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Source: Journal of Raptor Research, 45(3) : 236-243

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-10-66.1

J. Raptor Res. 45(3):236–243

SEX-RELATED DIFFERENCES IN HABITAT ASSOCIATIONS OF WINTERING AMERICAN KESTRELS IN CALIFORNIA'S CENTRAL VALLEY

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ABSTRACT.—We used roadside survey data collected from 19 routes over three consecutive winters from 2007–08 to 2009–10 to compare habitat associations of male and female American Kestrels (*Falco sparverius*) in the Central Valley of California to determine if segregation by sex was evident across this region. As a species, American Kestrels showed positive associations with alfalfa and other forage crops like hay and winter wheat, as well as grassland, irrigated pasture, and rice. Habitat associations of females were similar, with female densities in all these habitats except rice significantly higher than average. Male American Kestrels showed a positive association only with grassland and were present at densities well below those of females in alfalfa, other forage crops, and grassland. Males were present in higher densities than females in most habitats with negative associations for the species, such as orchards, urbanized areas, and oak savannah. The ratio of females to males for each route was positively correlated with the overall density of American Kestrels on that route. Our findings that females seem to occupy higher quality habitats in winter are consistent with observations from elsewhere in North America.

KEY WORDS: *American Kestrel*; Falco sparverius; *Central Valley*; *habitat association*; *sex*; *winter*.

DIFERENCIAS DE ASOCIACIÓN DE HÁBITAT RELACIONADAS CON EL SEXO EN INDIVIDUOS INVERNANTES DE *FALCO SPARVERIUS* EN EL VALLE CENTRAL DE CALIFORNIA

RESUMEN.—Utilizamos datos recolectados en 19 rutas en carreteras durante tres inviernos consecutivos desde 2007–08 a 2009–10 para comparar las asociaciones de hábitat de machos y hembras de *Falco sparverius* en el Valle Central de California y para determinar si la segregación por sexo fue evidente en esta región. Como especie, *F. sparverius* mostró asociaciones positivas con el cultivo de alfalfa y otros forrajes como heno y trigo de invierno, así como pastizales, pastos de regadío y cultivos de arroz. Las asociaciones de hábitat de las hembras fueron similares, con densidades de hembras significativamente mayores a la media en todos estos hábitats con excepción del cultivo de arroz. Los machos mostraron una asociación positiva sólo con pastizales y estuvieron presentes en densidades muy inferiores a las de las hembras en el cultivo de alfalfa, otros forrajes y pastizales. En la mayoría de los hábitats los machos estuvieron presentes en densidades más altas que las hembras y con asociaciones negativas para la especie con huertos, zonas urbanizadas y la sabana de roble. El cuociente entre hembras y machos para cada ruta se correlacionó positivamente con la densidad total de individuos de *F. sparverius* en esa ruta. Nuestro hallazgo, de que las hembras parecen ocupar hábitats de mayor calidad en invierno, son consistentes con las observaciones de otras partes de América del Norte.

[Traducción del equipo editorial]

The American Kestrel (*Falco sparverius*) shows marked sexual segregation by habitat type throughout much of its winter range (Smallwood and Bird 2002). Females tend to occupy more open habitats

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than males in California (Koplin 1973, Meyer and Balgooyen 1987), Georgia (Stinson et al. 1981), Florida (Bohall-Wood and Collopy 1986, Smallwood 1987), Pennsylvania (Ardia and Bildstein 2001), and in several areas of southwestern North America (Mills 1976). Females occupy habitats of higher quality than males (Smallwood 1987, 1988, Meyer and Balgooyen 1987, Ardia and Bildstein 1997, 2001, Ardia 2002). Arnold and Martin (1991) found no difference in habitat use between males and females in winter in Ontario, Canada. However, they concluded this was due to the fact that lower densities of American Kestrels at the northern edge of the winter range (Root 1988, Arnold 1991) produce less competition between sexes, thus permitting more uniform distribution by sex across habitat types. Ardia and Bildstein (2001) also suggested a relationship between local density of kestrels and female dominance of better habitats.

Hypotheses proposed to explain sexual segregation by habitat in the American Kestrel fall into three categories. Koplin (1973), Stinson et al. (1981), and Meyer and Balgooyen (1987) proposed that males and females are adapted to use different habitat types, possibly to minimize intraspecies competition during winter. Mills (1976), Ardia and Bildstein (1997, 2001) and Ardia (2002) suggested that females exclude and/or displace males from the best habitats. Smallwood (1988), although agreeing that females occupy the better habitats, proposed that they dominate those habitats mainly because females arrive on the wintering grounds earlier than males.

We used data from 19 roadside survey routes throughout the Central Valley of California to compare winter distribution of female and male American Kestrels across different habitat types. We tested the hypothesis that females occupy higher quality habitats in winter. We examined this question across a broader geographic scale and using more precisely determined habitat categories than any prior study.

METHODS

Study Area. The Central Valley is one of California's dominant geographic features. It is divided into the Sacramento Valley, which drains southward, the San Joaquin Valley, which drains northward, and the Sacramento–San Joaquin River Delta, where these rivers converge. For the purposes of this study, we defined the Central Valley as the valley floor up to 300 m and including a portion of the San Francisco Bay Delta region in Sacramento, Solano, and San Joaquin counties.

Survey Routes and Habitat Assessment. We established 19 roadside survey routes throughout the Central Valley, from Shasta County in the north to Kings County in the south (Fig. 1), to count open-country raptors during winter. These surveys were designed as area searches for raptors along the chosen survey road. Average route length was 59 km (range 44–81 km, SD = 8). We selected routes that covered mostly open country to facilitate location of raptors. Routes generally followed secondary roads with low to moderate traffic to facilitate safe observation and identification of perched and flying raptors. We also attempted to include representative examples of all major land cover types within the area.

We characterized habitat along routes just prior to each survey season by driving each route. Beginning at the start of each route, we established habitat blocks on either side of the survey road at 0.8 km intervals. Each block measured 500 m $\times$ 800 m, with the roadside edge centered at each 0.8 km point and extending away from the road 500 m perpendicular to the road, and up and down the survey road 400 m in each direction. UTM coordinates were recorded at each point. We visually determined the dominant (>50%) habitat type of each block. In the great majority of cases (>90%), a given block consisted of a single habitat type. We calibrated survey vehicle odometers to that of the vehicle used on habitat assessments to ensure mileages recorded on raptor surveys matched habitat block locations.

Habitat Categories. We assigned a dominant habitat to each block chosen from 12 habitat categories (Table 1). For our purposes, these habitat categories are based almost entirely on the dominant vegetative cover present. For planted crops, our assessments did not differentiate the stage of development, which ranged from recently planted to post-harvest stubble.

Survey Methods. Survey teams included a minimum of two observers, at least one of whom was experienced at raptor identification and capable of consistently identifying all expected species. Surveys were run at least once per month during winter (December through February). We used this period since this better represents the meteorological winter season in California than the calendar definition of winter (Alpert et al. 2004). Surveys began between 0800–1000 PST and ended no later than 1500 PST. Each route was run in the same direction

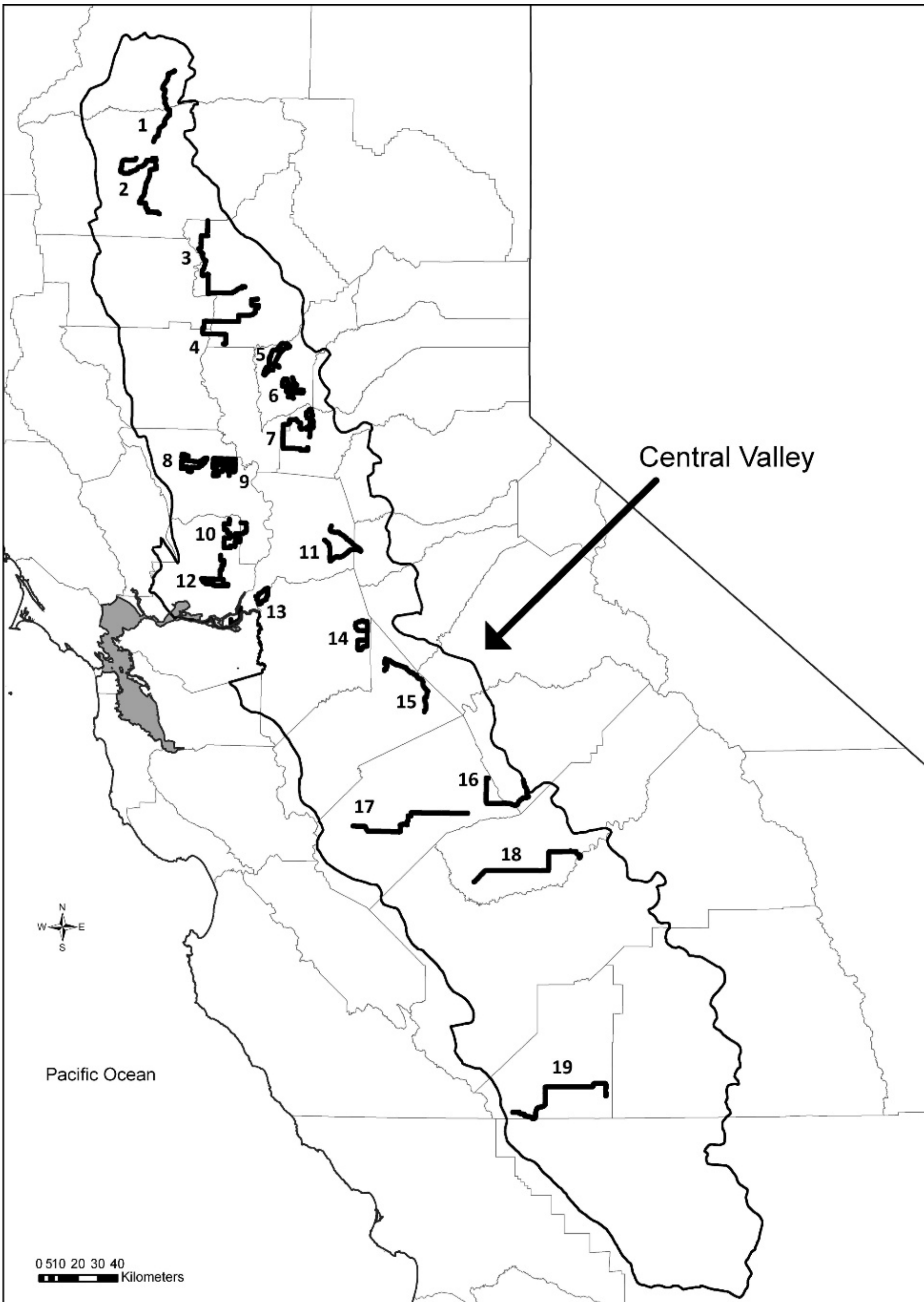

Figure 1. Map of the survey routes. Routes are numbered as follows: 1-Shasta, 2-Tehama, 3-Butte N., 4-Butte S., 5-Yuba, 6-Beale, 7-Lincoln, 8-Dunnigan Hills, 9-Woodland, 10-Davis, 11-Folsom, 12-Jepson, 13-Delta, 14-Linden, 15-Oakdale, 16-LeGrand, 17-Los Banos, 18-Madera, 19-Kings.

Table 1. Descriptions of habitat categories.

HABITAT CATEGORY	DESCRIPTION
Grassland	Grazed, ungrazed, and burned annual grasslands and scrub grasslands with some salt-tolerant shrubs (all nonirrigated)
Row crop	Row crop planted in spring and summer consisting mainly of plowed fields in winter
Rice	Rice fields, mostly flooded or burned in winter
Orchard	Wide variety of crops (almond, walnut, etc.) and ages of trees
Urbanized	Mainly residential and rural residential
Pasture	Irrigated pasture
Savannah	Mainly blue oak (*Quercus douglasii*) at 10–30% canopy cover
Alfalfa	Both unharvested and recently harvested fields
Wetland	Natural and human-made wetlands
Other forage	Mainly hay and winter wheat
Vineyard	Mostly mature plants and typical vineyard support structures
Other	Diverse group of habitats, each present in small amounts, including fallow fields, open water, riparian-dominated areas, etc.

to facilitate the use of odometer readings to place bird observations in the correct habitat block. Bunn et al. (1995) showed time-of-day effects on numbers and behavior of some raptors, though not for American Kestrels. Given the large number of routes we surveyed, the wide variety of habitats on each route, and the fact that each survey included both morning and afternoon hours, it is unlikely that time-of-day would have had significant effects on observed habitat associations. Surveys were postponed or interrupted for heavy fog, precipitation, high winds (>30 km/hr or Beaufort scale 4) or any condition that limited visibility to less than 500 m. Average driving speed was 15 km/hr (range 11–25 km/hr, SD = 4) with frequent stops to identify birds or allow traffic to pass. All raptors observed within 500 m of the survey road were counted. We recorded species, sex, behavior (perched or flying), perch type, side of the survey road, and mileage to the nearest tenth of a mile from the start of the survey. We recorded location and behavior when a bird was first observed and recorded the mileage along the survey road at the shortest perpendicular distance from the survey road to the bird. The mileage was used to place each observation into a specific habitat block, after calibration of the survey vehicle odometer to that of the habitat assessment vehicle.

Statistical Analyses. We used generalized linear models (McCullagh and Nelder 1989) with an assumed Poisson distribution, using numbers of individuals per block as the response variable. We limited our fixed effects to habitat and sex. We ran all possible combinations of models (including the interaction of habitat and sex). Results presented are model-averaged density predictions based on model weights developed from AICc scores of each model (Burnham and Anderson 2002). Birds were considered to show a positive association with a given habitat when the predicted density in that block was significantly greater than the average density over all habitats, and considered to show a negative association when the density was significantly less than the average. To determine if female:male ratios by habitat were relatively consistent between different survey routes, we compared those ratios in given habitat types across all routes that included at least 200 ha of that habitat type. We also examined correlations between American Kestrel density and the ratio of females:males using linear regression.

RESULTS

The average number of surveys of each route during the study was 9.5 (SD = 1.3, range 7–12). We recorded 3672 observations of American Kestrels, 1575 of which were identified as females and 1239 of which were identified as males, with the remainder identified only to species. Overall, the species showed significant positive associations with alfalfa, other forage, grassland, pasture, and rice and negative associations with orchards, urbanized areas, oak savannah, vineyards, row crops, and other (Fig. 2).

We used Akaike's Information Criterion (AICc) to assess model fit for each possible model (Table 2). Model predictions were calculated as the model-averaged values for predictions from all 5 of the alternative models, weighting each models' predictions by the model-weight, derived from the

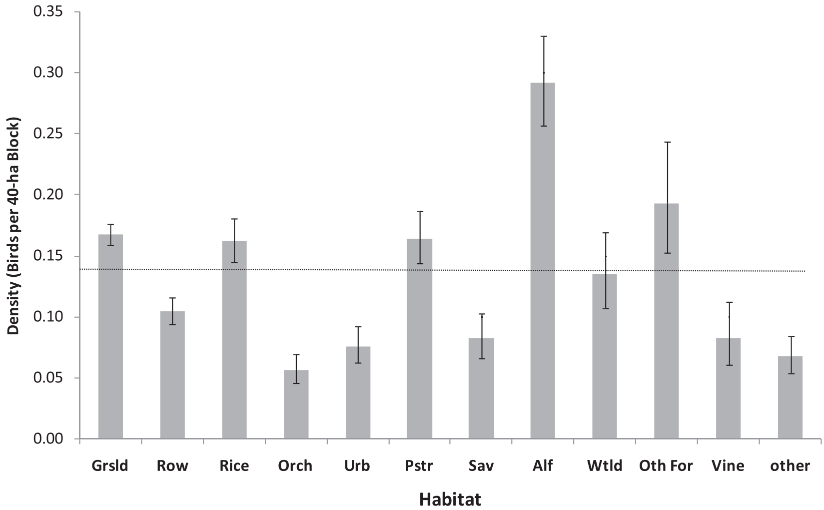

Figure 2. Density (birds per 40 ha block) all American Kestrels by habitat type. The horizontal line represents the average density over all habitats. Error bars represent 95% C.I. (Grsld = grassland, Row = row crop, Orch = orchard, Urb = urbanized, Pstr = irrigated pasture, Sav = savannah, Alf = alfalfa, Wtld = wetland, Oth For = other forage, Vine = vineyard).

AICc score. Thus, these predictions incorporate not only the variation around the prediction of the model, but also model selection uncertainty (Burnham and Anderson 2002).

Females showed positive associations with most (4 of 5) habitats with which the species was positively associated, with rice the only exception. However, males showed a positive association only with grassland. Overall, males were more evenly distributed across the habitat types than females. Females showed significant negative associations with urbanized areas, savannah, orchards, wetland, and other. All these, except wetland, also showed negative associations for the species as a whole. The density of females and males by habitat type (Fig. 3) showed marked differences in distribution with females present in alfalfa and other forage at densities nearly 4 times that of males. Male density in savannah, orchard, and wetland was approximately twice as high as female density in these habitats.

We determined that the distribution of females and males by habitat type was consistent between different survey routes by comparing ratios of females to males for selected habitats across all routes that included at least 200 ha of that habitat type (Table 3). Across most routes, females outnumbered males in habitats with which the species was positively associated and males outnumbered females across most routes in habitats with which the species was negatively associated. There was a significant positive correlation between overall American Kestrel density across a route and the ratio of females to males on that route (Fig. 4; $r^2 = 0.4$, $P < 0.01$).

Table 2. Models and model selection statistics used to predict the number of individuals detected per block.

MODELS	k[a]	AIC_c	DELTA AIC_c	MODEL WEIGHT	MODEL LIKELINESS
Habitat + sex + habitat × sex	24	21943	0.0	1	1
Habitat + sex	13	22063	120	7.38E-27	7.38E-27
Habitat	12	22103	161	1.37E-35	1.37E-35
Sex	2	22469	526	5.13E-115	5.13E-115
Intercept only	1	22509	567	9.53E-124	9.53E-124

[a] Number of parameters estimated by each model.

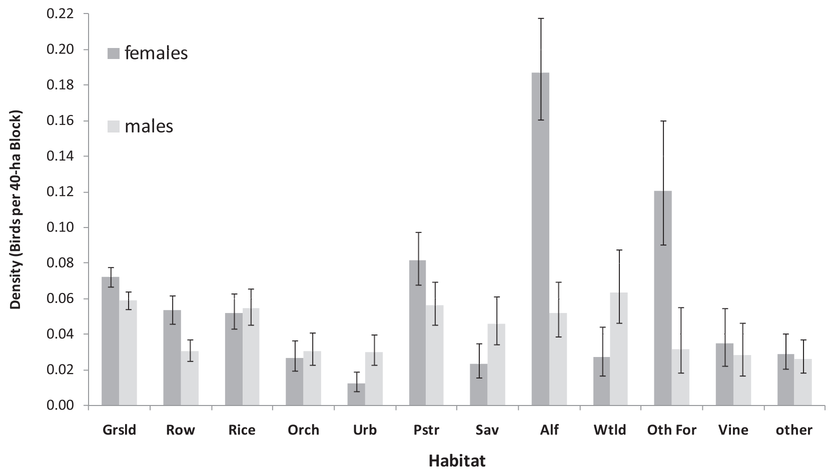

Figure 3. Comparison of density (birds per 40 ha block) of female and male American Kestrels by habitat type. Error bars represent 95% C.I. (Grsld = grassland, Row = row crop, Orch = orchard, Urb = urbanized, Pstr = irrigated pasture, Sav = savannah, Alf = alfalfa, Wtld = wetland, Oth For = other forage, Vine = vineyard).

DISCUSSION

Our results confirm previous work documenting significant winter segregation of American Kestrels by sex (Smallwood and Bird 2002) and are consistent with the findings of most authors (Mills 1976, Smallwood 1988, Ardia and Bildstein 1997, 2001, Ardia 2002) that females generally occupy the better habitats. We found that habitat associations of females closely resembled that of the species as a whole, with strong positive associations with alfalfa and other forage crops, whereas males showed a positive association with only grassland. Female densities were much higher than those of males in alfalfa and other forage, whereas males' densities were higher than females' in negatively associated habitats like urbanized areas and oak savannah. This appears to be true across a wide geographic scale in the Central Valley, as most routes recorded more females than males in positively associated habitats and more males than females in negatively associated ones. These findings suggest that habitat

Table 3. Comparison of percent of routes with female: male American Kestrels ratios greater than 1.0 between habitat types.

HABITAT TYPE	NUMBER OF ROUTES[a]	ROUTES WITH FEMALE:MALE >1 FOR THAT HABITAT	
		n	(%)
Habitats with positive association			
Alfalfa	6	6	(100%)
Other forage	4	3	(75%)
Grassland	17	11	(65%)
Pasture	13	7	(54%)
Rice	4	2	(50%)
Habitats with negative association			
Orchard	8	3	(38%)
Other	10	4	(40%)
Urbanized	14	4	(27%)
Savannah	6	2	(33%)
Vineyard	4	2	(50%)
Row crop	13	5	(38%)

[a] Routes which include ≥200 ha of the specified habitat type.

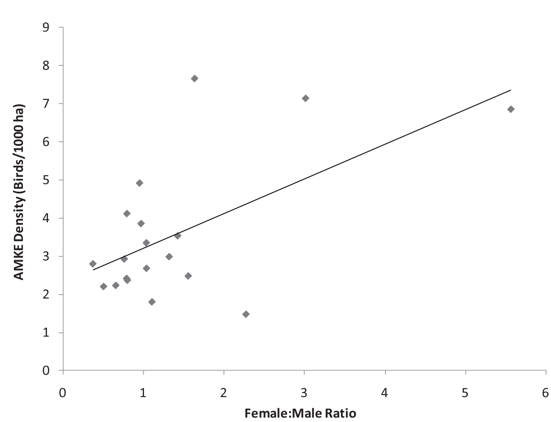

Figure 4. Linear regression of American Kestrel (AMKE) density (birds/1000 ha) by route vs. ratio of females:males on that route.

quality may play a significant role in determining the winter distribution of male and female American Kestrels in the Central Valley. Our intent was to compare distributions of female and male kestrels over a larger geographic scale and a wider variety of habitat types than previous studies. Therefore, we were not able to assess the potential importance of fine-scale elements within individual habitat blocks (e.g., perch types or density) to relative densities of the two sexes.

Prior studies proposed two different hypotheses to explain the preponderance of females in higher quality habitats. Mills (1976), Ardia and Bildstein (1997, 2001) and Ardia (2002) all suggested that females outcompete males for the best winter habitats. Smallwood (1998) proposed that females dominate those habitats by arriving earlier than males and that either sex, once established on a winter territory, is usually able to hold that territory.

Analyses of Christmas Bird Count data (Root 1988, Arnold 1991) showed that density of American Kestrels is highest in the more temperate areas of the species' winter range. Arnold and Martin (1991) and Ardia and Bildstein (2001) both suggested that higher local density of American Kestrels creates more competition for winter territories, which leads to the higher ratios of females to males observed in these areas. We found a positive correlation between the density of American Kestrels and female to male ratios on the routes we surveyed, consistent with this suggestion. However, this correlation does not necessarily support the notion that females are dominating higher quality habitats by directly competing with males. Higher kestrel density on these routes could be a result of a higher proportion of high quality habitat on those routes, which could be dominated by females due to their arriving earlier than males.

Our results support the suggestion that female American Kestrels occupy the higher quality habitats in winter. Whether this dominance is due to direct competition between the sexes during winter or is the result of females arriving earlier on the wintering grounds is debatable. Further studies to test the dynamics of interactions between female and male American Kestrels in fall, especially in areas with high winter ratios of females to males, could shed light on this question.

ACKNOWLEDGMENTS

This work would not have been possible without the devotion of considerable time and effort by the volunteers who helped run the surveys: Steve Abbott, Roger Adamson, Dan Brown, Ken Burton, Walt Carnahan, Chuck Carroll, Helene Cavoir, Debbie Daley, Bruce and Kathy Deuel, Julie Dinsdale, J. Frank, Alan England, Tim Fitzer, B. Getty, Jim Groesser, Ed Harper, Ken Hashagen, Lois Hoy, Scott and Liam Huber, Sami LaRocca, John Lewis, E. Long, Len Mackenzie, Joe Medley, Zach Miller, Frances Oliver, Harold and Sue Reeve, Phil Robertson, Jeff Seay, Mike Skram, Dan Stewart, Steve and Priscilla Summers, Craig Swolgaard, Dave Wagner, Heath Wakelee, Bruce Webb, Gary Woods, Lowell Young, and Bob and Carol Yutzy. We thank Stacie Hooper for preparing the map of the survey routes. Sid England and John Sterling provided suggestions for improving the study design. Daniel Ardia made very helpful suggestions on an earlier draft of this manuscript. The final product was much improved by suggestions from Keith Bildstein, Cheryl Dykstra, Chris Farmer, and Daniel Varland. We are grateful for logistical support from Central Valley Bird Club and for funding received from Altacal Audubon Society, California Rangeland Conservation Coalition, California Rice Commission, Central Valley Bird Club, Sacramento Audubon Society, San Joaquin Audubon Society, Sierra Foothills Audubon Society, Stanislaus Audubon Society, U.S. Fish and Wildlife Service, and Yolo Audubon Society.

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Received 29 July 2010; accepted 29 March 2011
Associate Editor: Christopher J. Farmer