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RESEARCH ARTICLE

Balancing model specificity and transferability: Barn owl nest box selection

Matthew D. Johnson[1] | Jaime E. Carlino[1] | Samantha D. Chavez[1] | Rebecca Wang[2] | Christian Cortez[1] | Laura M. Echávez Montenegro[1] | Doris Duncan[3] | Bill Ralph[4]

[1]Department of Wildlife, Cal Poly Humboldt, Arcata, CA 95521, USA

[2]978 Valecito Court, San Luis Obispo, CA 93405, USA

[3]Sonoma County Wildlife Rescue, Petaluma, CA 94952, USA

[4]41932 Bessie Jacobs Road, Raymond, CA 93653, USA

Correspondence

Matthew D. Johnson, Department of Wildlife, Cal Poly Humboldt, Arcata, CA 95521, USA.
Email: mdj6@humboldt.edu

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Abstract

Examining the transferability of habitat selection models is vital when they are used to forecast predictions in new times or places, but this issue is too often neglected. Nest boxes are often installed in agricultural landscapes to attract barn owls (*Tyto* spp.) and the ecosystem services they provide. For this practice to be effective, farmers need actionable guidelines for nest box design and placement to optimize nest box use. We addressed 3 primary objectives: 1) develop a nest box selection model in the well-studied region of Napa Valley, California, USA, 2) evaluate this model's predictive performance in other regions of California, and 3) use data from all regions to build a more generalizable model. Based on data from 6 years of monitoring used and unused American barn owl (*Tyto furcata*) nest boxes in Napa Valley, we found that nest box selection was best predicted by nest box attributes (e.g., pole height, box height, and entrance orientation), local land cover (e.g., grassland within 75 m), and landscape-scale metrics (e.g., grassland within 2.81 km). This model's predictions were strongly correlated with observed nest box use in Napa, but the model performed poorly when used to predict nest box use in other regions that are ecologically similar (Sonoma County) or dissimilar (Fresno, Merced, and Madera counties). A model pooling data from all regions fit the data well and again showed effects of box, local, and landscape predictors. It was more generalizable than the Napa-only model and lost little precision when applied with forecasting predictions to Napa in

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particular. Taken together, our results indicate that local data should be used to make the most reliable predictions of nest box use. Until those data are available, general recommendations should be made from models that pool data from as many regions as feasible and should provide appropriate caveats. Results of this work can inform nest box design and placement for the benefit of farmers and owls in California, and future research should examine nest box selection by barn owls in other areas of the world with different climates and local habitats.

KEYWORDS

barn owl, generality, habitat selection, nest box, nest site, prediction, specificity, transferability, *Tyto alba*, *Tyto furcata*

Predicting the distribution of species in time and space is a cornerstone of animal ecology (Scott et al. 2002, Guisan and Thuiller 2005, Peterson et al. 2011, Guisan et al. 2017, Matthiopoulos et al. 2020). Ecologists have developed a range of statistical models to associate species distribution with biotic and abiotic factors, including those based solely on occurrence data (niche distribution models, maximum entropy models; Elith and Leathwick 2009), those based on detection and non-detection data (site occupancy models; MacKenzie et al. 2017), and those based on used versus available or non-used sites (resource selection functions [RSFs]; Johnson et al. 2006, Lele et al. 2013). The latter, more recently called habitat selection analyses (Fieberg et al. 2021, Northrup et al. 2022), provide indices of habitat use (when used cases are compared to those randomly available, RSFs) or estimates of the actual probability of habitat use (when used and unused cases are compared, resource selection probability functions [RSPFs]; Lele et al. 2013). In some cases, these models are constructed primarily to identify which environmental covariates influence species distribution (i.e., ecological revealers), and in other cases, practitioners aim to predict species distribution for conservation and management purposes (i.e., applied predictors; Lawler et al. 2010, Matthiopoulos et al. 2023). Applied predictive models are especially useful if they can be generalized to project species distribution to a place or time other than that used to create the model, such as to investigate a species' response to changing environmental conditions or to provide insight about its distribution in a poorly studied region (Franklin 2010). The value of such predictions of course depends on a model's validity and generality, so model evaluation is a vital analytical step but is too often neglected (Randin et al. 2006, Guisan et al. 2017).

The simplest form of model evaluation involves assessing how well a model fits the data used to create the model in the first place (i.e., resubstitution), a circular approach likely to overestimate a model's generality (Fielding and Bell 1997). Partitioning the available data into training and testing sets is more rigorous and can be done with bootstrapping methods to maximize the use of all data, but these internal evaluation methods may still fail to reveal how a model performs in other times or places (Randin et al. 2006). Testing habitat models on independent data sets (i.e., external evaluation) is usually considered the most robust type of model evaluation (Guisan et al. 2017), but it is comparatively rare in the literature (Elith and Burgman 2002, Lee-Yaw et al. 2022). A model's generality can be examined by testing its ability to predict species distribution in the same place where the model was built but in a new time (temporal transferability) or by testing its predictive power in a similar time but in a new place (spatial transferability; Guisan et al. 2017, Werkowska et al. 2017). There may be trade-offs in transferability and specificity when building predictive models, with models trained on a particular region providing more temporal transferability in that area specifically, whereas models built from data more widely distributed in space may offer more spatial transferability while possibly sacrificing some specificity to a given region (Randin et al. 2006). Despite tremendous advances in model sophistication and the availability of remotely sensed environmental covariates, research indicates species distribution models often show limited temporal and spatial transferability (Randin et al. 2006, Lee-Yaw et al. 2022), prompting a need for caution when applying models to new times or places.

Model transferability relies on assumptions of species distribution at equilibrium, analogous environments, matched resolutions, and stationarity of habitat associations. First, transferability requires the target species' distribution to be approximately equilibrated with its environment (Werkowska et al. 2017), both where and when the model is created and to where and when it is transferred (Pulliam 2000), sometimes called the equilibrium rule. If a species is far below its carrying capacity where the model is built, for example, then it will not occupy all suitable sites, and the model will underestimate the range of suitable conditions for the species, leading to underestimates of its distribution in a new location (i.e., many omission errors). In contrast, if a model is created from a region in which the species is equilibrated but transferred to a place where it is far below equilibrium, the model will overestimate the distribution in the transferred location (many commission errors). Second, the environmental conditions should be similar between the time and place where the model is created (i.e., the training set) and where and when it is transferred. This is sometimes referred to as the analogous environments rule (Elith and Leathwick 2009, Rousseau and Betts 2022). Violations of this rule are particularly problematic if the species' response to an environmental gradient is non-linear and shows a differently shaped response in the model's training set compared to where it is transferred (Van Horn 2002, Randin et al. 2006), which is exacerbated when the model is extrapolated to conditions outside the range of training data. Third, if the resolution at which distribution data are available does not coincide with the interests of conservation and management, practitioners may be tempted to transfer the model to a finer or coarser resolution (called downscaling or upscaling, respectively), but doing so can lead to severe biases in predicted presence and absence (Araújo et al. 2005, Werkowska et al. 2017). Lastly, for a model to be widely transferable, a species needs to have a consistent niche and habitat association over time and across locations, sometimes called the stationarity rule (Rousseau and Betts 2022). Spatial variation in species' niches can occur if there are genetic differences among populations (Pearman et al. 2008), or if a species experiences strong spatial differences in interspecific competition, predation, or disease that affect its response to other environmental attributes (Araújo and Luoto 2007, Daskin and Alford 2012, Rousseau and Betts 2022). Thus, before using a predictive model widely, it is essential to consider the various obstacles to its transferability and to test the model against geographically and temporally new datasets (Fielding and Bell 1997, Araújo et al. 2005, Randin et al. 2006) to properly assess the conditions under which it can be reliably transferred in space and time (Werkowska et al. 2017).

Assessing the transferability of species distribution models is especially important for secondary cavity-nesting animals willing to use human-made nest or roost boxes. For these species, nest box selection models are inherently intended to be transferable because they are used to understand how those boxes should be designed, inform where new boxes should be deployed, and predict their subsequent colonization for conservation and management of the target species. This type of work is relevant for a wide range of animals, from flying squirrels (*Glaucomys* spp. Carey et al. 1997, Fokidis and Risch 2005) and martens (*Martes* spp.; Delheimer et al. 2018), to bats (Rueegger 2016, Pschonny et al. 2022), bluebirds (*Sialia* spp.), tree swallows (*Tachycineta bicolor*; Munro and Rounds 1985, Courtois et al. 2021), ducks (Dow and Fredga 1985, Lacki et al. 1987), and cavity-nesting raptors such as kestrels (*Falco* spp.; Rohrbaugh and Yahner 1997) and barn owls (*Tyto* spp.; Lambrechts et al. 2012, Wendt and Johnson 2017).

Nest boxes for western barn owls (*Tyto alba*) and American barn owls (*T. furcata*; we follow nomenclature of Aliabadian et al. 2016) have particular interest in the agricultural community because of their role in helping to reduce rodent populations (Meyrom et al. 2009, Browning et al. 2016, Luna et al. 2020, Hansen and Johnson 2022). This is an old idea; before the widespread application of chemical pesticides, systematic studies of the potential role of birds as pest control agents were produced for the then-named field of economic ornithology (Evenden 1995). Barn owls were among the first birds recognized for their potential to control rodent pests (Fisher 1983). By the late 1930s, however, depictions of birds as useful agents of pest control declined, and the field of economic ornithology all but disappeared (Whelan et al. 2015). The emerging dominance of chemical pesticides was clearly underlying this change, but economic ornithology also collapsed because it failed to offer practical methods for harnessing the role of birds as pest eaters (Johnson et al. 2018). This history illustrates the importance of applied research on animals' selection of nest box designs and placement to provide farmers and other practitioners with the information necessary to maximize nest box use. Currently, gray literature provides farmers with several barn owl nest box designs and general recommendations for box placement (Wild Farm Alliance 2022, Cornell Lab of Ornithology 2024), and there are a few careful studies of barn owls' selection of nest box attributes and habitat in various locations (e.g., Charter et al. 2010, Frey et al. 2011, Hindmarch et al. 2012, Zmihorski et al. 2020, Huysman and Johnson 2021*a*, Charter and Rozman 2022) but no examination of whether those patterns of selection vary regionally (Lambrechts et al. 2012).

In this study, we address this research gap by building a model of American barn owl nest box selection using 6 years of data (2015–2020) from Napa Valley, California, USA, and then examining the model's performance by testing its ability to predict nest box use in 3 other settings. First, we examined the model's temporal forecasting ability by assessing its predictive accuracy in Napa Valley in the following year (2021). Second, we examined the model's spatial transferability by testing it against data from a neighboring county, Sonoma, with a similar overall landscape composition. Both counties are known for wine production and have heterogenous landscapes composed of vineyards, grassland, oak savanna, forests, and urban areas. Third, we tested the model's transferability with data from boxes monitored in other agricultural counties in California with much larger farms, less heterogeneity, and different crops, including more row crops and orchards (especially pistachio, almond, and fig; Madera, Merced, and Fresno counties). Thus, we tested a model from a focal region with abundant data in several settings arranged in decreasing environmental analogy and increasing order of challenge to the model. Fourth, and finally, we examined whether a different model built with data pooled from all regions better predicted owl nest box use overall, and if that model sacrificed some specificity for Napa Valley in particular. Results of these analyses allowed us to make recommendations for barn nest box design and placement, assess the generality of those recommendations, and present a case study of evaluating trade-offs between model specificity and transferability.

STUDY AREA

American barn owls are widely distributed and common in California (Marti et al. 2020). We collected data from 4 agricultural regions in the state: Napa Valley, where researchers from Cal Poly Humboldt have monitored >300 nest boxes since 2015 (Huysman and Johnson 2021*a*); Sonoma County, where the Sonoma County Wildlife Rescue recently launched a barn owl nest box installation and monitoring program; Merced County and portions of neighboring Madera County (hereafter Merced for brevity), where nest boxes have been monitored for several years (B. Ralph, unpublished data); and Fresno County, where nest box use was monitored on a pistachio orchard in 2019.

Napa Valley is approximately 100 km north of San Francisco (Figure 1) and is bordered by the Mayacamas Mountains on the west and the Vaca Range on the east. It is a world-renowned winegrape growing region, contributing an estimated $42.4 billion to the United States economy (Stonebridge Research Group 2017). The region is characterized by a Mediterranean climate (summer highs 28–31°C) that, together with its unique geologic history, microclimates, and diverse soils, supports 16 viticultural appellations (Elliott-Fisk 1993, Napa Valley Vintners 2020). Precipitation from February to July averages 21.2 cm (National Oceanic and Atmospheric Administration [NOAA] 2024). Around the vineyards, the northern region of the Valley is primarily composed of mixed oak scrub and conifer forests, whereas the southern region of the Valley is primarily composed of grasslands and oak savannas (Napa 2010, Wendt and Johnson 2017). Vineyard cultivation dominates the valley floor, with over 200,000 ha under cultivation across more than 2,000 vineyards (Stonebridge Research Group 2017).

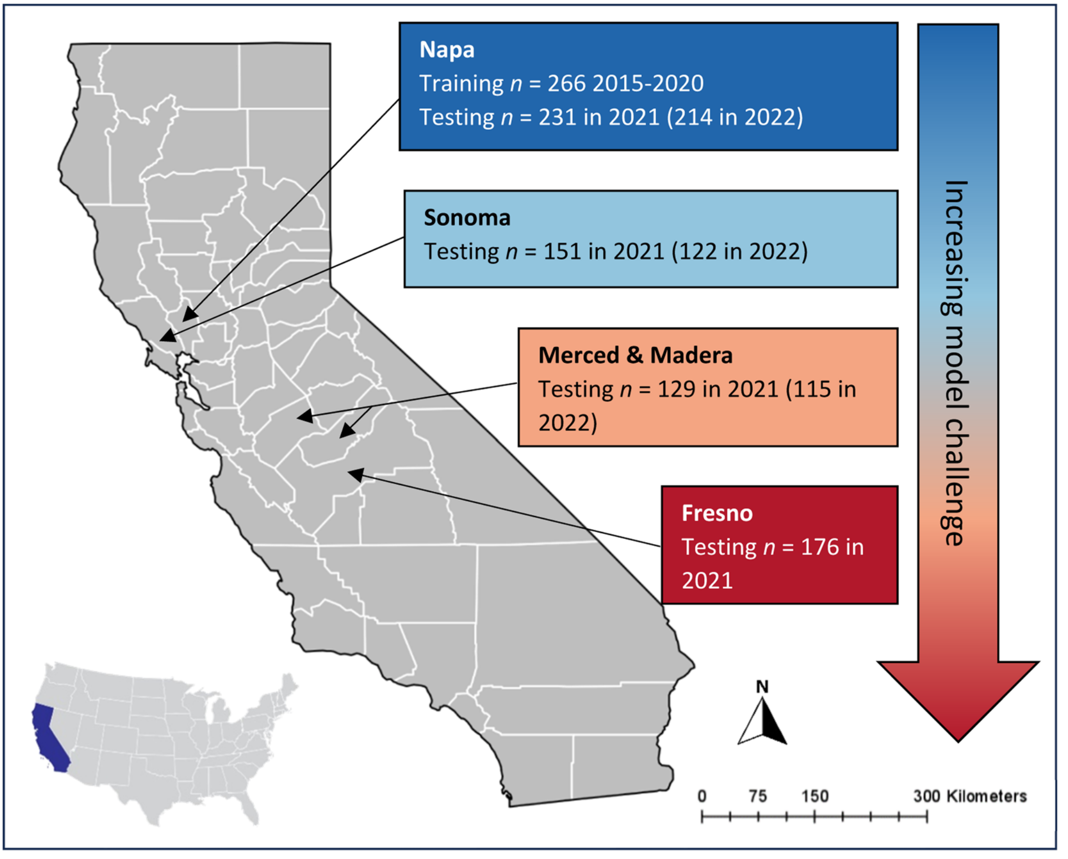

FIGURE 1 California, USA, counties where we monitored barn owl nest boxes (2015–2022) to build and test models of nest box selection.

The nest boxes included in this research were independently and opportunistically installed by land owners within and along vineyard edges (see Wendt and Johnson 2017 for further details). They varied in placement, size, height, material, and orientation, and the vineyards varied in size, surrounding land cover, urban development, and growing techniques. The number of nest boxes on each vineyard varied from 1 to 27 and the distance between the nearest boxes varied from 20–1,353 m, but the average distance between boxes was 170 ± 127 m (mean ± SD).

In Sonoma, we assessed nest boxes deployed and managed by Sonoma County Wildlife Rescue's Barn Owl Monitoring Program (BOMP). Most boxes were purchased from the BOMP program by private landowners and thus nearly all had essentially the same design and dimensions, and were relatively new (erected from 2015–2020). A few boxes (~8% of the total sample) were pre-existing and these varied in design. The average distance between boxes was 310 ± 239 m. The local and landscape conditions varied depending on box placement; most were deployed in the cultivated valleys and foothills of Sonoma County on winegrape vineyards, though some were deployed at private residences or near pastures. Sonoma County is immediately to the west of Napa County, and as noted earlier, the agricultural valleys in these counties share a very similar climate and land cover. Winegrape cultivation (>25,000 ha) and pastures dominate agricultural activities, with winegrapes and milk as the top 2 agricultural commodities (Sonoma County 2023). However, Sonoma is slightly cooler (summer highs 25–28°C) and wetter than Napa, with average precipitation from February to July averaging 34.0 cm (NOAA 2024).

In Merced, the owl box locations ranged from approximately Snelling in Merced County (about 183 km southeast of Sonoma and Napa) to Madera (about 180–250 km southeast of Sonoma and Napa); the average distance between boxes was 119 ± 98 m. The climate is warmer in this region than in most of Sonoma or Napa, with summer highs ranging from 28–34°C, and precipitation from February to July averaging 15.3 cm (NOAA 2024). These are highly productive counties with agricultural commodities grossing >$6.6 billion in 2022, and they are known especially for almonds, pistachios, other nuts and hulls, figs, and grapes (Madera County 2022).

In southern Fresno County (Ingleby Farms), the average distance between boxes was 178 ± 79 m. Like Merced, Fresno County is warmer and drier than Sonoma or Napa counties, with summer highs 28–34°C, and average precipitation from February to July averaging 16.0 cm (NOAA 2024). It contains 1.88 million acres of highly productive agricultural land, dominated by almonds, grapes, and pistachios. Agriculture in Fresno County contributes more than 5.6 billion dollars to the state's economy. Pistachios ranked third in the top 10 crops grown in Fresno County, bringing in roughly $8.6 million (County of Fresno Department of Agriculture 2018). The landscape in this study area consisted primarily of agriculture with sloughs running through the orchards that create riparian ecosystems. The pistachio fields were lined with pomegranate trees and surrounding fields produced almonds, corn, and winegrapes.

METHODS

Nest box surveys

Ongoing research on nest box monitoring and selection in Napa Valley began in 2015 with 297 nest boxes (Wendt and Johnson 2017). In 2016 and 2017, we monitored a random sample of 150 of those boxes. From 2018–2022, we monitored the existing original 297 boxes plus newly erected nest boxes throughout the breeding season, with some losses due to damaged or removed boxes. For this analysis, we used 266 boxes that included data for at least 6 of the 8 years between 2015–2022. We monitored nest boxes with a camera (Hero Session and Hero 7; GoPro, San Mateo, CA, USA) fitted with a light-emitting diode (LED) flashlight mounted on an extendable pole, which we inserted into the nest box entry hole (Huysman and Johnson 2021*b*). The camera was wirelessly connected to a smartphone, allowing us to view the contents of the nest box from the ground. This minimized disturbance and potential for abandonment during sensitive nesting periods (M. D. Johnson, Cal Poly Humboldt, unpublished data). Our emphasis was on breeding nest box use because breeding is essential for sustaining a local population (Carlino et al. 2022) and because a nesting family of owls removes far more rodents than do non-breeding adults (Johnson and St. George 2020). Therefore, we considered a nest box to be used if there were barn owl eggs or nestlings at any point in the breeding season.

With most barn owl courtship beginning in January, peak egg-laying often occurs from late February through March (Bourbour et al. 2022). Egg laying lasts approximately 10–15 days with eggs being laid every 2–3 days and an average clutch size of approximately 5 (Marti et al. 2020). Incubation lasts 29–34 days and offspring fledge at 50–65 days (Marti et al. 2020). Monitoring schedules differed slightly from 2015–2020 and 2021–2022. From 2015–2018, we checked nest boxes every 10 days in March. After these initial 3 checks, we monitored all boxes with barn owl presence monthly at least 3 more times to determine or confirm breeding use. In 2020, because of COVID restrictions, we conducted a single survey during the month of May, which is the month with peak detection probability (M. D. Johnson, unpublished data). In 2021–2022, we monitored all nest boxes for use monthly from March through July. These monitoring protocols limited the event of a used box going undetected. Using multi-season occupancy modeling for years 2015–2018, we estimated overall detection probability to be over 97% (A. E. Huysman, Cal Poly Humboldt, unpublished data), and single-season modeling for 2022 showed the detection probability to be over 98% (J. E. Carlino, Cal Poly Humboldt, unpublished data). Thus, for analytical purposes, we assume boxes with no detected use were unused, enabling the analysis of used and unused resource units to estimate an RSPF (Lele et al. 2013).

Nest box surveys in Sonoma, Fresno, and Merced generally followed a similar protocol, though many boxes in Sonoma and Merced were examined by a field worker plugging the entrance hole, climbing a ladder, and visually inspecting contents. Nest box checks in Fresno (monthly from January through May) and in Merced (once every 2 weeks starting in mid-March) were similar to monitoring schedules in Napa, but nest box checks were less frequent in Sonoma (1–2 times per season). In Sonoma the monitoring was timed to optimize detection with nest checks occurring in late April and again in May when detection probability is maximized locally (M. D. Johnson, unpublished data). We were unable to model detection probability with these datasets outside of Napa, and though the resulting estimates of nest box use are likely slight underestimations of true box use owing to some small number of missed nesting attempts, these study areas showed rates of nest box use within the range observed in Napa Valley, so we considered the data useful for measures of model performance.

Land cover and nest box attributes

We conceptualized barn owl nest box selection to operate at 3 levels: nest box attributes, local land cover composition within 75 m, and landscape land cover composition within a 2.81-km radius. We chose the local radius to reflect the immediate flight environment of adults frequenting the nest box and the immediate habitat experienced by recently fledged owlets. The larger landscape radius was the mean maximum distance traveled from nest boxes based on a previous telemetry study in Napa (Huysman and Johnson 2021*b*). We hypothesized that the local land cover composition affects nest box selection because of physical attributes (i.e., flight path), safety (e.g., proximity to forest), and favorable local habitat for recently fledged chicks (e.g., grassland). We hypothesized that landscape composition affects nest box selection because hunting adult owls show clear selection for a high proportion of uncultivated land cover within their hunting radius in our study region (Huysman and Johnson 2021*b*). We hypothesized that 10 nest box attributes affect the selection of boxes by barn owls because of their relation to thermoregulation and predator avoidance (Table 1). Researchers measured all nest box attributes by hand in the field. We report imperial units for nest box dimensions to be consistent with nest box building plans and construction materials commonly available in the United States. We visually assessed local habitat composition (%) within 75 m in the field with 5 categories (grassland, forest, vineyard-orchard, road-building, or other crop) and quantified landscape composition from

TABLE 1 Barn owl nest box attributes investigated in 4 regions of California, USA, 2015–2021.

Variable	Units/measurements[a]	Rational
Pole height	Feet	Minimize predation
Pole material	Binary (wooden [e.g., mounted to a tree] or metal)	Minimize predation
Box height	Inches	Space for adults and nestlings
Box area	Inches squared	Space for adults and nestlings
Hole diameter	Inches	Minimize predation and competition
Entrance direction	Categorical (N, E, S, W)	Thermoregulation
Appendage (perch or platform on exterior of box)	Binary (yes or no [Y/N])	Minimize predation (if N) or aid in prey delivery of nestling development (if Y)
Thermoregulation (ventilation holes or heat shield)	Binary (Y/N)	Thermoregulation
Box material	Binary (plastic or wooden)	Thermoregulation or other
Partial wall (interior)	Binary (Y/N)	Minimize predation or thermoregulation

[a]Imperial units are used to be consistent with nest box building plans and construction materials commonly available in the United States.

CropScape (Center for Spatial Information Science and Systems 2024), a land cover data layer created annually for the continental United States using moderate resolution satellite imagery and extensive agricultural ground truthing. This layer was well-suited for our purposes because it is year-specific and wide-scale, offering the potential for our model to be used in other times and places. It also distinguished among many more crop types than other land cover layers, and its resolution (30 × 30 m) was adequate for barn owls, which have relatively large home ranges (Roulin 2020). We reclassified CropScape's numerous land cover types into 9 categories based on their relevance to barn owls, including 4 uncultivated types (forest, oak and shrubland, riparian, and grassland), 3 cultivated types (orchard-vineyard, grassy crops, and other crops), and 2 unsuitable types (water-wetland and urban-barren). We pooled orchard and vineyard crop types because they offer similar attributes to barn owls (perennial, with structure for perching), and we pooled several crop types into grassy crops (e.g., hay, alfalfa, wheat) because they are structurally similar and offer near uniform ground cover that likely supports more rodent prey than do other row crops (e.g., tomatoes, onions, leafy greens). We used ArcGIS Pro version 2.9 (Esri, Redlands, CA, USA) and program R version 4.1.3 (R Foundation for Statistical Computing, Vienna, Austria) to extract the proportion of each land cover type within a 2.81-km radius around each nest box. We statistically compared the nest box attributes, local land cover, and landscape composition among regions (Napa, Sonoma, Merced, Fresno) using multivariate analysis of variance (MANOVA) and linear discriminant analysis (using the MASS package in R; Venables and Ripley 2002) for land cover at local and landscape scales, Kruskal-Wallis tests followed by Wilcoxon rank sum tests for *post hoc* pairwise comparisons on continuous box attributes (e.g., pole height, box height), and χ^2 tests of independence on categorical nest box attributes (e.g., entrance orientation, presence–absence of partial wall), using $P < 0.05$ as an indicator of strong evidence, with Bonferoni adjustments for multiple comparisons where necessary.

Nest box selection models

Using data from 266 nest boxes monitored in Napa Valley from 2015–2020, we built a nest box selection model. We then used this model to forecast use of 231 nest boxes in Napa in 2021, comparing predicted versus observed nest box use to assess the model's temporal transferability (Figure 1). Next, we used the Napa model to predict the use of 151 nest boxes monitored in Sonoma county in 2020, and again compared predicted versus observed nest box use to assess the model's spatial transferability to that region with a relatively similar landscape composition and climate. We similarly used the Napa model to predict the use of 129 boxes monitored in Merced in 2020 and 176 monitored in Fresno in 2019, quantifying transferability to those regions with less similar landscapes and climates. Finally, we pooled data from all 4 regions ($n = 687$) to build a transregional nest box selection model, and we used data from 451 boxes in Napa, Sonoma, and Merced monitored in 2022 to examine its predictive performance (Figure 1).

We used generalized linear models (GLMs) with a binomial error distribution to examine nest box selection with the proportion of years each box in Napa Valley was monitored and used from 2015–2020 (training data) as the response variable. Predictor variables included box attributes, local land cover, and land cover composition at the landscape scale. Generalized linear models have been shown to be better for model transferability than generalized additive models (GAMs), which can lead to overfitting models to the local training set (Randin et al. 2006). We examined pairwise collinearity using Pearson's correlation coefficients with $|r| \geq 0.70$, and retained the variables that were more ecologically relevant to barn owls (Dormann et al. 2013). We used unscaled data because we did not encounter problems with convergence and because coefficients needed to be on raw scales to be forecast and transferred to other times and places with different ranges of predictor variable values. For the final analysis of top models and reporting, however, we used scaled variables (standardized by subtracting the mean and dividing by the standard deviation prior to fitting) so that coefficients could be more intuitively compared among predictors. In addition to linear responses, we explored a quadratic relationship with hole diameter (hypothesizing a selection for intermediate sizes) and quadratic and pseudo-threshold functional responses for grassland composition in the landscape radius based on previous work (Castañeda et al. 2021). We then explored the effect of each predictor on nest box use using univariate GLMs to conservatively remove uninformative predictors and narrow down the variables to include in our candidate model set and avoid overfitting. We retained variables explaining at least 10% of the deviance as strong predictors and variables explaining 5–9% of the deviance as moderate predictors. Finally, we fit 18 *a priori* candidate GLMs including combinations of strong and moderate predictors from each level (box, local, and landscape), a null model, and models based on earlier work (Wendt and Johnson 2017, Huysman and Johnson 2021*b*, Carlino 2024). We used corrected Akaike's Information Criterion (AIC_c) for model selection and considered all models with ≤2 ΔAIC_c of the top model as competitive (Burnham and Anderson 2002). We considered variable coefficients with 95% confidence intervals that did not overlap zero to show strong selection or avoidance; we considered variables with coefficients ± 1 standard error that did not include zero to show a tendency for selection or avoidance. We followed the same procedure to build a transregional model pooling data from all boxes from Sonoma, Fresno, Merced, and the 2021 data from Napa to align with single-year data of the other regions; total $n = 687$ boxes), which yielded a transregional model set containing 16 candidate models.

We first validated the Napa model against the data used to build it by regressing the proportion of years each box was used (2015–2020) against the top model-predicted probability of nest box use (analogous to resubstitution), with the expectation of a significant positive relationship with a slope close to 1.0. We did not model-average because there was a single clear top model and because of concerns with using model-averaged coefficients (Cade et al. 2015). Next, we assessed the model's capacity to forecast to a new time by using the coefficients from the top model to obtain predicted probabilities of nest box use for each nest box monitored in Napa in 2021 ($n = 231$). We then computed the correct classification rate (CCR) using a default threshold (0.5) and one that maximized CCR. We also computed the Kappa statistic, the true skill statistic (TSS; Allouche et al. 2006), and the threshold independent area under the receiver operating characteristic (AUC) using the package PresenceAbsence in R (Freeman and Moisen 2008). We interpreted AUC values using the classification of Araújo et al. (2005): excellent AUC > 0.90, good AUC > 0.80 – 0.90, fair AUC > 0.70 – 0.80, poor AUC > 0.60 – 0.70, fail AUC ≤ 0.60. We interpreted Kappa values also using a classification suggested by Araújo et al. (2005): excellent K > 0.75, good K > 0.4 – 0.75, poor K ≤ 0.40. Similarly, we assessed the Napa model's spatial transferability by using the top model's coefficients to obtain predicted probabilities of nest box use for nest boxes in Sonoma, Merced, and Fresno, again computing the CCR, Kappa, TSS, and AUC to quantify performance. Finally, we used coefficients from the top transregional pooled models and the top Napa model to forecast nest box use for a subset of boxes monitored in 2022 in Napa ($n = 214$), Sonoma ($n = 122$), and Merced ($n = 115$), and we computed CCR, Kappa, TSS, and AUC to assess and compare the transferability of those models. There were several competitive models for the transregional model, so we created weighted average predictions using coefficients from all models within 2 AIC_c of the top model (Cade et al. 2015).

RESULTS

As expected, land cover composition at the landscape scale (within 2.81 km of nest boxes) differed among all 4 regions in the study (Wilk's lambda = 0.039, $F_{27,\ 1972} = 147.9$, $P < 0.01$), but Napa and Sonoma were comparatively more similar to each other than either was to Merced and Fresno (Figure S1). For example, nest boxes in Napa and Sonoma had, on average, more forest (9% and 18%, respectively) and shrubland (10% and 17%) within 2.81 km than did either Merced or Fresno (<2%). In contrast, the more intensively cultivated regions of Merced and Fresno had, on average, more vineyard-orchard within 2.81 km of their nest boxes (42% and 62%) than did boxes in Napa and Sonoma (35% and 15%). All 4 regions had similar proportions of grassland-pasture or grassy crops (e.g., alfalfa) around their nest boxes (means of 23–38% for all regions). The other land cover types were generally rarer, though Napa and Sonoma had more urban space near nest boxes (13% and 17%) than did either Merced or Fresno (<7%), and Fresno had very little riparian land cover (<0.1%). Local habitat conditions within 75 m of nest boxes were comparatively more similar among regions (Figure S2; Wilk's lambda = 0.546, $F_{15,\ 1875} = 30.6$, $P < 0.01$). Nest boxes were deployed by farmers within fields or along their margins, so vineyard-orchard was the most common local land cover type near nest boxes, ranging from 42% (Sonoma) to 68% (Fresno). The amount of grass (10–21%) and road or buildings (10–19%) near best boxes was similar among all 4 regions. Sonoma and Napa had more forest (17% and 7%) than did Fresno and Merced (<2%), and Fresno had more other crops (14%, especially corn and pomegranates) than did the other regions (<4%). Thus, as the Napa model was transferred to Sonoma, Merced, and Fresno, the environments were decreasingly analogous.

Nest box attributes differed among regions in several ways. Nest box installation guidelines in California often advise installers to orient boxes so their entrances face either eastward or northward (generally away from prevailing winds and direct sun in the afternoon; Wild Farm Alliance 2022), and these 2 orientations were indeed most common in our study. However, all nest box entrances were facing eastward in Sonoma, whereas eastward-facing boxes comprised 37% (Napa) to 58% (Merced) and 60% (Fresno) in the other regions (Figure 2). Northward-facing boxes were the next most common, ranging from 13% (Fresno) to 27% (Merced) to 36% (Napa). Pole heights were tallest in Napa and Sonoma, and lowest in Fresno (Figure 2). Nest box heights were overall taller in Napa (mean ± 1 SE; 20.9 ± 0.28 inches; 53 ± 0.7 cm) and Sonoma (21.6 ± 0.29 inches; 55 ± 0.7 cm) because they contained proportionally more 24-inch (61-cm) nest boxes, whereas most boxes in Merced (16.6 ± 0.09; 42 ± 0.2 cm) and Fresno (16.5 ± 0.01; 42 ± 0.03 cm) were smaller (Figure 2). Overall, most boxes included partial interior walls, though this proportion varied from 66% in Napa, to 88% in Sonoma, and 100% in Merced and Fresno. All boxes in Fresno and Merced were wooden, whereas 18% and 2% were plastic in Napa and Sonoma, respectively.

The proportion of nest boxes used in Napa varied over years, with a low of 31% in 2015 to a high of 52% in 2018. The top model for nest box selection from 2015–2020, carrying 67% of the model weight in the candidate set (Table 2), was the global model. No other model was within 2 AIC_c. Model coefficients (scaled, Figure 3) indicated that the owls most strongly selected boxes that were tall, mounted on tall poles, facing south, and with abundant grassland within 75 m (95% CIs around coefficients excluded zero). They also showed tendencies (coefficients ± 1 SE excluded zero) to select boxes that included a partial interior wall, facing north, and with abundant grassland-pasture within 2.81 km. They avoided boxes with extensive forest or shrubland-oak savanna within 2.81 km and showed some tendency to avoid boxes that were made of plastic, with extensive forest within 75 m, and with other crops within 2.81 km.

The Napa model performed well when tested against data from Napa. The observed frequency of use (from years 2015–2020) among boxes was strongly positively correlated with their predicted probability of use ($t_{264} = 20.62$, $P < 0.001$, $r = 0.79$), with a slope that did not differ from 1.0 (1.01 ± 0.05), indicating the model fit the data used to build it very well. When forecasting this model to assess its capacity to predict nest box use in Napa the following year in 2021 (temporal transferability), the model showed good predictive power with a correct classification rate of 76%, a Kappa statistic of 0.55, which is considered good, and a TSS of 0.58. The AUC value for this model was 0.85, which is also considered good (Araújo et al. 2005). A threshold value of 0.43 maximized the correct classification rate at 78%.

The Napa model performed worse when transferred to other regions. When applied to data from Sonoma in 2020, the 2015–2020 Napa model had a correct classification rate of 74%, but a Kappa statistic of only 0.24, which is considered poor, and a TSS of 0.25. The AUC value for this model was 0.65, which is also considered poor (Araújo et al. 2005). With a relatively low proportion of nest box use in the Sonoma data (16%), the correct classification was maximized at a high threshold value (0.95), peaking at 84% (when the model predicted all absences). When applied to data from Merced in 2021, where the rate of nest box use was 67% and the landscape is more homogenous and with different types of farms than those in Napa or Sonoma, the Napa model performed even worse. The correct classification rate was 40%, the Kappa statistic was 0.08, which is poor, and the TSS was 0.11. The AUC value was 0.57, which is considered a failure (Araújo et al. 2005). A threshold value of 0.085 maximized the correct classification rate at 67% by predicting all presences. In Fresno, which has a similar landscape to Merced but a much lower rate of nest box use (26%), the Napa model again performed poorly. The correct classification rate was 74%, but the Kappa statistic was 0.17, which is

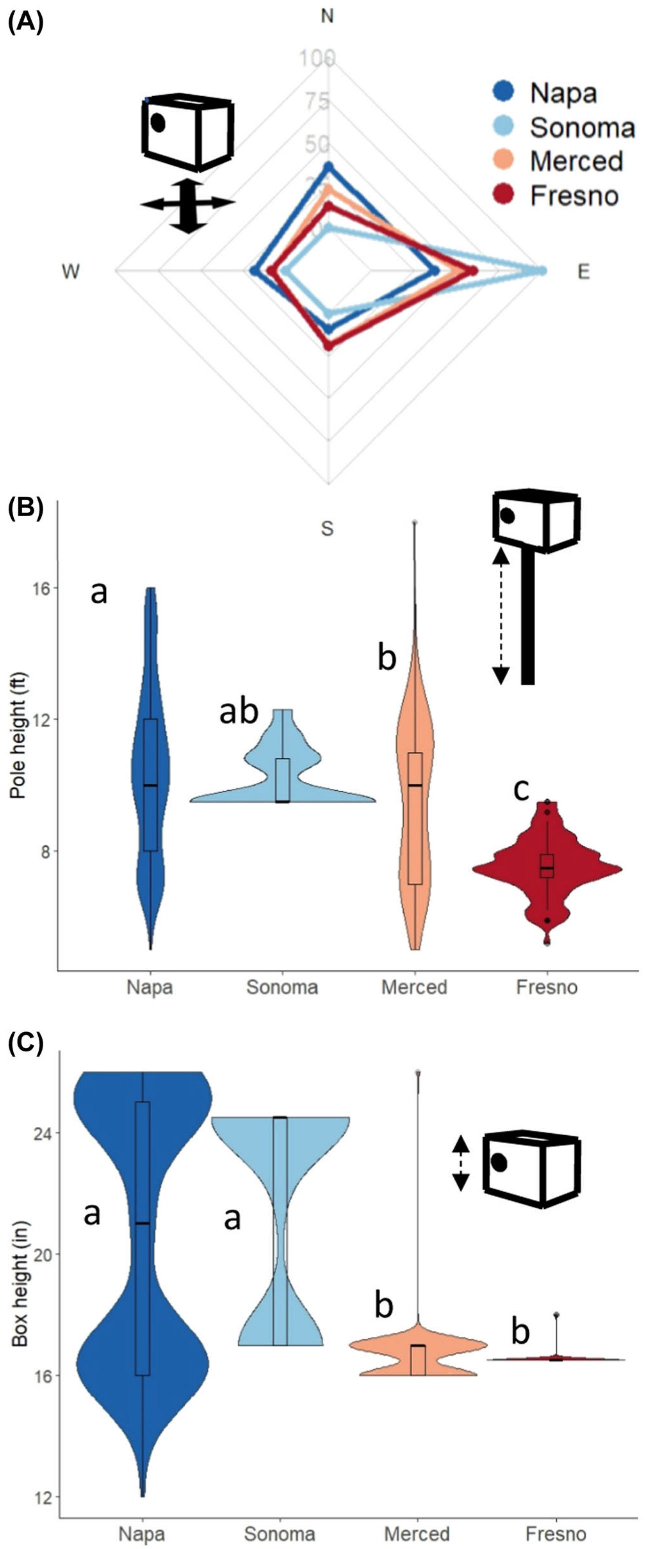

FIGURE 2 (See caption on next page).

TABLE 2 Candidate model set based on corrected Akaike's Information Criterion (AIC_c) for barn owl nest box selection among 266 nest boxes monitored in Napa, California, USA, 2015–2020.

Model	Number of parameters	Residual deviance	AIC_c	ΔAIC_c	Weight
Global (box[a] + local[b] + landscape[c])	17	432.48	739.80	0.00	0.67
Box + landscape	15	439.98	742.76	2.96	0.15
Simple box[d] + landscape	11	450.25	744.14	4.34	0.08
Simple global (simple box + local + simple landscape[e])	10	453.07	744.8	5.00	0.05
Carlino et al.[f]	8	457.89	745.31	5.51	0.04
Box + simple landscape	12	453.27	749.36	9.56	0.01
Simple box + simple landscape	8	463.02	750.44	10.64	<0.01
Huysman and Johnson[g]	6	511.43	794.62	54.82	<0.01
Wendt and Johnson[h]	10	503.05	794.77	54.97	<0.01
Landscape + local	9	581.03	870.59	130.79	<0.01
Simple landscape + local	6	588.46	871.64	131.84	<0.01
Landscape	7	588.86	874.16	134.36	<0.01
Box + local	11	581.20	875.10	135.30	<0.01
Simple landscape	4	599.55	878.56	138.76	<0.01
Simple box + local	7	609.84	895.14	155.34	<0.01
Box	9	619.43	909.00	169.20	<0.01
Simple box	5	668.50	949.59	209.79	<0.01
Null	1	947.62	1,220.50	480.70	<0.01

[a]Pole height, box height, partial wall (present or absent), box material (wood or plastic), box area, entrance category (N, S, E, W).
[b]Grassland within 75 m, forest within 75 m.
[c]The amount of the following within 2.81 km: grassland-pasture, shrubland-oak savanna, vineyard-orchard, forest, grassy crops, other (non-grassy) crops.
[d]Same as box but without box area or entrance category.
[e]Same as landscape but without forest, grassy crops, other (non-grassy) crops.
[f]Pole height, box height, box material, forest within 75 m, grassland within 75 m, forest within 2.81 km, grassland within 2.81 km.
[g]Pole height, box material, and the following within 2.81 km: grassland-pasture, forest, shrubland-oak savanna.
[h]Pole height, entrance category, box material, and the following within 2.81 km: grassland-pasture, forest, shrubland-oak savanna, riparian.

considered poor, and the TSS was 0.13. The AUC value for the Napa model transferred to Fresno was 0.53, which is again considered a failure. A threshold value of 0.19 maximized the correct classification rate at 76%.

When pooling nest boxes from all regions (n = 687), the top nest box selection model combined 6 variables of nest box attributes, 1 local habitat variable, and 2 landscape variables (Table 3). Three other similar models were competitive ($\Delta AIC < 2$), by either including an additional landscape variable (global model), dropping the local habitat

FIGURE 2 Distribution of barn owl nest box entrance orientations (A) and violin plots of nest pole height (B) and box height (C) of barn owl nest boxes in 4 regions of California, USA, 2015–2021. Regions not sharing a lowercase letter had strong evidence that they were different from each other based on Tukey *post hoc* pairwise comparisons.

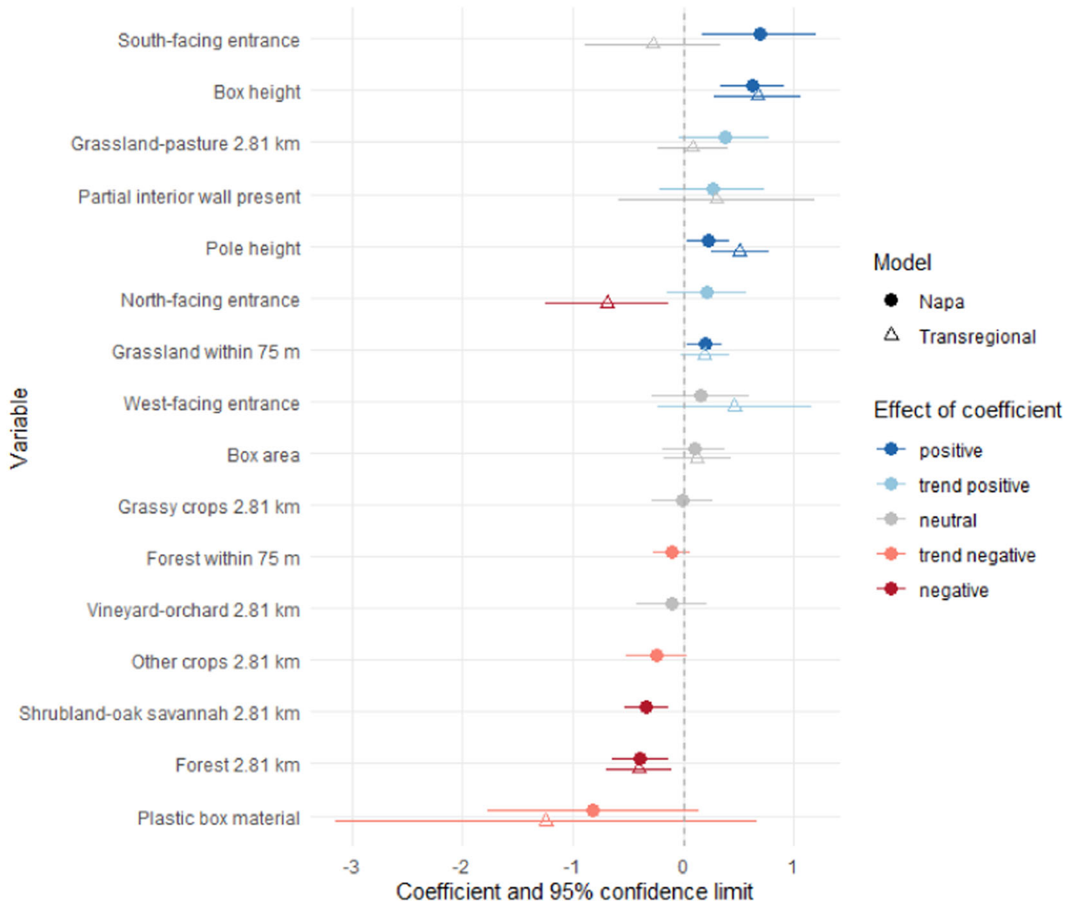

FIGURE 3 Coefficients (scaled) and their 95% confidence limits from the top barn owl nest box selection model trained on data from Napa County, 2015–2020, and the top transregional model, 2019–2021, trained on data from 4 study regions (Napa, Sonoma, Merced, and Fresno) in California, USA. Coefficients with 95% confidence intervals that excluded zero show strong selection (positive) or avoidance (negative); coefficients with standard errors that excluded zero were considered to show tendencies for selection or avoidance. Variables are arranged in order from most selected (top) to most avoided (bottom) according to the Napa model. Reference categories were partial interior wall absent, wooden box material, and east-facing entrance.

variable, or both. Together these 4 models contained over 92% of the model weight in the candidate set. Top model coefficients (Figure 3) indicated that the owls most strongly selected for tall boxes mounted on tall poles, and selection was negatively associated with north-facing boxes and with the amount of forest within 2.81 km (95% CIs around coefficients excluded zero). Our transregional model indicated that, all else being equal, a 24-inch (61-cm) box was 4.09 times more likely to be used than a 16-inch (40.6-cm) box (95% CI = 1.80–9.31 times more likely). It also indicated, all else being equal, that a box with 10% of the surrounding landscape (2.81-km radius) in forest was 2.23 times more likely to be used than a box with 33% landscape forest (95% CI = 1.25–4.00 times more likely). They also showed tendencies (coefficients ± 1 SE excluded zero) to select boxes that were facing west and with a large amount of local grassland (within 75 m). They showed a tendency to avoid boxes made of plastic. When validating the weighted predictions (from top 4 models) against the data used to build the transregional model, the performance was strong. The correct classification rate was 78%, the Kappa was 0.50, which is considered good, and the TSS was 0.49. The AUC value for this model was 0.81, which is considered good. A threshold value of 0.52 maximized the correct classification rate at 78%.

TABLE 3 Candidate model set based on corrected Akaike's Information Criterion (AIC_c) for a transregional model of barn owl nest box selection among 687 nest boxes monitored in Napa, Sonoma, Merced, and Fresno, California, USA, 2019–2021. We used predictions from the top 4 models for measures of model performance (cumulative model weight > 0.92).

Model	Number of parameters	Residual deviance	AIC_c	ΔAIC_c	Weight
Box[a] + local[b] + simple landscape[c]	13	699.20	725.76	0.00	0.336
Box + simple landscape	12	702.20	726.63	0.87	0.217
Global (box + local + landscape[d])	14	698.10	726.72	0.96	0.208
Box + landscape	13	700.70	727.22	1.46	0.162
Simple global (simple box[e] + local + simple landscape)	9	711.40	729.63	3.87	0.048
Simple box + simple landscape	8	716.00	732.24	6.48	0.013
Simple box + landscape	9	714.60	732.83	7.07	0.010
Box+local	11	711.90	734.28	8.52	0.005
Simple box + local	7	724.00	738.12	12.36	0.001
Box	10	718.60	738.91	13.15	0.000
Simple box	6	732.00	744.16	18.40	0.000
Landscape	5	793.30	803.35	77.59	0.000
Local + landscape	6	792.90	805.01	79.25	0.000
Simple landscape	4	797.40	805.46	79.70	0.000
Local + simple landscape	5	796.80	806.89	81.13	0.000
Null	2	825.80	829.81	104.05	0.000

[a]Pole height, box height, partial wall, box material (wood or plastic), box area, entrance category (N, S, E, W).

[b]Grassland within 75 m.

[c]The amount of the following with 2.81 km: grassland-pasture, forest.

[d]Same as simple landscape but with addition of vineyard-orchard within 2.81 km.

[e]Same as box but without box area and entrance category.

Finally, when tested against data from 2022, the transregional model performed a little better overall than did the model from Napa 2015–2020, sacrificing little in terms of specificity for predictions in Napa (Figure 4). The model built from data from Napa 2015–2020 only performed well in Napa in 2022, with failing scores (AUC values < 0.6 and Kappa < 0.1) in both Sonoma and Merced. The transregional model also failed when transferred temporally to Sonoma in 2022, but it performed comparatively better in Merced, though it was still graded as poor. The transregional model's performance in Napa and among all regions pooled was generally fair (AUC > 0.7, Kappa = 0.39–0.49).

DISCUSSION

We found that a barn owl nest box selection model built from abundant data in a single region (Napa) performed well when used to forecast nest box use in that same region the following year, but it generally performed poorly when transferred to different regions, even to a neighboring county (Sonoma) with a relatively similar land cover

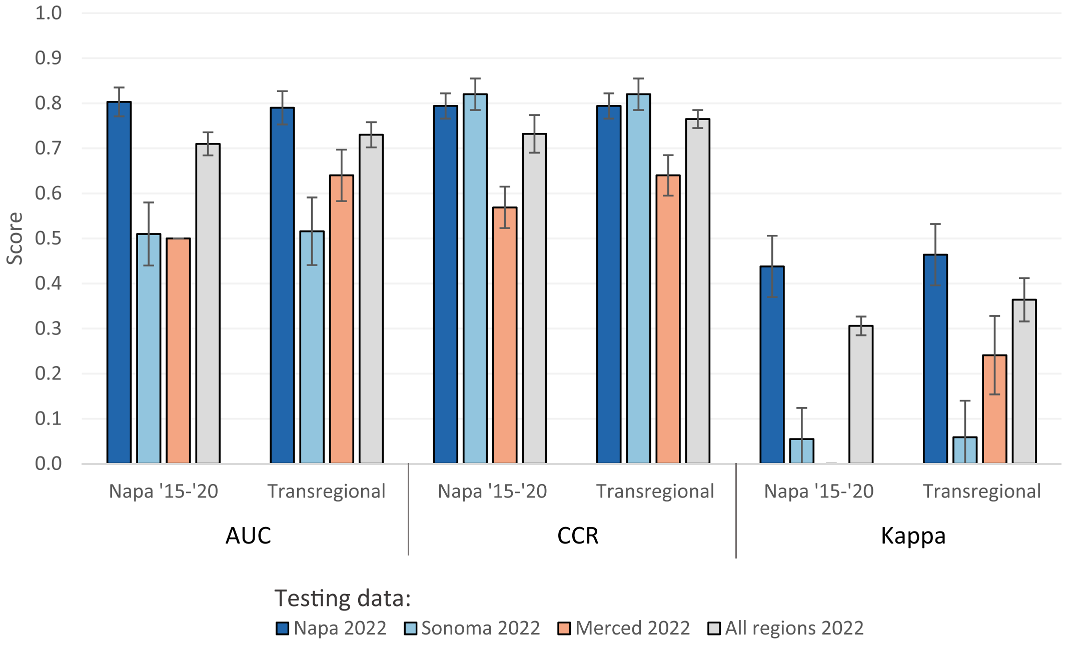

FIGURE 4 Performance metrics of the top barn owl nest box selection model trained on data from Napa County, 2015–2020, and the top transregional models, 2019–2021, trained on data from 4 study regions (Napa, Sonoma, Merced, and Fresno) in California, USA. Testing data used to examine performance were from 3 regions in 2022 (Napa, Sonoma, and Merced) and all regions pooled. Area under the receiver's operating curve (AUC), the maximum correct classification rate (CCR), and Kappa values and their standard deviations are shown.

composition. These are sobering results, suggesting caution when attempting to transfer habitat selection models in space. Though this is among the first studies of model transferability for nest box selection models specifically, other researchers have also found limited transferability for habitat selection models for a range of taxa (Graf et al. 2006, Randin et al. 2006, Rousseau and Betts 2022). Reviews across studies indicate that models are most likely to show low transferability for species that have large distributions (i.e., non-analogous environments), distributions located in areas with low topographic relief (i.e., difficult for models to be sensitive enough), shorter lifespans (i.e., species tend to be less selective), and phenotypic plasticity or ecotypes across their range (non-stationarity; Randin et al. 2006, Werkowska et al. 2017, Lee-Yaw et al. 2022, Rousseau and Betts 2022). American barn owls have an expansive distribution among generally low-lying areas, and they are relatively short-lived for a raptor species (Roulin 2020), so the low transferability we documented is perhaps not surprising. However, many species distribution models are built with coarse-scale remotely sensed data with only indirect correlative associations with distribution (e.g., bioclimatic variables), whereas our models included variables with plausible biological mechanistic relationships to nest box use (see methods and Table 1), which should yield models that are more transferable in space (Rousseau and Betts 2022). Moreover, our system focused on the selection of nest boxes with similar designs and placements across several agricultural regions in a single state, and the local habitats in the most intensive training dataset (Napa) were similar to those in the other regions (Figures 2 and S2), requiring very little ecological extrapolation. Nonetheless, the Napa model failed when transferred to regions >240 km away, which had more dissimilar landscape compositions (i.e., Merced and Fresno; Figure S1).

Several factors can diminish a model's transferability, including compromises of the equilibrium, analogous environment, or stationary rules. Barn owl numbers track notoriously dynamic rodent populations (Roulin 2020), and likely also respond to weather extremes (Hindmarch and Clegg 2024), so in any given year their local population could be above or below carrying capacity, which would violate the equilibrium rule and could lead to over- or under-estimating nest box use. In this study, we used multiple years of data to train the Napa model, during which the proportion of nest boxes used ranged from 31% to 55%. Moreover, in the 10 years this population has been monitored, the rate of nest box use has shown a central tendency between these extremes (tending to fall after rising and rise after falling; M. D. Johnson unpublished data). Thus, we suspect the barn owls in this study were likely at equilibrium in Napa, at least approximately. In contrast, the nest box use rate in Sonoma in 2020 was only 16%, and we suspect it was not yet at equilibrium. Of the boxes in Sonoma used in this study, 46% were <4 years old. Barn owls are known to sometimes take several years to colonize new boxes (Meyrom et al. 2009, Charter et al. 2010, M. D. Johnson, unpublished data). Therefore, even though Sonoma is very similar to Napa, consistent with the analogous environment rule, the low rate of nest box use in Sonoma may be due to a time lag, which would cause the Napa model to overpredict Sonoma's nest box use (high commission errors), which is consistent with our results. We expected the Napa model to perform worse in Merced and Fresno, which are more distant and dissimilar to Napa than is Sonoma (Figures S1 and S2), consistent with the geographic distance hypothesis (Rousseau and Betts 2022). We found that it was almost a total failure, barely able to predict nest box use better than chance alone. Certainly, a compromise to the analogous environment rule is partially responsible, as the distribution of nest box attributes and landscape compositions varied among the study regions. However, the range of values in Napa for most variables encompassed those in Fresno and Merced, so this test did not involve much mathematical extrapolation beyond the range of training data. Napa is about 240–320 km from Fresno and Merced counties, and the median natal dispersal distance for American barn owls varies from 15 km to 57 km (Marti 1999, Roulin 2020). However, there are no geographical barriers between these regions, and relatively few long-distance dispersal events per generation are needed to prevent local adaptation being formed or maintained, so non-stationarity in patterns of habitat selection seems unlikely. Future work should investigate possible differences in populations among regions, including variable habitat selection emerging from different local climates. Examining local adaptation is especially important for widespread taxa that use nest boxes in highly variable environments, such as the nearly cosmopolitan barn owls.

Our research has several caveats worth noting to inform future work. First, the data from Napa used to train the Napa model spanned 6 years (2015–2020) and are likely not temporally independent, though we summarized data across years for each box so this lack of independence should not compromise results. We have not yet quantified adult survival or site fidelity in this study system, but work in other areas shows that nest site fidelity can be high especially where nest sites are limited, though there is considerable turnover of breeding birds among nest sites where mortality is high or nest sites are abundant (Roulin 2020). Second, as previously described, our nest box monitoring procedures in Napa resulted in extremely high detection probability (approaching 100%), and it was likely the same in Merced and Fresno where similar methods were used, but this was not the case in all regions. In Sonoma, workers typically check nest boxes once or twice per season, which could lead to lower detection probabilities and could contribute to the high commission errors we found. However, nest box checks in that region are usually timed to coincide with peak detection likelihood (informed from more detailed data in Napa), and though nesting dates can vary between regions with different climates (Bourbour et al. 2022), we have no evidence that the timing of nesting varies between Napa and Sonoma. Thus, we suspect the detection probability was generally high even in Sonoma. Third, although our list of predictors was long, informed by previous research, and linked to ecological mechanisms, our work likely omitted some factors worth investigating. Road density has been shown to affect barn owl distribution in some regions (Hindmarch et al. 2012), though initial investigation indicated it was not a strong variable in our study system (Wendt and Johnson 2017). Zmihiorski et al. (2020) innovatively incorporated socio-economic variables (e.g., unemployment rate, age of local citizen) to improve models of barn owl use of old churches in Poland, hypothesizing these factors capture variation that could meaningfully affect owls but remain unaddressed by typical land cover and climate variables (e.g., repairs to churches that could seal nest cavities, amount of untended field margins). Future work should consider this approach, though these indirect variables may be even less transferable in space or time (Rousseau and Betts 2022). Fourth, our study enabled us to test a model built with abundant data in a single region to 3 other regions with increasingly challenging contexts. However, all were within central California, and American barn owls are distributed throughout much of North America, so we cannot know how well our models apply to other distant regions. Our results indicate that biologists should develop models for their own regions, as we describe in more detail below.

Although our models may not mathematically predict nest box use in other regions, natural history information and additional analyses allow us to make several more general recommendations. Regarding design, nest boxes should be tall (i.e., 24 inches; 61 cm). Not only did barn owls show clear selection for tall boxes, taller boxes are likely beneficial for at least 3 reasons. First, fledgling barn owls need to open their wings and practice flapping to strengthen before their first flights (Bunn et al. 1982), and small boxes may constrain their ability to do so inside the nest box. Second, nesting debris (mainly old, regurgitated pellets, feces, and unconsumed rodent parts) can build up quickly within nest boxes containing multiple nestlings, effectively raising the floor and putting chicks at greater risk of falling out of the nest entrance of short nest boxes. Indeed, collaborators at rehabilitation centers report that barn owl nestlings are frequently brought to them after falling out of boxes with debris built up to the level of the entrance hole. For this reason, we recommend nest entrance holes be at least 16 inches (40.6 cm) from the bottom of a nest box (measured from the bottom of the hole). There is a cottage industry of barn owl nest box providers in the United States and elsewhere, and some producers suggest even larger boxes than the largest in our study (Humane Wildlife Control 2019), which we cannot disagree with, though they may be larger than necessary and are certainly more expensive and difficult to deploy. We also recommend that used nest boxes be cleaned relatively regularly, especially those with large broods (Bourbour et al. 2022). However, old nesting material may function as informative cues in making nest box selection decisions, as has been shown for European kestrels (*Falco tinnunculus*; Mingju et al. 2019), so we recommend leaving a layer of old nesting debris, and possibly avoiding cleaning every year, though the effects of cleaning and residual nest debris need to be studied more. Third, larger boxes may be better for thermoregulation. Evidence from Yolo County California, which has a climate intermediate between cooler Napa and hotter Fresno counties, indicates that larger and taller boxes stay cooler than smaller and shorter boxes, and have shorter durations of temperature out of the owls' thermoneutral zone (Phillips et al. 2024). Our Napa data clearly indicate that owls selected wooden over plastic boxes in that region, but other authors report high rates of use for plastic boxes in other areas of California (Browning et al. 2016) and elsewhere in the country (M. Browning, Barn Owl Box Company, personal communication), including in Florida, USA, so this needs additional study. Selection for wooden or plastic boxes could vary regionally owing to climatic variation; however, the most common plastic box design we have encountered is shorter (~18 inches; 45.7 cm) than we recommend (≥24 inches; 61 cm).

For nest box placement, we strongly suspect that deploying barn owl nest boxes with abundant grassland nearby will help maximize their probability of being used in most areas of their range. This is based on the effects of this variable at multiple scales in both our Napa and our transregional models (Figure 3) and the association with grasslands noted for this species generally (Charter et al. 2010, Frey et al. 2011, Hindmarch et al. 2012, Marti et al. 2020, Zmihorski et al. 2020); also, when we ran region-specific models using data only from Sonoma and Merced, nest box selection was routinely positively associated with grasslands (M. D. Johnson, unpublished data). We also recommend deploying boxes away from forests. Great-horned owls (*Bubo virginianus*) are known predators of barn owls, and our data from Napa and the other regions show that barn owls avoid nest boxes with abundant forest land cover nearby (Figure 3) that may harbor such predators.

We also found that nest box use increased with pole height, but in our experience very tall boxes (>15 feet; 4.6 m) are sometimes left unmaintained and can become dilapidated or packed full of pellet debris. Very tall boxes are also difficult and dangerous to access depending on terrain and personnel, and may require specialized equipment, which could increase the financial cost and difficulty of maintaining barn owl nest box networks. Considering this trade-off, we recommend pole heights 10–15 feet (3–4.6 m). Nest hole orientation and box material (wood or plastic) merit further study, particularly with respect to microclimate (temperature, prevailing winds). Despite finding relatively low transferability of mathematical nest box use predictions, we found similar variables emerging as important predictors among regions, so we expect these recommendations to apply well for our study regions in California. However, we cannot know how well they may apply elsewhere, and we suggest other researchers perform similar analyses in other regions.

Lastly, even data-informed recommendations for nest box design and placement may not translate to high fitness potential for their occupants. Nest site selection is not always adaptive, as animals can for various reasons select poor sites or avoid good ones (see review Chalfoun and Schmidt 2012). In extreme cases, this could lead to ecological traps (Battin 2004). Lee-Yaw et al. (2022) recently showed that even accurate species distribution models often fail to predict population fitness. However, in our study system, we have confirmed that nest box selection is adaptive, as reproductive success tends to be higher in boxes with selected attributes (Carlino 2024). Moreover, using simple demographic simulations informed by estimates of reproductive success obtained locally and survival estimates obtained from the literature, we showed that the owl nest boxes in Napa Valley are not an ecological trap (Carlino et al. 2022). We encourage other researchers, especially those promoting the use of human-made nest boxes for species of conservation concern, to undertake similar investigations.

MANAGEMENT IMPLICATIONS

We found that although the model trained with Napa data did not transfer in space very well, the transregional model built with data from all regions was a little better, and it sacrificed very little in accuracy when applied to Napa specifically. Taken together, our results indicate 2 generalizations of nest box model transferability. First, local data should be used to make the most reliable predictions of nest box use, which will require biologists to build nest box selection models for many different regions where their study animals occur, a substantial task especially for species with distributions as extensive as those of barn owls. Second, if that is not feasible, or until those data are available, general recommendations should be made from models that pool data from as many regions as feasible, and practitioners should be properly warned that said recommendations may not maximize local nest box use if the animals show regional patterns of nest box selection. Though the models we examined struggled to accurately predict exactly which boxes would be used in a new time or place, the top Napa and the transregional models included similar variables with similar relationships with nest box selection (Figure 3), indicating these patterns are fairly robust, at least in California. Both the Napa model and the transregional model indicated that owls show some selection for tall boxes mounted on tall poles, with abundant grassland within 75 m, while avoiding plastic boxes and those with abundant forest within 2.81 km (Figure 3), so these are tendencies likely to operate elsewhere in California. The largest discrepancy in variables selected in the top models for Napa and the transregional model was in the direction of the nest box entrance, perhaps because of different prevailing wind directionalities among regions. Additional work should investigate the mechanism for the owls' selection for nest box orientations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This research was approved by Cal Poly Humboldt's Institutional Animal Care Use Committee (protocol 2021W12-A) and was conducted under a United States Geological Survey Federal Master Bird Bander Permit (09379).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Matthew D. Johnson http://orcid.org/0000-0003-3662-2824

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