**Cacti and shrubs enhance avian community diversity through non-trophic and different functions depending on the season.**

Malory Owen[[1]](#footnote-1), Christopher J. Lortie1, 2, and Nargol Ghazian1\*

1Department of Biological Science, York University, 4700 Keele St, Toronto, ON M3J 1P3, Canada

2National Centre for Ecological Analysis and Synthesis (NCEAS), 735 State St #300, Santa Barbara, CA 93101, United States

\*Corresponding Author: Department of Biological Science, York University, 4700 Keele St, Toronto, ON, M3J 1P3, Canada. Email: [nargolg1@my.yorku.ca](mailto:nargolg1@my.yorku.ca)

# Abstract

Habitat heterogeneity can be a critical determinant of animal community composition and structure in some systems, impacting the ability of the resident wildlife to colonize different microsites. Plants can increase habitat heterogeneity and resources for animal communities. However, interactions with plants may be species-specific and can depend on the season. Foundation plants can function as agents of structural facilitation, providing different niches for habitat selection. We tested if foundation plant species, specifically cacti and shrubs, effects on animal communities are species-specific and temporally dependent. We used line transects to record habitat associations of birds at a protected site in the Mojave Desert. We found that the bird biodiversity and behaviour were not equally represented across all microhabitats or seasons. Diversity and evenness of the bird communities and territorial behaviors were significantly greater at shrubs microhabitats in spring. Shrubs can provide structural heterogeneity for the avian community to use as perches, nests, and other non-trophic services because foraging and consumption were observed less often. The diversity of birds was greater at cacti than at open microhabitats in the summer; hence, seasonal timing is also an important component of facilitation by foundation plants for bird communities in deserts. This study suggests that non-trophic interactions with plants in addition to direct resource provision are also important ecological mechanisms for maintaining local bird diversity in deserts.

**Keywords:** Arid, bird, cacti, community, desert, diversity, facilitation, foundation species, habitat heterogeneity, microhabitat, mutualism, positive interactions, shrubs.

# Introduction

Positive interactions or facilitation at the landscape level can influence ecosystem infrastructure (Stachowicz 2001). Facilitation is defined as any positive interaction wherein a benefactor species increases the fitness or survival of associated species (Bertness and Callaway 1994; Bruno et al. 2003). However, competitive interactions often happen concurrently alongside facilitation (i.e. competition for pollinators between benefactors and beneficiaries) (Braun 2018). There are many mechanisms for facilitation between interacting taxa (Landero and Valiente-Banuet 2010), and several categories are common across plant-animal interactions with plants often providing food resources such as nectar, fruit, and seeds (Narango et al. 2017; Feinsinger 1987; Saracco et al. 2004). Benefactor plants can also indirectly facilitate carnivores or insectivores by attracting their prey items (Ruttan et al. 2016). Non-trophic interactions between plants and animals are relatively limited when compared with plant-plant studies, with most studies examining hypotheses that supported the function of shrubs as seed traps for beneficiary animals (Lortie et al. 2016). In the more specific example of bird-plant interactions, plants aid birds in foraging and defining their territory (Wiens 1973; Craig 1990; Devereux et al. 2000; Longland and Price 1991). All of these trophic and non-trophic interactions can be relevant for desert birds; however, the relative frequency of these interactions within a given system or for a specific community is not well documented.

Foundation species can be benefactors that facilitate other species within an ecosystem using some or all of the mechanisms previously described (Angelini et al. 2011; Almeida and Mikich 2018). In many ecosystems, including deserts, plants are foundation species. The traits of a foundation plant species (such as growth pattern, life histories, and origins of neighbors and targets) can influence the mechanism of the interaction (He et al. 2013). Traits can also shift the net outcome of interactions from facilitative to competitive (Callaway and Walker 1997). Shrubs and cacti have been documented as common foundation species globally (Filazzola and Lortie 2014). These large, sturdy plants are often responsible for habitat infrastructure of wildlife throughout an ecosystem (Callaway 1997; Gelmi-Candusso et al. 2017). In relatively high-stress environments like deserts, events like mega-droughts and other inter-annual variations are stressful for many species in the ecosystem (Siegal et al. 2013). This physical stability helps maintain the presence of many other species in a habitat (Lortie et al. 2018). While most studies have focused on plant-plant facilitation (Callaway 2007), positive plant-animal interactions are also frequent in deserts (Lortie et al. 2016; Bertness et al. 1999; Arsenault and Owen-Smith 2002). A more comprehensive understanding of the types of associations between foundation plant species and animals will enable better predictions of how biodiversity will respond to a changing climate and to the relatively extreme existing variation in desert climates seasonally. The extent that positive effects are specific species is also an important ecological issue (Callaway 1998; Villarreal-Barajas and Martorell 2009) because we need to know whether the benefits are generic and thus more easily restored and managed or specific to certain foundation species.

We study bird-plant interactions specifically for two key reasons. Birds can function as indicator species for ecosystem health because they are easily tracked and respond to large- and small-scale changes in the environment (Carignan and Villard 2002). Birds also typically respond to the environmental changes with seasonal shifts sometimes by migrating (Salewski and Bruderer 2007). Secondly, the timing of life cycles in desert ecosystems can vary widely due to the extreme variation in temperature and precipitation inherent in these climates (Henen et al. 1998). For animals that rely on or associate with plants for resources (nectar, fruit, seeds, etc.), timing is critical (Buler et al. 2007), and specifically, floral and fruiting timing of plants (Schwartz 2003; Beatley 1974; Jordan and Nobel 1982; Nobel and Hartsock 1981) is necessary for the success of birds during migration breeding seasons (Sillett and Holmes 2002; Runge and Tulloch 2017; Fahse et al. 1998). Thus examining the avian community does not only help in de-coupling pathways of animal-plan positive interactions but also gives us insight into temporal and seasonal variations that may influence these dynamics.

Climate change can introduce many novel drivers of change in natural systems and exacerbate existing challenges to local biota. The changes in these desert systems will further intensify the frequency, strength, and duration of severe weather events such as droughts (Ye and Grimm 2013), mega-droughts (i.e. long-term sustained inter-annual drought events) (Williams et al. 2020), and significantly warming annual temperatures (Kunkel et al. 2013). If foundation species are extirpated or become functionally extinct locally, other species can also disappear (Berger et al. 2008; Säterberg et al. 2013). Furthermore, if positive effects are specific to certain functions provided by species or even their unique architecture, then their loss can ultimately translate to the loss of the associated taxa. Desert bird communities have already severely declined primarily due to desert climate change (Iknayan and Beissinger 2018) because increased temperatures in already hot ecosystems are linked with decreases in the frequency of trophic interactions (Plessis et al. 2012). Many of these threatened interactions are species-specific and thus cannot be restored after their disappearance (Valiente-Banuet et al. 2015), and our study thus provides a framework for determining benchmarks for bird-plant interactions in desert ecosystems.

In this study, two common desert foundation plant species and the resident avian community were examined to explore the relative importance, specificity, and sensitivity of avian associations by behaviour with these dominant plants. We tested the hypothesis that birds associate with different foundation species in deserts as microhabitats and temporal shifts in plant flowering and fruiting changes the frequency and nature of these associations. We used association patterns through time and at fine spatial scales to test the following predictions. (1) The abundance, richness, and diversity of a desert avian community are greater near foundation plants relative to open-gap microhabitats without a foundation plant. (2) The bird-plant associations estimated by observed bird behaviours will vary across microhabitats (cactus, shrub, or open) and by season (spring versus summer) because of changes in plant and bird reproductive timing.

# Materials & Methods

## **Study Site**

The field work was conducted at the Sweeney Granite Mountains Desert Research Center (34°48′20″N 115°39′50″W) in the Mojave Desert (Supplemental material A, Fig. 1). The elevation of the 3600 hectares of land ranges from 1128 to 2071 m and is not accessible to the public and is thus safe from visitor disturbance. Rainfall varies significantly throughout the year with a mean annual precipitation ranging from 34 to 310 mm per year (Urban et al. 2009). Typically, there is limited to no precipitation in the summer months. The July maximum and minimum temperatures are 33 C and 20 C respectively. The site is dominated by perennial woody and succulent shrubs such as *Cylindropuntia acanthocarpa, Yucca mohavensis, Larrea tridentata, Ambrosia salsola, Pinus monophylla*, and numerous other shrub species (André 2006). There have been 159 birds, 42 mammals, 35 reptiles, 2 amphibians, and 504 species of vascular plants documented at the reserve (Gurin et al. 2012; “Mammals of the Granite Mountains”; Stewart and Lappin 2008; André 2006).

***Study species***

While the Mojave boasts an array of diverse plants, a handful of foundational plant species dominate the landscape. *Cylindropuntia acanthocarpa*, or Buckhorn Cholla, is a shrub-like cactus with an irregular branching pattern (Pinkava 1999). *Larrea tridentata*, or Creosote Bush, is a large, long-lived deciduous shrub that is a highly reliable floral producer due to its low rainfall threshold (Bowers and Dimmitt, 1994). *Yucca schideigera*, or Mojave Yucca, is a flowering plant native to the region with several specialist and generalist relationships to fauna of the region. While there are many other plant species found in the study site, these three are the most abundant plant species and accounted for the greatest number of interactions documented in this study. Mojave Yucca, however, was included as a cactus in our study due to its succulent leaves ending in sharp points which make it functionally similar to other cacti in the region. All three of these species have been documented as foundation species in the region (Smith 1995; Schafer et al. 2012). During the spring surveys, these three species were flowering; in summer, however, all three had fleshy fruits available.

## **Experimental Design**

We conducted observations during 27 surveys from 5/1/2019 to 5/10/2019 for spring observations and repeated 20 surveys recording the observations for summer from 8/14/2019 to 8/24/2019. A 500-meter line transect was used over two-hour period blocks to sample the bird community from 7-10 am or 5-8 pm, depending on daily temperatures. Two individual line transects were used and spaced 80 meters apart. The starting coordinates for transects 1 and 2 were (34.78299, -115.662) and (34.78303, -115.663), respectively. A single observer familiar with the local bird species recorded all visual or auditory bird cues and identified each observation to species. As most non-shrub or non-cactus spaces constituted a relatively open microhabitat, this included some vegetative areas, but none with the level of heterogeneity that shrubs or cacti provide to their open surroundings. In addition to species, we also recorded behaviour as designated by an ethogram (Supplemental material C Table 8), microhabitat, geographic coordinates, and the time of the sighting/hearing. We only included visual observations of birds in microhabitat and behavioural analyses as birds that were heard but not seen could not be documented at any microhabitat, and birds may have been exhibiting behaviors that should be prioritized over singing or calling as defined by the ethogram, but these behaviors could not be observed. Flyovers (defined as birds flying roughly 25 feet above the highest vegetation at the site that did not land within sight) were not included as observations.

## **Statistical analyses**

Behaviour and microhabitat were treated as dependent variables for each independent bird observation documented. Behavioural observations were then categorized into broader behaviours (active movement, cleaning, feeding, inactive, and territorial/mating). Microhabitats were classified as cactus, shrub, or open-gap. Trophic guild and migratory class abundances, defined as the number of individuals within a trophic guild or migratory class at a seasonal microhabitat during a particular survey, were used to define functional diversity in further detailed analyses. We categorized all observed species into trophic guilds using “Foraging Guilds of North America” (De Graaf et al.1985) and into migratory classes using *Common Birds of the Sweeney Granite Mountains Desert Research Center* (Gurin et al. 2012). Taxonomic diversity was recorded to species level and is thus represented in the primary statistical analyses.

Generalized linear models (GLM) were used to compare bird abundance, richness, diversity, trophic guild abundance, migratory class, or behaviour with microhabitat type and season while including average maximum air temperature for the hour and survey replication as random factors (Donald et al. 2001; Morris et al. 2014). Species, trophic guild, or migratory class abundance are defined in this study as the number of individuals represented in each species, trophic guild, or migratory class. Species richness is the number of species in a community (i.e. a seasonal microhabitat during one survey). Diversity is represented as the Shannon Index, a biodiversity measure that accounts for rare species, more so than Simpson’s Diversity which more heavily incorporates species evenness. We then compared contrasted terms using estimated marginal means using the *emmeans* function (Lenth and Herve 2019) in R Version 4.0.2 (R Development Core Team 2020). We repeated these analyses excluding the Black-throated Sparrow, which made up ~36% of observations to ensure that this abundant species was not unduly influence detected outcomes. We also used a Non-metric Multidimensional Scaling analysis followed by a PERMANOVA (Legendre and Legendre 1998) to explore the influence of season on community composition and associations.

All code is published on Zenodo (Owen and Lortie 2020a). Photo documentation of birds is published at Figshare (Owen 2020), and a complete dataset of bird observation is published in the Knowledge Network for Biocomplexity Data Repository (Owen and Lortie 2020b).

# Results

A total of 755 birds were observed and an additional 467 bird calls were recorded during both seasons for a total of 1222 bird records over a total of 94 hours. Birds that were not seen were excluded because these instances could not be classified by microhabitat or behaviour. During the spring, 539 individual birds were visually observed, and 216 birds were visually observed in summer. Thus, there were significantly more individual birds observed in spring than in summer (Fig. 1; Table 1; post-hoc contrast at p = 0.0327).

Avian communities associated with shrubs in spring were the most species-rich and diverse (Fig. 1; Table 1; GLM richness; p = 0.024; post-hoc contrast at p = 0.0144; GLM Shannon index; p = 0.0001; post-hoc contrast at p = 0.0038). Open microhabitats in summer had the lowest bird species richness and biodiversity across all census periods (Fig. 1; Table 1; Richness: GLM; p = 0.024; post-hoc contrast at p < 0.0001; Shannon index: GLM; p = 0.0001; post-hoc contrast at p = 0.0216). The total abundances of birds were, however, greatest at open microhabitats in summer and lowest at open microhabitats in spring (Fig. 1; Table 1; GLM; p = 0.0254; post-hoc contrast at p = 0.0327). All iterative analyses findings were robust that excluded the Black-throated Sparrow (Supplemental material D). Bird trophic guild abundances were highest at shrubs in spring (Fig. 1; Table 2; GLM; p = 0.0233; post-hoc contrasts at p = 0.0384, respectively). However, there was no difference in the abundance of birds by migratory class between microhabitats or by season (Fig. 1; Table 1; p = 0.318). There was no significant difference between the composition of the avian communities by season or by microhabitats (Supplemental Material E Table 10 and Figure 4; PERMANOVA; F2 = 1.523; R2 = 0.0081; p = 0.178).

The most frequent activity observed was territorial behaviours in the spring at shrubs (Fig. 2; Table 3; GLM; p-value < 0.0001; post-hoc contrast at p = 0.0291). Cleaning behaviours were the least common, and we observed cleaning at shrubs four times in spring and once in the summer (Fig. 2; Table 3; GLM; p-value < 0.0001; post-hoc contrast at p = 0.0291). Feeding, active, and cleaning behaviors at all communities were equally frequent (Fig. 2; Table 3; GLM; p-value < 0.0001); thus, there was no termporal effect for these factors.

# Discussion

The relative importance of the two categories of foundation plant species for the avian community was examined through associational pattern analyses by season, and the hypothesis that positive effects were species and season-specific was supported. Bird species richness, diversity, and trophic guild abundances were higher at foundation plants. Diverse bird communities were most likely to be associated with foundation shrubs rather than at open or cacti microhabitats. This suggests that foundation plant species effects are species-specific at a given site within a region (or that different species of birds use these habitats differently) and they are still important for community composition (Ellison 2019). Foundation plants change community structure by modifying community assembly and generally support a higher α-diversity and a larger species pool relative to the open-gap (Kikvidze et al. 2015). Both mechanisms were likely relevant drivers of the observed bird-plant association patterns in this system. Additionally, bird behaviour varied by season and microhabitat. Benefits estimated through observed behaviors were mostly non-trophic such as using plants for structural purposes as we observed increased territorial displays at shrubs in the spring. Thus, foundation species are structural agents of facilitation that aid in increasing the diversity of the local avian community but interactions with these microhabitats differ seasonally.

Habitat heterogeneity, being fine-scale differences of habitats between microsites, was observed as important for bird community composition. Open and cacti microhabitats supported some birds though to a much lesser extent than shrubs in both spring and summer. Abiotic factors such as ultraviolet radiation, water scarcity, and heat are more intense in summer, which accounts for the lower diversity of many vertebrate species in open microhabitats in deserts (Koyama 2015). However, we observed some birds at cacti and open microhabitats, which can provide seeds and nest sites to birds (Simons and Martin 1990; Kelt et al. 2004). For example, when seeds and fruit begin to drop beneath the canopy of the mother plant, seed predators (i.e. granivorous birds) forage for these trophic resources (Racskó et al. 2007; Janzen 1970); but this is equally common in open areas (Milesi et al. 2019). However, summer foraging at open sites was not observed in this study and thus is likely not a reason for desert birds to be in open sites. While cacti can provide services like cover from predator and nesting sites to many species (Kozma and Mathews 1997), the family Cactaceae is morphologically diverse (Boke 1980) and unique cactus species thus provide functionally different opportunities for animals. The importance of cacti for birds in regions with other dominant cactus species has been well-documented (Drezner 2014). Our findings suggest that it is hence not one or the other (shrub or cacti) that enhaces community assembly, but in fact, it is the existence of both species in the area, as well as the open-gap, even in times of trophic resource abundance such as spring that contributes to heterogeneity and heterogeneity itself is crucial for the maintenance of biodiversity in arid ecosystems.

Food availability was not the primary driver of bird community diversity at shrub microhabitats. Birds in this system were typically observed associating with shrub microhabitats for their structural benefits, i.e. perching sites for territorial displays. Territorial displays allow birds to express honest signals to potential mates (Searcy et al. 2006) and provide population information to conservationists (Lewis et al. 2020). These findings support previous research that shrubs are valuable to migrating birds in the spring when they are seeking new territories (Lima 2009) and that perching sites are used differently for foraging and territorial displays (Collins 1981; Beck and George 2000). The expression of these behaviors is necessary for birds to maintain social connections and territories, both of which are important for bird reproductive success (Wilkins et al. 2013; Cooney et al. 2018). Birds likely associate more with foundation plant as they possibly provide structurual resources through architecture, shade, branching, height, spatial continuity, or even the presence of some animals near them and not other species. Future work could examine the importance of structural characteristics for bird communities. Benefactor rocks have been shown to facilitate plants and provide habitat for desert birds (Peters et al. 2008; Warning and Benedict 2015). Plant architecture, i.e. the nature and relative arrangement of a plant’s parts (Barthélémy et al. 2007), has already been documented as important for bird communities and should be examined in desert ecosystems more fully. Perch height is an important influencer of bird aggression, and thus plant and branch height should continue to be explored. Anthropogenic development of the American Southwest has provided an abundance of structures that may be beneficial to birds, such as fence posts and solar panels (Prather and Messmer 2010). However, these artificial structures may have negative implications such as the loss of seed dispersal over a landscape as birds over-use towers and poles. Careful attention should be paid to comparisons between these natural and non-natural or biotic and abiotic structures to see what native species are restored through these interactions and how they are mixed, locally.

Environmental stress in desert ecosystems is likely to increase in the upcoming years. Temporal environmental fluctuations are likely to affect bird diversity from spring to summer in deserts (Tonkin et al. 2017), and thus the decrease in bird individuals in summer was expected. Increased seasonal temperatures in summer pressure birds to avoid hotter areas in the open, as has been documented among other vertebrates (Ivey et al. 2020). Open gaps between vegetation in deserts are particularly harsh for animals and plants due to increased seasonal temperatures (Ivey et al. 2020; Lortie et al. 2016; Smith et al. 2018), and this decrease in bird richness and diversity from spring to summer suggests that temperatures at fine scales can be an environmental limitation for bird communities (Barrientos et al. 2007). Changes in biodiversity due to the arrival and departure of migratory species (in addition to anthropogenic impacts) have been shown to influence resident species’ success in reproduction and resource acquisition (Cox 1968; Greenberg et al. 1993; Ramírez-Cruz et al. 2020). Our study supports previous work that has clearly documented avoidance by vertebrates of open gaps in desert summer landscapes. This suggests that birds likely used foundation species structure as perches and shade to avoid experiencing the peak of environmental stressors, including temperature and solar radiation.

Environmental managers and conservationists must make restoration decisions regarding planting, genetic management, and distribution of expensive resources like seeds, seedlings, and fencing (among other things) to support plant growth (Aavik and Helm 2018). Commonly, managers may resort to planting one easily accessible plant species that is functionally similar to a rarer plant to provide microhabitat at lower costs and effort (Holl and Howarth 2000). However, birds (and likely other vertebrate species) require a range of microhabitats in environments with varying degrees of stress and varying types of pressures to exclude competitors; for successful, community-wide restoration efforts, this shifting range of needs must be fully considered. By protecting current plant diversity and investing in a diverse set of plant microhabitats when restoring degraded habitat, managers may better protect bird communities, which rely on habitat heterogeneity.

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**Author’s Contributions**

CJL and MO conceived the ideas and the experimental design; MO collected the data; MO analyzed the data with input from CJL; MO led the writing on the manuscript; NG and CJL thoroughly edited the manuscript and contributed critically to drafts for publication.

**Data Availability**

The dataset of bird observation is published in the Knowledge Network for Biocomplexity Data Repository: Owen, M., and C. Lortie. 2020c. Mojave Desert Bird Microhabitat and Behavioral Line Transect Observations. All other codes and data are publicly available on Zenodo and Figshare: Owen, M., and C. Lortie. 2020a. Mojave Desert Bird Survey Photos 2019; Owen, M., and C. Lortie. 2020b. Desert Bird Microhabitat Associations Analyses.

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**Tables**

**Table 1.** General linear models testing taxonomic abundance, richness, and Shannon index at three microhabitats (shrub, cactus, and open) during two different seasons (spring and summer).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Measure | Effect | d.f. | Deviance Residuals | P-value |
| Species Abundance (A) | Microhabitat | 2 | 3.3587 | 0.3618 |
|  | Season | 1 | 4.9182 | 0.0845 |
|  | **Microhabitat x Season** | **2** | **12.1427** | **0.0254** |
|  | Survey | 0 | 0 | - |
|  | Temperature | 0 | 0 | - |
| Species Richness (S) | **Microhabitat** | **2** | **23.528** | **0.0071** |
|  | **Season** | **1** | **121.103** | **<0.0001** |
|  | **Microhabitat x Season** | **2** | **22.262** | **0.024** |
|  | Survey | 0 | 0 | - |
|  | Temperature | 0 | 0 | - |
| Shannon Index (H) | **Microhabitat** | **2** | **5.0558** | **0.0036** |
|  | **Season** | **1** | **26.459** | **<0.0001** |
|  | **Microhabitat x Season** | **2** | **8.0337** | **0.0001** |
|  | Survey | 0 | 0 | - |
|  | Temperature | 0 | 0 | - |

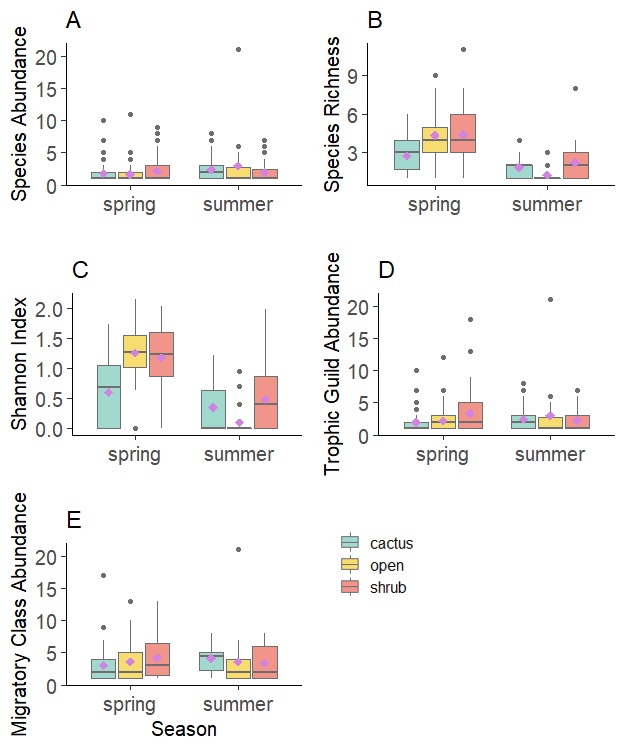
**Table 2.** General linear models testing functional diversity metrics for bird communities as defined by bird trophic guild and migratory class between three microhabitats (shrub, cactus, and open) during two different seasons (spring and summer).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Measure | Effect | d.f. | Deviance Residuals | P-value |
| Trophic Guild Abundance | **Microhabitat** | **2** | **14.6185** | **0.0363** |
|  | Season | 1 | 0.1855 | 0.7718 |
|  | **Microhabitat x Season** | **2** | **16.5826** | **0.0233** |
|  | Survey | 0 | 0 | - |
|  | Temperature | 0 | 0 | - |
| Migratory Class Abundance | Microhabitat | 2 | 2.7772 | 0.6178 |
|  | Season | 1 | 0.032 | 0.916 |
|  | Microhabitat x Season | 2 | 6.6078 | 0.318 |
|  | Survey | 0 | 0 | - |
|  | Temperature | 0 | 0 | - |

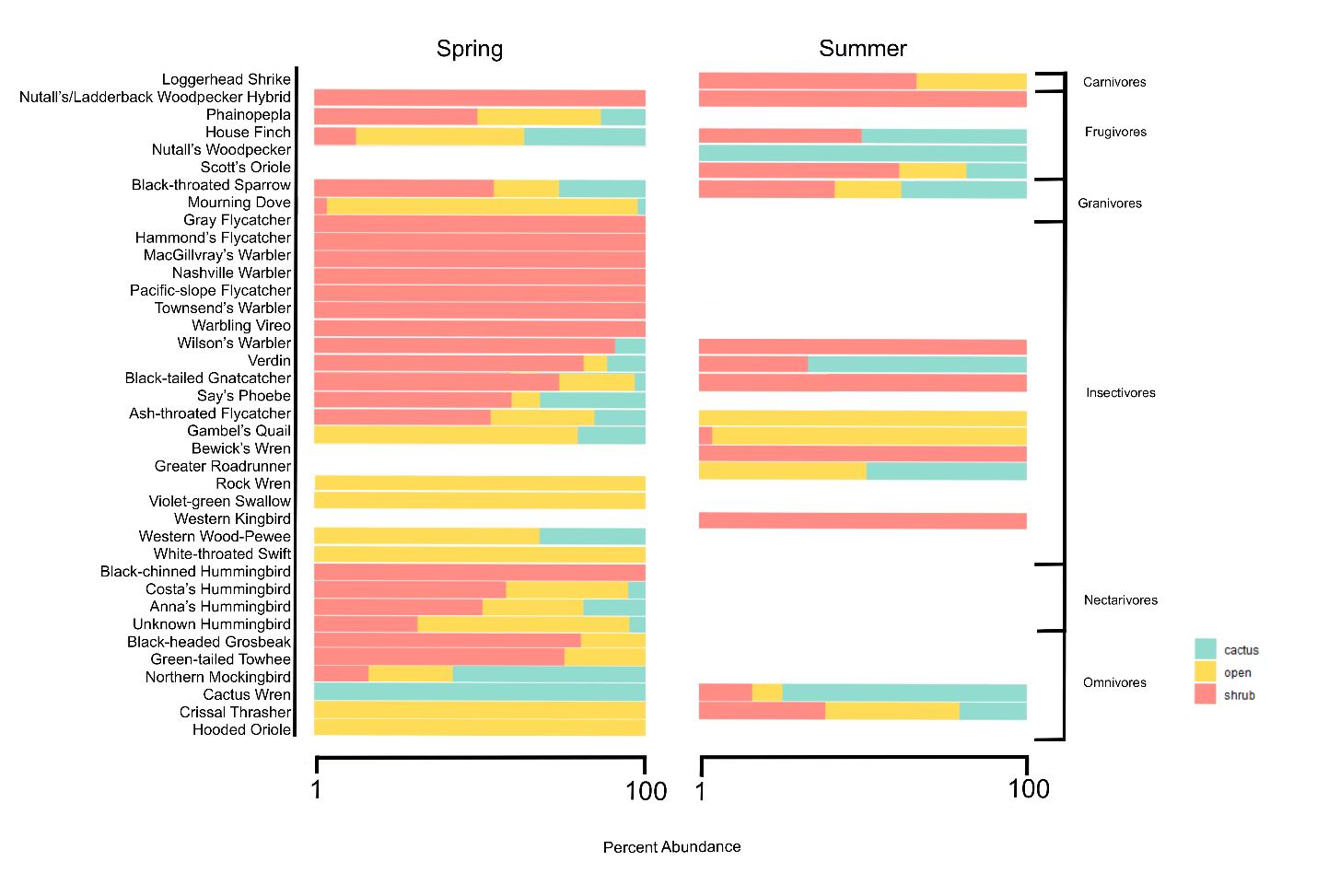
**Table 3.** Statistical output of the general linear model testing for differences in behavior frequency at three different microhabitats (shrub, cactus, and open sites) between two different seasons (spring and summer).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Measure | Effect | d.f. | Deviance Residual | P-value |
| Behavior Abundance | **Microhabitat** | **2** | **20.282** | **0.0012** |
|  | Season | 1 | 5.133 | 0.0642 |
|  | **Behavior** | **4** | **44.712** | **<0.0001** |
|  | Microhabitat x Season | 2 | 4.011 | 0.2624 |
|  | **Microhabitat x Behavior** | **6** | **25.668** | **0.0088** |
|  | **Season x Behavior** | **4** | **33.332** | **0.0002** |
|  | **Microhabitat x Season x Behavior** | **6** | **45.038** | **<0.0001** |
|  | Survey | 0 | 0 | - |
|  | Temperature | 0 | 0 | - |

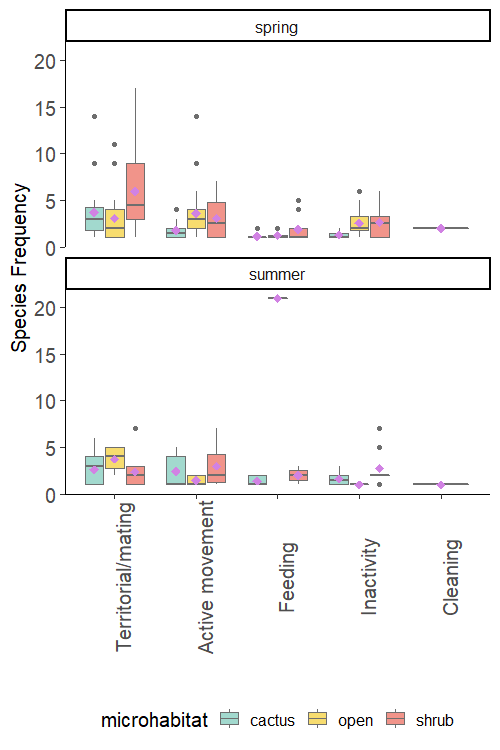
**Figures**



**Figure 1**. Boxplots of (A) species abundance, (B) species richness, (C) species diversity as the Shannon Index, (D) trophic guild abundance, and (E) migratory class abundance of all visually observed birds at either cacti, shrub, or open microhabitats in both spring and summer. Purple diamonds represent the means value among surveys of each bird community metric. Shrubs in spring had the highest species richness (p = 0.024) and species diversity (p < 0.0001) relative to all other seasonal microhabitats.



**Figure 2:** Species frequency as a percent of all observed avian species at cactus, shrub, and open microhabitats during spring and summer. More species and more individuals were present in spring.



**Figure 3:** Boxplots of frequencies of behaviors exhibited by birds during surveys at cactus, shrub, and open microhabitats during spring and summer. The purple diamonds represent the mean frequencies of each behavior with survey as the level of replication. The most common behavior exhibited at a single seasonal microhabitat was territorial/mating behaviors at spring shrubs (p < 0.0001).

1. [↑](#footnote-ref-1)