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Authors: Winchell, Clark S., Huyvaert, Kathryn P., Doherty, Paul F., Taylor, John M., and Grant, Tyler J.

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Ecological correlates to habitat use in the Cactus Wren (*Campylorhynchus brunneicapillus*)

Clark S. Winchell,[1]* Kathryn P. Huyvaert,[2] Paul F. Doherty Jr.,[2] John M. Taylor,[3] and Tyler J. Grant[4]

ABSTRACT—Conversion of natural habitats to urban landscapes is happening at a rapid pace around the globe. Establishing a preserve system and restoring lands within these preserves is one way to offset the loss of natural habitats. However, often when preserves are being developed little data exists outlining the distribution of species and the habitat parameters on which they depend. We used populations of the Cactus Wren (*Campylorhynchus brunneicapillus sandiegensis*) inhabiting the coastal slope of California to demonstrate how to refine the general gestalt of habitat conditions for the wren into defined parameters that can be used to develop strategic restoration plans. We found that wren habitat use declined to nearly 0% when cactus patches were spaced farther than 800 m apart, regardless of size. The probability of occupancy, or habitat use, rose above 60% when cactus patches were 0.15 ha in size or greater. Elderberry is an important factor in areas with little topographic relief, as it provides perching sites. Buckwheat may not be important to the wren but could be used to select sites that have drier conditions conducive to cacti. Planting cactus to restore ruderal sites properly selected for xeric conditions, and within relatively close proximity to each other, could help meet conservation goals of connecting and increasing wren populations by establishing ecological functions at a landscape level. *Received 2 December 2019. Accepted 1 October 2021.*

Key words: cholla, habitat restoration, occupancy, prickly pear cactus, sage scrub.

Correlaciones ecológicas con el uso de hábitat en la matraca *Campylorhynchus brunneicapillus*

RESUMEN (Spanish)—La conversión de hábitats naturales a ambientes urbanos está ocurriendo a un paso acelerado en todo el mundo. El establecimiento de un sistema de reservas y la restauración de tierras al interior de estas reservas es una forma de contrarrestar la pérdida de hábitats naturales. Sin embargo, el desarrollo de reservas con frecuencia dispone de pocos datos que definan la distribución de las especies y los parámetros del hábitat de los cuales dependen. Usamos poblaciones de la matraca *Campylorhynchus brunneicapillus sandiegensis* que habita en la vertiente costera de California para demostrar cómo se puede refinar la percepción general de condiciones de hábitat de esta matraca en parámetros definidos que puedan ser usados en el desarrollo de planes estratégicos de restauración. Encontramos que el uso de hábitat de la matraca declinó a cerca de 0% cuando los parches de cactus estaban espaciados a distancias mayores de 800 m entre sí, independientemente de su tamaño. La probabilidad de ocupación o de uso de hábitat se elevó a más de 60% cuando los parches de cactus tenían tamaños de 0.15 ha o mayores. El sauco es un factor importante en áreas con poca pendiente, pues provee sitios para perchar. El alforfón podría no ser de importancia para la matraca pero podría ser utilizado para seleccionar sitios que tienen condiciones más secas y proclives a los cactus. La siembra de cactus para restaurar sitios ruderales apropiadamente seleccionados para condiciones xéricas, y con una relativa cercanía unos de otros, podría ayudar a alcanzar las metas de conservación de conectar e incrementar las poblaciones de matracas a través del establecimiento de funciones ecológicas en nivel de paisaje.

Palabras clave: cholla, matorral costero, nopales, ocupación, restauración de hábitat.

Conversion of natural habitats to urban landscapes is happening at a rapid pace around the globe (Ramalho and Hobbs 2012). In the latter part of the 20th century, urbanization has been especially prominent in southern California, particularly in areas supporting coastal sage scrub where conversion to urban areas has reduced the natural habitat to 10–30% of its original extent (Atwood 1993, McCaull 1994). In addition, large portions of native vegetation in southern California have been converted to agricultural lands; in 2011 San Diego County had the fourth highest number of individual farms of any county in the United States, and agriculture was the fifth largest component of the county's economy (San Diego County 2011).

Coastal sage scrub is a native plant community that is patchily distributed along the California coast extending from the San Francisco Bay region into northwestern Baja California (Axelrod 1978, Westman 1981). California sagebrush (*Artemisia californica*) predominates in coastal sage scrub but patches can also feature several species of sage (*Salvia* spp.), California buckwheat (*Eriogonum fasciculatum*), and evergreen shrubs such as lemonade berry (*Rhus integrifolia*) (DeSimone 1995). The suite of plant taxa comprising the

[1] United States Fish and Wildlife Service, Carlsbad Fish and Wildlife Office, Carlsbad, CA, USA
[2] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, USA
[3] U.S. Fish and Wildlife Service, Palm Springs Fish and Wildlife Office, Palm Springs, CA, USA
[4] Department of Natural Resource Ecology and Management, Iowa State University, Ames, IA, USA
* Corresponding author: clark_winchell@fws.gov

community varies geographically, changing gradually with latitude (Axelrod 1978). The distribution of a particular dominant species is associated with soil, topography, and climate characteristics (Kirkpatrick and Hutchinson 1980, Westman 1981, DeSimone and Burk 1992). For example, cacti taxa such as prickly pear (*Opuntia* spp.) and cholla (*Cylindropuntia* spp.) are characteristic of coastal sage scrub patches in the southerly "Diegan sage" division of this plant community where warmer winters and more irregular precipitation make this important habitat for a unique suite of organisms (Axelrod 1978).

Coastal sage scrub, particularly where cactus is prominent, is the principal habitat of the Coastal Cactus Wren (*Campylorhynchus brunneicapillus sandiegensis*; hereinafter referred to as "wren"). In southern California, this wren is thought to be strongly associated with coastal sage scrub dominated by California sagebrush and buckwheat at elevations below 460 m and wrens build nests in coastal sage scrub habitat where large patches of cactus, especially prickly pear and cholla plants over 75 cm tall, are prominent (Rea and Weaver 1990). Also noted for its importance to wrens is the presence of blue elderberry (*Sambucus nigra* ssp. *caerulea*; hereinafter "elderberry") on which wrens feed and roost (Mitrovich and Hamilton 2007). Given its association with imperiled coastal sage scrub habitats in southern California, the wren is considered a taxon of special conservation concern (San Diego County 1998) and may be a potentially useful "indicator species" (Chase et al. 2000) given its sensitivity to fragmentation (Soulé et al. 1988) and relatively easy detection (Chase et al. 2000).

The principal anthropogenic threats to wrens include habitat fragmentation, loss of habitat, and altered fire regimes. Fragmentation of natural habitats may play a role in interrupting dispersal patterns and increasing isolation of breeding pairs (Deutschman and Strahm 2012). Recent genetic studies show a high degree of population structure, lending support to the theory that dispersal of wrens across the landscape is low (Barr et al. 2015). The combination of urbanization, construction of major freeways, and conversion of habitat to agricultural land uses, processes that lead to habitat fragmentation and a loss of suitable nesting habitat, is also linked to a regional decline of wrens (Regan et al. 2006). In addition, intense wildfires in southern California have further impacted populations that are now limited to smaller patches of remaining habitat. For example, estimates of territory occupancy by wrens of coastal sage scrub affected by the 1993 Laguna Fire in Orange County, California, declined by ~87% between 1992 and 2006 (Mitrovich and Hamilton 2007).

In response to apparent declines in wren populations in coastal southern California, natural resource agencies have placed wrens in "Risk Group 1," a designation reflecting the highest risk of decline or extirpation (Regan et al. 2006, 2008) and prompted population monitoring and conservation activities as a high priority.

Given land use changes in San Diego County, California, and the potential for continued declines in wren populations, we set out to establish the degree and predictors of habitat use of coastal sage scrub by wrens in southern California. Our primary objective was to estimate wren habitat patch occupancy (i.e., habitat use) in an occupancy framework in relation to (1) cactus density and distribution and (2) metrics of human-related development. In particular, we hypothesized that cactus density and distance to other cactus patches are important predictors of wren habitat use primarily due to the species' use of cacti for nesting and feeding (Rea and Weaver 1990). Similarly, we expected metrics of urbanization, like distance to urban features and the proportion of the survey plots covered with development and associated infrastructure, to be associated with limited habitat use by wrens because of changes in factors such as predation risk and habitat or vegetation structure (Preston and Kamada 2012, Barr et al. 2013) linked to habitat conversion. We also examined the relationships between wren habitat use and the presence of elderberry and buckwheat, hypothesizing that wrens would be more likely to use plots with more of these vegetation types because of their utility as food plants (Rea and Weaver 1990, Mitrovich and Hamilton 2007). Lastly, we evaluated the relationship between the aspect of the plots and habitat use by wrens, acknowledging that plots with more southwest-facing exposures in the northern hemisphere are more suitable for cactus-dominated plant communities (Parker 1991). By establishing baseline habitat use and linking wren usage to landscape features, we can track changes in habitat thereby informing science-based decisions regarding wren management.

Methods

Field methods

Our survey sample frame was limited to areas located in coastal sage scrub on publicly accessible parcels (SANDAG 1995) and preserve lands within the San Diego Multiple Species Conservation Plan area in southwest San Diego County, California (San Diego 1998). The centroid of our study area was at 32°49′55.9″N, 117°03′42.2″W. Available habitat was defined as those areas with a southern aspect (70–280°) and below 460 m in elevation (Rea and Weaver 1990). We divided aspect into 2 categories: for our latitude, we defined southeast aspect as 70–170° and southwest aspect as 171–280°. Using publicly available geospatial datasets, and following the parameters identified above, we modeled potential wren habitat within accessible parcels using ArcGIS (ESRI, Redlands, California, USA).

Once parcels were selected as probable candidates containing potential wren habitat, surveyors systematically inspected these parcels to delineate "patches" of prickly pear and/or cholla cactus if present. Every land parcel within the sample frame was surveyed for cactus and each patch was mapped using a Trimble Juno (Sunnyvale, California, USA) GPS unit. We defined a cactus patch as a group of 3 or more cacti at least 0.75 m tall and/or a single cactus measuring at least 2 m in width and at least 0.75 m high. Cacti within 15 m of each other were included in the same "patch." The survey effort initiated in 2009 focused on southwest aspect. In 2011, the survey effort was repeated and expanded to the entire southern aspect.

Cactus patches equal to or greater than 0.01 ha in size were assigned plot numbers. Plots to be retained in our wren sampling process were delimited further using the following criteria: (1) at least one patch of cactus, as described above, was present, and (2) field staff could observe the entirety of the survey plot from a randomly chosen point. Thus, survey plots varied in size and could be isolated or adjacent to other survey plots; adjacent plots had either large expanses of cactus or crossed shared topographic features such as ridges. We had a total of 695 plots available to sample for wren occupancy.

Plots were surveyed for wren occupancy 3 times during the peak of the breeding season, from 18 April 2011 to 18 June 2011. The 3 visits were equally spaced within this 8 week period. However, if weather disrupted field schedules, plot visits were spaced at least 2 d apart. Our attempt at timing site visits was to avoid behavioral biases from the previous surveys and ensure all plots were sampled within the breeding season. In practice, surveys were conducted at a randomly selected sample point within each plot. Surveys occurred between sunrise and sunset when wind speeds were less than 20 km/h, precipitation did not exceed a drizzle, and ambient temperatures were above 4.5°C. Wind speed and air temperatures were measured with a pocket weather station (Kestrel, Boothwyn, Pennsylvania, USA) averaged over a 1 min period upon arrival at the survey point.

Wren surveys were conducted over two 5 min observation periods. During the first observation period, surveyors listened and scanned the plot for wrens, noting both auditory and visual detections. In the second 5 min period, surveyors used digital playbacks of wren songs to elicit responses of wrens on the plots to aid in their detection. Following Mitrovich and Hamilton (2007), playbacks were conducted for three 40 s intervals with 60 s of silence in between. Surveyors carefully listened and watched for wren responses as the playback was played and for 1 min after each playback. Wrens could respond with their own song or by simply moving about, making themselves more easily detected by surveyors. We recorded the presence or absence of wrens on the plot detected during the survey, as well as whether a single bird or pair was detected on the plot. While monitoring during playback, wrens that flew into the plot were noted separately from wrens that were detected within the plot. We also noted whether or not nests were observed within the plot.

Analytical methods

We modeled occupancy (Ψ) and detection (p) of wrens using the methods of MacKenzie et al. (2002). Because we cannot confirm that our survey plots were closed to movement, we interpret the occupancy parameter, Ψ, as "habitat use" rather than

Table 1. Ecological variables used to model Cactus Wren habitat use in San Diego County, California, USA. Cumulative variable Akaike information criterion (AICc) weights calculated from the entire, balanced model set are included as measures of relative variable importance. The beta (β) estimates, standard error (SE), and lower (LCI) and upper (UCI) 95% confidence limits from the global model are presented.

Notation	Variable description	Prediction	Cumulative AICc weight	β estimate	SE	LCI	UCI
Aspect	Direction plot faces	Southwest-facing plots will have higher use	1.000	1.915	0.331	1.266	2.564
VegCat	Presence of the buckwheat category	Higher use with presence of buckwheat	1.000	1.741	0.453	0.852	2.629
NearDist	Distance to the next plot containing cactus	Negative relationship; increasing use with shorter distance	0.999	−0.004	0.001	−0.007	−0.001
TotCactA	Area of continuous cactus in which a survey plot resides	Positive relationship; increasing use with increasing area	0.998	0.202	0.049	0.107	0.298
ElderPres	Elderberry presence within 100 m of the center of a plot	Positive relationship; increasing use with elderberry presence	0.691	0.542	0.299	−0.043	1.127
DistUrb	Distance to urban (including roads)	Positive relationship; increasing use with increasing distance	0.441	−0.001	0.001	−0.003	0.000
Cac100p	Proportion of the area within 100 m of the center of a plot covered by cactus	Positive relationship; increasing use with higher proportion	0.409	0.021	0.020	−0.018	0.060
Urb1000p	Proportion of the area within 100 m of the center of a plot covered by development	Negative relationship; increasing use with lower proportion	0.359	−0.009	0.008	−0.024	0.006
Cac1000p	Proportion of the area within 1,000 m of the center of a plot covered by cactus	Positive relationship; increasing use with higher proportion	0.296	−0.007	0.016	−0.038	0.024

occupancy (MacKenzie 2006). We considered detection as a function of time (i.e., across 3 visits) or as a constant across time. We also considered Ψ as a function of a number of ecological variables related to cactus and human-related development. Specifically, we modeled Ψ as a function of distance (m) to the nearest plot containing cactus, proportion of the area within 1,000 m of the center of the plot that was covered in cactus, proportion of the area within 100 m of the center of the plot covered in cactus, and the overall area (m^2) of a survey plot that was covered in continuous cactus where continuous cactus was classified as a patch of prickly pear and/or cholla. We also modeled Ψ as a function of distance to urban structures (including roads), as well as the proportion of the area within 100 m of the center of the plot covered by human-related development; this was defined as any type of building and excluded utilities. Finally, we thought Ψ could be influenced by the presence of elderberry, by the presence of plant communities dominated by either buckwheat, white sage (*Salvia apiana*), or black sage (*S. mellifera*), and the aspect category of the plot (Table 1).

Following recommendations outlined by Doherty et al. (2012), we modeled all possible additive combinations of these variables to produce a balanced model set. We used Akaike's information criterion with a small sample size correction (AICc) for model selection and we calculated cumulative AICc weights for each variable as a measure of relative variable importance (Burnham and Anderson 2002). Following Barbieri and Berger (2004), we used a cumulative AICc weight of >0.5 as the cutoff for identifying variables with predictive power.

Results

We surveyed 6,710 ha, mapping 265 ha of cactus patches, which comprised 695 plots. We surveyed the 695 plots and we detected wrens on

Table 2. Models of Cactus Wren habitat occupancy/use (Ψ) within 2 Akaike information criterion units (ΔAICc) of the top model (Minimum AICc = 1036.480) in San Diego County, California, USA. Only models with detection (p) modeled as a constant ranked highly. Variables in models included distance to the nearest plot containing cactus (NearDist), area of continuous cactus in which a survey plot resides (TotCactA), presence of elderberry (ElderPres), presence of buckwheat (VegCat), aspect, percent of the area within 100 m (Cac100p) and 1,000 m (Cac1000p) of the center of a plot covered by cactus, and the distance to an urban structure. AICc model weights (AICc wt), Number of parameters (*N* pmtrs), and the –2 log-likelihood (–2log(L)) for each model are also presented.

Ψ Model	ΔAICc	AICc wt	*N* pmtrs	−2log(L)
NearDist+TotCactA+ElderPres+VegCat+Aspect	0.000	0.098	7	1022.317
NearDist+TotCactA+ElderPres+VegCat+Aspect+Cac100p	0.504	0.076	8	1020.774
NearDist+TotCactA+ElderPres+VegCat+Aspect+DistUrb+Urb1000p	1.344	0.050	9	1019.561
NearDist+TotCactA+ElderPres+VegCat+Aspect+DistUrb	1.390	0.049	8	1021.660
NearDist+TotCactA+ElderPres+VegCat+Aspect+Cac1000p	1.526	0.046	8	1021.796
NearDist+TotCactA+ElderPres+VegCat+Aspect+DistUrb+Cac100p	1.527	0.046	9	1019.744
NearDist+TotCactA+VegCat+Aspect	1.818	0.040	6	1026.176
NearDist+TotCactA+ElderPres+VegCat+Aspect+Urb1000p	1.866	0.039	8	1022.136

157 (22.6%) of the plots. Wrens were relatively easy to detect and models that included detection as a constant probability consistently ranked highly (cumulative variable weight = 0.867; Table 2). The probability of detection of wrens on a single visit was 0.703 (SE 0.026) and the probability of detecting wrens at least once over the 3 visits was 0.974.

The best models of wren habitat use were complex with the models including distance to the nearest plot containing cactus (AICc cumulative weight = 0.999), area of continuous cactus (AICc cumulative weight = 0.998), presence of elderberry (AICc cumulative weight = 0.691), presence of buckwheat (AICc cumulative weight = 1.000), and southwest aspect (AICc cumulative weight = 1.000) all ranking highly. Other variables were less important and/or functioned as pretending variables (Anderson 2008); these variables were included in high-ranking models without adding additional explanatory power (Tables 1, 2).

In general, wrens used plots close to other plots containing cactus to a higher degree than plots that were farther away from cactus-containing plots (Fig. 1). Wrens were more likely to use plots in large areas of cactus than in small areas (Fig. 2). Plots containing elderberry were more likely to be used by wrens than plots without elderberry (Fig. 3). Plots dominated by buckwheat, and not dominated by white or black sage, were more likely to be used by wrens (Fig. 4). Finally, wrens were more likely to use plots facing southwest than other directions (Fig. 5).

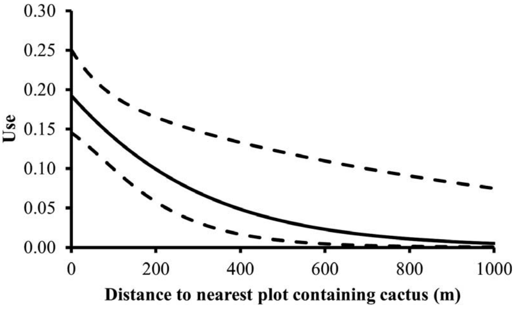

Figure 1. Probability of survey plot use by Cactus Wrens as related to distance to cactus-containing plots. Dashed lines illustrate 95% confidence limits.

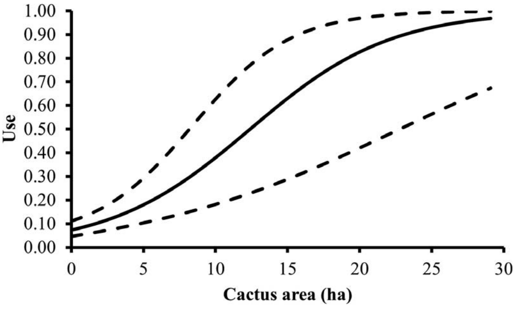

Figure 2. Probability of survey plot use by Cactus Wrens as related to the area of cactus in which the plot was placed. Dashed lines illustrate 95% confidence limits.

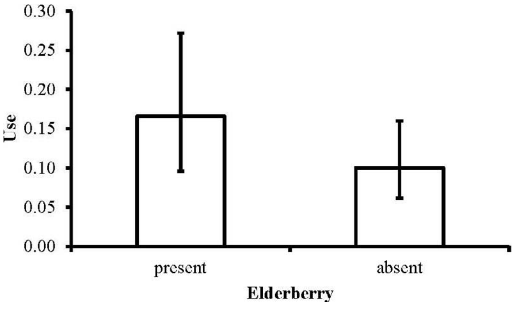

Figure 3. Cactus Wren use of survey plots with and without elderberry. Error bars represent 95% confidence intervals.

Discussion

We showed that vegetation aspect and the topography characteristic of the sage scrub are important in shaping habitat use by Cactus Wrens in coastal slope areas in southern California. Not surprisingly, the presence and extent of cactus was associated with occupancy probability (our metric of habitat use): use was higher when nearby plots also have cactus and when the cactus is in larger continuous patches. Habitat use was also higher with the presence of elderberry and buckwheat and when plots were situated with a southwest aspect.

Rea and Weaver (1990) suggested that wrens disappear from small habitat patches. Thus, as wrens are relegated to smaller and smaller patches, the potential of local extinction increases (Soulé et al. 1988). The exact mechanism for extirpation in small patches may be a combination of stochasticity, inbreeding, and other factors. A smaller population is more likely to become extirpated in the face of stochastic events such as dry years and/or fire (Barr et al. 2013, 2015). Whereas a larger

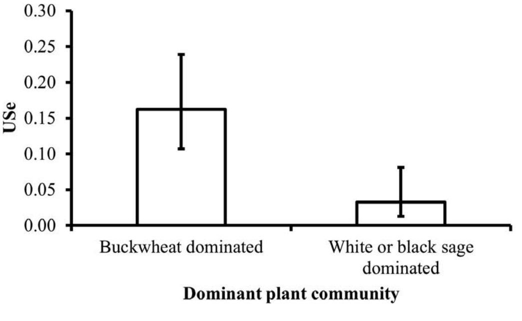

Figure 4. Cactus Wren use of buckwheat-dominated and white or black sage-dominated plant communities. Error bars represent 95% confidence intervals.

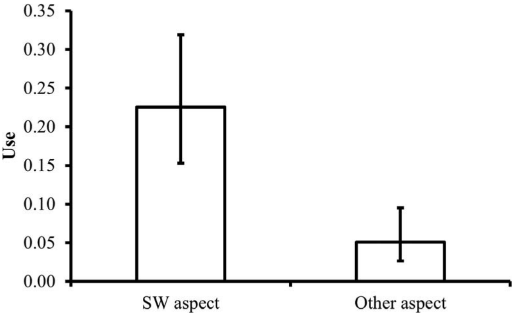

Figure 5. Cactus Wren use of areas with southwest aspects favored over southeast-facing aspects. Error bars represent 95% confidence intervals.

population may recover, a smaller population is less likely to recover (Barr et al. 2015). Inbreeding can directly reduce reproduction, or closely related birds may attempt to disperse to find less closely related mates (Crooks et al. 2001). Our work showed that plots with >0.13 ha of cactus had a 50% chance or greater probability of being used by wrens (Fig. 2).

Dense stands of cactus are an important habitat component for wrens as the cactus spines provide protection from predation (Short 1985) and the structure provides cooler microhabitats (Ricklefs and Hainsworth 1968). Wrens construct bulky, globular nests (Proudfoot et al. 2000) that can be relatively heavy. Dense stands of cactus provide firm structures to which wrens can attach nests. Large nests are important to wrens as nests are used both for rearing young and night roosting by adults. Further, wrens often construct several nests within an area, which would favor large cactus patches in which to distribute nests (Rea and Weaver 1990).

Connectivity between large patches of cactus also is important for wren conservation. We found that cactus patches with neighboring patches that form large aggregates of cactus have a greater than 60% chance of being used by wrens. Similarly, plots containing cactus that are within 200 m of other plots with cactus are twice as likely to be used by wrens than plots without neighboring cactus (Fig. 1).

Little is known regarding wren dispersal factors. However, habitat fragmentation is thought to be one of the primary causes for declining wren populations in southern California (Preston and Griswold 2011). Our work showed that cactus patches separated by 800 m have almost no chance of being utilized by wrens. With conversion of habitat due to agricultural practices and permanent loss of habitat due to development, such long distances between patches are not uncommon. Our results suggest that wrens have little chance for recovery across their range in southern California until appropriately large patches of habitat are restored near occupied patches of habitat.

While the presence and extent of cactus across the landscape appear to be important for wren habitat use, we found that the composition of the rest of the plant community was also associated with wren plot use. In particular, plots with elderberry (Fig. 3) and those dominated by buckwheat (Fig. 4) were more likely to be used by wrens. Elderberry may play an important role by providing roosting locations (Mitrovich and Hamilton 2007) and forage, primarily fruit pulp (Hamilton et al. 2011). A combination of different fruit pulp is reported to make up 17% of the bird's diet (Proudfoot et al. 2000, Hamilton et al. 2011). Elderberry is a small tree or tall shrub and, across our study plots, it was the only consistent feature that provided structural height that produced fruit. Other fruit-bearing vegetation, such as lemonadeberry (*Rhus integrifolia*), toyon (*Heteromeles arbutifolia*), or red berry (*Rhamnus crocea*), were not broadly distributed across the landscape at the scale we sampled. While such vegetation has been reported from stomach contents of wrens sampled in other parts of the species' range (Proudfoot et al. 2000), the structural height of elderberry may be the more prominent feature of the plant influencing wren occupancy in our plots rather than fruit availability. Elderberry grows along stream terraces and bottomlands that have alluvium soils (Sawyer et al. 2009). These areas can periodically flood creating relatively flat areas where perch sites provided by the tall elderberry may be an important feature of the landscape that wrens use. Elderberry trees were not found on plots with slope, and topographic relief may provide the same function for perching. Elderberry is a strong indicator of wren habitat use on alluvial soils but may not be a factor outside of these bottomlands.

We have no firm explanation for the strong relationship between wrens and buckwheat. We tested buckwheat as Rea and Weaver (1990) report the plant as closely associated with wrens, without a specific explanation. Buckwheat is a major component of Diegan Coastal Sage Scrub (Sawyer et al. 2009) and is generally associated with habitats not invaded by nonnative vegetation (Montalvo 2004). These habitats, not dominated by thick invasive grasses and forbs, most likely support a great diversity and number of prey items (Burger et al. 2003). Our general observation is that the canopy is open with some distance between shrubs in areas where buckwheat is the dominant shrub; this open habitat may be more conducive to capturing prey.

In addition, buckwheat may be more tolerant of drier conditions given its xeromorphic leaf characteristics. Harrison et al. (1971) measured a sclerophylly index of nine coastal sage scrub and chaparral plants. Ashyleaf buckwheat (*Eriogonum cinereum*), which occurs in coastal sage scrub in San Diego County, had sclerophylly values near the average index for chaparral plants and set the maximum value for coastal sage scrub plants.

Our results also showed that aspect is an important factor affecting habitat use, with southwest-facing aspects favored over southeast-facing aspects (Fig. 5). Our results align with those of Vaughan (2010) using ArcGIS to model habitat preferences of wrens. Southwest aspects are generally drier as these areas heat up earlier in the day and cool off later in the evening (Kumar et al. 1997). Abiotic factors contributing toward drier conditions tend to favor cactus and, potentially, buckwheat. Therefore, buckwheat may be an indicator of habitat that is drier and has not been invaded by invasive grasses or forbs.

Our results indicated that habitat adjacent to urbanized areas did not influence habitat use. However, habitat loss is a major factor limiting wren distribution and Barr et al. (2015) documented genetic isolation within the range of wrens across southern California. Urbanization may not negatively affect habitat use of those parcels that also support immediately adjacent large cactus patches, but development does impact wrens' ability to exchange genetic information across the landscape such that habitat loss will limit population numbers and distribution (Emlen 1974, Rea and Weaver 1990, Barr et al. 2015). Thus, habitat lost to development cannot be restored for wrens.

Conservation biologists working to restore wren populations may want to strategically select where to place their efforts. Biologists should consider working outward from areas that currently support wrens, restoring habitat concentrically because wrens tend to occupy cactus patches adjacent to other occupied patches. Restoring areas greater than 800 m from occupied sites, or restoring areas that are completely isolated, may not meet the goal of increasing wren populations across the landscape. Areas for restoration would be most beneficial if they occur within 200 m of occupied habitat, selecting the driest areas on southwest-facing aspects. Cactus plantings, if used, should cover a large area, possibly greater than 0.13 ha. This recommendation of 0.13 ha is a starting point that can be tested or refined using an adaptive management framework. Colonization by wrens of restored sites might be good indicators that conservation goals of connecting and increasing wren populations are being met and ecological functions are being maintained at a landscape level.

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