginal and conditional R^2 values (Nakagawa and Schielzeth 2013).

We then examined whether occupancy rates and habitat characteristics were good indicators of habitat quality by

TABLE 1. Significant variables from our 3 analyses for 5 oak woodland species on our study area in the outer coast range of central California, USA, with the direction of coefficients indicated in parentheses. Scientific names of species are given in the text.

Species	Occupancy	Nesting success	Fledging success
Ash-throated Flycatcher	Edge density (+)	Occupancy rate (+)	Occupancy rate (+)
	Percentage of grassland (−)		
House Wren	Percentage of grassland (−)	Occupancy rate (+)	Occupancy rate (+)
Oak Titmouse	Distance to stream (−)	Occupancy rate (+)	Occupancy rate (+)
	Percentage of chaparral (+)	Percentage of chaparral (+)	
	Percentage of grassland (−)		
Violet-green Swallow		Occupancy rate (+)	Occupancy rate (+)
Western Bluebird	Distance to stream (+)	Occupancy rate (+)	Occupancy rate (+)
	Percentage of chaparral (−)		
	Percentage of grassland (+)		

using them as predictors of reproductive success, which we calculated in 2 ways. First, nest success was described as a binary variable, with "success" defined as a box that produced at least one fledgling in a given year. Second, "fledging success" was defined as the raw number of fledglings produced per box in a given year, described with a Poisson distribution. The first measure examined whether a pair had any success, which would be predominantly affected by predation, whereas the second measure examined relative success, which could also be influenced by other conditions such as food availability. To examine reproductive success, we followed the analysis methods described above and included all models for which the cumulative weight (w_i) reached 80% in the box occupancy analysis, both alone and in combination with the variable of occupancy rate.

Finally, we tested whether migratory status affected the habitat characteristics that were important predictors of box occupancy for each species. Our study species included two resident species, Western Bluebird and Oak Titmouse; and two migratory species, Ash-throated Flycatcher and Violet-green Swallow. The House Wren is a partial migrant and so was not included as either a resident or a migrant in separate analyses. We assumed that all boxes were available to resident species but not necessarily to migratory species, whether due to late arrival dates or to competition with residents. We tested 2 hypotheses regarding box availability for migrants to determine whether the habitat characteristics affecting occupancy differed, which would suggest that migratory status had an influence on box occupancy and success. First, we tested the hypothesis that migratory status had no effect on box occupancy and success, by assuming that all boxes were available to all species, regardless of migratory status. Second, we tested the hypothesis that migratory status did have an effect on box occupancy and success, by assuming that all boxes occupied by residents in a given year were not available to migrants. This represented the most conservative assumption about the impact of migratory status on box availability with the maximum number of boxes deemed unavailable. It is also the most reasonable, because Western Bluebirds were the most frequent box occupant, using the boxes 6× as much as Ash-throated Flycatchers, the second most frequent occupant, and because Western Bluebirds are territorial year-round, often using the same box year after year (Dickinson et al. 2014). We followed the analysis methods outlined above to test our 2 hypotheses about the influence of migratory success on box occupancy and success.

RESULTS

During the 12 yr study period, a total of 380 distinct box locations on Hastings–Oak Ridge were monitored for a total of 4,261 different nesting opportunities or box-years. Together, the 5 study species accounted for 1,740 box occupancy events (box-years).

Western Bluebird was the primary box occupant. The rank order of box occupancies across all years was Western Bluebird (29% of box-years), Ash-throated Flycatcher (5%), Oak Titmouse (3%), House Wren (2%), and Violet-green Swallow (2%). Although we provide considerable detail on the analyses in the text below, the results are best summarized in Table 1. The main results are that (1) occupancy for each species was predicted by a slightly different set of habitat variables and (2) occupancy was the best predictor of both nest success (whether or not a nest was successful) and fledging success (the number of young fledged at successful nests) for all 5 species. Full results of AIC analyses and slope estimates of significant variables are presented online in the Supplemental Materials.

Distribution of Nest-Box Use

Before asking which habitat factors influenced nest-box selection in our study area, we determined whether each species' nest-box use was consistent with random use or the result of some kind of selective process, be it active choice or exclusion. Box use for all 5 species differed statistically from random expectations (Ash-throated Flycatcher: $\chi^2 = 15{,}136.1$, df $= 121$, $P < 0.001$, $n = 367$;

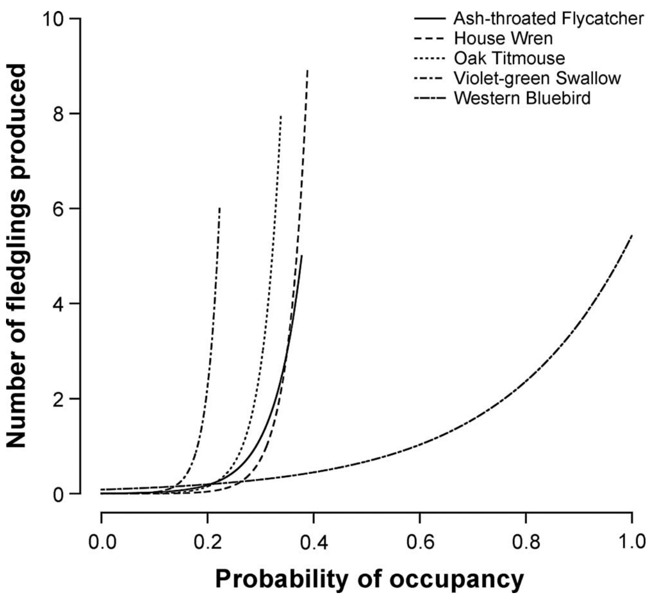

FIGURE 2. Influence of the number of years a nest box was occupied on the number of fledglings produced by 5 oak woodland species on our study area in the outer coast range of central California, USA. The probability of occupancy was calculated from the occupancy rate, which was a score (0–12) for each nest box that represented the number of years that a given species used it to breed.

House Wren: $\chi^2 = 4{,}131.8$, df = 45, $P < 0.001$, $n = 367$; Oak Titmouse: $\chi^2 = 9{,}071.5$, df = 75, $P < 0.001$, $n = 367$; Violet-green Swallow: $\chi^2 = 3{,}400.8$, df = 121, $P < 0.001$, $n = 367$; Western Bluebird: $\chi^2 = 77{,}913.5$, df = 286, $P < 0.001$, $n = 367$). Graphs of the species distributions are presented in the Supplemental Materials.

Ash-throated Flycatcher

Ash-throated Flycatchers occupied a total of 204 boxes and had 139 successful nests. They occupied a mean of 16.2 ± 1.7 boxes each year (n = 4,240), and successful nests produced a mean of 3.9 ± 0.1 fledglings. In the analysis examining box occupancy, the percentage of grassland was in the top 2 models, representing 83% of model weight. When coefficients were model-averaged, edge density and percentage of grassland were both significant (Table 1). The marginal R^2 and conditional R^2 for the top model, which included edge density and percentage of grassland ($\Delta AIC_c = 0$, $w_i = 0.59$), were 0.01 and 0.30, respectively. In the analysis examining nesting success, occupancy rate was in all 3 top models, representing 100% of the model weight. In the analysis examining fledging success (Figure 2), occupancy rate was again in the top 3 models, accounting for 100% of model weight. In both analyses examining reproductive success, occupancy rate was the only variable considered significant (Table 1). For the top model predicting nesting success, which included just occupancy rate ($\Delta AIC_c = 0$, $w_i = 0.63$), the marginal R^2 and conditional R^2 were 0.18 and 0.24, respectively. The marginal R^2 and conditional R^2 for the top model predicting fledging success, which included occupancy rate and percentage of grassland ($\Delta AIC_c = 0$, $w_i = 0.62$), were 0.26 and 0.64, respectively.

Ash-throated Flycatcher box occupancy and reproductive success were also examined under the assumption that all boxes occupied by residents were not available. Using this assumption did not alter the results. The same variables were important for predicting both box occupancy and reproductive success, and the distribution of model weight between the candidate models agreed closely with the first analysis described above.

House Wren

House Wrens occupied a total of 95 boxes and had 74 successful nests. They occupied a mean of 7.5 ± 1.0 boxes each year (n = 4,247), and successful nests produced a mean of 6.4 ± 0.2 fledglings. In the analysis examining box occupancy, percentage of grassland was in the top 2 models, representing 82% of model weight, and distance to nearest stream was in 2 of the top 3 models, representing 72% of model weight. When coefficients were model-averaged, only percentage of grassland was significant (Table 1). The marginal R^2 and conditional R^2 for the top model, which included distance to nearest stream and percentage of grassland ($\Delta AIC_c = 0$, $w_i = 0.60$), were 0.02 and 0.81, respectively. In the analysis examining nesting success, occupancy rate was in all 3 top models, representing 100% of the model weight. In the analysis examining fledging success (Figure 2), occupancy rate was again in the 3 top models, accounting for 100% of model weight. In both analyses examining reproductive success, the only variable considered significant was occupancy rate (Table 1). For the top model predicting nesting success, the marginal R^2 and conditional R^2 for the top model, which included only occupancy rate ($\Delta AIC_c = 0$, $w_i = 0.50$), were 0.16 and 0.32, respectively. The marginal R^2 and conditional R^2 for the top model predicting fledging success, which included occupancy rate ($\Delta AIC_c = 0$, $w_i = 0.58$), were 0.18 and 0.88, respectively.

Oak Titmouse

Oak Titmice occupied a total of 147 boxes and had 113 successful nests. They occupied a mean of 11.9 ± 2.8 boxes each year (n = 4,248), and successful nests produced a mean of 5.8 ± 0.1 fledglings. In the analysis examining box occupancy, distance to nearest stream was in the top 6 models, representing 100% of model weight. Percentage of chaparral was in the top 2 models, representing 68% of model weight, and percentage of grassland was in 3 of the top 7 models, representing 27% of model weight. When coefficients were model-averaged, percentage of chaparral, percentage of grassland, and distance to nearest stream were all significant (Table 1). The marginal R^2 and conditional R^2 for the top model, which included distance to nearest stream, percentage of mixed oak–madrone forest, percentage of chaparral, and edge density ($\Delta AIC_c = 0$, $w_i = 0.40$), were 0.01 and 0.55, respectively. In the analysis examining nesting success, occupancy rate was in all 4 top models, representing 100% of the model weight, and percentage of chaparral was in the top 2 models, representing 73% of model weight. The only variables considered significant were occupancy rate and percentage of chaparral (Table 1). The marginal R^2 and conditional R^2 for the top model, which included distance to nearest stream, percentage of mixed oak–madrone forest, percentage of chaparral, and occupancy rate ($\Delta AIC_c = 0$, $w_i = 0.53$), were 0.002 and 0.34, respectively. In the analysis examining fledging success (Figure 2), occupancy rate was again in the 4 top models, accounting for 100% of model weight. The only variable considered significant was occupancy rate (Table 1). The marginal R^2 and conditional R^2 for the top model, which included just occupancy rate ($\Delta AIC_c = 0$, $w_i = 0.47$), were 0.33 and 0.80, respectively.

Violet-green Swallow

Violet-green Swallows occupied a total of 69 boxes and had 46 successful nests. They occupied a mean of 5.7 ± 0.7 boxes each year ($n = 4{,}248$), and successful nests produced a mean of 3.7 ± 0.2 fledglings. In the analysis examining box occupancy, distance to nearest stream was in the top 2 models, representing 68% of model weight, and percentage of chaparral was in 2 of the 4 top models, representing 35% of model weight. The marginal R^2 and conditional R^2 for the top model, which included distance to nearest stream ($\Delta AIC_c = 0$, $w_i = 0.45$), were 0.03 and 0.58, respectively. In the analysis examining nesting success, occupancy rate was in all 4 top models, representing 100% of the model weight. In the analysis examining fledging success (Figure 2), occupancy rate was again in the 4 top models, accounting for 100% of model weight. In both analyses examining reproductive success, the only variable considered significant was occupancy rate (Table 1). For the top model predicting nesting success, the marginal R^2 and conditional R^2 for the top model, which included occupancy rate, distance to nearest stream, and percentage of chaparral ($\Delta AIC_c = 0$, $w_i = 0.41$), were 0.03 and 0.15, respectively. The marginal R^2 and conditional R^2 for the top model predicting fledging success, which included occupancy rate and distance to nearest stream ($\Delta AIC_c = 0$, $w_i = 0.35$), were 0.03 and 0.61, respectively.

Violet-green Swallow box occupancy and reproductive success were also examined under the assumption that all boxes occupied by residents were not available, but the results did not change using this assumption. The same variables were important for predicting both box occupancy and reproductive success, and the distribution of model weight between the candidate models closely agreed with the first analysis described above.

Western Bluebird

Western Bluebirds occupied a total of 1,225 boxes and had 672 successful nests. They occupied a mean of 101.4 ± 10.2 boxes each year ($n = 4{,}337$), and successful nests produced a mean of 4.0 ± 0.1 fledglings. In the analysis examining box occupancy, distance to stream was in the top 3 models, representing 99% of model weight. Percentage of grassland and percentage of oak woodland were both in 3 of the top 4 models, representing 86% and 85% of model weight, respectively. When coefficients were model averaged, percentage of chaparral, percentage of grassland, and distance to nearest stream were all significant (Table 1). The marginal R^2 and conditional R^2 for the top model, which included percentage of oak woodland, percentage of grassland, and distance to nearest stream ($\Delta AIC_c = 0$, $w_i = 0.72$), were 0.008 and 0.40, respectively. In the analysis examining nesting success, occupancy rate was in all 3 top models, representing 100% of the model weight. In the analysis examining fledging success (Figure 2), occupancy rate was again in the 3 top models, accounting for 100% of model weight. In both analyses examining reproductive success, the only variable considered significant was occupancy rate (Table 1). For the top model predicting nesting success, the marginal R^2 and conditional R^2 for the top model, which included occupancy rate ($\Delta AIC_c = 0$, $w_i = 0.76$), were 0.23 and 0.29, respectively. The marginal R^2 and conditional R^2 for the top model predicting fledging success, which included only occupancy rate ($\Delta AIC_c = 0$, $w_i = 0.73$), were 0.23 and 0.38, respectively.

DISCUSSION

All 5 study species appeared to use nest boxes nonrandomly. Given that the nest boxes were identical in size and shape, individuals were presumably actively choosing nest sites on the basis of criteria other than the box itself. The habitat characteristics influencing nest-site selection differed among the 5 species, a pattern that could be due either to different preferences or to interspecific competition. Ash-throated Flycatchers were associated with nest boxes with less grassland and higher edge density. House Wrens were also associated with less grassland but showed a preference for sites surrounded by riparian vegetation, reflecting their tendency to nest close to streams. Oak Titmice were associated with similar habitat types as House Wrens, favoring less grassland and more riparian vegetation, but were also associated with chaparral habitat. Violet-green Swallows favored chaparral but tended to choose sites away from riparian corridors. Western

Bluebirds were associated with nest sites away from riparian corridors but avoided chaparral, and preferred areas with more grassland and oak woodland.

Although few directly comparable studies exist, our results generally agree with those of previous studies of Ash-throated Flycatchers (Cardiff and Dittmann 2002), House Wrens (Lawler et al. 2004, Johnson 2014), Oak Titmice (Wilson 1992), Violet-green Swallows (Brown et al. 2011), and Western Bluebirds (Garrett and Dunn 1981, Dickinson and McGowan 2005, Dickinson et al. 2014). However, our results differed from some previous work for some species. Although previous researchers similarly found that House Wrens preferred wooded areas, they also observed a strong preference for areas with sparse understory and low foliage density (DeGraaf 1987, Sedgwick and Knopf 1987). Our broad measures of habitat did not include small-scale differences such as foliage density within a habitat type, so this association was not detectable in our analysis. Another study conducted on a larger scale found that land-cover characteristics—including the amount of coverage by, but not proximity to, different stream types within the habitat—did not adequately capture habitat preferences of House Wrens (Lawler et al. 2004). This suggests that future studies should examine microhabitat choices in addition to broader classifications of vegetation. Previous work on "plain titmice," now split into Oak and Juniper titmice, indicated that they preferred moderately dense woodlands (Wilson 1992), which could be represented by riparian vegetation or the mixed oak–madrone forests on north-facing slopes in our study system. However, we also found a strong association with chaparral habitat, which seems to contrast with a preference for woodlands. This could simply reflect a lack of information on the behavior of Oak Titmice; while Oak Titmice may choose actual nest sites in woodlands, they may preferentially forage in chaparral. To investigate such potential differences in function, further information on the ways in which the study species are using the different habitats is necessary. Finally, our results suggest a strong association of Western Bluebirds with grassland habitats, contrasting with a previous study that found that Western Bluebirds did not favor large meadows (Guinan et al. 2008). This difference could reflect the scale at which habitat use was examined. We quantified the habitat within 100 m of each nest box, but it is possible that if habitat use were examined at a larger scale, observed use would differ.

Although there were distinct differences in habitat characteristics related to box occupancy for each of the 5 species, the R^2 values for all of the models predicting box occupancy were low, which suggests that, although the models fit the data reasonably well, there was substantial variation in occupancy that remained unexplained by the habitat variables examined here. This variation could be explained by additional habitat variables, such as microhabitat characteristics, that were not analyzed. Alternatively, habitat may not be the most important predictor of nest-box selection in these species, with other factors, such as food availability, playing a larger role.

Adding the more stringent assumption that residents' boxes were not available to migrants had no influence on the importance of habitat characteristics for nest-site selection by Ash-throated Flycatchers and Violet-green Swallows. This suggests that both migratory species were choosing the same kinds of sites, regardless of whether boxes were available or not due to prior occupation by residents. This may indicate that there is little competition between migrants and residents for nest boxes in this naturally fragmented landscape. However, more information is needed regarding the direct interactions among these species and how those interactions can affect habitat selection.

For all 5 species, occupancy rate was the best predictor of reproductive success. This suggests that box occupancy is a good indicator of habitat quality in the relatively undisturbed habitat of Hastings–Oak Ridge, further supporting the idea that these species' use of boxes is determined more by fitness-based preferences than by interspecific competition. This finding corresponds to previous studies that have found territory occupancy to be a strong predictor of species-specific territory quality (Sergio and Newton 2003, Doran and Holmes 2005, Dawson and Bortolotti 2006, Janiszewski et al. 2013, Jones et al. 2014). However, our results suggest that occupancy is a better predictor of habitat quality than the physical habitat characteristics, which contrasts with previous studies that found a link between occupancy, habitat, and reproductive success based on a single, simple, habitat characteristic that was important for each study species (Doran and Holmes 2005, Janiszewski et al. 2013, Jones et al. 2014). Our results do not identify any simple, straightforward habitat characteristics important to our study species. Given that occupancy was a better predictor of habitat quality than the physical habitat characteristics examined here, other factors, including microhabitat characteristics, available food supply, or the abundance of predators, may be more proximate causes of nesting success for these 5 species. Although habitat factors may still be important cues for these species, other habitat factors may actually be mediating the probability of success and nest-site selection; this possibility merits further analysis.

Alternatively, cues such as predator abundance may remain elusive to birds, such that box selection is close to random. If individuals show high site fidelity and survival, over time there could be an association between occupancy and reproductive success but not between occupancy and habitat characteristics. More information is also needed on the relationship between habitat quality, territory occupancy, and specific demographic parameters. A high-quality territory could allow a single pair to survive and breed successfully over multiple years, leading to high occupancy. This raises the possibility that occupancy does not always reflect settlement or preferences; it also indicates that survival, and perhaps age, may be involved in the increases we see in a pair's chances of successfully fledging young—a pattern that has been seen in other species, such as Song Sparrows (*Melospiza melodia*; Nol and Smith 1987). Without population-wide banding and following of known, marked individuals, it is impossible to differentiate between the influences of habitat quality and adult survival on occupancy and their independent associations with fledging success. Only Western Bluebirds have been followed in this way on Hastings–Oak Ridge; further work to tease apart the effects of habitat on adult survival compared to territory settlement is in progress.

In the models predicting box occupancy for all species, the conditional R^2 values, which included both fixed and random effects, were much higher than the marginal R^2 values. Although this pattern is to be expected, the large difference between the marginal and conditional R^2 values suggests that the random effects could have a disproportionately large influence. Given that year was included as a random variable, this pattern is likely explained by a large variation among years. Our study site has highly variable weather conditions, including periodic El Niño years, 3 of which occurred during the study period. Although the habitat variables may still be important, nest-box selection could be strongly dependent on the year, which is likely a proxy for other factors, including weather, food availability, and other year-dependent conditions. Future analyses should examine other parameters, such as rainfall, that vary between years, in addition to habitat characteristics.

In conclusion, all 5 species using the nest boxes on our study area nested nonrandomly, and the habitat characteristics influencing nest-site selection differed among species. In addition, occupancy rate was the strongest predictor of reproductive success. This suggests that occupancy may be a valuable proxy for habitat quality for these 5 species when nest boxes are provided.

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