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FLUCTUATING POPULATIONS OF HOUSE WRENS AND BEWICK'S WRENS IN FOOTHILLS OF THE WESTERN SIERRA NEVADA OF CALIFORNIA[1]

JARED VERNER AND KATHRYN L. PURCELL
USDA Forest Service, Pacific Southwest Research Station, 2081 East Sierra Avenue, Fresno, CA 93710, e-mail: jverner/psw_fresno@fs.fed.us

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, Kennedy 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 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 km hr^{-1} (by Beaufort scale) were repeated the following count day. Windy-

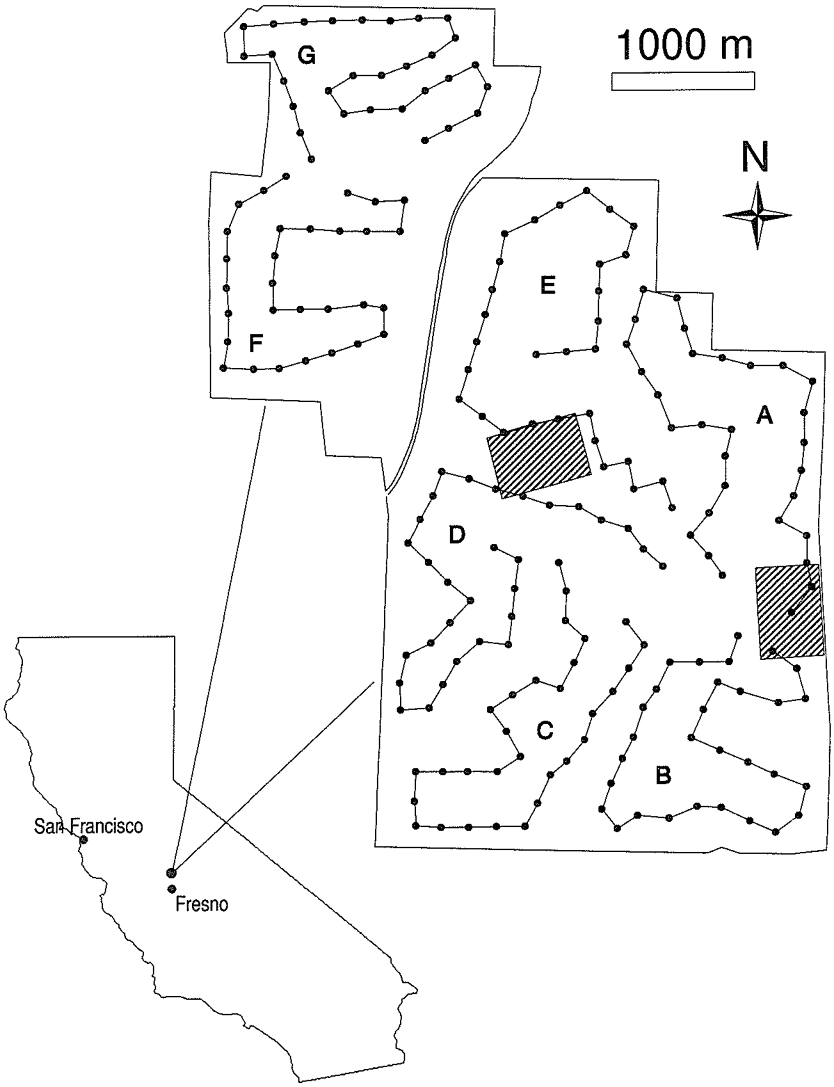

FIGURE 1. General location map and boundary map of the San Joaquin Experimental Range in foothills of the Sierra Nevada, California, showing locations of point-counting stations along each of the seven sampling lines (A–G); the two spot-mapping grids are shown as shaded rectangles. California State Highway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