

# FLUCTUATING POPULATIONS OF HOUSE WRENS AND BEWICK'S WRENS IN FOOTHILLS OF THE WESTERN SIERRA NEVADA OF CALIFORNIA<sup>1</sup>

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**Abstract.** In foothills of the western Sierra Nevada, 31 km east of Madera, California, we studied whether Bewick's Wrens (*Thryomanes bewickii*) tend to be excluded from an area occupied by House Wrens (*Troglodytes aedon*) as reported in several studies in the eastern United States. Neither point counts from 1985 to 1997 nor spot mapping from 1989 to 1993 suggests any interaction between these species. The study period included the most prolonged drought and the most severe period of winter weather in the 64-year climatological record from the study site. House Wren abundance was significantly related to the 4-year running average of annual precipitation and to the lowest temperature recorded in the winter months preceding survey counts. We speculate that House Wrens cannot maintain their numbers by local recruitment during droughts in the oak-pine woodlands that dominate our study area and that recovery of their population following droughts involves recruitment from other areas, probably riparian zones and other mesic habitats elsewhere in the Sierra foothills and Central Valley of California. There was no influence of precipitation on abundance of Bewick's Wrens and, although they apparently sustained heavy mortality during a period of extreme winter weather, their numbers otherwise were not related to the lowest temperature during the winter preceding counts.

**Key words:** *Bewick's Wren, House Wren, interspecific competition, population trends, precipitation, Thryomanes bewickii, Troglodytes aedon.*

## INTRODUCTION

Declining numbers of Bewick's Wrens (*Thryomanes bewickii*) have been well documented over much of the species' range in the eastern and midwestern United States (Wilcove 1990, Kennedy and White 1996). In spite of the fact that evidence is mainly circumstantial, probably the most widely held opinion is that Bewick's Wrens have declined in the face of expanding populations of House Wrens (*Troglodytes aedon*) (Simpson 1978, Wilcove 1990, Kennedy and White 1996). Some observers have reported overt aggression and interspecific territoriality between the species (Roads 1929, Brooks 1947, Newman 1961), but we know of no study that has established a direct cause-and-effect relation between the invasion of House Wrens into an area and the consequent disappearance of Bewick's Wrens. Alternate explanations warrant attention (Mengel 1965, Simpson 1978, Wilcove 1990).

In the most compelling study to date of interactions between breeding populations of these two species east of the Rocky Mountains, Ken-

nedy and White (1996), using nest boxes, found that destruction of eggs or nestlings by House Wrens accounted for 81% of the nesting failures of Bewick's Wrens in their study area near Manhattan, Kansas. They suggested that "range expansion by nest-vandalizing House Wrens, probably related to long-term habitat changes such as widespread secondary growth on abandoned agricultural land . . . , may be sufficient to explain the declining numbers and contracting ranges of Bewick's Wrens."

Few studies of interactions between these species have been reported from west of the Rocky Mountains. Root (1969) suggested interspecific territoriality in a limited study in coastal California. Kroodsma (1973), on the other hand, reported extensive overlap among territories of Bewick's and House Wrens at the Finley National Wildlife Refuge in western Oregon. Bewick's Wrens are permanent residents and House Wrens are migrants in both of these regions.

Both species breed in oak-pine woodlands in the western foothills of the Sierra Nevada of California. At the San Joaquin Experimental Range (SJER) we have been monitoring the relative abundance of breeding bird species since

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1985 and report here on a comparison of the year-to-year changes in counts of House and Bewick's Wrens. We test the null hypothesis that annual changes in counts of Bewick's Wrens are unrelated to annual changes in counts of House Wrens. Alternate hypotheses are that (1) counts of the two species exhibit opposite trends from year to year, and (2) counts of the two species exhibit parallel trends from year to year. The former hypothesis corresponds to expectation if range expansion by House Wrens results in displacement of Bewick's Wrens.

Using 5 years of spot-mapping data (1989–1993) on two 30-ha grids at SJER, we also explore the spatial relations among song perches and territorial boundaries of these two species for evidence of interspecific competition or avoidance: were song perches of Bewick's Wrens less likely to occur near those of House Wrens, or vice versa, and were their territories exclusive?

## METHODS

### STUDY AREA

With an area of approximately 1,875 ha, SJER ranges in elevation from 215 to 520 m in the western foothills of the Sierra Nevada, 31 km northeast of Madera, California (Fig. 1). A sparse woodland overstory of blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus sabiniana*) occurs over most of the landscape. An understory of scattered shrubs includes mainly buckbrush (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), redberry (*Rhamnus crocea*), and Mariposa manzanita (*Arctostaphylos viscida mariposa*). In a few smaller patches, the overstory is primarily blue oak, and a shrub understory is meager or missing. Some areas of typical annual grassland extend throughout the remainder of SJER where the overstory and understory are missing or not dense enough to shade out the grasses and forbs.

The climate at SJER is Mediterranean, with cool, wet winters and hot, dry summers. Mean annual precipitation (summing from July through June) from 1934 through 1997 was 47.4 cm. Snow is unusual, and daily maximum temperatures have exceeded freezing on all but 2 days in 64 years of weather data at SJER. Precipitation has fluctuated markedly from year to year, with extremes of 23.60 (1976–1977) and 94.34 cm (1983–1984). If we define a drought

as any period  $\geq 2$  years with annual precipitation  $\leq 75\%$  of the long-term mean, three droughts occurred from 1934 to 1997: July 1946 through June 1948 (precipitation 73.1% of the long-term mean); July 1975 through June 1977 (precipitation 57.7% of the long-term mean); and July 1987 through June 1991 (precipitation 62.6% of the long-term mean).

### POINT COUNTS

From three to seven observers completed 5-min point counts with unlimited distance at all counting stations in all years from 1985 to 1997. Extreme counting dates ranged from 25 March (1992) to 4 May (1988), encompassing the peak of breeding by most species in the community. We selected observers known to be expert in bird identification, especially in identifying the birds at SJER by sight and sound. In addition, observers underwent intensive training over a 2-week period to sharpen their identification skills and to familiarize them with details of the method to be used. Each observer's hearing was tested during the field season each year.

The sampling array consisted of 210 counting stations, with 30 stations distributed along each of seven lines established primarily in oak-pine woodlands throughout SJER (Fig. 1). The stations were about 200 m apart along each line and between the separate lines. Although this spacing did not assure independent samples in all cases, our intent was to obtain only an index of relative abundance of bird species in this community for comparison among years. By following the same sampling protocol each year, we believe potential biases resulting from a lack of independence in the counts of some species are consistent from year to year.

Observers were randomly assigned to the lines of counting stations such that only one observer sampled a given line each day, and all observers eventually sampled all lines only once. Counting at the first station on a line began 10 min after official sunrise and continued at the other stations along the line at 10-min intervals, producing counts at 6 stations  $\text{hr}^{-1}$  and completing the 30-station line within 5 hr. Stations were counted in the same sequence each time a line was sampled, further standardizing results. Counts were not done during rainy mornings, and counts done during days when wind consistently exceeded 32  $\text{km hr}^{-1}$  (by Beaufort scale) were repeated the following count day. Windy-

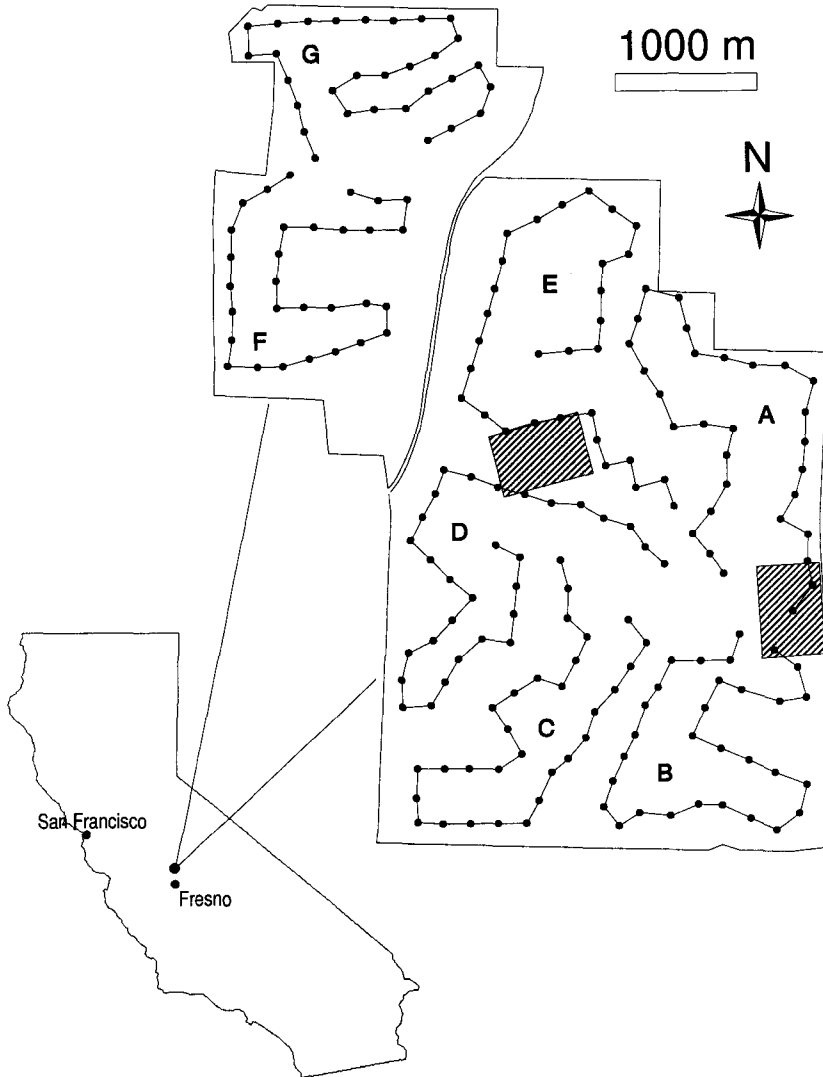


FIGURE 1. General location map and boundary map of the San Joaquin Experimental Range in foothills of the Sierra Nevada, California, showing locations of point-counting stations along each of the seven sampling lines (A–G); the two spot-mapping grids are shown as shaded rectangles. California State Highway 41 bisects the study area just west of sampling line E.

day counts were not included in the present analysis.

Results presented here are based on means of the total counts of each species by all observers each year. Pooling results of at least three observers was shown earlier by Verner and Milne (1989) to be a sufficient control for observer variability in this vegetation type, reducing Type I statistical errors to the 5% level assumed by an alpha of 0.05, as opposed to a rate of 17%

when counts by single observers were compared.

#### SPOT MAPPING

In a detailed study of the spot-mapping method from 1985 through 1993, we estimated the numbers of territorial birds on two plots  $660 \times 450$  m, gridded at 30-m intervals (Fig. 1). One, the "grazed plot," had been grazed at a moderate level, probably for at least 100 years. The other,

the "ungrazed plot," was similarly grazed until 1934, when it was closed to grazing. Steel fence posts bearing alphanumeric codes identified each grid intersection. Methods generally followed international standards (Anonymous 1970, Robbins 1970) during the early years of the study but included some important exceptions in later years as we learned more about the method. Consequently, only results from 1989 through 1993 have been used in the present analysis because our methods were well standardized by 1989 and we continued spot mapping only through 1993.

Dates of the first visit to the plots ranged from 22 to 28 March, and dates of the last visit ranged from 26 to 30 April. Members of the field crew most skilled in bird identification did the bird surveys on the plots, while other observers searched for nests and/or followed individuals, pairs, and family groups of individual species to augment results of the spot mapping. Each year, three or four spot mappers completed four or three visits each, respectively, to each of the two plots (total of 12 visits), with random assignments to starting points on the grid. Because daily visit maps were digitized each day, species maps could be produced at any time during the survey period when the field crew wished to review them to guide their subsequent field efforts. When 12 visits were completed at each plot, final species maps were computer generated, the spot mappers collectively interpreted them to attain consensus, and lines were drawn around clusters of mapped locations (registrations) judged to indicate territories.

From these mapping efforts, we examined the spatial relations between territories of the two species and between locations of their song perches, using only song perches located visually (hereafter, song posts). We plotted locations of song posts on maps of the two plots, grouping them into four sets of three consecutive survey dates (i.e., visits 1–2–3, 4–5–6, 7–8–9, and 10–11–12) so that mapped song posts of the two species were relatively contemporary. If a singing bird was located at the same song post on more than one visit in any group of three visits, we tallied each instance because repeated use of the same song post was an added measure of a male's tendency to stake its claim over space within a given cell in the mapping grid.

Using cells 30 × 30 m, we tallied for each of the four grouped survey intervals (1) the number

of song posts located for each species, as mapped by observers each day, (2) the number of cells with one song post, two song posts, etc., (3) the number of cells with Bewick's Wren song posts that also contained at least one House Wren song post, and (4) the number of cells with House Wren song posts that also contained at least one Bewick's Wren song post. This procedure was repeated using cells 50 × 50 m in an effort to make some allowance for scale effects in territory sizes of the two species. Sample size for these analyses was 40 (5 years × 2 plots × 4 grouping intervals).

The number of House Wren (HOWR) song posts expected in cells with Bewick's Wren (BEWR) song posts =

$$\frac{\text{Number of cells with BEWR songposts}}{\text{Total cells}} \times \text{Total HOWR songposts}$$

A comparable computation gave the number of Bewick's Wren song posts expected in cells with House Wren song posts. We used two-tailed, paired *t*-tests to explore whether differences between the observed and expected numbers of song posts of each species in cells with song posts of the other suggested significant avoidance or attraction between the two species.

Results of this analysis may be biased by lack of independence. First, we undoubtedly recorded data from the same males in the same territories during consecutive visits in a given breeding season. Second, the same males may have been on the same territories in one or more years of the study.

#### WEATHER

Daily precipitation and minimum/maximum temperatures were available from a small weather station maintained at SJER's headquarters since 1934. We tested the relation between yearly counts of each wren species and total precipitation from 1 July of the year preceding point counts through 30 June of the year of counting; about 88% of the precipitation during this period falls before counts begin each year. Additional independent variables were the lowest temperature recorded during the winter preceding counts, the 2-, 3-, 4-, and 5-year running averages of annual precipitation, and the summed "winter" precipitation values from October through February, through March, and through

April. Relations between annual counts of the wrens and those winter values were explored for the immediate season's precipitation and that for 1, 2, and 3 years prior to the immediate survey year.

## RESULTS

### WREN POPULATIONS AND WEATHER

Annual counts of both House and Bewick's Wrens differed markedly among years (Table 1). Neither their counts ( $r = 0.20$ ,  $P = 0.51$ ,  $n = 13$ ) nor the percentage changes in their year-to-year counts ( $r = 0.39$ ,  $P = 0.22$ ,  $n = 12$ ) were significantly correlated. In 8 of the 12 year-to-year intervals, however, populations of both species changed in the same direction (Fig. 2) (binomial test,  $P = 0.39$ ). Both species exhibited sharp increases in counts between some years. For example, mean counts of Bewick's Wrens increased 74% from 1987 to 1988, 69% from 1991 to 1992, and 117% from 1993 to 1994.

TABLE 1. Mean annual counts ( $\pm$  SE) of House Wrens and Bewick's Wrens at the San Joaquin Experimental Range. Sample size equals the number of different observers who completed counts at all 210 counting stations each year, except in 1986 and 1987 when seven observers each completed two full sets of counts.

Year	<i>n</i>	House Wren	Bewick's Wren
1985	3	120.3 $\pm$ 13.3	96.7 $\pm$ 15.3
1986	14	138.5 $\pm$ 8.6	112.1 $\pm$ 11.1
1987	14	91.2 $\pm$ 5.0	63.9 $\pm$ 8.4
1988	4	88.8 $\pm$ 5.8	111.3 $\pm$ 14.5
1989	7	45.1 $\pm$ 8.5	88.4 $\pm$ 6.0
1990	7	22.4 $\pm$ 6.7	89.6 $\pm$ 6.9
1991	4	29.0 $\pm$ 7.6	33.8 $\pm$ 6.0
1992	4	131.5 $\pm$ 27.2	57.0 $\pm$ 23.7
1993	4	116.8 $\pm$ 17.7	35.0 $\pm$ 5.0
1994	4	146.8 $\pm$ 8.6	75.8 $\pm$ 11.4
1995	4	150.3 $\pm$ 15.6	77.3 $\pm$ 10.9
1996	4	134.8 $\pm$ 17.3	113.3 $\pm$ 11.1
1997	5	108.6 $\pm$ 6.5	109.8 $\pm$ 3.1

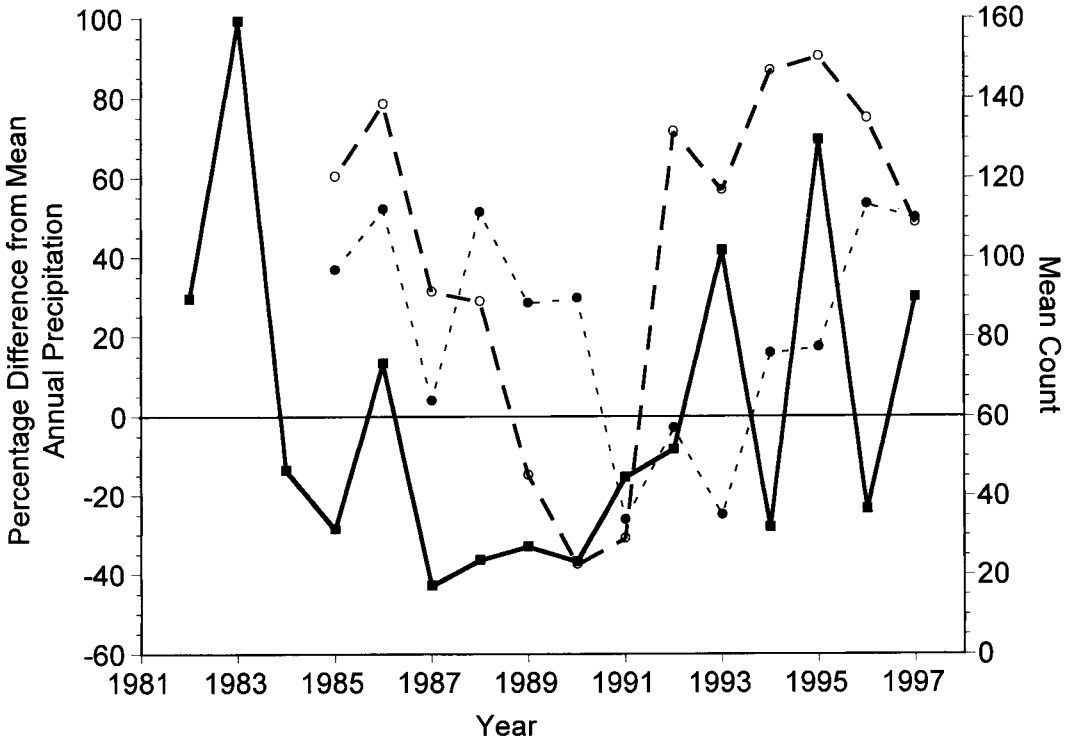


FIGURE 2. Relations of mean annual counts of House Wrens (heavy dashed line) and Bewick's Wrens (light dashed line) to the percentage deviation from mean annual precipitation (solid line) at the San Joaquin Experimental Range. The "zero" line for precipitation corresponds to mean annual precipitation of 47.4 cm; for these data, "1985" refers to the period from 1 July 1984 through 30 June 1985, and similarly for other years.

Counts of House Wrens increased 353% from 1991 to 1992.

Exploratory linear regressions between mean annual counts of each species and our various measures of precipitation gave mixed results. Adjusted  $R^2$  values were low and nonsignificant for most tests. They were relatively high, however, between counts of House Wrens and all four running averages of annual precipitation (2-year average:  $R^2 = 0.52$ ,  $P = 0.003$ ; 3-year average:  $R^2 = 0.50$ ,  $P = 0.004$ ; 4-year average:  $R^2 = 0.57$ ,  $P = 0.002$ ; 5-year average:  $R^2 = 0.39$ ,  $P = 0.013$ ). Bonferroni adjustment for these multiple tests requires  $P \leq 0.013$  for significance at the 0.05 level. Because results from the 4-year running average gave the best fit and the point scatter suggested a curvilinear relation, we fitted the 4-year running average to an equation of the form

$$y = a(1 - e^{-bx - cx^2}) + \epsilon$$

where estimates of  $\hat{a} = 133.707$ ,  $\hat{b} = -0.103$ ,

and  $\hat{c} = 0.004$  (Fig. 3). The root mean-square error was 23.9, a 17% improvement over the best linear model, based on the 4-year running average of precipitation. Visual inspection of the curve in Figure 3 suggests a threshold effect, seen in the steep ascent in mean annual counts of House Wrens between about 35 and 40 cm of annual precipitation, with an asymptote corresponding to a mean annual count of about 130 individuals within the range of precipitation observed during this study.

Correlations between counts of Bewick's Wrens and the prior year's total precipitation and the 2-, 3-, 4-, and 5-year running averages were not significant at the 0.05 level, nor were correlations between counts and winter precipitation for the current year, the previous year, or the previous 2 years. Although the probabilities of all correlations between counts and winter precipitation from 3 years prior to the counts ranged from 0.035 to 0.043, Bonferroni adjustment for these multiple tests requires  $P \leq 0.017$

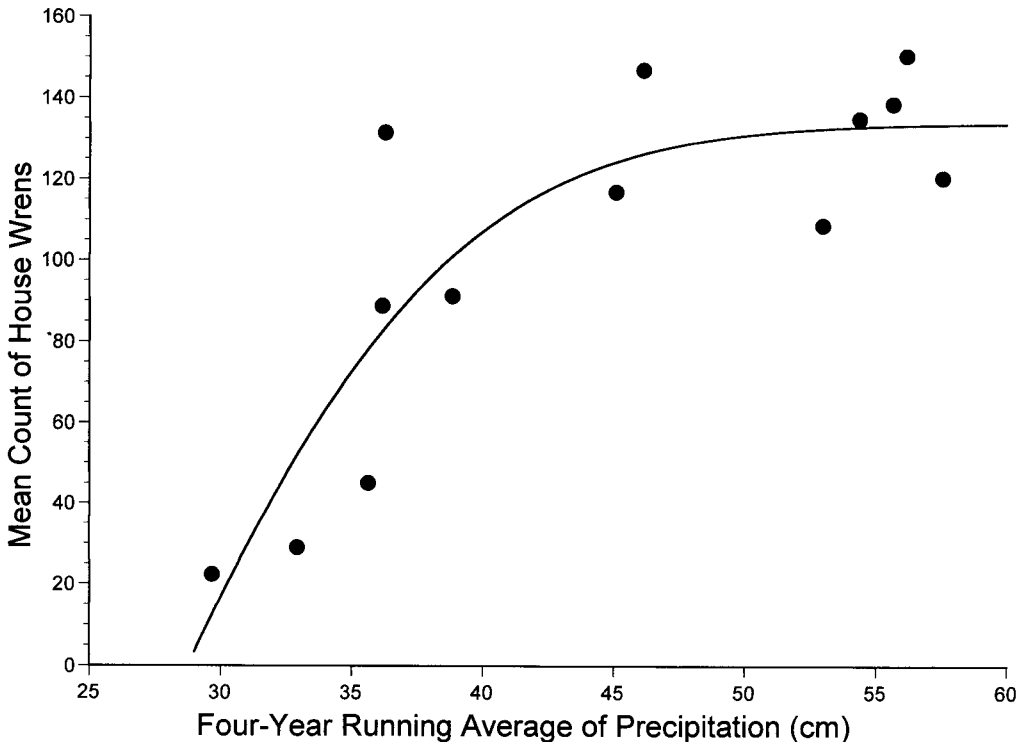


FIGURE 3. Curvilinear relation between the 4-year running average of precipitation and mean annual counts of House Wrens (adjusted  $R^2 = 0.57$ ,  $P = 0.002$ ). Note the apparent threshold effect suggested by the steep ascent in mean annual counts between about 35 and 40 cm of annual precipitation, with an asymptote corresponding to a mean annual count of about 130 individuals.

for significance at the 0.05 level. The sharp decline (62%) of Bewick's Wrens from 1990 to 1991 (Fig. 2) followed the most severe period of winter weather on record at SJER. Temperatures dropped below freezing every night from 13 December 1990 through 2 January 1991, reaching  $-11.7^{\circ}\text{C}$  (the lowest temperature in the 64-year record) on the night of 21 December,  $-10.6^{\circ}\text{C}$  on 22 December, and  $-8.3^{\circ}\text{C}$  on 23 December. This was accompanied by snow cover of 9–10 cm that remained for several days. Even a light dusting of snow is unusual at SJER, and it normally melts away within a day.

The correlation between counts of Bewick's Wrens and the lowest temperature recorded during the winter immediately preceding the counts was not significant ( $r = 0.37$ ,  $P = 0.21$ ), nor did minimum winter temperature add explanatory power to the regression model including total precipitation from October through March, 3 years prior to the counts—the precipitation measure with the highest  $R^2$ -value for Bewick's Wren counts (Type III sums of squares,  $F_{1,10} = 2.10$ ,  $P = 0.18$ ). Furthermore, removal of the data for 1991–1993, when the Bewick's Wren population was strongly influenced by the severe winter of 1991, dropped the  $R^2$ -value from 0.29 ( $P = 0.035$ ) to 0.0036 ( $P > 0.10$ ). Apparently the sharp drop in numbers of Bewick's Wrens associated with the severe winter of 1990–1991 positively biased the correlation between the winter period precipitation and Bewick's Wren abundance.

House Wren abundance, on the other hand, was strongly correlated with the lowest temperature recorded during the winter months preceding the counts ( $r = 0.77$ ,  $P = 0.002$ ), and adding minimum winter temperature to the regression model with the 4-year running average of total precipitation (the measure with the highest  $R^2$  for House Wrens) significantly improved the model (Type III sums of squares,  $F_{1,10} = 5.33$ ,  $P = 0.04$ ).

SPATIAL RELATIONS BETWEEN HOUSE AND BEWICK'S WRENS

In a plot of the observed vs. expected values of song posts of one species in cells with at least one song post of the other, data points would lie along the 45-degree line if all observed values equaled their paired, expected values. Results indicated neither attraction nor avoidance in song post locations between singing males of the two

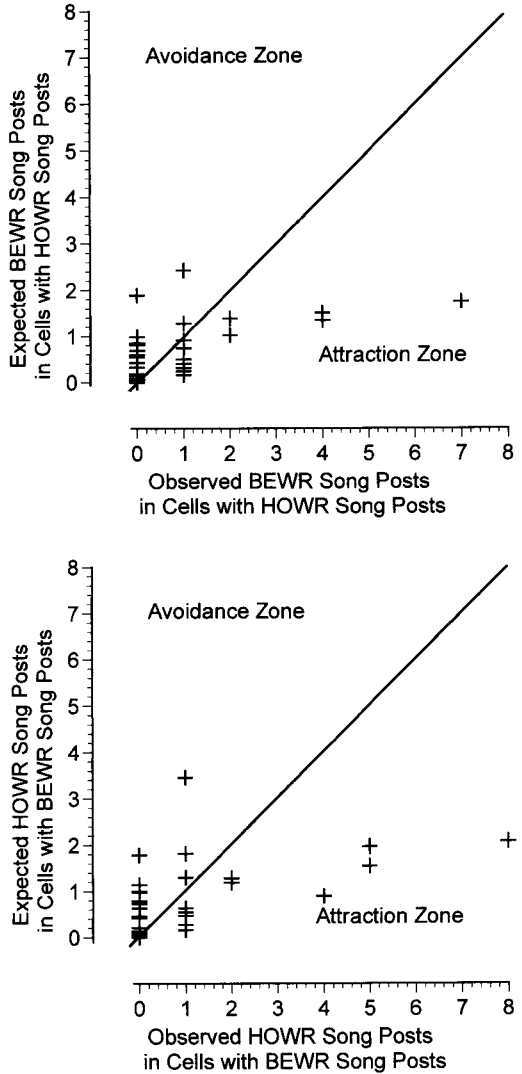


FIGURE 4. Above, the number of observed vs. expected song posts of Bewick's Wrens (BEWR) in cells 30 x 30 m that contained song posts of House Wrens (data pooled for the grazed and ungrazed spot-mapping plots). Below, the comparable data for song posts of House Wrens (HOWR) in cells containing song posts of Bewick's Wrens. Points would be concentrated in one or the other of the two zones if one species tended to avoid or to be attracted to the other. The true sample size (40) is obscured in each of these figures because several data points were identical or so similar that plotted points were coincident.

species (Fig. 4), and none of four paired *t*-tests of differences between means of the number of expected and observed song posts of one species in cells with song posts of the other even ap-

TABLE 2. Means  $\pm$  SE of the observed and expected numbers of song posts of one species in cells of the spot-mapping grid that had one or more song posts of the other, pooling data from the two plots ( $n = 40$ ).

	Observed	Expected	<i>t</i> -value <sup>a</sup>	<i>P</i>
House Wren song posts in Bewick's Wren cells				
30-m grid	0.85 $\pm$ 0.27	0.67 $\pm$ 0.12	0.77	0.45
50-m grid	1.53 $\pm$ 0.38	1.56 $\pm$ 0.27	-0.15	0.88
Bewick's Wren song posts in House Wren cells				
30-m grid	0.70 $\pm$ 0.22	0.55 $\pm$ 0.10	0.81	0.42
50-m grid	1.15 $\pm$ 0.31	1.17 $\pm$ 0.20	-0.08	0.93

<sup>a</sup> Two-tailed, paired *t*-tests.

proached statistical significance (Table 2). Power of the tests averaged 0.57 (range = 0.48–0.75) to detect a difference of 0.5 song post between observed and expected values and 0.99 (range = 0.97–1.00) to detect a difference of 1.0 song post. We cannot estimate the extent to which these results may be biased by a lack of independence; it is the case, however, that nonindependence is more likely to produce a false positive than a false negative result. In addition, the negative results of this analysis are supported by the territorial relations between these species as determined from spot mapping.

Although we do not contend that the spot-mapping method accurately maps territories of species on a study grid, it does provide some understanding of territory sizes and the general locations of boundaries. Superimposed maps of the registrations of the two wren species in this study indicated that Bewick's Wrens held much larger territories than House Wrens at SJER and, when both species were relatively abundant, their territories overlapped extensively. In fact, the boundaries of a given Bewick's Wren territory sometimes overlapped boundaries of several House Wren territories and sometimes completely surrounded a delineated House Wren territory (Fig. 5). These observations are consistent with the those of Kroodsma (1973) in Oregon but not with those of Root (1969) in coastal California.

## DISCUSSION

Our results provided no evidence of interspecific competition between House and Bewick's Wrens. Estimates of abundance based on point counts indicated that neither species was competitively excluding the other. Indeed, although

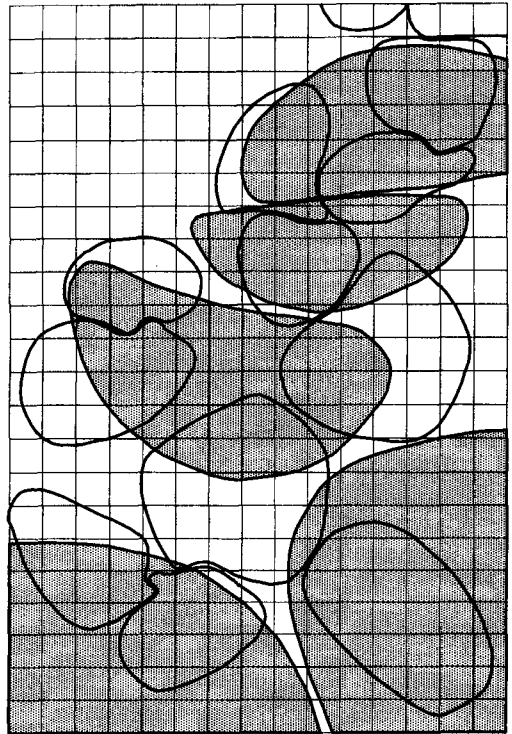


FIGURE 5. Territory boundaries of House Wrens (solid lines) and Bewick's Wrens (shaded) as delineated from spot-mapping data on the ungrazed plot, 1993. Grid lines of the mapping plot were at 30-m intervals.

not a significant pattern, annual population changes of the two species were in the same direction twice as often as in opposite directions. Spot-mapping indicated extensive territory overlap between the two species. Finally, analysis of the locations of song posts supported the null hypothesis of no difference between the expected and observed numbers of song posts of one species in grid cells containing at least one song post of the other. Interestingly, most plotted points fell into the "avoidance" half of Figure 4 when counts were low, but most fell into the "attraction" half when counts were high, as we might expect if males of the two species selected song posts independently of one another. Alternatively, the prevalence of points in the "attraction" half when counts were high may reflect overlap between the species in the habitat attributes that influence their selection of song posts.

Results of other studies at SJER (Purcell 1995; Verner, pers. observ.) indicate that these two wren species do not overlap in their selec-



tion of nest sites. Nest sites of Bewick's Wrens were generally atypical for cavity nesters and almost exclusively in natural cavities, including nests on the ground under a shrub or rock, or at the mouth of a vacant rodent burrow. Their nests were significantly lower than those of House Wrens, and they used nest boxes only twice over the 6-year period from 1989 to 1994 (44 boxes were in place from 1989 to 1991, and 92 were in place from 1992 to 1994). House Wrens used boxes frequently, and typically about 25% of the nest boxes were not used in a given year, suggesting no limitation of nest sites for these two species, a conclusion supported by Waters et al. (1990) in an earlier study at SJER. Unlike the study by Kennedy and White (1996) in Kansas, we have never observed a case of House Wrens at SJER usurping an active nest cavity of Bewick's Wrens, and Bewick's Wrens at SJER had the highest nest success among all secondary cavity-nesting species (Purcell 1995).

We do not view our results as necessarily in conflict with the many other studies implicating interspecific competition as a mechanism leading to the extirpation of Bewick's Wrens in the face of range expansion by House Wrens. Most of those studies were done east of the Rocky Mountains, where we need not expect similar conditions. Moreover, western populations of the Bewick's Wren have not exhibited declines as severe as those in the east (Wilcove 1990, Kennedy and White 1996).

The rather sharp changes in relative abundance seen between some years for both species probably have a complex explanation beyond the present study. Although we have 13 years of data on these populations and their relations to weather, in another sense our sample size is only one because the data included only one drought cycle and the most severe period of winter weather on record at SJER. In the context of the periodicity of these events, studies of much longer duration are needed to sort out the details of cause and effect.

Visual inspection of Figure 2 suggests that the Bewick's Wren population held fairly well during most of the severe drought years of 1987–1990, suggesting that even very severe droughts have little effect on their population. On the other hand, we suspect that Bewick's Wrens suffered high mortality as a direct result of the cold snap in the winter of 1990–1991, producing a drop in their population that was not paralleled

by a decline of House Wrens. Because the Bewick's Wren is a permanent resident at SJER, and the House Wren is a migrant, only the former could have been directly affected by the cold snap. Numbers of Bewick's Wrens then remained relatively low until 1994, when the population began to recover.

The decline of House Wrens during the severe drought of 1987–1991, followed by their dramatic recovery at the end of the drought, was not the first time such a change in abundance has been observed at SJER. We know from early spot-mapping studies at SJER, in 1978 and 1979, that House Wrens were rare on both the grazed and ungrazed plots following the severe drought of 1976–1977 (Verner, pers. observ.). When spot mapping was resumed in 1985, however, the House Wren was the most abundant breeder on both plots.

Our results raise the question of whether oak-pine woodlands at SJER comprise "sink" habitat for House Wrens, *sensu* Pulliam (1988). During years of more normal precipitation (at least 35 cm, as suggested by Fig. 3), House Wrens had high reproductive output compared with other secondary cavity nesters at SJER, often successfully completing two nesting cycles (Purcell, pers. observ.). Because of their low numbers during drought years, data were insufficient to estimate with confidence their productivity and nesting success then. We suspect, however, that the oak-pine woodlands at SJER are at least "intermittent" sinks for House Wrens; i.e., they support at least maintenance-level reproduction during years of normal precipitation but not during drought years. Similar dynamics of other species are reviewed by O'Connor (1986) and Wiens (1989). The question is whether House Wrens would persist in these woodlands, over the long term, if it were not for periodic immigration from other habitats to "jump-start" the population after severe droughts. Probable source habitats include riparian and other mesic sites elsewhere in the nearby Sierra foothills and Central Valley of California, which habitats do not exist at SJER. Such intermittent source-sink dynamics may be a common occurrence.

The monitoring work at SJER is continuing, so we expect to re-examine these relations after the next drought cycle. We predict that precipitation will again be a major factor for the House Wren. The apparent asymptote at a mean point

count of about 130 House Wrens (Fig. 3) in relation to the 4-year running average of annual precipitation may, of course, decline or increase under more extreme conditions of precipitation, but the dataset reported here included the lowest and the third highest 4-year running averages of annual precipitation in the 64-year record at SJER.

Many studies have described drought-induced effects on bird populations. For example, Hicks (1935), Cody (1981), Smith (1982), and Blake et al. (1992) reported reduced population levels during drought years compared to pre- and post-drought years. DeSante and Geupel (1987) documented reduced breeding success associated with drought, and Stiles (1992) reported higher mortality rates and reduced breeding success during a drought. Speculation as to a mechanism focuses primarily on reduced food supplies for the birds during droughts, and some researchers have suggested that lack of available water may directly affect some species. The studies of Cody (1981), Smith (1982), and Stiles (1992) provide data supporting their views that food supplies are depressed for various species during droughts.

In most previous studies, responses of populations to drought were noted only during the year of a drought. In the present study, however, precipitation apparently exerted its influence over more than one year, based on the fact that significant relations to House Wren counts were observed only with multiple-year running averages of precipitation. The apparent existence of a strong threshold effect of the 4-year running average of precipitation on House Wren abundance will be revisited as additional years of data are added to the study.

We believe the multiple-year influence of precipitation is more to be expected than an immediate effect confined to the current year. At the onset of a drought, for example, successful breeding may be curtailed or even prevented altogether, but death of all birds present at the time is unlikely. Instead we should expect to see a declining population that reflects reduced breeding success and probably increased mortality, leading to a gradual decline that continues for a period of years following the onset of the drought. When the drought is broken, the opposite pattern—increased breeding success and possibly lowered mortality—should generate a

lag of at least 1 year in the population's response to improved conditions.

Food supply also may explain the strong correlation between House Wren abundance and the lowest temperature in the winter months preceding counts, as winter temperature may influence over-winter survival of dormant insects. Alternatively, ambient temperature may influence the timing of leaf emergence on deciduous plants, which would influence insect productivity. To accept any hypothesis involving the influence of winter temperatures on spring food supply for House Wrens, however, we would need to understand how the wrens factor this into their settling responses as they return from their wintering grounds. Another possibility is that seasonal patterns of temperature change noted at SJER are indicative of similar patterns over a geographic region large enough to include the winter range of House Wrens that breed in foothills of the western Sierra Nevada. If true, the observed correlation may simply reflect temperature-related winter survival of the House Wrens.

Effects of density on song rates may have biased upward the high counts and downward the low counts of wrens in this study. Several studies have found that rates of territorial calls among various species were positively related to population density (references in Rappole 1995). For example, song rates of male Sedge Wrens (*Cistothorus platensis*) in Illinois increased when other males were singing in the neighborhood (Kroodsma and Verner 1978). In another case, male Marsh Wrens (*C. palustris*) in relatively dense populations in Washington State regularly averaged 20 or more songs  $\text{min}^{-1}$  for the first hour or more after daylight, but males within earshot of only one other male averaged fewer than 1  $\text{min}^{-1}$  during the same time of day (Kroodsma and Verner 1997). If similar effects occur among House Wrens and Bewick's Wrens at SJER, higher song rates of males during population highs would tend to make them more detectable, and possibly even lead to counting the same individuals more than once during the 5-min point counts used in this study. On the other hand, if song rates were markedly lower during population lows, birds may go undetected during a 5-min count. These effects may have exaggerated some of the extreme annual differences in counts we recorded.

Finally, the large, annual swings in abundance of these wrens caution against inferences about

long-term trends in their numbers in central California, based on comparisons of short-term studies in the past with short-term studies in the present.

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