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POST-DISTURBANCE CHANGES IN A DESERT BREEDING BIRD COMMUNITY

MICHAEL A. PATTEN AND JOHN T. ROTENBERRY
Department of Biology
University of California
Riverside, California 92521 USA

Abstract.—We examined breeding bird species richness, density, and community composition on a California desert riparian site in 1980 and, following construction of flood control structure and subsequent vegetation restoration, again in 1995. Both species richness and bird abundance declined markedly between 1980 and 1995. Except for turnover in locally scarce breeders, however, avian community composition did not shift significantly. Alteration and removal of much of the desert riparian habitat formerly on-site is probably responsible for the changes reflected in bird community structure, such that richness and density are now comparable to Breeding Bird Censuses conducted in other desert scrub habitats despite the intermittent stream that still transects the site. When examined in a broader context of desert bird community variation, overall community changes were slight if we emphasized species composition and abundance, but substantial if we emphasized species turnover. Community-level analyses emphasizing richness and composition are more sensitive to species turnover, whereas those incorporating bird density are more sensitive to changes in relative abundance.

CAMBIOS POST-DISTURBIOS EN UNA COMUNIDAD REPRODUCTIVA DE AVES DE DESIERTO.

Sinopsis.—Examinamos la riqueza de especies, la densidad, y la composición de la comunidad de aves en una localidad desértico-ribereña en California en 1980 y, posterior a la construcción de una estructura de control de inundaciones y la restauración subsecuente de la vegetación, de nuevo en 1995. Excepto por una reorganización en las aves de escasa reproducción local, la composición de la comunidad de aves no se modificó significativamente. La alteración y la remoción de mucho del habitat ribereño desértico en el lugar del estudio es probablemente responsable por los cambios reflejados en la estructura de la comunidad de aves, tales que la riqueza y la densidad son ahora comparables a la estimada de los "Censos de Aves en Reproducción" conducidos en otros habitats de chaparral desértico aunque una quebrada intermitente siga irrumpiendo en el área. Cuando la variación de la comunidad de aves del desierto es examinada en un contexto más amplio, los cambios generales en la comunidad fueron leves si se emfatiza la composición y la abundancia de especies, pero sustanciales si enfatizamos la reorganización de especies. Los analisis a nivel de comunidad enfatizando la riqueza y composición son más sensitivos a la reorganización de especies, mientras que aquellos que incorporan la densidad de aves son más sensitivos a los cambios en la abundancia relativa.

Human-induced disturbance can play a major role in the alteration of community structure and composition in natural systems. Although birds are perhaps more resilient to such disturbances than less vagile organisms (Wiens 1989), they can nevertheless be negatively affected by habitat modification or removal, either through direct loss or through habitat fragmentation. Measuring the response to disturbance can be difficult, however, because data seldom exist that sufficiently predate and postdate a disturbance such that more or less stable communities can be compared. If data do exist, they often are not in a comparable form. Perhaps most importantly, changes in community structure suspected to be the result of disturbance must be examined in the context of natural fluctuations in community composition at relatively undisturbed sites.

An additional complication is that different measurement techniques can lead to conflicting results (Magurran 1988, Gotelli and Graves 1996), and thus to different conclusions regarding the effects of disturbance on community structure. For example, it is possible for community composition to change little in terms of dominant species, but to change greatly in terms of overall richness. Thus, use of an index that emphasized species dominance (e.g., the Simpson diversity index) could yield a quantitatively different conclusion than use of a measure that emphasized rare species (e.g., the Shannon diversity index or simple species richness; see Remsen 1994, Gotelli and Graves 1996:22). Similarly, using an analysis technique that emphasizes species abundance and composition (e.g., ordination) can yield qualitatively different results from techniques concerned with richness (e.g., rarefaction).

In this paper we address these issues by (1) reporting the response to disturbance by a desert bird community using comparable pre- and post-disturbance spot-mapping data, and (2) setting the biological and statistical context for assessing such a response. In particular, we confront the issue that the determination of community stability is dependent on the analyses used and on the level at which analyses are conducted. Lastly, we demonstrate that despite limitations that necessarily arise in such studies, inferences can still be made if the data are properly analyzed and are placed into a broader context.

STUDY SITE

The study area was a 13.1-ha plot established in 1980 on the Tahquitz Creek alluvial fan at the northern edge of Palm Springs, Riverside County, California (Township 4 south, Range 4 east, Section 22, San Bernardino Baseline and Meridian, U.S. Geol. Survey 7.5′ Palm Springs quadrangle). The boundaries of this study plot corresponded to the proposed (i.e., pre-project) boundaries of a debris basin and spillway construction site, forming an L-shaped polygon with the long axis of 500 m aligned east to west (LaPré 1980). The plot extended to the base of rocky cliffs to the south.

Riverside County Flood Control and Water Conservation District completed construction of flood control structures in 1991. These structures consisted of a debris basin dam downstream from two unlined, channelized streams (Tahquitz Creek and Fern Canyon), and upstream from a single channel lined with rock and concrete. During construction, ±8.1 ha of desert vegetation was either removed or heavily impacted. Upon construction completion, vegetation restoration, a common mitigation measure for areas heavily impacted by construction projects, began through direct seeding and planting of saplings. After four years, restored vegetation had achieved the pre-defined success criterion of 15% total cover, although shrub cover, herb cover, and plant species richness was

TABLE 1. Breeding bird species and number of territories on the 13.1-ha Tahquitz Creek site, Palm Springs, California, comparing 1980 and 1995 spot-mapping data.

Species	Number of territories	
	1980	1995
Gambel's Quail (*Callipepla gambelii*)	3	—
Mourning Dove (*Zenaida macroura*)	2	—
Costa's Hummingbird (*Calypte costae*)	4	2.5
Black Phoebe (*Sayornis nigricans*)	—	2
Western Kingbird (*Tyrannus verticalis*)	1	—
Common Raven (*Corvus corax*)	—	0.5
Verdin (*Auriparus flaviceps*)	2	3
Cactus Wren (*Campylorhynchus brunneicapillus*)	1	—
Canyon Wren (*Catherpes mexicanus*)	1	—
Rock Wren (*Salpinctes obsoletus*)	—	1.5
Bewick's Wren (*Thryomanes bewickii*)	1	—
Blue-gray Gnatcatcher (*Polioptila caerulea*)	1	—
Black-tailed Gnatcatcher (*Polioptila melanura*)	—	1
Northern Mockingbird (*Mimus polyglottos*)	2	—
Phainopepla (*Phainopepla nitens*)	1.5	—
California Towhee (*Pipilo crissalis*)	1	1
Black-throated Sparrow (*Amphispiza bilineata*)	3	3
House Finch (*Carpodacus mexicanus*)	5	—

lower in the restored area compared to natural desert scrub habitat surrounding the construction area (Patten 1997).

METHODS

Vegetation was sampled in 1980 using the *relevé* method (Mueller-Dombois and Ellenberg 1974). Post-construction scrub vegetation cover was quantified 27 Aug.–2 Nov. 1993 in natural and restored areas by sampling randomly selected 3.3-m × 3.3-m plots (n = 132) within restored desert scrub and in surrounding desert scrub that was not impacted by construction; see Patten (1997) for more information. Plant taxonomy and nomenclature follows Hickman (1993), and scientific names for all bird species mentioned are listed in Table 1.

Breeding bird surveys were conducted in April and May 1980 by L. F. LaPré and in May–July 1995 by M. A. Patten. During both years, surveys followed standardized spot-mapping methodology (International Bird Census Committee 1970, Ralph et al. 1993). Fractional territories were considered in the total for the Tahquitz study site.

To set the biological context for examining avian community composition and variation of the Tahquitz Creek site, Breeding Bird Census data for 34 additional sites in the Mojave Desert of southern California (Appendix) were obtained from published summaries in *American Birds* (1978–1981 censuses) and the *Journal of Field Ornithology* (1992 and 1994 censuses); these years were used because they roughly coincided with the Tahquitz censuses. Sites were classified as either desert scrub (e.g., *Larrea* scrub, *Atriplex* flats; n = 23 sites) or as desert riparian (e.g., *Salix* woodland, *Prosopis* bosque, *Cercidium* wash; i.e., "xeroriparian" [Johnson et al. 1984]; $n = 11$ sites) based on habitat descriptions provided in each published summary. Because census plots varied in size, bird abundance was normalized for each site to number of territorial males per 100 ha. Two sites were censused roughly fifteen years apart at times coincident with the Tahquitz censuses: (1) Lanfair Valley 5, a desert scrub site sampled in 1978 and 1994, and (2) Morongo Valley, a desert riparian site censused in 1980 and 1994 (Table 1). No other sites in the California desert were sampled over this same span.

We examined changes in species richness at Tahquitz Creek by rarefaction (Heck et al. 1975, James and Rathburn 1981, Gotelli and Graves 1996:24). Specifically, we rarefied the 1980 Tahquitz abundance data to determine the number of species expected for the abundance we recorded in 1995, calculated the variance around that expected value (Heck et al. 1975), and then calculated a standard error estimate to determine if richness significantly differed between census years. We also calculated the expected number of species on average at desert riparian and scrub sites, along with standard errors for these expectations. Because census areas were roughly similar across all sites, and did not change at all on successive Tahquitz Creek surveys, individual abundances, rather than site areas, were rarefied to obtain expected species richnesses (James and Rathburn 1981).

Ordination techniques, particularly principal components analysis and detrended correspondence analysis (e.g., Rotenberry and Wiens 1980, Evans 1988), have been especially useful for assessing community-wide patterns without relying on diversity indices. Therefore, we further analyzed the Tahquitz breeding bird community data through a common ordination with other desert riparian and scrub sites. Ordination analyses were performed with these bird density data and with the Tahquitz Creek data to determine the relative shift in bird community structure at Tahquitz Creek in the broader context of bird community variation throughout other desert scrub and desert riparian sites in southern California. A second analysis was performed using only presence/absence data, which has the effect of emphasizing only species turnover. Proximity of sites in ordination space denotes similarity of overall species composition and abundance. Because principal components analyses (PCA) can lead to spurious curvilinear axes when used for ordination (Pielou 1984), especially with non-linear variables such as presence/absence data, we used detrended correspondence analysis (DCA). DCA is an ordination technique that, like PCA, is an eigenanalysis based on reciprocal averaging, but which breaks axes into segments that are renormalized, thus eliminating curvilinearity (Hill and Gauch 1980, Jackson and Somers 1991). Also, sequential renormalization results in axis linearity throughout its length. Despite critiques of this procedure (e.g., Wartenberg et al. 1987), we believe that it recovers the underlying gradient as well as any ordination technique that relies only on a species by site matrix. Indeed, DCA produces minimal distortion of unimodally distributed data such as these

(Peet et al. 1988, Rotenberry 1990, Jackson and Somers 1991). DCA axes are scaled such that a pair of censuses approximately four units apart share little overlap in species composition. We ran DCA ordinations of sites (PC-ORD 1995) using (1) bird abundance without downweighting of rare species and (2) species presence/absence.

RESULTS

Desert scrub habitat on the Tahquitz Creek alluvial fan site in 1995, even including the restoration areas, was like desert scrub on-site in 1980, but riparian vegetation was altered drastically (LaPré 1980, Patten 1997). In the desert scrub, *Encelia farinosa, Larrea tridentata,* and *Eriogonum fasciculatum* were the three dominant shrubs in both years, with non-native grasses composing the understory. In restored areas, *Encelia farinosa* and, to a lesser extent, *Eriogonum fasciculatum* were the only shrubs that established well, and understory cover was much lower. The most striking difference between vegetation structure and composition between 1980 and 1995 was in terms of plant species previously found on-site in washes and along Tahquitz Creek itself. Indeed, one species abundant along Tahquitz Creek in 1980, *Platanus racemosa,* no longer occurs on the site (they are found within 1–2 km upstream). There also was a substantial decline in the abundance of *Prosopis glandulosa* var. *torreyana* and *Chilopsis linearis* along the creek and in the associated washes. See Patten (1997) for more details about on-site vegetation.

There were fourteen breeding bird species on the Tahquitz site in 1980, at a total density of 217.6 pairs/km^2 (Table 1; LaPré 1980). This density was about double the average Breeding Bird Census density in desert scrub habitat (n = 23, mean number of species = 9.5, mean number of pairs/km^2 = 106.2), but was about half that for desert riparian habitats (n = 11, mean number of species = 15.5, mean number of pairs/km^2 = 465.8). In 1995, only eight species were found breeding on the site, and total breeding bird density had dropped to 110.7 pairs/km^2 (Table 1). Both 1995 figures are comparable to richness and abundance found in desert scrub habitats censused elsewhere in southern California. Rarefaction of the 1980 census data indicated that there was a significant decrease in species richness from 1980 to 1995, and that this decrease was not simply the result of lower bird abundance in the latter year (Fig. 1). Because the rarefaction curve for 1980 had already flattened, the expected number of species for 111 individuals (the total in 1995) was the same as the richness in 1980 ($E[S_n] = 14 \pm 0.036$ SE). Ten of 14 species found breeding in 1980 were not found in 1995, and four species found breeding in 1995 were not found in 1980 (Table 1). However, the House Finch probably bred on-site in 1995 because, although no definite territories were located, this species was a common nesting species at Tahquitz Creek in 1980, and was numerous in the area in 1995. Even so, the rarefaction confirmed the apparent pattern in the raw data: in terms of its bird community richness, Tahquitz Creek was more like a desert scrub site in 1995 than in 1980 (Fig. 1).

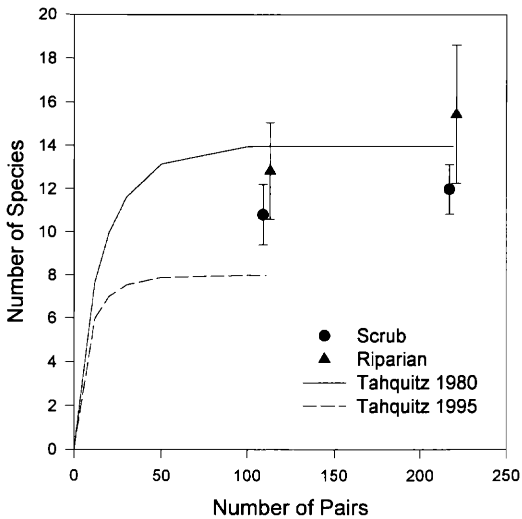

FIGURE 1. Rarefaction curves for bird species on the Tahquitz Creek site. Rarefaction was performed on bird abundance, with the 1980 Tahquitz census data (219 individuals) rarefied to the abundance found on the 1995 census (111 individuals). Average (± SE) expected species richness for eleven desert riparian and nine desert scrub sites (from Breeding Bird Census data) rarefied to 111 individuals and to 219 individuals are presented for comparison.

In contrast to the rarefaction analysis, Tahquitz Creek was intermediate to most riparian and scrub sites along DCA I, regardless of census year and of type of data used in the ordination (Figs. 2 and 3). The DCA performed on presence/absence data supported the idea of substantial community turnover at Tahquitz Creek; the distance moved in ordination space between 1980 and 1995 at Tahquitz was considerably greater than the distance moved by desert riparian and scrub sites conducted in comparable years (Fig. 2). The first DCA axis (DCA I) uncovered near complete turnover in species composition (gradient length = 4.51, $\lambda = 0.61$), and was clearly a mesic (low scores) to xeric (high scores) gradient. DCA II was also a long gradient (length = 3.54, $\lambda = 0.26$), with scrub sites more clustered along this axis than riparian sites (Fig. 2).

Unlike the results obtained by the rarefaction and the DCA on presence/absence data, which respectively consider only species richness and community membership, the DCA based on species abundance placed both Tahquitz Creek censuses fairly close to one another along both gradients represented along the first two axes (Fig. 3). Indeed, with abundance taken into account, the shift between census years at Tahquitz was the same as that shown by the undisturbed riparian and scrub sites with repeated data. The first axis of this DCA ($\lambda = 0.77$) provided near-complete separation of desert riparian and desert scrub sites (Fig. 3). As with the presence/absence DCA, DCA I appeared to be a mesic (values of 0)

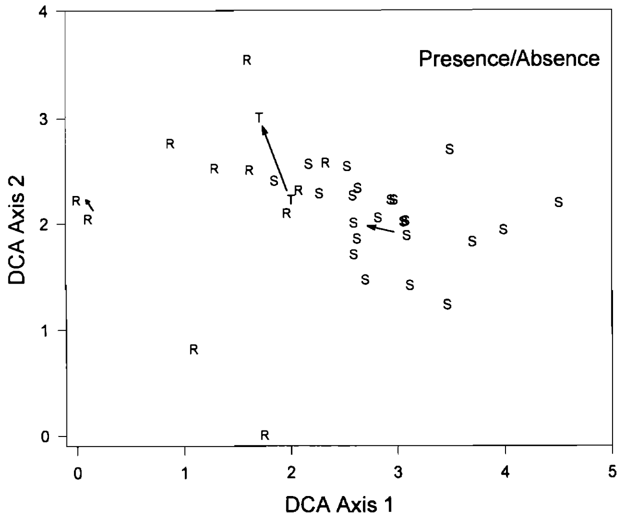

FIGURE 2. Detrended correspondence analysis ordination using Breeding Bird Census breeding bird presence/absence data for desert riparian (R), desert scrub (S), and the Tahquitz Creek (T) sites in the Mojave Desert of southern California. The arrows denote shifts from 1980 to 1995 for sites with comparable repeated censuses.

to xeric (values near 5) axis, and showed that there is a complete turnover of breeding bird community composition between desert riparian and desert scrub sites at opposite ends of the gradient (gradient length = 5.66). DCA I scores for Tahquitz Creek were not significantly different from mean riparian or mean scrub scores for this axis during either year ($P > 0.25$ for all four tests), signifying that it is a site with intermediate qualities, and that it has not shifted appreciably over the 15-yr period in terms of bird community composition. DCA II ($\lambda = 0.38$, gradient length = 3.72) provided most separation for riparian sites (Fig. 3).

DISCUSSION

Analyses of the comparative breeding bird data for Tahquitz Creek from 1980 and 1995 underscores the need to consider entire communities (i.e., a multivariate approach) instead of looking only at simple measures of diversity (a univariate approach). Diversity indices have been employed as the sole measure for most studies of patterns of variation in species richness and abundance (Wiens 1989:122), even though diversity indices provide little analytical or statistical information (Hurlbert 1971, Peet 1974), ignore community composition (James and Wamer 1982, Worthen 1996), and different ones frequently lead to conflicting results (Hill 1973, Magurran 1988). Because of these limitations, particularly with the Shannon index (Routledge 1980, Gotelli and Graves 1996:22), alternative methods such as rarefaction (James and Rathburn 1981), nested-subset analyses (Worthen 1996), and various ordination techniques

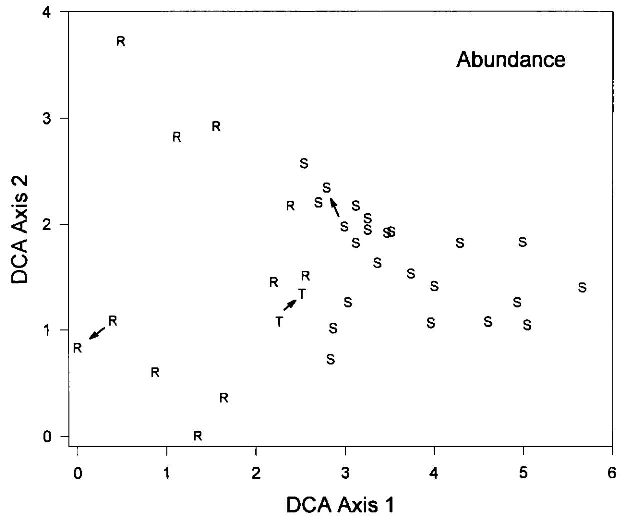

FIGURE 3. Detrended correspondence analysis ordination using Breeding Bird Census breeding bird density data for desert riparian (R), desert scrub (S), and the Tahquitz Creek (T) sites in the Mojave Desert of southern California. The arrows denote shifts from 1980 to 1995 for sites with comparable repeated censuses.

(Gauch 1982, Pielou 1984, Palmer 1993) have been used. For direct comparisons of species richness, rarefaction is the preferred technique, and yields more robust results than do diversity indices (Gotelli and Graves 1996:24). When considering only species richness, overall breeding bird abundance, and their resulting rarefaction, it would appear that the Tahquitz breeding bird community had shifted dramatically from predisturbance (1980) to postdisturbance (1995) conditions. Similarly, ordination of the predisturbance and postdisturbance communities using only presence/absence data suggests that the breeding bird community at Tahquitz changed greatly with respect to other desert riparian and desert scrub sites in southern California. Thus, if species composition is to be our primary measure of community stability, then the Tahquitz Creek site was drastically affected by construction of the dam and by channelization of the creek, and has yet to return to predisturbance composition.

By contrast, an ordination that included not only species composition, but also the relative abundances of these species, suggested that the Tahquitz Creek bird community was quite stable; it changed no more than did undisturbed sites supporting desert riparian and desert scrub in southern California. Although there was turnover in breeding bird species, most of these species were locally scarce (≤ 1 territory per 13.1 ha). This turnover was reflected in the rarefaction, which considers only species richness, and is thus sensitive to scarce species (Hill 1973, Routledge 1980). As noted above, only four of the eighteen bird species found nesting on the Tahquitz Creek site bred there in both 1980 and 1995. Three of these species, the Costa's Hummingbird, Verdin, and Black-throated Sparrow, are widespread, common breeders in Mojave Desert scrub habitats throughout southern California, and contributed greatly to the apparent "stability" of the community. The fourth species, the California Towhee, is at the eastern limit of its range at Tahquitz Creek, but suitable habitat for it exists throughout the southern edge of the study site.

Potential biases exist when observations are limited to certain years within a study period, and bird abundance and species richness may fluctuate drastically between short time periods (Wiens 1981, Diehl 1986). Whereas the results we report herein deal only with two study years, the differences in habitat alteration and temporal distance between the studies makes the results of interest. For example, two pairs of Black Phoebes were located in 1995, but none were detected in 1980. This species habitually uses artificial structures, particularly flood control structures and water diversion culverts, as nesting sites in southern California (Patten, pers. obs.). The construction of the debris basin dam likely provided nesting habitat for this species that did not exist before on the study site. Similarly, Rock Wrens were found nesting on-site in 1995, with one pair frequenting the rock revetments on the flanks of the dam. Abundant habitat for this species surrounds the site, but in 1980 rocky areas were confined to the bed of Tahquitz Creek and to the associated washes, both of which were fairly heavily vegetated. The other two species found nesting in 1995 that were not detected in 1980 were the Common Raven and Black-tailed Gnatcatcher. Both of these species nest fairly commonly in desert scrub habitats in southeastern California, and the lack of records in 1980 perhaps support warnings regarding short-term studies (Wiens 1981, Diehl 1986).

Similarly, several desert scrub breeders not detected in 1995, but found in 1980, may reflect only an annual "blip" in recording, again perhaps supporting previous contentions (Wiens 1981, Diehl 1986). The Gambel's Quail, Mourning Dove, and House Finch provide the best examples. All three of these species were observed regularly during both spot-mapping and other surveys being conducted on-site, yet no territoriality or other nesting behavior was observed. As a result, these species were not considered to be breeders on the site in 1995, although all three likely breed in the vicinity. Furthermore, Canyon Wrens are scarce on the desert slope in southern California, such that breeding should not be expected every year.

The remaining breeding bird species located in 1980, but not detected as breeders in 1995, are species typically found in riparian settings when in the desert, with some species, particularly the Blue-gray Gnatcatcher and Phainopepla, associated with *Prosopis* thickets and bosque in many desert areas (Patten, pers. obs.). Likewise, the Cactus Wren and Bewick's Wren frequently use this sort of habitat (e.g., at nearby Big Morongo Canyon). These species have almost certainly abandoned the site because of the substantial loss of *Prosopis* and other streamside/wash vegetation previously found there. In that regard, although both the Western Kingbird and Northern Mockingbird continue to breed in the Tahquitz vicinity (Patten, pers. obs.), the study site now lacks suitable nest trees.

In conclusion, there has been a substantial turnover in locally scarce breeding species at Tahquitz Creek, most of which we attribute to habitat alteration associated with the construction of flood control structures. From the standpoint of species richness and community composition with all species equally weighted, on-site disturbance has led to substantial community turnover. Nevertheless, the breeding bird community now using the Tahquitz site is hardly depauperate and, if we consider both species composition and relative abundance, it has remained relatively stable despite the disturbance. Thus, whether or not a community is considered stable is dependent upon the level of the analysis, with analyses emphasizing richness (e.g., rarefaction) and composition (e.g., a presence/absence ordination) being more sensitive to species turnover and those incorporating bird density (e.g., a standard ordination) more sensitive to changes in relative abundance. We recommend using all of these measures to assess community stability.

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APPENDIX

Breeding Bird Census data from the California desert (published in *American Birds* and *Journal of Field Ornithology*) that we used for comparative analyses in this study.

Desert scrub.—China Lake, Inyo County (1979); Cima, San Bernardino County (1978); Coso Junction 1, Inyo County (1979); Coso Junction 2, Inyo County (1979); Coso Junction 3, Inyo County (1979); Deep Springs Valley, Inyo County (1978); Haiwee Spring, Inyo County (1979); Johnson Canyon, Inyo County (1979); Lanfair Valley 1, San Bernardino County (1978); Lanfair Valley 2, San Bernardino County (1978); Lanfair Valley 3, San Bernardino County (1978); Lanfair Valley 4, San Bernardino County (1978); Lanfair Valley 5, San Bernardino County (1978); Lanfair Valley 5, San Bernardino County (1994); Lanfair Valley 6, San Bernardino County (1978); Lanfair Valley 7, San Bernardino County (1978); Mid Hills, San Bernardino County (1992); Mid Hills, San Bernardino County (1994); Milligan, San Bernardino County (1978); Palm Desert, Riverside County (1978); Palm Desert, Riverside County (1979); Rancho Mirage, Riverside County (1981); Vidal Wash, San Bernardino County (1978).

Desert riparian.—Amargosa River Gorge, Inyo County (1978); Chemhuevi Wash, San Bernardino County (1978); Corn Springs, Riverside County (1978); Coso Hot Springs, Inyo County (1979); East Bear Creek, Riverside County (1981); Morongo Valley, San Bernardino County (1980); Morongo Valley, San Bernardino County (1994); Pushwalla Springs, Riverside County (1978); Saline Valley, Inyo County (1978); Tecopa, Inyo County (1978); West Bear Creek, Riverside County (1981).