

# Factors Affecting the Abundance and Distribution of European Starlings at the San Joaquin Experimental Range<sup>1</sup>

Kathryn L. Purcell,<sup>2</sup> Jared Verner,<sup>2</sup> and Sylvia R. Mori<sup>3</sup>

## Abstract

We examined population trends and factors related to the abundance and presence of European starlings (*Sturnus vulgaris*) at the San Joaquin Experimental Range in the foothills of the western Sierra Nevada, 31 km east of Madera, California. Starlings first appeared there in low numbers in the late 1960s and are now abundant breeders. Simple models examining trends in starling numbers and presence/absence using point-counting data from 210 counting stations from 1985 through 2000 showed significantly increasing yearly trends in starling abundance and distribution. The yearly trend in abundance, however, became nonsignificant when weather patterns were included. Similarly, starling presence/absence showed an increasing trend over years, but the trend became sinusoidal when weather and habitat variables were included. Our data show that spurious results may occur when appropriate explanatory variables are not included in the analysis of population trends. Starlings were more abundant after years with cool summers, warm, wet winters, and on early and late count dates. Starling presence was related to habitat attributes generally considered necessary for foraging—level, open woodlands with fairly well-developed, accessible soil. Summer is the time of year when resources are most limiting for starlings in the foothill oak woodlands, as they primarily forage on arthropods in moist soils. Cool summers and wet winters permit the soils, especially swales, to remain moist and productive longer, thereby promoting higher starling abundance. Research is needed on the potential effects of starlings on native species of birds and the conservation and production values of the ecosystems they have invaded.

## Introduction

The European starling (*Sturnus vulgaris*) was introduced into North America in 1890 and rapidly spread throughout most of the United States (Kessel 1953). Breeding Bird Survey data from 1968 to 1975 showed an average increase of 16 percent per year in starling numbers in the western states (Robbins and Erskine 1975). Starlings are now among the most abundant species of birds in North America, with a breeding range extending from arctic Canada to the subtropics of Mexico (Feare 1984). As populations of exotic species increase from relatively few

---

<sup>1</sup> An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, 22-25 October 2001, San Diego, California.

<sup>2</sup> Research Wildlife Biologist, Forestry Sciences Laboratory, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, 2081 E. Sierra Avenue, Fresno, CA 93710.

<sup>3</sup> Mathematical Statistician, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, 800 Buchanan Street, Albany, CA 94710.

individuals and a limited distribution to abundant and widespread, we expect effects on ecosystems and their component biota to increase (Hobbs and Mooney 1998).

Starlings were first documented in California in 1942 (Jewett 1942) and are now likely the most abundant bird species in the state (Small 1994). They were not documented at the San Joaquin Experimental Range (hereafter SJER), located in the foothills of Madera County, California, until the late 1960s. By 1970, SJER was home to several nesting pairs, where they nested mainly in power poles around the headquarters buildings (Duncan and others 1985). Starlings are now widespread breeders throughout SJER and the foothill oak woodlands, although they avoid ungrazed pastures (Verner and others 1997).

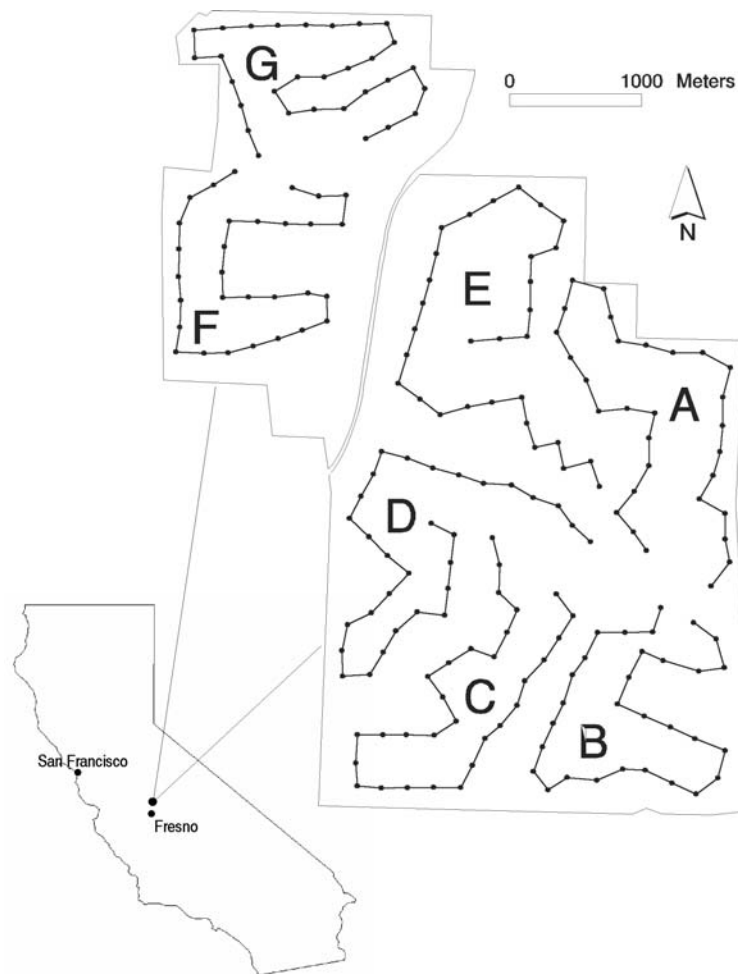
Cavity-nesting birds are an important and rich component of the breeding bird community in oak woodlands. Starlings are aggressive nest competitors and are known to usurp nest sites from other cavity-nesting birds (Ingold 1989, Short 1979, Troetschler 1976, Weitzel 1988, Zeleny 1978). Cavities are generally assumed to be limiting for cavity-nesting birds, and starlings use cavities similar in size and shape to those used by native species breeding at SJER, especially western bluebirds (*Sialia mexicana*) and violet-green swallows (*Tachycineta bicolor*) (Purcell 1995). Bird communities in oak woodlands are especially rich in cavity-nesting species, particularly nonexcavators that rely on cavities for nest sites that are excavated by other species (Purcell 1995, Verner and others 1997). Other than habitat loss, starlings may be the biggest threat to cavity-nesting birds in oak woodlands in California (Robbins and Erskine 1975).

Using point-count data collected at SJER since 1985, we explore trends in starling numbers and presence/absence to examine factors responsible for annual and long-term variation in starling abundance. We include weather and habitat variables to help understand the observed patterns of abundance and distribution of starlings at SJER.

## Methods

### Study Area

This study was done at the San Joaquin Experimental Range (SJER), in the western foothills of the Sierra Nevada, approximately 31 km northeast of Madera, California (fig. 1). SJER is approximately 1,875 ha in size and ranges in elevation from 215 to 520 m. Vegetation consists of a sparse woodland overstory of blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus sabiniana*). The understory of scattered shrubs includes mainly wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), hollyleaf coffeeberry (*Rhamnus ilicifolia*), and Mariposa manzanita (*Arctostaphylos viscida mariposa*). Some areas are typical blue oak woodlands, where few to no trees of other species occur, and the understory is open. Annual grasslands form a mosaic in dry areas with gentle slopes where the overstory and understory are missing. SJER has been lightly to moderately grazed since about 1900, except for a 29-ha Research Natural Area that has not been grazed since 1934.



**Figure 1**—General location map and boundary map of the San Joaquin Experimental Range in the foothills of the Sierra Nevada, California, showing locations of point-counting stations along each of the seven sampling lines (A-G). California State Highway 41 bisects the study area just west of sampling line E.

The climate is Mediterranean, with cool, wet winters and hot, dry summers. Long-term weather records from SJER are available since 1934, showing marked yearly variations in precipitation. If we define a drought as any period  $\geq 2$  years in duration with  $\leq 75$  percent of the long-term mean annual precipitation, a drought occurred from 1987 through 1991 (Verner and Purcell 1999). This was the most prolonged and severe of the three droughts that have occurred at SJER since 1934.

### ***Bird Counts***

From three to seven observers completed 5-min, unlimited-distance point counts from 1985 through 2000. Counts were done during the peak breeding period of most species that nest at SJER, from the last week of March through the end of April. Observers were carefully selected to be proficient at bird identification, especially by songs and calls. To help minimize observer variability, a 2-week training period prior

to counting helped observers sharpen their skills, and the same observers were used over as many years as possible (Verner and Milne 1989).

The sampling array consisted of 210 counting stations, with 30 stations distributed along each of seven lines established throughout SJER (*fig. 1*). Counting stations were at least 200 m apart along the same line and between the separate lines. Although this spacing is closer than ideal for independent samples, our intent was only to obtain an index of relative abundance for comparison across years. By following the same protocol each year, we believe potential biases resulting from a lack of independence in the counts are consistent from year to year. All counting stations were clearly identified by placement of yellow cattle ear tags wired to trees, shrubs, fences, and occasionally to steel fence posts, providing consistency in location across years; numerous red tags placed between stations helped guide observers from point to point along the lines.

Each year, observers were randomly assigned to lines and each observer eventually sampled all lines on seven different mornings, completing one count at each of the 210 stations. Consequently, each point was counted each year as many times as the number of observers in that year. Recording of birds at the first station on a line began at 10 minutes after official sunrise and continued at successive stations at 10-min intervals. By adhering to this schedule, each observer recorded birds at six stations per hour, with all 30 stations on a line sampled within 5 hours. Counts were not done on rainy days or when wind velocity exceeded 32 km/hr (Beaufort scale). Only results for European starlings are reported here.

We tested relations between yearly counts of starlings and nine precipitation and four temperature variables: total annual precipitation from 1 May of the year preceding the counts through 30 April of the counting year, and the 2-, 3-, 4-, and 5-year running averages of annual precipitation; winter precipitation values from October through March of the survey year, and those for 1, 2, and 3 years prior. About 86 percent of the annual precipitation falls in this period. Temperature variables included mean spring (March-May), summer (June-August), and winter (December-February) temperatures, and minimum winter temperature in the year preceding the counts. To examine the effects of the El Niño Southern Oscillation (ENSO) on starling abundance (see Sillett and others 2000), we examined five variables using annual mean monthly values of the standardized Southern Oscillation Index (SOI) to represent ENSO conditions for each calendar year. These variables included mean values for the current year, the previous year, and 2 years previous, based on the calendar year, and for April through March of the year preceding the counts and 2 years previous. High positive values of SOI indicate cold, dry La Niña conditions; low, negative values indicate warm, wet El Niño conditions (Kiladis and Diaz 1989).

### ***Vegetation Measurements***

Vegetation data were collected in 1988 at three 20-m radius plots at each of the 210 counting stations (Block 1989). Plot centers were located 40-80 m from the counting station along three axes radiating from each and separated by 120°, with the first bearing located randomly. Values for each of the three plots were averaged to describe the habitat at each station. Data from only one or two plots were available in two and 16 cases, respectively, and data from one station were missing entirely. Variables explored for inclusion in analyses were: slope (measured in degrees),

aspect, distance to water, litter depth (average of 10 measures taken at 4-m intervals along the axis of the plot), grass/forb height (average of 10 measures of the grass or forb located closest to the axis at 4-m intervals), percent cover of grasses, forbs, combined grasses and forbs, foothill pine, interior live oak, and blue oak trees (based on 40 points at 1-m intervals along the plot axis). Trees were defined as woody stems >10 cm in diameter and >2 m tall. Exploratory analysis of aspect data suggested that east-facing slopes were preferred by starlings during the morning counting period. Aspect was therefore transformed to a continuous variable via

$$A' = \cos(A_{\max} - A) + 1,$$

where  $A$  is the azimuth recorded clockwise from north and  $A_{\max}$  is east ( $90^\circ$ ), yielding a value of 2 for east and 0 for west (Beers and others 1966).

We collected another set of vegetation measurements in 2001 that included percent cover of the three primary tree species, shrubs, and rocks within a 50-m radius centered on each counting station. Visual estimates of cover were based on assigning 2 percent cover to substrates with a 7-m radius, 1 percent for a 5-m radius, and 0.5 percent for a 3.5-m radius. For example, a tree with a crown radius of 7 m has an area of  $154 \text{ m}^2$ , or 2 percent of the  $7,854 \text{ m}^2$  found in a 50-m radius plot. Global positioning system (GPS) northing and easting coordinates were also obtained for each counting station.

## Statistical Analyses

For analysis of starling abundance, the total number of individuals detected at each point was summed over route for each observer each year. This procedure obviated any potential between-point problems of nonindependence. We used nonparametric Poisson regression models as a subclass of generalized additive models (GAM) (Hastie 1993, Venables and Ripley 1997) as a first (exploratory) statistical approach to examine relations between the number of starlings (counts) and the independent variable candidates. Explanatory variables include annual or other temperature functions, annual or other precipitation functions, sampling day (Julian date), and location (route). This approach was used in lieu of prior knowledge of the functional shapes of relations between counts and explanatory variables. We did not assume linearity. Instead the data were used to visualize the simultaneous relations between explanatory variables and counts. Generalized additive modeling was also used to drop explanatory variables that appeared to have no relation to counts. We used analysis of deviance,  $F$ -tests, and visual examination of the partial residual plots to select the explanatory variables to be included in the model (Hastie and Tibshirani 1990, Knapp and Preisler 1999). The exception to this rule was the independent variable *year*, which was included in all possible regression models to explore annual trends in abundance of starlings. Parametric functional shapes for the explanatory variables were obtained by trying polynomial, logarithmic, or other parametric functions suggested by the output of GAM. We used the Poisson regression model as a subclass of the generalized linear models (McCullagh and Nelder 1991) for the parametric analysis of count trends. In general, the Poisson regression model, in either nonparametric or parametric models, was as follows:

$$\log \lambda_{ijk} = \text{intercept} + f(\text{year}_i) + f(\text{julian date}_i) + f(\text{temperature}_i) \\ + f(\text{precipitation}_i) + f(\text{SOI}_i) + \text{route}_j,$$

where

$$\text{Expected}(\text{count}_{ijk}) = \lambda_{ijk}$$

$i$  indexes year,  $j$  indexes route,  $k$  indexes observer,  $f$  is a smoothing (Loess) or parametric function, and the  $\text{count}_{ijk}$  for each year  $i$ , each route  $j$ , and each observer  $k$  has the Poisson ( $\lambda_{ijk}$ ) distribution. An error term (overdispersion term) was included in the model to account for the substantial variability among observers (see Verner and Milne 1989). For the parametric approach, the overdispersion term also accounted for the repeated measurement (the same observer counts birds at all the routes on different days). The GAM analysis was done with S-Plus (Mathsoft 1999) and the generalized linear models with the SAS GENMOD procedure (SAS Institute, Inc. 2000).

Because habitat data were collected at each of the 210 points, and counts at many points were zero (11 to 22 stations of the 30 per route, averaged over observers and years), we analyzed starling presence/absence at each point and for each observer instead of summing counts over routes. We again used the nonparametric generalized additive models (GAM) to model the presence/absence (odds) response, following the Logit regression model:

$$\text{Logit}(p_{ijkl}) = \log\left(\frac{p_{ijkl}}{1 - p_{ijkl}}\right) = \text{intercept} + \sum_{ijk} f(\text{explanatory}_{ijk}) + \text{route}_j,$$

where  $p_{ijkl}$  is the probability of starling presence in year  $i$ , on station  $k$  of route  $j$  for the  $l$  observer,  $f$  is a smoothing (Loess) or a parametric function of the explanatory variables, and response (presence) was assumed to have an overdispersed Bernoulli( $p_{ijkl}$ ) distribution. Assuming the above Logit model, the value of  $p_{ijkl}$  is given by

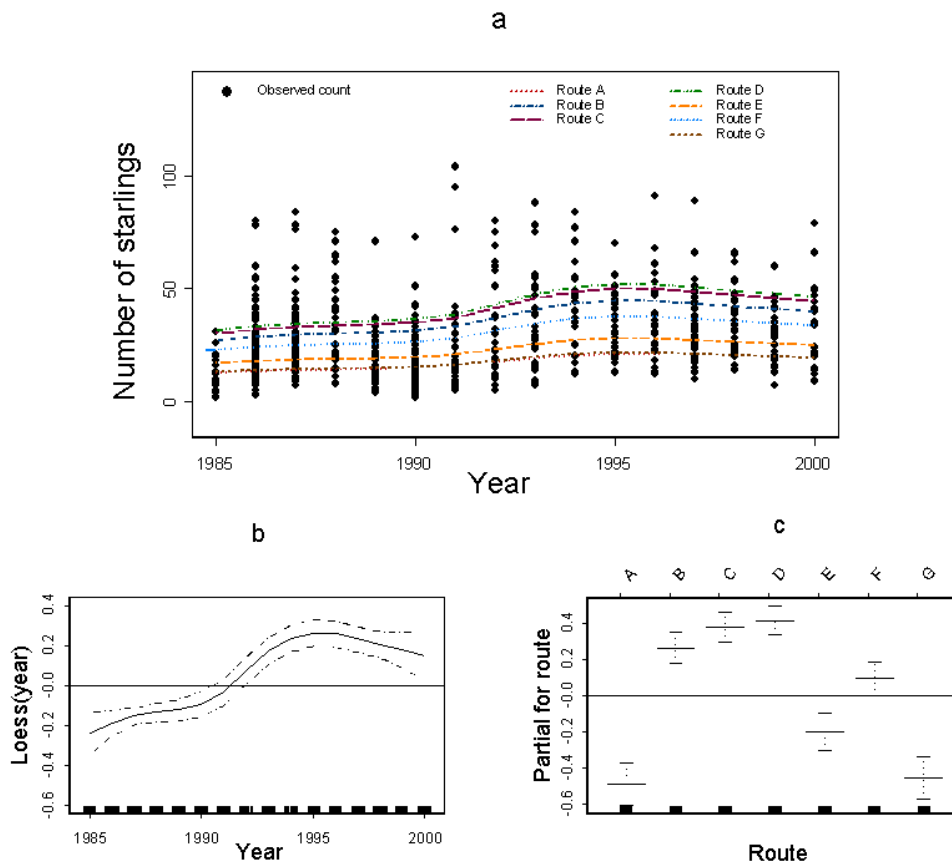
$$p_{ijkl} = \frac{e^{\text{intercept} + \sum_{ijk} f(\text{explanatory}_{ijk}) + \text{route}_j}}{1 + e^{\text{intercept} + \sum_{ijk} f(\text{explanatory}_{ijk}) + \text{route}_j}}.$$

After examining a simple model with only *year* and *route* as variables, all available variables were tried for inclusion in the habitat model, including date, time of day, and the weather variables. *Year* and the weather variables were considered due to possible relations with habitat variables, such as those related to soil moisture. Variable selection for the presence/absence response was aided by the use of classification trees (Venables and Ripley 1997). Bird-habitat relations, based on point-count data, are often weak because the habitat data describe only the general area used, not the actual location of the bird (Larson and Bock 1986). Our objective was not to produce a predictive model of starling presence, based on habitat variables, but only to see how the explanatory variables were related to starling abundance. For the presence/absence data, only the nonparametric models are presented here.

## Results

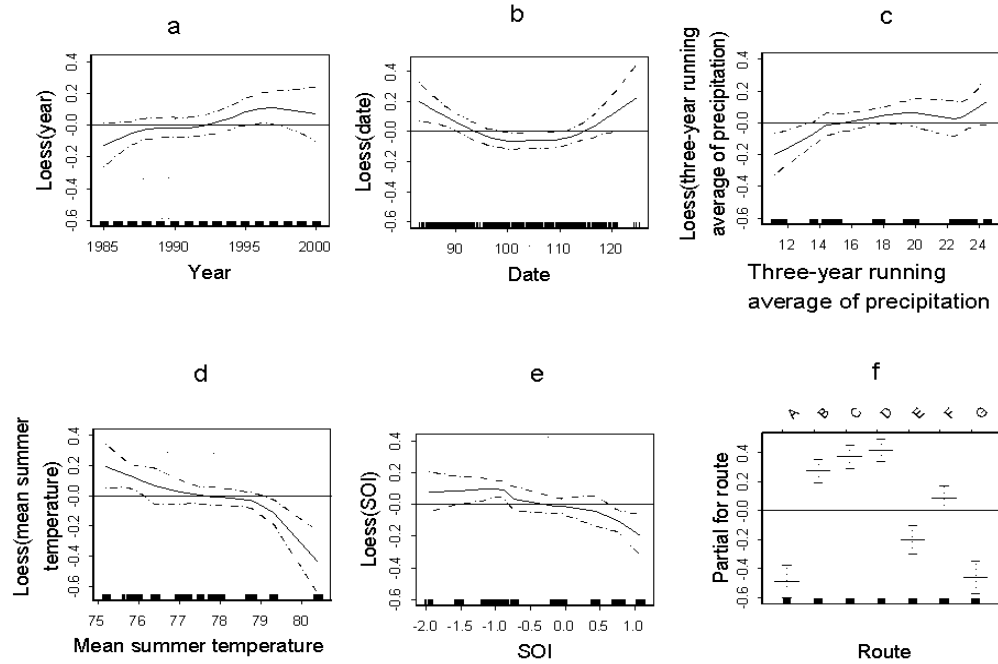
### Abundance (Counts)

The fitted nonparametric model including only *year* and *route* terms showed an increase in counts of starlings over the period of the study (fig. 2a). The *year* effect was significant ( $P < 0.001$ ), producing 10.2 percent drop in deviance, and the rate of change for counts was 40 percent (95 percent confidence interval was from 20 to 60 percent) from 1986 to 2000 (fig. 2b). The increasing trend from 1985 through 1995 was apparently damped by the 1987 through 1991 drought, and starling numbers leveled off or decreased slightly after 1995. High variability existed among counts by individual observers, and possibly even within the same observer (fig. 2a). Group foraging and flocking may also have contributed to variability in the counts. Differences among routes were especially significant ( $P < 0.001$ ), with *route* producing a 32.3 percent drop in deviance (fig. 2c).



**Figure 2**—(a) Plot of observed counts of European starlings (*Sturnus vulgaris*) (counts per observer per route) each year (observed counts) plus the smoothed intercept (predicted counts) by route. The model is  $\log(\text{expected count}) = \text{loess}(\text{year}) + \text{route}$ . (b) Plot for loess (*year*) (estimated smoothing function of *year*) showing a significant increasing trend in starling abundance. (c) Plot for estimated *route* (estimated smoothing function of *year*) effect showing significant differences among routes. The bars along the x-axis of panels b and c represent the data points.

In addition to *year*, three weather variables (*3-year running average of precipitation*, *mean summer temperature*, and *SOI*), *sampling date*, and *route* were selected with the exploratory GAM analysis to be included in the model (fig. 3). Together they produced a 49 percent drop in deviance. The *SOI* variable used was the mean of the monthly indices for the 12 months from April through March immediately preceding the counts. After these variables were added to the regression, *year* became statistically nonsignificant.



**Figure 3**—Plots of smoothing functions from the nonparametric Poisson model of log(expected count) estimated by GAM showing (a) nonsignificant, yearly trend in starling counts, (b) increasing counts on early and late counting dates (Julian calendar), (c) increasing counts with the *3-year running average of precipitation*, (d) decreasing counts with *mean summer temperature* (June through August), (e) the *Southern Oscillation Index* (SOI), and (f) significant differences among routes. The bars along the x-axis show the distribution of data along the axis.

Visual examination of the partial residual plots, and some trial and error, yielded the functional form for the selected explanatory variables, displayed by the following fitted parametric Poisson regression model:

$$\begin{aligned} \text{Log}(\hat{\lambda}) = & 390.3 - 0.007 * \text{year} - 0.1582 * \text{date} + 0.0008 * \text{date}^2 + 0.0323 * \text{pav3} \\ & - 5.2441 * \text{tja} + 0.7118 * \text{tja}^2 - 0.0321 * \text{tja}^3 \\ & - 0.1304 * \text{SOI} - 0.0703 * \text{SOI}^2 + \text{route}, \end{aligned}$$

where  $\hat{\lambda}$  is the estimated mean *count*, pav3 is the *3-year running average of precipitation*, and tja is *mean summer temperature*. The parametric model also showed a nonsignificant yearly trend when the other variables were present in the

model (*table 1*). The other five explanatory variables were statistically significant and their patterns generally remained the same.

To summarize, *year* did not reduce the deviance significantly for either the nonparametric or parametric approach (*fig. 3a, table 1*), and the confidence interval displayed by the plot of the estimated smoothing function contained the zero line (*fig. 3a*); the plot showed a tendency for an increasing trend. The relation between *year* and counts was stronger if the *3-year running average of precipitation* was not present in the model. Because *year* and the *3-year running average of precipitation* were highly correlated (0.63 for 1985-2000 and 0.91 for 1990-2000), the significance of both was weaker when *year* was included in both the nonparametric and parametric models. Removal of *SOI* from both models did not affect the behavior of *year* or the *3-year running average of precipitation*.

**Table 1**—The full parametric Poisson regression model for starling abundance (count) showed that *date*, the *3-year running average of precipitation*, *mean summer temperature*, the *Southern Oscillation Index*, and *route* were all significantly related to European starling abundance at SJER, while *year* was not. When the *3-year running average of precipitation* was not included, *year* showed a significant trend.

Independent variables	Full model	Without 3-year running average of precipitation
	P-value	P-value
Year	0.9740	0.0002
Date	<0.0001	<0.0001
Date <sup>2</sup>	<0.0001	0.0001
3-yr running average of precipitation	0.0982	-
Mean summer temperature	<0.0039	0.0258
Mean summer temperature <sup>2</sup>	<0.0035	0.0299
Mean summer temperature <sup>3</sup>	<0.0031	0.0307
Southern Oscillation Index	0.0068	0.0008
Southern Oscillation Index <sup>2</sup>	0.1011	0.0175
Route	<0.0001	<0.0001
Model deviance	3263	3358
Null model deviance	6403	

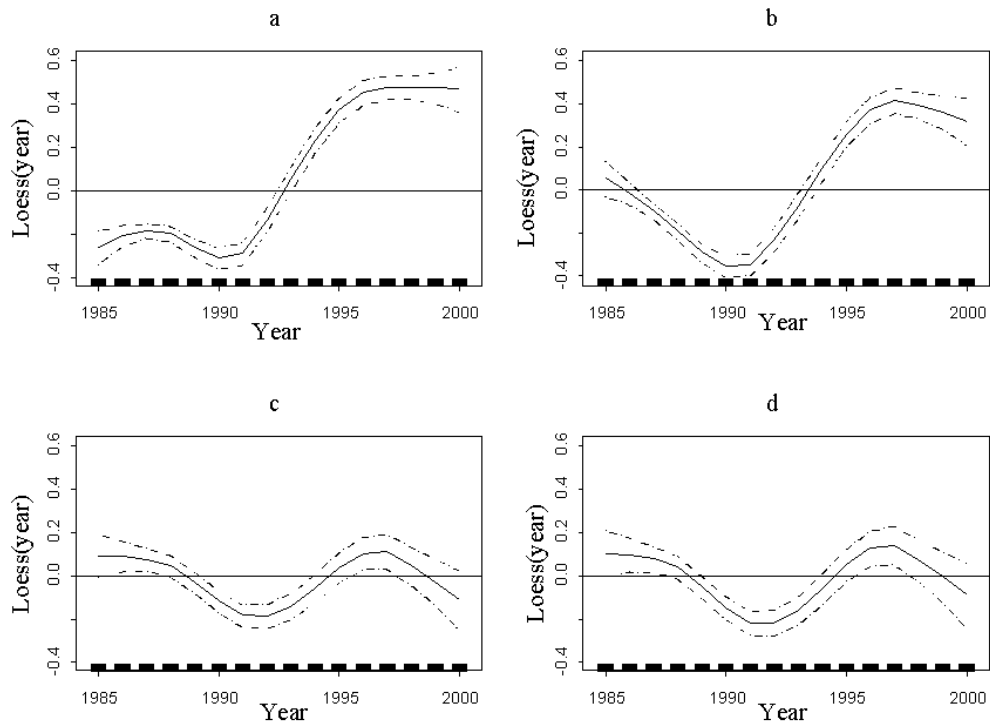
Results from both models showed that counts of starlings were high during the early and late count dates and high on routes B, C, D, and F (*fig. 3b, f*). *Route* (location) produced the largest drop in deviance. Starling abundance increased with low summer temperatures in the preceding year, with a high running average of precipitation during the 3 years previous to the counting year, and with low mean monthly indices of *SOI* in the preceding year (*fig. 3c, d, e*). Both precipitation variables—the *3-year running average of precipitation* and *SOI*—contributed significantly to the model and were not colinear (Pearson correlation = 0.13).

### Presence/absence

The nonparametric model including only *year* and *route* terms showed a statistically significant increase in starling presence over the study period ( $P < 0.000$ , *fig. 4a*) and accounted for a 6.2 percent drop in deviance. The effect of the 1987 through 1991 drought on starling distribution was especially marked; this was followed by a period of increasing distribution in the succeeding wet years until 1997

when presence leveled off. Differences among routes were again highly significant ( $P < 0.000$ ).

The weather variables appear to be modifying the behavior of the *year* effect and explaining the increasing trend in starling presence/absence. The addition of *mean summer temperature* to the model increased the drop in deviance to 6.7 percent and altered the yearly trend pattern (fig. 4b). Adding the *3-year running average of precipitation* further altered the pattern to a sinusoidal curve and reduced the scale of variability (fig. 4c). The best overall model, including habitat variables along with the weather variables and *year*, resulted in a 16.1 percent drop in total deviance (table 2). *Year* contributed significantly to the full model, and the pattern was the same as for the model containing *year*, *route*, and the two weather variables that showed a cyclic pattern around the mean, with reduced amplitude (fig. 4c,d). The variables included in the Poisson model were still important, providing confidence in their significance to starlings (table 2, fig. 5a-c). For the previous analysis of count data, we could not examine *time of day*, as counts were totaled over route. In this analysis, *time of day* was significant and showed higher starling detections in the first hour of counting (fig. 5d). Starlings were more frequently detected in areas that were more level than steep and that were generally east-facing, in areas with low cover of rocks, low litter depth, high blue oak cover, low live oak cover, high foothill pine cover, and low cover of shrubs (fig. 5e-l).



**Figure 4**—Plots of smoothing functions from the nonparametric logit model for starling presence/absence response (a) including only *year* and *route*, (b) adding *mean summer temperature* (June through August), (c) adding the *3-year running average of precipitation*, and (d) the full model including the habitat variables. As we add variables to the model, the year effect appeared to be driven by weather variables—both temperature and precipitation. Habitat variables did not alter the sinusoidal pattern but did contribute to the drop in model deviance. The bars along the x-axis represent the data points.

**Table 2**—Analysis of deviance for independent variables in the nonparametric logit regression model examining relations between starling presence/absence and year, habitat, weather, and other variables ( $n = 19,019$ ). P-values for the full model and all variables are  $< 0.0000$ .

Model	Model deviance	Test deviance <sup>1</sup>	Pct drop in deviance
Null model <sup>2</sup>	18,953		
Full model <sup>3</sup>	19,018	4225	16.1
Full model less			
Year	22,162	67	0.1
Date	22,124	29	0.1
3-year running average of precipitation	22,127	32	0.1
Mean summer temperature	22,175	80	0.3
Route	22,168	73	0.3
Time of day	22,162	67	0.3
Slope	22,221	126	0.5
East aspect <sup>4</sup>	22,146	51	0.2
Pct cover of blue oak	22,212	117	0.4
Pct cover of live oak	22,165	70	0.3
Pct cover of foothill pine	22,129	34	0.1
Pct cover of shrubs	22,236	141	0.5
Pct cover of rocks	22,218	33	0.1
Litter depth	22,191	96	0.4
Easting	22,274	179	0.7
Northing	22,140	45	0.2

<sup>1</sup>Test deviance = (deviance of full model less one covariate) - (deviance of Full model)

<sup>2</sup>Null model is the model with only the intercept parameter in it.

<sup>3</sup>Full model is the model including the intercept parameter and all six explanatory variables.

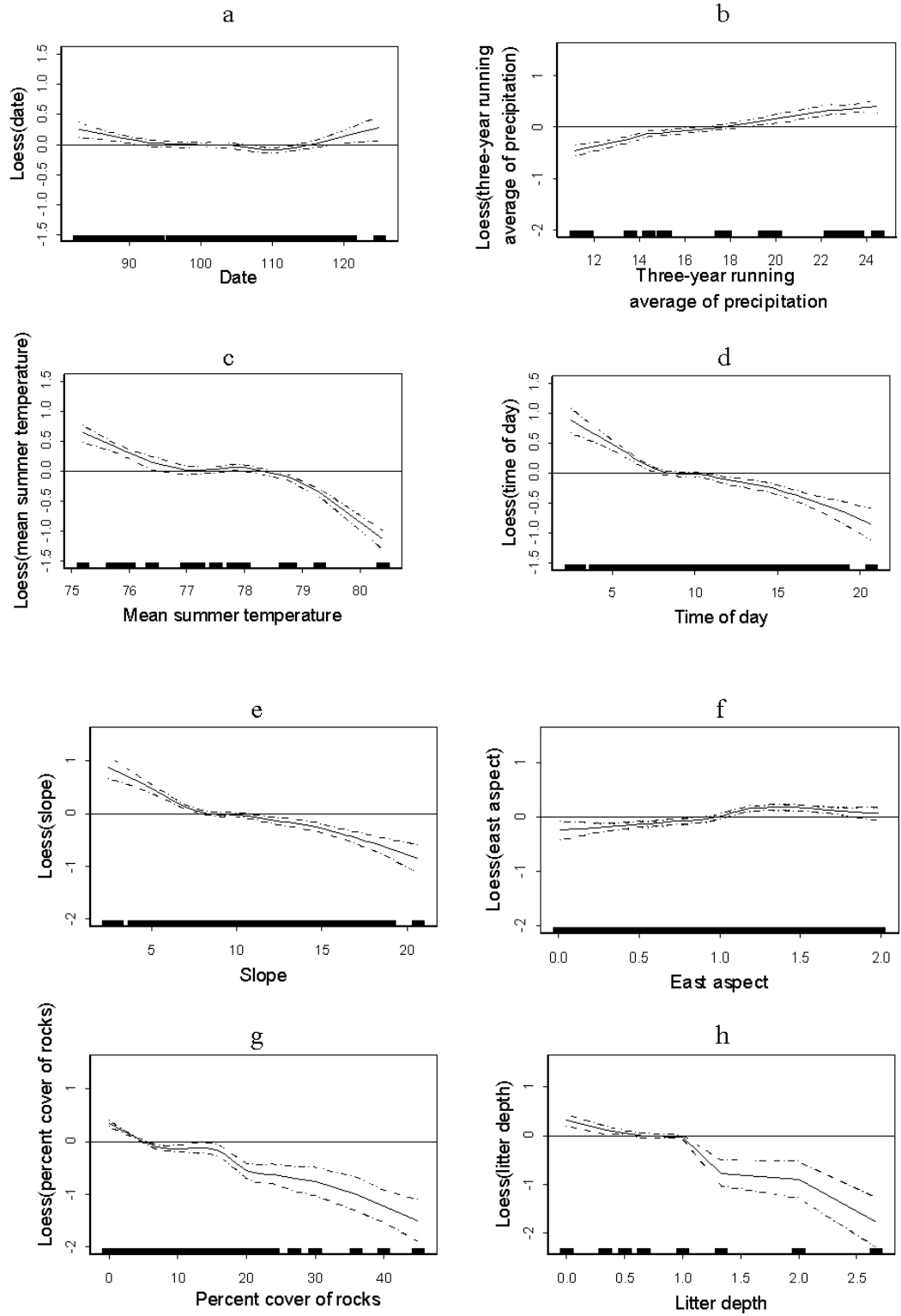
<sup>4</sup>Aspect is transformed to reflect east-west continuum as discussed in text.

## Discussion and Conclusions

### Trend in Abundance

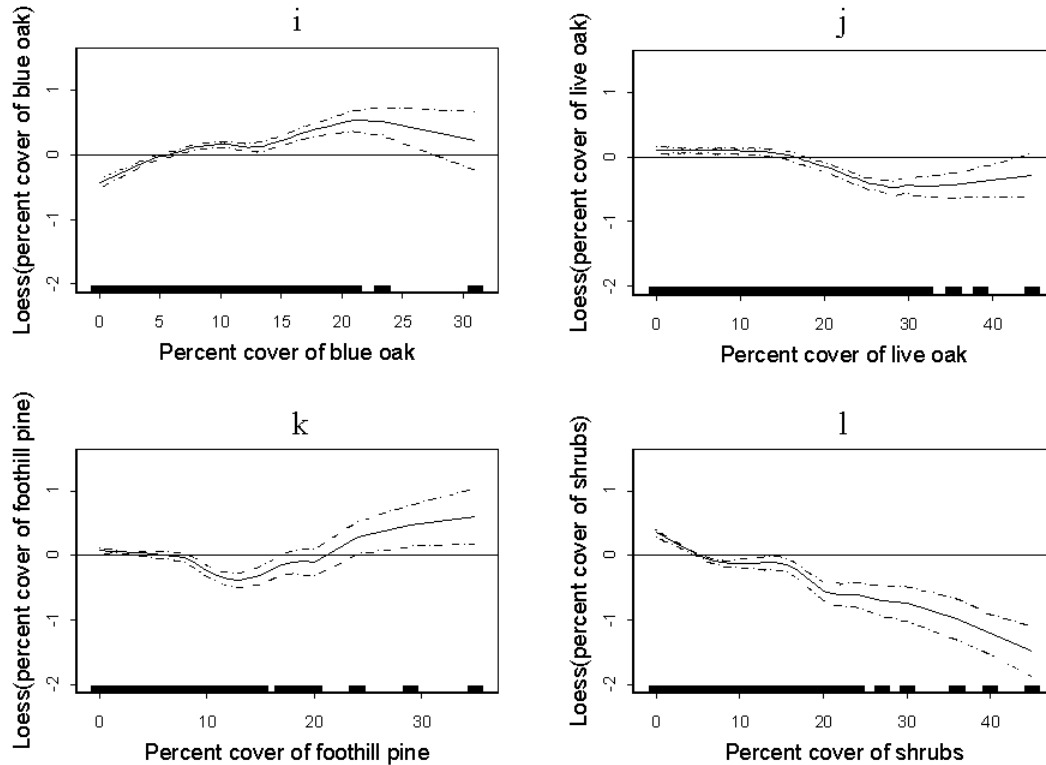
From the first sightings in the late 1960s to becoming an abundant breeding species, starlings have clearly increased at SJER. The primary period of increase, however, occurred prior to the initiation of this study. During the period of this study, it seems that numbers of starlings follow precipitation and temperature patterns.

Our results show that simple models of population trends can give spurious results when appropriate explanatory variables are not included. Correlated variables responsible for apparent, usually short-term, increases or decreases in population numbers need to be recorded, examined, and included in models if we are to have any faith in results of trend analyses. Starling abundance and presence showed a significant increasing trend over time when *route* and *year* were the only explanatory variables (*figs. 2a, 4a*), but with the best explanatory variables present in the model, the yearly trend in starling abundance was nonsignificant.



(Figure 5 continued on next page)

(Figure 5 continued)



**Figure 5**—Plots of smoothing functions from the full nonparametric logit model for starling presence/absence response estimated by GAM, showing (a) increasing presence on early and late counting dates; (b) increasing presence with the 3-year running average of precipitation; (c) decreasing presence with mean summer temperature; (d) higher detectability in the hour following sunrise; (e) decreasing presence with increasing slope; (f) increasing detections on east-facing slopes; (g) increasing presence with decreasing cover of rock and (h) decreasing litter depth; increasing presence with (i) increasing cover of blue oak, (j) interior live oak, and (k) foothill pine; (l) decreasing cover of shrubs. The bars along the x-axis show the distribution of data along the axis.

If multiyear rainfall patterns do, in large part, determine starling abundance at SJER, we expect that starling abundance will decrease during the next drought. The higher abundance of starlings in years after wet, warm winters and cool summers is probably indirectly related to higher productivity and resulting higher recruitment, although movement to more suitable or productive sites is also likely. The crucial question remains whether starling numbers have reached a plateau around which they will fluctuate at SJER, or whether they will continue to increase in the future.

Food resources are limiting for starlings in the summer months in Europe, where starlings are native (Feare 1985), and probably also here as described below. Arthropod numbers follow the pattern of soil moisture at SJER (Burdick and others 1989), and soil arthropods—the primary food of starlings during the breeding season (Feare 1985)—are most abundant during fall and winter, becoming scarce during the dry summer months as the ground dries and hardens and as insect larvae mature and leave the soil (Burdick and others 1989, Feare 1985). Thus, low starling abundance after hot, dry summers follows naturally. In dry years, starlings nearly disappear from SJER during July and August (K. Purcell, personal observation). Wet winters allow swales to remain moist longer into the summer months and are conducive to high starling abundance.

### **Habitat Relations**

The predictive power of our habitat model was low due to the loose association between locations where starlings were detected and where habitat data were collected. We do, however, have some idea of the scales involved. While starlings sometimes fly long distances between roost sites and foraging locations at other times of the year, foraging locations during the breeding season are closer to nests—generally within 200 m but rarely up to 500 m (Feare 1984). While the predictive power of our model would likely improve without the spatial sampling noise in our data, we believe that the distances starlings fly are generally smaller than the scale at which we see changes in most of the habitat variables. Starlings were found in level, open habitat that had low cover of shrubs and live oaks. The suitability of level or rolling terrain is likely related to the presence of swales and their moist soils. Duncan and others (1985) reported an early observation of large flocks of starlings feeding on crane fly larvae (*Tipulidae* spp.) in swales at SJER, and preliminary data on starling foraging indicate a preference for swales (V. Wible, personal communication). Starlings appeared to avoid areas with a high density of understory—areas with shrubs and live oaks, with a shrub-like growth form. Starlings were found in areas with high cover of blue oaks. Blue oak saplings are shade intolerant, and stands of blue oaks tend to be more open than mixed stands (Verner 1988). Litter depth and rock cover were also important variables in predicting starling presence, with starlings avoiding areas with deep litter and high rock cover. These results are all consistent with the foraging needs of starlings—open, level areas with comparatively well-developed, accessible soil. Also consistent with foraging needs, starlings were found on east-facing slopes during the cool morning hours of spring where the sun would warm both the birds and their soil-dwelling prey.

Starlings have the potential to affect the diversity and resilience of the ecological community and regional biodiversity as a whole, yet we have little knowledge of factors affecting their abundance and distribution. When starlings first appeared at SJER, their distribution was local and centered around areas of human disturbance. To successfully invade oak woodlands, they had to adapt to the physical and biological conditions present. Food resources in the soil were available as long as the soil retained moisture, but to breed successfully, starlings must locate adequate food resources during the entire breeding season. Although oak woodlands may not be optimal habitat for starlings, they have nonetheless adapted to local conditions and successfully invaded these woodlands in the foothills of central California.

## Future Work

Ongoing studies at SJER are investigating starling nesting and foraging ecology. One study is examining the overlap in laying dates and nest-site parameters between starlings and native cavity-nesting birds and the behavioral responses of native cavity nesters to starlings at their nests. We are also comparing soil arthropods among soil samples from starling foraging locations, random soil samples, and starling stomach samples. We continue to look for relations between starlings and their resource base. We hypothesized that starlings might avoid foraging in areas with tall grasses and forbs and high residual dry matter, such as the ungrazed Research Natural Area at SJER, because of a reduced ability to detect predators, reduced foraging efficiency, decreased maneuverability, or some combination of these factors. Our present results suggest that litter depth, not grass/forb height, explained starling occurrence and that the presence of residual dry matter is a deterrent to starling foraging. Differences in the abundance and composition of soil arthropods might also account for avoidance of ungrazed pastures. Preliminary results from our ongoing studies suggest that soil arthropods differ in abundance and species composition between ungrazed and grazed pastures. Grazed pastures were dominated by springtails (collembola), while samples from the Research Natural Area had a more balanced arthropod fauna.<sup>4</sup> Insectivorous birds of farmlands have been shown to prefer moderately or intensively grazed pastures (Söderström and others 2001). Morris and Thompson (1998) showed that the abundance of brown-headed cowbirds (*Molothrus ater*) was related to livestock presence and coincident high invertebrate densities, while grass height was of secondary importance. Our understanding of the starling's role in the foothill woodland ecosystem is still far from adequate. For example, we know little about their effects, if any, on the abundance and productivity of native cavity-nesting species, or about the effects of various management practices on their abundance. We do know from many studies elsewhere, however, that the addition of non-native species, compounded by habitat loss, may have significant deleterious effects on native species and the conservation and production values of ecosystems. Given the high species richness of the oak woodland avifauna, and specifically that of cavity-nesting birds (Verner and others 1997), the invasion by starlings is a real concern because of their potential for competition with native species.

## Acknowledgments

We thank those who assisted with fieldwork: Laura Arnow, Parker Backstrom, Susan Balch, Ken Burton, Sandra Cederbaum, Chris Cutler, Jeff Davis, Doug Drynan, Matt Georgeff, Brian Gibson, Ellen Hammond, Kim Kuska, Zev Labinger, Peter Landres, John Lovio, Rod MacDonald, Bill Maynard, Kevin Mazzocco, Rolf Miller, Kathy Granillo, Dan Nelson, Barbara North, Kathleen Brubaker, Coleen Pidgeon, Rick Reynolds, Jeff Seay, Tim Schantz, Curt Steggall, Susan Sutton-Mazzocco, Kim Suryan, Rob Suryan, Robert Suydam, Dan Taylor, Tracy Tennant, David Tibor, Jennifer Turner, and Ed Whisler. Doug Drynan prepared *figure 1*. Bill Block generously provided vegetation data for the counting stations. We thank Haiganoush Preisler for her statistical advice and review of an earlier version of this manuscript. Constructive reviews of a draft manuscript were provided by Walt Koenig and Barry Garrison. To all we extend our deep appreciation.

<sup>4</sup> Unpublished data on file, Nancy Rappaport, Pacific Southwest Research Station, Albany, Calif.

## References

- Beers, Thomas W.; Dress, Peter E.; Wensel, Lee C. 1966. **Aspect transformation in site productivity research.** *Journal of Forestry* 64: 691-692.
- Block, William M. 1989. **Spatial and temporal patterns of resource use by birds in California oak woodlands.** Berkeley: University of California; 364 p. Ph.D. dissertation.
- Burdick, Donald, J.; Duncan, Don A.; Hasegawa, Craig T.; Larson, Jeanne R. 1989. **Arthropods on an annual grassland at the San Joaquin Experimental Range.** CATI/890806. Fresno: California Agricultural Technology Institute, California State University; 68 p.
- Duncan, Don A.; Ritter, Lyman V.; Newman, Thomas F. 1985. **Vertebrate fauna of the San Joaquin Experimental Range, California: a 50-year checklist.** CATI/850901. Fresno: California Agricultural Technology Institute, California State University; 41 p.
- Feare, Christopher J. 1984. **The Starling.** New York: Oxford University Press; 315 p.
- Feare, Christopher J. 1985. **The Starling.** Aylesbury, UK: Shire Publications, Ltd.; 24 p.
- Hastie, Trevor J. 1993. **Generalized additive models.** In: Chamber, J.M.; Hastie, T.J., eds. *Statistical Models.* New York: Chapman & Hall; 250-307.
- Hastie, Trevor J; Tibshirani, Robert. 1990. **Generalized additive models.** London: Chapman and Hall; 335 p.
- Hobbs, Richard J.; Mooney, Harold A. 1998. **Broadening the extinction debate: population deletions and additions in California and Western Australia.** *Conservation Biology* 12:271-283.
- Ingold, Danny J. 1989. **Nesting phenology and competition for nest sites among Red-headed and Red-bellied Woodpeckers and European Starlings.** *Auk* 106: 209-217.
- Jewett, Stanley G. 1942. **The European Starling in California.** *Condor* 44: 79.
- Kessel, Brina. 1953. **Distribution and migration of the European Starling in North America.** *Condor* 55: 49-67.
- Knapp, Roland A.; Preisler, Haiganoush K. 1999. **Is it possible to predict habitat use by spawning salmonids? A test using California golden trout (*Oncorhynchus mykiss aguabonita*).** *Canadian Journal of Fisheries and Aquatic Science* 56: 1576-1584.
- Larson, Diane L; Bock, Carl E. 1989. **Determining avian habitat preference by bird-centered vegetation sampling.** In: Verner, Jared; Morrison, Michael L; Ralph, C. John, eds. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates.* Madison, WI: University of Wisconsin Press; 37-43.
- MathSoft. 1999. **S-PLUS 2000 user's guide.** Seattle, WA: Data Analysis Products Division, MathSoft, Inc; 557 p.
- McCullagh, Peter; Nelder, John A. 1991. **Generalized linear models.** New York: Chapman & Hall; 511 p.
- Morris, Dana L.; Thompson, Frank R. III. 1998. **Effects of habitat and invertebrate density on abundance and foraging behavior of brown-headed cowbirds.** *Auk* 115: 376-385.
- Purcell, Kathryn L. 1995. **Reproductive strategies of open- and cavity-nesting birds.** Reno: University of Nevada; 110 p. Ph.D. dissertation.
- Robbins, Chandler. S.; Erskine, Anthony J. 1975. **Population trends in nongame birds in North America.** *Transactions of the North American Wildlife and Natural Resources Conference* 40: 288-293.

- SAS Institute, Inc. 2000. **SAS procedures guide, version 8, volumes 1 and 2, release 8.2.** Cary, NC: SAS Institute, Inc; 1675 p.
- Short, Lester L. 1979. **Burdens of the picid hole-excavating habit.** *Wilson Bulletin* 91: 16-28.
- Sillett, T. Scott; Holmes, Richard T.; Sherry, Thomas W. 2000. **Impacts of a global climate cycle on population dynamics of a migratory songbird.** *Science* 288: 2040-2042.
- Small, Arnold. 1994. **California birds: their status and distribution.** Vista, CA: Ibis Publishing; 342 p.
- Söderström, Bo; Pärt, Tomas; Linnarsson, Erik. 2001. **Grazing effects on between-year variation of farmland bird communities.** *Ecological Applications* 11: 1141-1150.
- Troetschler, Ruth G. 1976. **Acorn Woodpecker breeding strategy as affected by starling nest-hole competition.** *Condor* 78: 151-165.
- Venables, William N.; Ripley, Brian D. 1997. **Modern applied statistics with S-PLUS.** New York: Springer; 548 p.
- Verner, Jared. 1988. **Blue oak—digger pine.** In: Mayer, Kenneth E.; Laudenslayer, William F., Jr., eds. *A guide to wildlife habitats of California.* Sacramento, CA: California Department of Forestry and Fire Protection; 80-81.
- Verner, Jared; Milne, Kathleen A. 1989. **Coping with sources of variability when monitoring population trends.** *Annales Zoologici Fennici* 26: 191-199.
- Verner, Jared; Purcell, Kathryn L. 1999. **Fluctuating populations of House Wrens and Bewick's Wrens in foothills of the western Sierra Nevada in California.** *Condor* 101: 219-229.
- Verner, Jared; Purcell, Kathryn L.; Turner, Jennifer G. 1997. **Bird communities in grazed and ungrazed oak-pine woodlands at the San Joaquin Experimental Range.** In: Pillsbury, Norman H.; Verner, Jared, Tietje, William D., tech. coords. *Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues.* Gen. Tech. Rep. PSW-GTR-160. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 381-390.
- Weitzel, Norman H. 1988. **Nest-site competition between the European Starling and native breeding birds in northwestern Nevada.** *Condor* 90: 515-517.
- Zeleny, Lawrence. 1978. **Nesting box programs for bluebirds and other passerines.** In: Temple, S. A., ed. *Endangered birds: management techniques for preserving threatened species.* Madison: University of Wisconsin Press; 55-60.