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A TWENTY-YEAR INVESTIGATION OF THE EFFECTS OF FIRE ON A COASTAL SAGE SCRUB BIRD COMMUNITY

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ABSTRACT: From 1983 to 2003 I examined the effects of fire on the bird community of two 1.25-ha tracts of coastal sage scrub, Box Canyon and F Canyon, 0.4 km apart in a 31-ha reserve in Los Angeles County, California. Wildfire burned Box Canyon in 1981 and both sites in 1989. I observed 90 species in F Canyon, 80 in Box Canyon, of which 73 were seen in both. The same species were common throughout the 20-year period. F Canyon had more species per count than Box Canyon in both summer and winter. Immediately after the 1989 wildfire, observations of some species of open habitat increased, and observations of some species confined to shrubs decreased. Effects of the 1989 fire on the sites were of short duration. Differences between the sites in number of species attributed to the 1981 fire in earlier studies are confounded by differences between the sites.

Long-term studies provide insight into the organization and dynamics of avian communities (Holmes et al. 1986, Brawn and Robinson 1996, Herrera 1998). Understanding differences among sites in richness of bird species is important in fragmented habitats such as coastal sage scrub, which has been reduced by urbanization and whose biodiversity is the subject of concern (Westman 1981, McCaull 1994, Chase et al. 2000, Cox and Allen 2008). In a brief period, such as a single breeding season, differences in species richness between sites may represent random variation, be transitory, or may indicate a long-term difference (Chase et al. 2000). Long-term data address this ambiguity.

The effect of fire on birds of southern California's coastal sage scrub has been examined with varying results and conclusions. Wirtz (1982) and Mendelsohn et al. (2008) reported increased species richness in chaparral and coastal sage scrub, respectively, but Moriarty et al. (1985) and Stanton (1986) reported richness in burned coastal sage scrub decreased from that at an unburned site. Mendelsohn et al. (2008) suggested discrepancies between their study and that of Stanton (1986) may have been due to differences

Table 1 Ranges of Dates of Blocks of Counts and Number of Species Seen by Season at the Voorhis Ecological Reserve, Pomona, California, 1983–2003

		F Canyon			Box Canyon			
Dates	n^a	Summer	Winter	Total	Summer	Winter	Total	Block total
20 Jan 1983–16 May 1984	56	49	47	65	46	38	60	79
17 Oct 1986–31 Dec 1988	41	38	29	44	31	18	37	54
30 Jul 1989–11 Nov 1991[b]	39	46	37	57	38	27	49	66
6 Dec 1992–31 Aug 1996	85	51	50	61	35	32	42	65
23 Jul 2000–22 Jul 2001	18	26	24	31	20	21	28	37
19 Oct 2002–30 Dec 2003	26	29	29	39	27	31	37	45
Total (all blocks)	265	78	71	90	66	60	80	97

[a]Number of paired counts in each block.

[b]The study area burned on 28 July 1989, two days before the start of the third count block.

between the sites they studied in San Diego and Los Angeles counties, respectively. Differences unrelated to fire may have confounded the results.

In this paper my objectives are (1) to describe species richness and community composition of birds at two sites in coastal sage scrub over 20 years, (2) to compare the two sites with respect to richness and composition and examine how these differences affect the conclusions of previous studies of the effect of fire at these sites (Moriarty et al. 1985, Stanton 1986), and (3) to describe the effect on richness and composition of a wildfire that burned both sites in the sixth year of the study.

METHODS

Study Sites

My study area was the 31-ha Voorhis Ecological Reserve in the San Jose Hills on the campus of California State Polytechnic University, Pomona, Los Angeles County, California (34° 03′ N, 117° 49′ W). I established two 1.25-ha sites at approximately 300 m elevation and 0.4 km apart, connected by contiguous vegetation. The first site (Box Canyon) was burned in a wildfire on 21 August 1981 (Moriarty et al. 1985). The second site (F Canyon) was not burned and was used as a control by Moriarty et al. (1985) and Stanton (1986). The sites are both south-facing canyons and appear similar in their topography and vegetation structure (Moriarty et al. 1985, Stanton 1986). A second wildfire of apparent accidental origin burned the entire reserve

Table 2 Numbers of Times Each Species Was Observed at the Voorhis Ecological Reserve, Pomona, California, 1983–2003, by Site and Season

Species[a] and residency status[b]	F Canyon		Box Canyon	
	Summer	Winter	Summer	Winter
1. **Anna's Hummingbird**, *Calypte anna*, P	98	117	115	110
2. **California Towhee**, *Melozone crissalis*, P	121	100	116	74
3. **Western Scrub-Jay**, *Aphelocoma californica*, P	100	87	111	83
4. **Northern Mockingbird**, *Mimus polyglottos*, P	106	**79**	94	**48**
5. **House Finch**, *Haemorhous mexicanus*, P	**104**	75	**74**	59
6. **Spotted Towhee**, *Pipilo maculatus*, P	**86**	**61**	**59**	**25**
7. **Wrentit**, *Chamaea fasciata*, P	**74**	**64**	**44**	**30**
8. **Mourning Dove**, *Zenaida macroura*, P	**89**	**39**	**41**	**20**
9. **California Quail**, *Callipepla californica*, P	53	**68**	46	**24**
10. **Cactus Wren**, *Campylorhynchus brunneicapillus*, P	**81**	**53**	**4**	**1**
11. **Bushtit**, *Psaltriparus minimus*, P	31	38	62	34
12. **California Thrasher**, *Toxostoma redivivum*, P	**58**	**44**	**36**	**19**
13. **Lesser Goldfinch**, *Spinus psaltria*, P	31	31	34	35
14. **Bewick's Wren**, *Thryomanes bewickii*, P	40	**38**	33	**16**
15. **Northern Flicker**, *Colaptes auratus*, P	10	36	15	65
16. **Red-tailed Hawk**, *Buteo jamaicensis*, P	20	**43**	9	**22**
17. **Rufous-crowned Sparrow**, *Aimophila ruficeps*, P	29	**37**	24	**12**
18. **Yellow-rumped Warbler**, *Setophaga coronata*, W	3	27	5	54
19. **Phainopepla**, *Phainopepla nitens*, S	**58**	1	**17**	0
20. **White-crowned Sparrow**, *Zonotrichia leucophrys*, W	7	**45**	5	**18**
21. **Nuttall's Woodpecker**, *Picoides nuttallii*, P	23	**23**	12	**2**
22. **Black Phoebe**, *Sayornis nigricans*, P	15	14	9	8
23. **Song Sparrow**, *Melospiza melodia*, P	16	14	7	6
24. **House Wren**, *Troglodytes aedon*, P	18	11	11	8
25. **Ash-throated Flycatcher**, *Myiarchus cinerascens*, S	24	1	17	2
26. **Ruby-crowned Kinglet**, *Regulus calendula*, W	3	**29**	0	**4**
27. **Black-headed Grosbeak**, *Pheucticus melanocephalus*, S	15	1	21	2
28. **American Kestrel**, *Falco sparverius*, P	7	6	6	12
29. **American Robin**, *Turdus migratorius*, W	2	17	0	14
30. **Brown-headed Cowbird**, *Molothrus ater*, S	16	1	15	1
31. **Cooper's Hawk**, *Accipiter cooperii*, P	7	7	4	8
32. **Blue-gray Gnatcatcher**, *Polioptila caerulea*, W	4	**15**	2	**1**
33. **Western Kingbird**, *Tyrannus verticalis*, S	8	1	11	1

(*continued*)

Table 2 (*continued*)

Species[a] and residency status[b]	F Canyon		Box Canyon	
	Summer	Winter	Summer	Winter
34. **California Gnatcatcher**, *Polioptila californica*, P	11	5	5	2
35. **Common Raven**, *Corvus corax*, P	4	7	2	9
36. Cedar Waxwing, *Bombycilla cedrorum*, W	1	13	0	8
37. Black-chinned Hummingbird, *Archilochus alexandri*, S	10	1	10	0
38. Wilson's Warbler, *Cardellina pusilla*, S	7	2	10	0
39. Cliff Swallow, *Petrochelidon pyrrhonota*, S	8	0	9	1
40. Bullock's Oriole, *Icterus bullockii*, S	10	0	7	1
41. American Goldfinch, *Spinus tristis*, W	3	7	2	5
42. Loggerhead Shrike, *Lanius ludovicianus*, P	6	5	3	1
43. Hermit Thrush, *Catharus guttatus*, W	5	8	0	1
44. Western Bluebird, *Sialia mexicana*, W	0	8	0	10
45. Say's Phoebe, *Sayornis saya*, W	0	1	3	10
46. Sharp-shinned Hawk, *Accipiter striatus*, W	0	8	0	5
47. Western Meadowlark, *Sturnella neglecta*, XP	4	3	3	6
48. Pacific-slope Flycatcher, *Empidonax difficilis*, S	8	1	4	1
49. Dark-eyed Junco, *Junco hyemalis*, W	1	4	0	7
50. Acorn Woodpecker, *Melanerpes formicivorus*, P	3	6	2	1
51. Lazuli Bunting, *Passerina amoena*, XS	5	0	8	0
52. American Crow, *Corvus brachyrhynchos*, S	4	3	2	2
53. Northern Harrier, *Circus cyaneus*, W	0	7	0	3
54. Hooded Oriole, *Icterus cucullatus*, S	6	0	4	0
55. Turkey Vulture, *Cathartes aura*, XP	1	4	2	5
56. Golden-crowned Sparrow, *Zonotrichia atricapilla*, W	1	5	0	2
57. Cassin's Kingbird, *Tyrannus vociferans*, XP	2	3	2	1
58. White-tailed Kite, *Elanus leucurus*, XP	4	1	0	1
59. Western Tanager, *Piranga ludoviciana*, XM	3	0	3	0
60. Rock Wren, *Salpinctes obsoletus*, W	0	5	0	0
61. Greater Roadrunner, *Geococcyx californianus*, XP	4	0	1	0
62. Fox Sparrow, *Passerella iliaca*, W	1	3	0	1
63. Western Wood-Pewee, *Contopus sordidulus*, XS	2	1	2	0
64. Chipping Sparrow, *Spizella passerina*, XP	0	2	3	0
65. Costa's Hummingbird, *Calypte costae*, XS	0	0	5	0
66. Yellow Warbler, *Setophaga petechia*, XS	3	1	1	0
67. Violet-green Swallow, *Tachycineta thalassina*, XP	2	1	1	0
68. Orange-crowned Warbler, *Oreothlypis celata*, XW	0	3	1	0
69. Townsend's Warbler, *Setophaga townsendi*, XW	2	0	1	1

(*continued*)

Table 2 (*continued*)

Species[a] and residency status[b]	F Canyon		Box Canyon	
	Summer	Winter	Summer	Winter
70. Allen's Hummingbird, *Selasphorus sasin*, XS	3	0	0	0
71. Swainson's Thrush, *Catharus ustulatus*, XM	2	1	0	0
72. Band-tailed Pigeon, *Patagioenas fasciata*, XP	1	1	1	0
73. Vaux's Swift, *Chaetura vauxi*, XM	1	0	0	2
74. Purple Finch, *Haemorhous purpureus*, XP	0	0	0	3
75. Lark Sparrow, *Chondestes grammacus*, XP	1	1	0	0
76. Lawrence's Goldfinch, *Spinus lawrencei*, XP	1	1	0	0
77. Prairie Falcon, *Falco mexicanus*, XP	0	2	0	0
78. Great Horned Owl, *Bubo virginianus*, XP	2	0	0	0
79. Spotted Dove, *Streptopelia chinensis*, XP	1	1	0	0
80. European Starling, *Sturnus vulgaris*, XP	1	0	1	0
81. House Sparrow, *Passer domesticus*, XP	1	0	1	0
82. Gray Flycatcher, *Empidonax wrightii*, XS	1	0	1	0
83. Red-winged Blackbird, *Agelaius phoeniceus*, XP	0	0	1	1
84. White-throated Swift, *Aeronautes saxatalis*, XP	0	0	1	1
85. Golden Eagle, *Aquila chrysaetos*, XP	1	0	1	0
86. Lincoln's Sparrow, *Melospiza lincolnii*, XW	0	1	0	0
87. Oak Titmouse, *Baeolophus inornatus*, XP	0	1	0	0
88. Warbling Vireo, *Vireo gilvus*, XM	0	1	0	0
89. Savannah Sparrow, *Passerculus sandwichensis*, XW	1	0	0	0
90. Mountain Chickadee, *Poecile gambeli*, XP	1	0	0	0
91. Cassin's Vireo, *Vireo cassinii*, XS	1	0	0	0
92. Northern Rough-winged Swallow, *Stelgidopteryx serripennis*, XS	1	0	0	0
93. Sage Sparrow, *Artemisiospiza belli*, XP	0	1	0	0
94. Rufous Hummingbird, *Selasphorus rufus*, XM	1	0	0	0
95. Plumbeous Vireo, *Vireo plumbeus*, XS	0	0	1	0
96. MacGillivray's Warbler, *Geothlypis tolmiei*, XM	0	0	1	0
97. Common Poorwill, *Phalaenoptilus nuttallii*, XP	0	0	0	1

[a]Listed from most to least frequently seen; those in **bold** are the 35 most common species used in some statistical analyses. Numbers in **bold** represent species seen significantly more often in F Canyon than in Box Canyon within a season; numbers underlined are species seen significantly more often within season in Box Canyon (χ^2 goodness of fit to 1:1 ratio with exact probabilities, all $P < 0.05$).

[b]Residency status determined from data: P, permanent resident; S, summer (April–September) resident; W, winter (October–March) resident; M, migrant; X, categorized not from the infrequent observations but from range maps (Sibley 2000) and personal observation.

including both sites on 28 July 1989. The fire was restricted mainly to the reserve. Adjacent undeveloped coastal sage scrub in the San Jose Hills, as well as developed areas, did not burn.

The region encompassing the Voorhis Ecological Reserve has cool, wet winters, dry, hot summers, and is prone to fire (Westman 1981, Minnich 1983). The dominant native shrubs at both sites were the California Sagebrush (*Artemisia californica*), California Buckwheat (*Eriogonum fasciculatum*), and Black Sage (*Salvia mellifera*). Large shrubs and trees were present, including Coast Live Oak (*Quercus agrifolia*), Western Sycamore (*Platanus racemosa*), Laurel Sumac (*Malosma laurina*), California Walnut (*Juglans californica*), Elderberry (*Sambucus mexicana*), and Toyon (*Heteromeles arbutifolia*). Prevalent exotic herbs were Mediterranean Mustard (*Hirschfeldia incana*), Black Mustard (*Brassica nigra*), Tocalote (*Centaurea melitensis*), Red Brome (*Bromus rubens*), Ripgut Grass (*Bromus diandrus*), and Horehound (*Marrubium vulgare*) (Moriarty et al. 1985, Stanton 1986, Clark 1990).

Bird Counts

Bird counts commenced on 20 January 1983, but I define 21 August 1981, the date of the first fire, as "day zero." The 265 pairs of counts, of one count each in Box Canyon and F Canyon, were distributed in six blocks or periods of 1 to 3 years from 1983 to 2003 (Table 1). Within each block, paired counts were conducted approximately twice per week. Within a pair, each site was visited sequentially on one day, then the order of sites was switched on the next count day. Counts began shortly after sunrise, and entailed the observer standing quietly at a defined peripheral location that allowed an unobstructed view of the entire site. Birds flying over the sites were not recorded. Individual birds were not marked and density was not estimated, so analysis is restricted to presence/absence and numbers of species.

I define counts from April through September as summer (n = 135), those from October through March as winter (n = 130). These broad seasonal categories did not provide resolution to distinguish categories such as migrants or juveniles but did allow each commonly observed species to be categorized as a summer resident (observed in at least four of the six summer months, n = 12, Table 2) winter resident (observed in at least four of the six winter months; n = 16), or permanent resident (observed in at least four months of both seasons; n = 27). I categorized species not meeting any of these criteria (n = 42) (Table 2) on the basis of range maps (Sibley 2000) and personal observation. There were few observations of these 42 species on the 265 field days. Six were seen on 6 to 13 days, the remaining 36 on 5 or fewer days.

Statistical Analysis

Counts of the first block (1983–84, Table 1) were 50 min in duration; all later counts were 30 min in duration. For analyses involving the mean number of species per count, I adjusted the value for each count in the first block as an estimate of the number of species expected if the count had been for 30 min. As a basis for this adjustment, I made an additional 45 paired counts of 50 min duration between 7 November 2002 and 1 May 2003, recording the time a species was first seen. I used data from these 45 paired counts only for

the adjustment, not in any other analyses. In F Canyon, the mean number of species seen was 12.4 ± 0.4 (± SE) in 50 min, 1.8 ± 0.2 after the first 30 min. In Box Canyon, the mean number of species seen was 8.9 ± 0.4 in 50 min, 1.4 ± 0.2 after the first 30 min. I adjusted counts for F Canyon and Box Canyon separately because the number of species seen on these 45 paired counts in 50 min was higher in F Canyon (paired-sample $t = 7.77$, df = 44, $P < 0.001$). The number of species seen after 30 min was positively correlated with the total number of species seen in the 50 min count (Box Canyon, $r = 0.44$, df = 43, $P = 0.001$; F Canyon, $r = 0.26$, df = 43, $P = 0.04$). Therefore, I figured the adjustment for each count in the 1983–84 block by using ordinary least-squares linear regression to predict the number of species that would be seen after 30 min and subtracting that number from the total number seen in the count. For F Canyon, the adjustment function was adjusted number = total species seen – (–0.01 + 0.15 total species seen); for Box Canyon it was adjusted number = total species seen – (–0.41 + 0.20 total species seen). The phrase "adjusted number of species" indicates an analysis using the adjustment of the 1983–84 data. Data from the other five blocks were not adjusted because those counts were 30 min in duration.

I analyzed differences in adjusted number of species among count blocks and sites with split-plot ANOVA. Each count (whole unit) was split into the two sites (F Canyon and Box Canyon) as subunits. I tested the whole-unit effect of count block by using unexplained variation among counts as an error term, the subunit effects of site and site-by-count-block interaction by using unexplained variation within counts as an error term. I used Tukey's honestly significant difference (HSD) test for multiple comparisons among count blocks and tested for a difference between the sites within each count block by separate paired-sample t tests. Because analyses within a count are paired by date, I used the actual number of species per count rather than the adjusted number. I analyzed winter and summer data separately.

Because the data were not normally distributed, I assessed correlation in the number of species observed between count blocks within canyons and seasons by the nonparametric Spearman rank correlation. The concomitant loss of power was minimal because 95% of the Spearman values were significant at $P < 0.05$. I used the Fisher exact test to evaluate differences within canyons by season in the proportional use of sites in the count block before the 1989 fire (1986–88) and the count block after the fire (1989–91). Means are reported ± one standard error. For statistical analyses I used SAS software version 9.2 (SAS Institute, Inc., Cary, NC).

RESULTS

Bird Species Richness and Community Composition

Over the 20-year study I made 3753 observations representing 97 species and 12,619 individuals (Table 2). During the 16 months of the first count block (Table 1), 79 species were seen. The remaining 18 species were accumulated over the next 19 years. Ninety species were seen in F Canyon, 80 in Box Canyon. Seventy-three species (75%) were seen in both canyons. No commonly seen species was restricted to a single canyon. Of the 24 species seen in only one canyon, 12 of these were seen once, seven were

seen twice, three were seen three times, and two were seen five times. The California Gnatcatcher, listed as threatened by the U.S. Fish and Wildlife Service, was seen 19 times beginning in 1994.

A small number of species dominate the counts. The six most common species (Anna's Hummingbird, California Towhee, Western Scrub-Jay, Northern Mockingbird, House Finch, Spotted Towhee) account for 36% of the 3753 observations. Addition of the next five species (Wrentit, Mourning Dove, California Quail, Cactus Wren, Bushtit) encompasses 50% of the observations. The 35 most commonly seen species (Table 2, in bold) account for 90% of the observations. Fifty-one species were seen on fewer than 5% of the 265 count days.

Numbers of species recorded in the six blocks of counts were significantly different in summer ($F_{5, 129} = 18.3$, $P < 0.0001$) and in winter ($F_{5, 124} = 21.8$, $P < 0.0001$). The first count block (1983–84) and the last count block (2002–03) were more similar to each other and had more adjusted species per count than the four count blocks in between (Figure 1). However, results of the Tukey HSD multiple-comparisons tests (Figure 1) indicate some overlap. For example, the 1992–96 block is always grouped with either the first or the last block in both canyons and in both seasons. Therefore, although the count blocks were a significant source of variation in the number of adjusted species observed, there was no block that was unique.

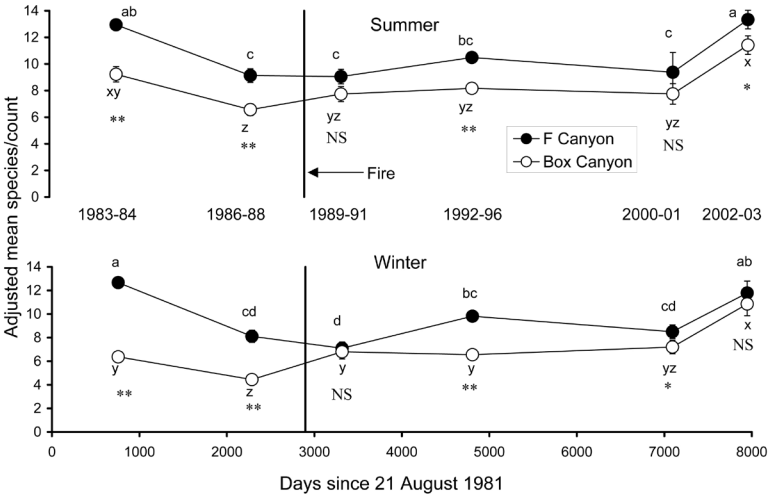

Figure 1. Mean adjusted species per count in F Canyon and Box Canyon, Voorhis Ecological Reserve, Pomona, California, in summer (top panel) and winter (lower panel) through six blocks of counts (Table 1), 1983–2003. Vertical bars at the means represent one standard error. Lower-case letters indicate groupings by the Tukey HSD test within a season, not between seasons. Results of paired-sample *t* tests of the difference between F Canyon and Box Canyon for each count block in each season: NS, not significant ($P > 0.05$); *, $P < 0.05$; **, $P < 0.001$. The vertical line indicates the date of the fire (28 July 1989) that burned both sites and the surrounding reserve.

Site Differences

During the summer (Figure 1), the adjusted mean number of species per count was significantly higher at F Canyon (10.7 ± 0.25) than at Box Canyon (8.3 ± 0.23; $F_{1, 129} = 64.6$, $P < 0.0001$). There was no significant interaction between the site and count blocks ($F_{5, 129} = 1.9$, $P = 0.1$). When count blocks are examined individually (Figure 1), the canyons were significantly different in all except the 1989–91 and the 2000–01 block. During the winter (Figure 1), the adjusted mean number of species per count was also significantly higher at F Canyon (9.9 ± 0.27) than at Box Canyon (6.7 ± 0.24; $F_{1, 124} = 120.9$, $P < 0.0001$). At this season, there was a significant ($F_{5, 124} = 16.8$, $P < 0.0001$) interaction between site and count block but no significant difference in the 1989–91 and 2002–03 blocks (Figure 1). More species were seen in F Canyon than in Box Canyon on 214 (81%) of the 265 paired counts. The same number of species was seen on 21 counts (8%), and more species were seen in Box Canyon on the remaining 30 counts (11%). The ratio of 214:30 is significantly different from the 1:1 expected if the higher number of species seen was distributed randomly (sign test, $P < 0.001$). In comparisons within seasons, F Canyon had more species observed than Box Canyon in all count blocks except in winter of the 2002–03 block (Table 1).

Of the 35 most common species, 16 were seen significantly more often in F Canyon than in Box Canyon (Table 2). Five of these (Spotted Towhee, Wrentit, Mourning Dove, Cactus Wren, California Thrasher) preferred F Canyon in both summer and winter. Nine species (Northern Mockingbird, California Quail, Bewick's Wren, Red-tailed Hawk, Rufous-crowned Sparrow, White-crowned Sparrow, Nuttall's Woodpecker, Ruby-crowned Kinglet, Blue-gray Gnatcatcher) preferred F Canyon only in the winter. The House Finch and Phainopepla preferred F Canyon only in the summer. Three species were seen significantly more often in Box Canyon (Table 2). The Bushtit preferred Box Canyon in the summer, whereas the Northern Flicker and Yellow-rumped Warbler preferred Box Canyon only in the winter. The remaining 16 species had no preference in either season (Table 2).

Within canyons and seasons, there was significant positive correlation between count blocks in the ranks of the 35 most common species in 57 of the 60 comparisons (Table 3). In other words, the species observed most often in one block were the species observed most often in the other blocks. The three exceptions to this all involved the count block immediately after the 1989 fire (1989–91) in F Canyon in the winter (Table 3). In summary, the general results of these correlations are that the same species occurred at similar relative frequencies over the entire 20-year study. The species in Table 2 are listed by decreasing number of total observations, and this order is generally representative of both sites, both seasons, and the count blocks.

Effects of the 1989 Wildfire

The mean adjusted number of species per count immediately after the fire (1989–91) at both sites and in both seasons was similar to that both before the fire and much later after the fire (Figure 1). The 1989–91 block was the only block in which there was no significant difference between F Canyon

Table 3 Spearman Rank Correlations of the 35 Most Common Species[a] at the Voorhis Ecological Reserve, Pomona, California, 1983–2003[b]

	1983–84	1986–88	1989–91	1992–96	2000–01	2002–03
F Canyon						
1983–84		0.77	0.26*	0.74	0.81	0.72
1986–88	0.90		0.23*	0.65	0.83	0.79
1989–91	0.45	0.34		0.34	0.13*	0.36
1992–96	0.83	0.79	0.56		0.78	0.83
2000–01	0.73	0.77	0.45	0.72		0.79
2002–03	0.76	0.77	0.37	0.77	0.80	
Box Canyon						
1983–84		0.46	0.62	0.53	0.35	0.40
1986–88	0.61		0.67	0.59	0.61	0.58
1989–91	0.78	0.65		0.36	0.47	0.50
1992–96	0.67	0.73	0.74		0.74	0.71
2000–01	0.46	0.64	0.60	0.67		0.79
2002–03	0.52	0.58	0.64	0.69	0.87	

[a]See Table 2.

[b]In the matrix for each canyon, the lower left triangle contains summer correlations, the upper right triangle winter correlations. All correlations except the three marked with an asterisk (*) are significant ($P < 0.05$, $n = 35$).

and Box Canyon in the number of adjusted species per count in both summer and winter, although there was no significant difference in the summer of 2001–01 and the winter of 2002–03 as well (Figure 1). Examination of both seasons in Figure 1 suggests a tendency for a decrease in adjusted species per count in F Canyon and an increase in Box Canyon immediately after the fire, but statistical support for the trend is weak.

In addition to the only three nonsignificant rank correlations involving the count block immediately after the fire, correlations involving the 1989–91 count block are significantly weaker than correlations involving other count blocks (Wilcoxon rank-sum test, exact $P < 0.05$). This indicates that of all the count blocks, the post-fire block was the most different. In F Canyon in the summer, the Wrentit and Cactus Wren (Table 4) were seen significantly more often before the fire (1986–88) than after the fire (1989–91), while the American Kestrel was seen significantly more often after the fire. In F Canyon in the winter, the Western Scrub-Jay, Spotted Towhee, Wrentit, California Quail, and Cactus Wren were seen significantly more often before the fire, while the House Finch and Lesser Goldfinch were seen significantly more often after the fire (Table 4). In Box Canyon in the summer, the only significant difference was the Rufous-crowned Sparrow, which was seen more often after the fire. In Box Canyon in the winter the Yellow-rumped Warbler and White-crowned Sparrow (both winter residents) were seen significantly more often after the fire (Table 4). Six species were only seen in the 1989–91 count block: the Rock Wren, White-throated Swift, Lark Sparrow, Golden Eagle, Cassin's Vireo, and Prairie Falcon.

Table 4 Percentages of Counts in Which the 35 Most Common Species at the Voorhis Ecological Reserve Were Observed before (1986–88) and after (1989–91) the 1989 Fire by Site and Season[a]

	F Canyon				Box Canyon			
	Summer (n = 23)		Winter (n = 18)		Summer (n = 19)		Winter (n = 20)	
	86–88	89–91	86–88	89–91	86–88	89–91	86–88	89–91
Anna's Hummingbird	65	68	94	80	78	84	83	90
California Towhee	83	89	78	30	91	74	28	60
Western Scrub-Jay	91	42	89*	20*	70	68	67	55
N. Mockingbird	43	63	39	10	78	68	33	10
House Finch	61	74	17*	75*	48	63	39	35
Spotted Towhee	61	32	50*	5*	17	42	0	10
Wrentit	96*	5*	72*	0*	22	11	17	0
California Quail	39	5	33*	0*	0	11	0	0
Mourning Dove	35	74	6	20	30	16	11	15
Bushtit	9	11	6	5	22	26	22	5
California Thrasher	35	16	22	0	17	11	0	0
Cactus Wren	48*	0*	39*	0*	4	0	0	0
Lesser Goldfinch	13	42	0*	60*	13	21	0	10
Bewick's Wren	22	16	39	20	9	37	6	35
Northern Flicker	9	11	22	20	13	11	56	75
Rufous-crn. Sparrow	4	16	0	5	0*	37*	0	0
Red-tailed Hawk	4	21	22	35	13	0	28	45
Yellow-rumped Warbler	0	11	22	45	0	5	6*	65*
Phainopepla	35	16	0	0	22	26	0	0
White-crn. Sparrow	9	11	22	35	0	0	0*	45*
Nuttall's Woodpecker	13	32	11	0	9	5	0	5
House Wren	13	0	6	0	4	5	0	0
Black Phoebe	0	21	0	30	0	16	6	0
Ash-throated Flycatcher	13	11	0	0	17	5	0	0
Song Sparrow	13	0	11	0	4	0	0	5
Black-headed Grosbeak	17	0	0	0	13	0	0	0
Ruby-crn. Kinglet	0	11	11	10	0	0	0	5
American Robin	4	0	11	10	0	0	6	0
Brown-headed Cowbird	4	16	0	0	0	5	0	0
American Kestrel	0*	32*	0	15	4	11	6	15
Cooper's Hawk	0	5	0	15	0	0	0	0
California Gnatcatcher	0	0	0	0	0	0	0	0
Blue-gray Gnatcatcher	4	0	39	5	0	0	0	0
Common Raven	0	5	0	25	0	5	6	40
Western Kingbird	0	16	0	0	0	11	0	0

[a]Asterisks (*) indicate a significant difference between 1986–88 and 1989–91 within the site and season (Fisher exact test, $P < 0.05$).

DISCUSSION

Bird Species Richness and Community Composition

The Voorhis Ecological Reserve contains some species typical of urban habitats and others dependent on the reserve's shrub habitat, but its avifauna is dominated by several common species that are generally found in urban habitats. While they use fragments of sage scrub, they are not shrub-obligate species (Soulé et al. 1988, Crooks et al. 2004). The six most common (Table 2) species (Anna's Hummingbird, California Towhee, Western Scrub-Jay, Northern Mockingbird, House Finch, Spotted Towhee) fit this description. But some of the other common species, such as the Wrentit, California Quail, Cactus Wren, and California Thrasher, tend to be scrub specialists (Soulé et al. 1988, Bolger et al. 1991, Crooks et al. 2001).

Site Differences

One interesting result of this study was the consistent difference in the number of adjusted species per count between the sites, F Canyon averaging two to three more species than Box Canyon. The amount of difference fluctuated over the count blocks and by season, but F Canyon had a higher adjusted mean number of species per count in all blocks, and the fact that F Canyon had more species in 81% of the counts is notable.

I selected the sites after the 1981 fire because of their similar vegetation, physical similarity, close proximity, connection with continuous coastal sage scrub within the reserve, and because Box Canyon burned in the 1981 fire while F Canyon did not (Moriarty et al. 1985, Stanton 1986). Moriarty et al. (1985) and Stanton (1986) compared these two sites to assess the effect of the 1981 fire on avian species richness in coastal sage scrub. Both studies found significantly fewer species seen in Box Canyon than F Canyon and concluded that fire reduced avian species richness.

The conclusions of Moriarty et al. (1985) and Stanton (1986) are substantially mitigated by the long-term results I report here. The consistently higher number of bird species seen in F Canyon suggests that the sites are not equivalent and that F Canyon was not a "control" for the burned Box Canyon. The difference in the number of species per count attributed to fire effects was four by Moriarty et al. (1985), and 5.9 by Stanton (1986), but these differences may have been due, at least in part, to inherent differences between the sites. The long-term results (a difference of about three species) do not completely contradict the earlier (Moriarty et al. 1985, Stanton 1986) conclusions, but they certainly confound the conclusions to the point where an inference on the effect of fire on avian species richness in coastal sage scrub cannot be drawn from those studies. Furthermore, comparison of the count blocks immediately before and after the 1989 fire suggested the response to fire was different at the two sites and may also have varied by season.

This finding demonstrates the difficulty of selecting appropriate comparison sites for study of the effect of uncontrolled fires (Diamond 1986). I attempted to match a burned and unburned area with respect to size, aspect, topography, proximity, and vegetation in order to control for any effect except the fire. Yet the long-term data strongly suggest the sites differ. If multiple burned and

unburned canyons were available after the 1981 fire, such replication may have detected the effect of site, although such replication would have been approximate and may not have demonstrated the effect (Hargrove and Pickering 1992, Underwood 2009). Adequate replication of sites in field situations requires prior knowledge of perturbations and detailed analysis (Silva-Lugo and Tanner 2010), and these conditions could not be met at my study sites.

Given the two canyon's similarity and proximity, what causes the effect? The data do not provide an answer to that question, but possibilities may be suggested. Perhaps the vegetation structure and/or composition differ in some way important to the birds that is not obvious to human observers. Perhaps predators such as Cooper's Hawk spend more time in the Box Canyon area than F Canyon, resulting in smaller birds spending more time in F Canyon. The composition of the avian community at the two sites is similar. That is, the same species were observed in the two canyons at the same approximate relative frequency but more often in F Canyon than in Box Canyon. This suggests that the factors in which the sites differ may be subtle. It is possible that it was easier to detect species in F Canyon than in Box Canyon. There was nothing in the field experience that suggested such a bias, but it cannot be conclusively ruled out.

The increase in the number of species seen at both sites and in both seasons in 2002–03 (Fig. 1) is consistent with these possibilities. However, such an interpretation is predicated on the 2002–03 data representing a biological effect and not random variation, and distinguishing between these possibilities would require more long-term data. As seen above, conclusions based on short-term (1–2 years) data without adequate control are subject to error.

Effects of Wildfire

Having discussed the importance of site effects and lack of replication in comparisons before and after the fires, I stress that this discussion of the effect of the 1989 fire is descriptive, anecdotal rather than inferential. In contrast to the conclusions of Moriarty et al. (1985) and Stanton (1986) after the 1981 fire, the number of species did not decline after the 1989 fire. There was an increase in species after the fire in Box Canyon, paralleling the findings of Mendelsohn et al. (2008) after San Diego County's Cedar Fire of 2003, but only during the winter.

The fire did appear to have some effect on the composition of the species. Not surprisingly, species associated with dense vegetation (e.g., Wrentit, California Quail, Spotted Towhee) were seen less often after the fire (Knick and Rotenberry 1995, Mendelsohn et al. 2008). The Cactus Wren was seen less often after the fire, presumably because of the destruction of the *Opuntia* cactus with which the bird associates. Some species were seen more often after the fire, apparently taking advantage of the more open habitat. These included ground-feeding species such as the House Finch, Lesser Goldfinch, Rufous-crowned Sparrow, Yellow-rumped Warbler, and White-crowned Sparrow. The American Kestrel was also more frequently seen after the fire, perhaps because prey was easier to detect. A few species such as the Golden Eagle, Prairie Falcon, and Lark Sparrow, perhaps responding to open habitat, were seen only within the first two years following the fire. Some of the most common species (e.g., Anna's

Hummingbird, California Towhee, Northern Mockingbird, Mourning Dove) did not show any significant change in their use of the sites after the fire. These four species are common in both shrub and urban habitat (Soulé et al. 1988, Crooks et al. 2004), and this flexibility may extend to using burned and unburned areas.

These apparent effects of the fire did not last long. By the start of the fourth count block, approximately three years post-fire, most of the effects described above were no longer apparent. The 1989 fire did not cause any long-lasting change to the bird community. The effects of fire on bird communities vary greatly, with the severity of the fire being critical to species' responses (Smucker et al. 2005). In addition to severity, I suggest that the proximity of habitat suitable for common species also contributes to a fire's effect on the community. In this study, adjacent undeveloped areas of coastal sage scrub habitat in the San Jose Hills did not burn. Many of the common species are also found in nearby urban areas (Mills et al.1989, Crooks et al. 2004). Therefore, there were numerous potential refugia as well as sources of birds to repopulate the reserve. The appearance of the California Gnatcatcher in 1994 (five years post-fire) suggests recovery of the scrub (Atwood and Bontrager 2001). Results of this study largely parallel those of Mendelsohn et al. (2008) in low-elevation coastal sage scrub. But because of birds' inconsistent response to fire (Smucker et al. 2005) and lack of replication in my study, it would not be appropriate to consider the effects I discuss here as general features of the response of coastal sage scrub birds to fire. Such replication may not be feasible, given the patchy distribution, dynamics, and disturbance of coastal sage scrub (Crooks et al. 2001, Cox and Allen 2008).

Long-term studies contribute to our understanding of avian community dynamics (Holmes et al. 1986), and suggest questions for future work. Studies of the breeding birds of the Voorhis Ecological Reserve could emphasize demographics (Brawn and Robinson 1996), particularly of the threatened California Gnatcatcher. Study of migrants or vagrants could address these species' use of the reserve. Such research may help clarify bases of the differences between F Canyon and Box Canyon, as well as provide a baseline for comparison following any future fires.

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