Factors Affecting Detection Probability of Burrowing Owls in Southwest Agroecosystem Environments

Author(s): Jeffrey A. Manning
Source: Journal of Wildlife Management, 75(7):1558-1567. 2011.
Published By: The Wildlife Society
URL: http://www.bioone.org/doi/full/10.1002/jwmg.192

The Journal of Wildlife Management 75(7):1558–1567; 2011; DOI: 10.1002/jwmg.192

Research Article

Factors Affecting Detection Probability of Burrowing Owls in Southwest Agroecosystem Environments

JEFFREY A. MANNING,[1] *Fish and Wildlife Resources, College of Natural Resources 107, University of Idaho, Moscow, ID 83844-1136, USA*

ABSTRACT Estimating range-wide population trends of western burrowing owls (*Athene cunicularia*) requires standardized survey protocols that correct for detection bias in environments that support large owl populations. High concentrations of owls exist in irrigated agroecosystems within the southwest United States, yet little is known about the factors that affect detection bias during owl surveys in these systems. I used closed-population capture-recapture models to evaluate 4 factors that could affect the probability of a surveyor detecting an owl activity center (i.e., nest burrow) during visual surveys where owls are the focal object and analyzed the relationship (linear or curvilinear) between specific factors and detection probability. I recorded 1,199 detections of owls from 132 capture-recapture surveys within 12 sites of the Imperial Valley agroecosystem in California, USA between 16 April and 20 May 2006. I also conducted 96 time budget surveys throughout the day and used mixed linear models to evaluate the effect of each factor on probability of an owl activity center being available for detection (i.e., $\geq$1 owls above ground) during surveys. Model selection results indicated that detection probability was influenced by ambient air temperature interacting with wind speed. Detection probability followed a curvilinear relationship that resembled bell-shaped curve along a temperature gradient, with the maximum detection probability shifting as a function of wind speed. At low temperatures, detection probability declined with increased wind speed, but this relationship was reversed at high temperatures, producing a 3-dimensional pattern in detection probability characterized by a saddle-shaped hyperbolic paraboloid response surface. The probability of an activity center being available for detection declined curvilinearly with increased temperature and explained 51% of the variation in detection probability. Given the broad range of detection probabilities, correcting visual survey counts for detection bias is necessary for comparing population estimates among regions and through time. Survey designs intended to estimate abundance of owls in southwest agroecosystems should incorporate methods to estimate and correct for variation in detection probability that include measurements of ambient temperature and wind speed for use as covariates. © 2011 The Wildlife Society.

KEY WORDS agroecosystem, activity center, *Athene cunicularia*, availability for detection, burrowing owl, detection probability, monitoring, population estimation, survey methods.

Populations of the western burrowing owl (*Athene cunicularia*) have declined or disappeared at the northern edge of the species' breeding range in southern Canada and northern United States, whereas populations in the southern portion of their range (southwestern U.S. and northwestern Mexico) have increased and support some of the highest breeding densities recorded (James and Espie 1997, Wellicome and Holroyd 2001, Klute et al. 2003, Desante et al. 2004, Sauer et al. 2008). These diverging population trends may be linked to different human land uses, owls appear to be increasing in irrigated agriculture but declining in natural landscapes (Moulton et al. 2006). A range-wide survey protocol has been recommended to estimate population trends across all habitats (James and Espie 1997, Holroyd et al. 2001, Conway and Simon 2003). The accuracy and efficiency of a range-wide survey protocol for estimating population trends depends on a survey design that accounts and corrects for factors that influence detection probability differentially among habitats (Anderson 2007). Identifying sources of variation where large concentrations of owls occur is especially important for detecting range-wide population trends because the accuracy of population estimates in high-abundance areas can have a profound affect on the accuracy of total population estimates (Caughley 1977, Cochran 1977). Accurate models of the relationships between environmental factors and detection probability can be integrated into an efficient range-wide survey protocol by modifying existing protocols to account for relationships specific to agricultural habitats.

The development of sampling protocols and analytical methods that account for variation in detection probability is a focus of research in population ecology (Otis et al. 1978, Pollock and Kendall 1987, Kery and Schmid 2004). Some methods correct for known sources of variation in detection

Received: 19 May 2010; Accepted: 13 February 2011;
Published: 26 July 2011

[1]*E-mail: jeffmanning@vandals.uidaho.edu*

probability, such as group size and vegetation cover, distance from observer, and propensity to call (Royle et al. 2004, Diefenbach et al. 2007, Pearse et al. 2008). Other methods, such as double-survey methods and mark–recapture, directly estimate and correct for detection bias attributed to a wide range of sources, as long as the appropriate predictors are measured and the correct relationship (e.g., linear, asymptotic, or curvilinear) is applied (Lebreton et al. 1992, Nichols et al. 2000).

Sources of variation in detection probability during avian surveys are numerous and include bird behavior, habitat characteristics, and weather (Thompson 2002, Anderson 2007). Early studies of burrowing owls found that owls were not readily available for detection during midday visual surveys because they retreated into their burrows (Coulombe 1971, Thomsen 1971). Others have reported that male and female adult owls differ in the time spent in the burrow throughout the day during the breeding and non-breeding seasons (Plumpton and Lutz 1993, LaFever et al. 2008). Weather conditions can affect owl behavior and reduce detection probability in southern Alberta, Canada, and detection probability during auditory surveys in the Mojave Desert is affected by probabilities of owl availability and detection (Haug and Didiuk 1993, Shyry et al. 2001, Crowe and Longshore 2010). Several studies have also provided estimates of detection probability in irrigated agricultural areas (e.g., Coulombe 1971, Rosenberg and Haley 2004), although factors affecting detection probability in these systems have not been investigated. Conway et al. (2008) completed the most comprehensive study on factors that affect detection probabilities of burrowing owl nest burrows in various land uses, including irrigated agriculture, in northern portions of the owl's range (Washington and Wyoming) and found that detection probability depended on linear interactions between timing within the breeding cycle and time of day, study area and percent cloud cover, time of day and ambient temperature, and temperature and wind speed. These studies have proven valuable in demonstrating that detection probability varies across the owl's range and that environmental conditions influence detection probability. However, an effective and accurate range-wide survey protocol also requires information on factors influencing detection probability of burrowing owls in southwest agricultural areas. My objective was to identify sources of variation and their relationships with detection probability of burrowing owl activity centers in southwest agroecosystem habitats that support a high density of owls.

STUDY AREA

The study area was the 337,000-ha agroecosystem in the Imperial Valley of California, USA (32°58′N, 115°31′W), an important region for burrowing owls that supports one of the highest densities of owls in North America (Coulombe 1971, Desante et al. 2004, Sauer et al. 2008). Extensive landscape change occurred in this desert ecosystem during the early 20th century, when a large portion of the valley became cultivated for agricultural production with irrigation water supplied by the Colorado River (Bailey 1994). The primary land use was irrigated cropland but also included urban, suburban, industrial, pasture, abandoned fields, and roadside embankment. Remnant patches of wetland, desert dry wash, and riparian woodland vegetation communities were also present. During this study, fields that were in agricultural production were intensively managed year-round, with alfalfa, Sudan grass, Bermuda grass, and wheat as the dominant crops (Falkowski and Manning, in press). Burrowing owls nested almost entirely within or along irrigation ditches that were either concrete-lined water-delivery canals or earthen irrigation drains that spanned the margins of agricultural fields and paralleled dirt maintenance roads. Average elevation was 40 m below sea level and average annual precipitation was <3.0 cm. Average annual low and high temperatures were $-15.6°$ C and $51.1°$ C, respectively, and average low and high temperatures during the study period were $14.9°$ C and $32.2°$ C, respectively (Western Regional Climate Center 2010).

METHODS

Detection Probabilities

Although burrowing owls in this landscape tend to perch in visible areas, nest burrows are usually located along the slope of irrigation ditches and can be difficult to see from access roads. Additionally, classifying the status of unoccupied and occupied burrows is not without error (Garcia and Conway 2009). Thus, I used visual observations of owls as the basis for detecting nest burrows, as others have (Conway et al. 2008, Crowe and Longshore 2010, Manning and Goldberg 2010). I recorded point-coordinate capture-recapture (PCCR) locations of owls obtained during visual surveys of owls, considered nest burrows associated with owl locations as individual burrowing owl activity centers, and used owl locations to calculate detection probabilities of activity centers with capture-recapture models, following methods described by Manning and Goldberg (2010). The PCCR method is well suited for estimating detection probabilities of activity centers from owl locations because it uses the spatial coordinates from detected unmarked owls to construct encounter histories associated with activity centers.

I conducted point-coordinate capture-recapture surveys in 12 randomly selected linear nesting sites (each approx. 6 km) between 16 April and 20 May 2006. I used ArcGIS 9.2 (ESRI, Redlands, CA) to randomly choose replicate nesting sites from a vector layer of all possible 6-km segments of irrigation drains and canals (5,385 km) maintained by the Imperial Irrigation District (Imperial, CA) in the study area. I arbitrarily chose the starting point of each segment. All of the randomly chosen segments were occupied by burrowing owls, and I later reduced 2 segments by 0.3 km at a terminal point due to restricted access. Although I did not collect data to determine breeding status of occupied burrows, it was most likely the early part of the breeding cycle because others have reported first egg-laying as early as 7 April, average clutch completion dates on 29 April and 14 May, and average date of newly hatched young on 16 May in this system (Coulombe 1971, Rosenberg and Haley 2004).

Additionally, no nestlings were observed above ground during this study until 19 May (J. A. Manning, University of Idaho, personal observation).

Observers conducted point-coordinate capture-recapture surveys using the single vehicle stop method with 2 surveyors, as described by Manning and Kaler (2011). I used the same make and model vehicle for all surveys. Observers completed 11 separate 1-hr PCCR survey occasions throughout the day at each site, one for each hour between 0630 hour and 1830 hour, except for 1230–1330 hours. One observer and one driver surveyed from a vehicle that traveled 11 km/hr in the same direction along the dirt maintenance road closest to the irrigation ditch. The time required for a vehicle to travel the entire length of a survey site varied from 33 min to 45 min, depending on the number of owls encountered. After traversing the entire length of a site, observations paused for $\geq$15 min to complete the 1-hr survey occasion and drive along an alternate route back to the initial start point. All 11 1-hr survey occasions were conducted by the same observer and driver at a site. To reduce problems with increased detection over the 11 consecutive occasions due to repeated surveys by the same surveyors, I did not mark owls or locations of owls, and I trained observers and drivers to focus on detecting owls during each occasion rather than landscape features such as nest burrows. Drivers also alerted observers of any owls they observed that were not detected by the observer. Drivers based the direction of travel at each site on positioning the observer side of the survey vehicle closest to the irrigation ditch. To reduce double counting owl activity centers, the driver and observer maintained a field of view in the direction of travel, noted where owls that flushed resumed perching, and did not look behind the vehicle.

At every detected owl, surveyors exited the vehicle and used a Trimble GeoXM (Trimble Navigation Limited, Westminster, CO) Global Positioning System (GPS) receiver, laser range finder, and magnetic compass with sighting mirror to record the owl's perch location or its burrow if the owl was <20 m from an active burrow. I considered a burrow active if an owl retreated into or flushed from it or if the entrance contained regurgitated pellets, feathers, nest lining, whitewash, or footprints without cobwebs (Conway et al. 2008). I excluded locations of owls observed only flying ($n = 2$). If an owl was first observed flying and then landed, I recorded the landing site as the perch. To further avoid double counting activity centers during the same PCCR survey occasion, I considered owls <20 m apart to be a nesting pair and recorded them as a single observation (following Manning and Goldberg 2010).

I used the 11 PCCR survey occasions to construct PCCR encounter histories with the maximum likelihood estimate of the maximum distance moved (58 m) reported by Manning and Goldberg (2010). This estimate of maximum distance moved was appropriate for constructing PCCR encounter histories because the estimate was derived from data collected in this study area during the same time of year. Additional details on applying the PCCR method to owls in this system are provided by Manning and Goldberg (2010).

Six different observers conducted PCCR surveys. The influence of vehicle-based surveys on burrowing owl behaviors when 2 observers exit a vehicle is the topic of a previous study (Manning and Kaler 2011). I assumed that variation among observers in detecting owls was negligible because observers received the same level of standardized field training (40 hr).

I examined the extent to which the following 4 factors influenced detection probability of burrowing owl activity centers: survey segment, time of day, wind speed, and ambient temperature. I included study site because sites differed in the type and physiognomic stage of crops; above-ground structures that were available to owls for perching such as shrubs, boulders, posts, debris piles, machinery, hay bales, water conveyance structures, and utility poles; and abundance of owls. I assumed that detection probability did not vary within each PCCR survey occasion and used discrete variables by classifying each occasion into one of 11 periods of day. Periods were every hour, starting at 0630 hours, ending at 1829 hours, and skipping 1230–1329 hours. I included the 2 weather variables because wind and temperature have been shown to influence the detection of burrowing owls in the northwest (Conway et al. 2008). I recorded percent cloud cover and precipitation (present, absent) during each PCCR survey, but I excluded them from analyses because both were nearly non-existent in 98% (3 of 132) of surveys. I recorded ambient air temperature (° C) and wind speed (km/hr) at each site repeatedly during each PCCR survey occasion with a Kestrel 3000 Pocket Weather Monitor (Nielsen-Kellerman, Boothwyn, PA) and used it to compute site-specific hourly averages of each variable throughout the day.

To estimate detection probability (p_d), I fit closed-population models available in Program MARK to the PCCR encounter histories (White and Burnham 1999, Manning and Goldberg 2010). I used the PCCR encounter histories as a closed capture data type, applied a multinomial logit link function, and fit models that assumed recapture probability would not differ from initial capture probability (i.e., $c = p$) because I could not envision a situation in which my sampling activity would affect probability of subsequent capture (i.e., I did not include a behavioral response to initial capture). My candidate set of models included all possible additive and 2-way interactions, except I did not include variables that were highly correlated ($r < 0.6$) in the same model. I included time as a second-degree quadratic function to represent a curvilinear relationship with detection probability because detections have been reported to decline during midday in this region (Coulombe 1971). I also modeled time as a linear trend to test whether prior knowledge of owl locations by surveyors at a site influenced subsequent detection probabilities. I modeled the relationship between detection probability and temperature as both linear and second-degree quadratic because bell-shaped curves typically represent organism responses to environmental continua (Morrison et al. 1998); I postulated detection probability would follow a bell-shaped pattern because high temperatures in my study area may stabilize or reduce detections during peak temperatures if owls use their burrows to minimize heat stress (Morrison et al. 1998). I ranked models using second-order Akaike's Information Criterion corrected for small sample sizes (AIC_c) and used Akaike weights w to assess the relative importance (weight of evidence) of each model (Akaike 1973, Burnham and Anderson 2002). I used a plot of deviance residuals to heuristically assess the fit of my global model and tested for overdispersion by calculating a variance inflation factor ($\hat{c}$) generated from 1,000 bootstrap simulations with the median $\hat{c}$ procedure (Cooch and White 2007). To assess generality of the best model, I subset the data according to 4 categories based on aspect of slopes (north–south or east–west) and type (earthen drain and cement-lined canal or only earthen drain) of irrigation ditch that was present at each site, which has been shown to influence presence of nesting burrowing owls in this system (Bartok and Conway 2010), and I refit the closed-population models.

Availability for Detection

To estimate probabilities of a burrowing owl activity center being available for detection (p_a), I conducted time budget surveys at one randomly selected occupied burrow in each study site to determine the proportion of time (min/hr) $\geq$1 owls were above ground. Following a repeated measures design, observers continuously observed each burrow throughout a day from 0630 hours to 1930 hours, except between 1230 hours and 1330 hours. Observers completed surveys between 7 May and 17 May 2006 and within 2 weeks of a detection survey at a site. I used an instantaneous, focal-animal sampling approach to record the start and stop times when $\geq$1 owls were above ground (Altmann 1974). I recorded the same weather variables as those measured during PCCR detection surveys during each hour of a time budget survey.

Observers conducted observations with binoculars and a spotting scope from vehicles parked at a distance believed to not disturb owls in this agroecosystem (approx. 160 m; Coulombe 1971). Drivers positioned vehicles close to the edge of the slope above the irrigation ditch to maximize visibility along its length. If an owl flew out of sight, the observer continuously scanned the area and focused attention back to the vicinity of the burrow (or burrow complex) to determine when the owl retreated into its burrow; I considered an owl available for detection until the owl retreated into the burrow. If both owls flew out of sight, the observer recorded when each owl returned and retreated into the burrow. The flat agricultural landscape enabled us to maintain sight of most owls or detect them upon returning from far distances before they re-entered burrows.

Observers arrived at each observation location 15 min prior to starting observations to locate target owls prior to data recording. If no owls were detected by the start of a time budget survey, the observer continuously scanned the general vicinity of the burrow and surrounding area to determine if an owl was already above ground at the start of the survey. Observers did not detect 4 of the 12 owls prior to starting the survey, preventing me from verifying whether they were above or below ground at the start of the survey; I excluded those owls from analyses.

I considered the proportion of time $\geq$1 owls were available for detection during each 1-hr interval throughout a time budget survey as a multivariate response under different conditions (i.e., different time of day, wind speed, and temperature), and I fit linear mixed effects models to the repeated measurements of the proportion of time ($n = 96$; 8 activity centers $\times$ 12 hr). I considered individual activity centers as random effects and applied an arcsine square-root transformation to the proportions (Lindstrom and Bates 1990, Ramsey and Schafer 2002). This process assumed that variation among the sample of activity centers was random during each 1-hr time interval, such that the effect of each activity center was randomly selected from the wider owl population, which parallels the benefits of a randomized block design (Ramsey and Schafer 2002). I constructed all possible additive and 2-way interactions. However, I did not include time of day and temperature in the same model because these were strongly correlated. I used AIC_c and w to determine the most parsimonious model and pseudo r^2 to measure the amount of deviance in proportion of time available that was explained by each mixed model (McFadden 1973, Dobson 2002).

To assess how much variation in detection probability was attributed to the probability of a burrowing owl activity center being available for detection, I used the detection probabilities I estimated from each 1-hr PCCR survey occasion at each site with the best capture-recapture detection model as a response variable in a simple linear regression model where the corresponding probability of being available predicted from the best availability model was the explanatory variable. I restricted this analysis to data ($n = 84$) from PCCR surveys where temperature was 20–41° C and wind speed was <9.6 km/hr to reflect the conditions during time budget surveys. I did not include site as a random effect because I wanted to estimate the amount of variation in detection that was explained by availability across all sites (i.e., a reliable r^2-value). I computed statistics using the nlme package in R (Bolker 2008; nmle Version 3.1–89, http://cran.r-project.org/web/packages/nlme/index.html, accessed 31 Mar 2008; R Version 2.11.1, www.r-project.org, accessed 31 Mar 2008).

RESULTS

I recorded 1,199 burrowing owl detections during 132 PCCR surveys in 12 replicate sites between 16 April and 20 May 2006, and used these to model detection probability. Ambient temperature and wind speed during surveys varied from 15° C to 41° C and 0–17 km/hr, respectively. The global model fit the data well and exhibited a symmetric and narrow pattern of deviance residuals close to zero and $\hat{c} = 1.1$. Because temperature and time of day were highly correlated ($r = 0.88$, $P = 0.01$), I did not include these in the same model. I found strong evidence that detection probability was influenced by ambient temperature interacting with wind speed and differed among sites (second-degree quadratic temp $\times$ wind + site; model $w = 0.99$). There was no evidence for support of the remaining 20 models (all $\Delta AIC_c \geq 9.3$ and $w_i \leq 0.009$; Table 1; Fig. 1), including a time trend attributed to prior knowledge of owl locations by observers (all ΔAIC_c of time trend models >51.0 and $w_i \leq 0.001$; Table 1). The best model predicted detection probability as a second-degree quadratic function of ambient temperature, with maximum detection probability at the vertex (Fig. 1). Wind speed negatively affected detection probability at low temperatures and positively influenced it at high temperatures (Fig. 1). Thus, the maximum detection probability shifted to the right along the temperature gradient as wind speed increased, creating a saddle-shaped hyperbolic paraboloid response surface (Fig. 1). Detection probability was highest at 21° C when wind was absent and at 38° C when average wind speed was 30 km/hr (Fig. 1). On 3 of the 4 site categories (based on aspect and irrigation ditch type), second-degree quadratic temp × wind was the best model. On the fourth, it was competitive ($\Delta AIC_c = 1.67$) with second-degree quadratic temp + wind. Combined, the 12 sites supported a derived estimate of 227 activity centers, and densities varied among sites from 1.8 to 5.0 activity centers/km ($\bar{x} = 2.9$ activity centers/km, SD = 0.86).

During availability surveys, ambient temperature and wind speed varied between varied from 20° C and 41° C and 0 km/hr and 9.6 km/hr, respectively. I found that the probability of ≥1 owls being available for detection at an activity center was a curvilinear function of temperature, as expressed in the relationship between the arcsine square-root transformed proportions of time available and temperature ($w_i = 0.72$, pseudo $r^2 = 0.44$; Table 2; Fig. 2). There was less evidence for time of day ($\Delta AIC_c \geq 2.4$ and $w_i \leq 0.23$; Table 2) and no evidence for wind as single, additive, or interactive factor affecting availability (Table 2). The probability of a burrowing owl activity center being available for detection had a positive effect on detection probability and explained half of the variation in detection probability (adjusted $r^2 = 0.51$, $F_{1, 82} = 84$, $P = 0.001$; Fig. 3). This model predicted an average detection probability of 0.61 when availability was 100%, indicating that the remaining 39% of detection probability at this level of estimated availability was attributable to factors other than availability.

DISCUSSION

Detection probability of burrowing owl activity centers in southwest agroecosystems during early stages of the breeding cycle was affected by ambient air temperature and wind speed, with the magnitude of influence by these interacting factors varying among sites. Additionally, the relationship between these factors and detection probability was not linear. I found that detection probability followed a bell-shaped response curve with ambient temperature, but this relationship was affected by wind speed such that maximum

Table 1. Closed-population capture-recapture models predicting detection probability of burrowing owl activity centers during 132 point-coordinate capture-recapture survey occasions conducted at 12 6-km nesting sites within the agroecosystem of the Imperial Valley, California, USA, 2006. I conducted surveys during the incubation and early nestling stages of the breeding cycle. Predictors were: ambient air temperature (temp), wind speed, 1-hr time intervals throughout the day (time, $n = 11$), and site ($n = 12$).

Model[a]	K	ΔAIC_c	w_i	Dev
Second-degree quadratic temp × wind + site	16	0	0.986	1,979.89
Second-degree quadratic temp + site	14	9.34	0.009	1,993.27
Second-degree quadratic temp + wind + site	15	10.77	0.005	1,992.68
Second-degree quadratic temp × wind	5	34.46	0	2,036.54
Second-degree quadratic time + site	14	37.23	0	2,021.16
Wind + second-degree quadratic time + site	15	38.81	0	2,020.72
Wind × second-degree quadratic time + site	16	39.70	0	2,019.59
Wind × time trend + site	15	51.70	0	2,033.61
Time trend + site	13	52.48	0	2,038.44
Wind + time trend + site	14	53.71	0	2,421.90
Temp + site	13	55.95	0	2,041.91
Temp + wind + site	14	57.76	0	2,041.69
Temp × wind + site	15	58.11	0	2,040.02
Site	12	60.82	0	2,048.80
Wind + site	13	62.83	0	2,048.79
Second-degree quadratic temp + wind	4	78.09	0	2,082.18
Temp + wind	3	78.38	0	2,084.48
Wind + second-degree quadratic time	4	80.70	0	2,084.78
Wind + time trend	3	83.87	0	2,089.96
Second-degree quadratic temp	3	97.53	0	2,103.63
Temp	2	113.54	0	2,121.64
Second-degree quadratic time	3	113.61	0	2,119.70
Temp × wind	4	118.77	0	2,122.86
Wind	2	127.28	0	2,135.39
Time trend	2	128.21	0	2,139.31
Constant detection	1	136.17	0	2,146.27

[a] Model notation refers to parameters of detection probability. Abbreviations are: number of parameters (K), difference in Akaike's Information Criterion adjusted for sample size (ΔAIC_c), Akaike weight (w_i), and deviance (Dev). I constructed encounter histories from visual detections during driving surveys using the point-coordinate capture-recapture method with the maximum distance moved set at 58 m (Manning and Goldberg 2010). I modeled recapture and initial capture probabilities as equal ($c = p$). The best approximating model had an $AIC_c = 2{,}368.19$.

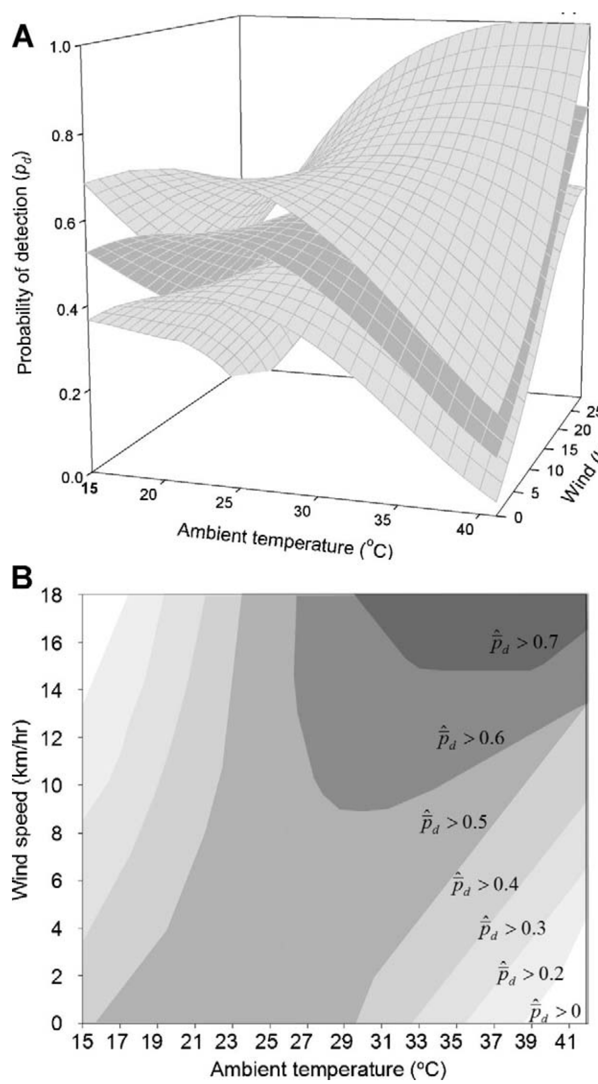

Figure 1. Best model (A) of detection probability of burrowing owl activity centers as predicted by ambient temperature and wind speed in the agroecosystem of the Imperial Valley, California, USA, 2006. Data are from 132 point-coordinate capture-recapture visual driving surveys from 0630 hours to 1830 hours during the incubation and early nestling stages of the breeding cycle. I averaged detection probability over 12 sites. Upper and lower surfaces are 95% confidence limits. A 2-dimensional plot (B) can be used to select ambient temperature and wind speeds that maximize detection probability.

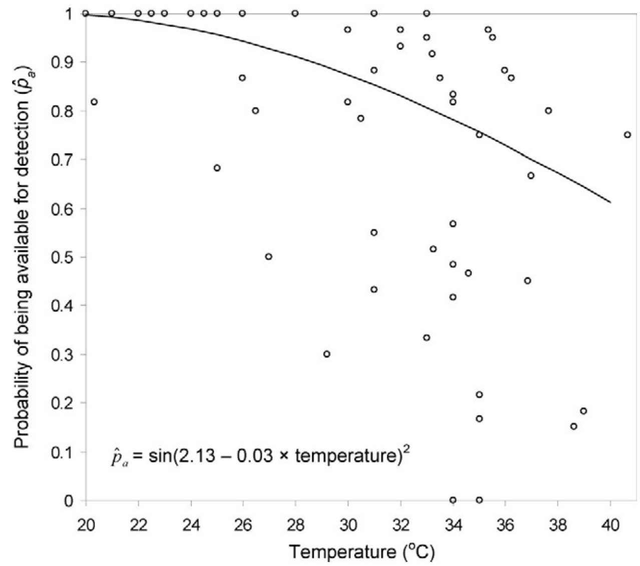

Figure 2. Probability that burrowing owl activity centers were available for detection (i.e., ≥1 owls aboveground) predicted by the best linear mixed model as a curvilinear function of temperature, expressed as a relationship between arcsine square-root transformed proportions of time and temperature in the agroecosystem of the Imperial Valley, California, USA, 2006. Circles are untransformed proportions of time owls were available for detection. Data are from 96 time budget surveys repeated during 11 consecutive daytime hours at 8 activity centers.

detection probability shifted along the temperature gradient as a function of wind speed, creating a saddle-shaped hyperbolic paraboloid response surface. The same model was the highest ranked or competing best model in all 4 groups, and the same basic shape was present in sites grouped according to aspect of slopes and type of irrigation ditch, showing that the saddle-shaped pattern in detection was consistent across sites. Nonlinear relationships between factors that affect detection probability of burrowing owls have not been reported elsewhere. This curvilinear response surface may depict a broader response pattern to temperature and wind gradients across the owl's range and can bias range-wide estimates of burrowing owl population size or population trends if not accounted for in survey protocols and data

Table 2. Linear mixed models predicting probability of a burrowing owl activity center being available for detection (≥1 burrowing owls is aboveground) during 96 time budget surveys over 11 consecutive daytime hrs at 8 activity centers in the agroecosystem of the Imperial Valley, California, USA, 2006. I conducted surveys during the incubation and early nestling stages of the breeding cycle.

Model[a]	K	ΔAIC_c	w_i	Psuedo r^2
Temp	4	0	0.721	0.44
Second-degree quadratic time	5	2.4	0.221	0.38
Temp + wind	5	6.2	0.032	0.32
Wind	4	7.8	0.014	0.31
Wind + second-degree quadratic time	6	8.8	0.009	0.31
Second-degree quadratic temp	5	11.8	0.002	0.26
Temp × wind	6	14.5	<0.001	0.22
Second-degree quadratic temp + wind	6	18.1	<0.001	0.21
Wind × second-degree quadratic time	7	22.1	<0.001	0.21
Second-degree quadratic temp × wind	7	35.2	<0.001	0.01

[a] Model notation refers to parameters of detection probability. Abbreviations are: number of parameters (K), difference in Akaike's Information Criterion adjusted for sample size (ΔAIC_c), Akaike weight (w_i), and pseudo r^2 (McFadden 1973). I considered activity centers random effects, and I arcsine square-root transformed availability. The best approximating model predicted availability as a curvilinear function of temperature, expressed by the relationship between arcsine square-root transformed proportions of time and temperature. The best approximating model had an AIC = 78.6.

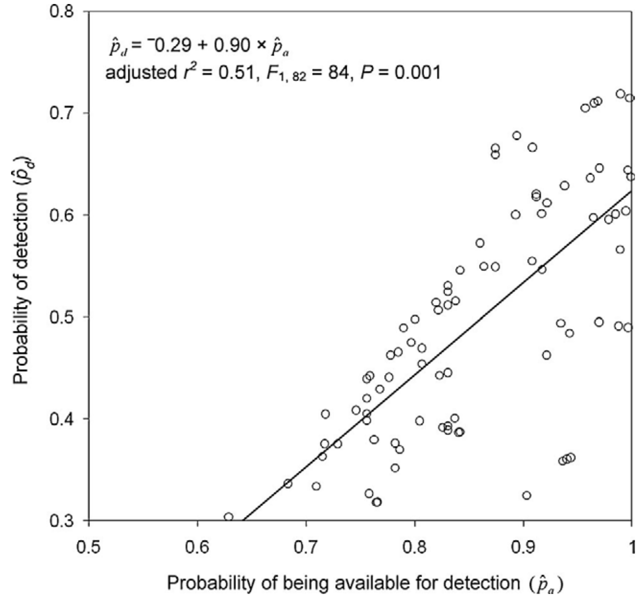

Figure 3. Detection probability of burrowing owl activity centers as a function of probability of being available for detection (i.e., ≥1 owls aboveground) in the agroecosystem of the Imperial Valley, California, USA, 2006. Data are from 84 point-coordinate capture-recapture visual driving surveys and time budget surveys from 0630 hours to 1930 hours during the incubation and early nestling stages of the breeding cycle where temperature and wind speed were 20–41° C and <9.6 km/hr, respectively. I estimated detection probability based on the best model (Table 1).

analyses, particularly in southwest agroecosystems where large concentrations of breeding burrowing owls exist.

Availability for detection declined as temperature increased, and followed the same trend as detection probability at temperatures ≥20° C. In another study, availability of owls declined to its lowest level in mid-afternoon, when temperatures would be highest, at which time surveys of abundance estimated only 10–25% of the population (Thomsen 1971). If owls use their burrows to aid in thermoregulation at temperatures <20° C, the probability of being available may begin to decline with continued decreases in temperature below those temperatures recorded during my PCCR surveys; such a decline in detection probability with decreasing temperature was reported in the northern portion of the owl's breeding range (Conway et al. 2008). Thus, availability for detection is an important source of variation in detection probability during burrowing owl surveys intended for documenting distribution and estimating abundance and should be considered in future local and range-wide survey protocols.

The probability of a burrowing owl activity center being available for detection during time budget surveys explained 51% of the variation in detection probability during PCCR surveys, indicating that availability for detection is an important component of detection probability during standardized owl surveys. Detection probability would be expected to be lower than the probability of being available for detection (Fig. 3), although my estimates of availability may have been high because I considered owls that were aboveground during time budget surveys to be available for detection, regardless of whether observers lost sight of them. Although this consideration may have lowered the estimated intercept in the simple linear regression model, probabilities of detection and availability were linearly related, indicating that the factors affecting imperfect detection appear to be reasonably constant across a range of probabilities of being available for detection. Additionally, the residual scatter between probabilities of detection and availability can be attributable to imperfect probabilities explained by the measured variables, with both explained largely by similar nonlinear declines associated with temperature.

The bell-shaped response of detection probability to ambient temperature may have been detectable during this study because of the wide range of daily April and May temperatures (3.3–47.8° C; Western Regional Climate Center 2010). These temperatures constitute an environmental gradient, across which owls need to maintain thermoneutrality (Coulombe 1970). Burrowing owls exhibit mild heat stress at 41° C and use shaded areas, burrows, and raised perches such as utility poles, utility wires, shrubs, and hay stacks to reduce body heat at high temperatures (Coulombe 1970, 1971). Use of hay stacks, shrubs, and other raised perches that offer shaded areas may obscure owls from observers, and owls that retreat into burrows are unavailable for detection, all of which can reduce detection probability during standardized surveys. Additionally, other researchers have reported a positive relationship between temperature and detection probability similar to what I found for temperatures below those associated with maximum detection probability. For example, Conway et al. (2008) reported an increase in detection probability with increased ambient temperature during detection trials in eastern Washington and Wyoming, and most (95%) of their detection trials occurred at temperatures ≤26° C.

There are several possible explanations for why wind speed was important for detection but not availability for detection above ground. First, I considered owls that were aboveground during time budget surveys to be available for detection, regardless of whether observers lost sight of them. Although I did not evaluate effects of wind speed on owls being visible while above ground during these surveys, it is possible that wind reduced foraging efficiency, causing owls to forage at greater distances away from burrows and irrigation ditches where observers were less likely to detect them during PCCR detection surveys. Alternatively, the interaction between wind and temperature may have affected the detection process by altering aboveground behaviors and perch use. I suspect high wind speeds may have reduced heat stress during high temperatures, allowing owls to remain outside of burrows and be available for detection, because I often observed owls nestled down next to burrow entrances or rocks, as well as other debris near the burrow entrance when wind and temperature were high, enabling observers to readily detect the owls.

Factors in addition to those I included may also be important sources of variation in detection probability of burrowing owls. Variation among sites may have been due to the amount of time owls spent standing at the entrance of nest burrows (Conway et al. 2008). Variable land uses, vegetation characteristics, and types of perches used by burrowing owls may further reflect differences among sites (Coulombe 1971, Williford et al. 2007). Although prior knowledge of owl locations did not influence detection probability in subsequent survey occasions at a site, different observers conducted surveys at the 12 replicate sites, and variation between observers may have also contributed to differences in detection probability I found among sites (Diefenbach et al. 2003). However, the hyperbolic paraboloid pattern in detection probability should be robust to observer differences, as the same model and basic shape consistently described the variation in detection probability in the 4 categories of sites even though different observers were involved in conducting surveys. Potential effects of cloud cover were not considered here because drought conditions led to most PCCR surveys (98%) being conducted during cloud-free days, although periods of high cloud cover were found to lower detection probability in southeastern Washington (Conway et al. 2008).

Additionally, I did not investigate the effect of stage of the breeding cycle on detection probability because my goal was to identify factors that affect detection probability during brief survey periods to achieve a critical assumption of closed-population estimators: the population is closed to emigration, immigration, births, and deaths (Otis et al. 1978). Although the stage of the breeding cycle does affect detection probability of burrowing owls (Conway et al. 2008), my surveys were restricted to the period including only the incubation and early nestling stages because nestlings and incubating females are underground (Coulombe 1971, Thomsen 1971, Plumpton and Lutz 1993). I also did not control for variation in early stages of nesting phenology because owl surveys often involve the detection of nests that differ in phenological stage; these stages are difficult to ascertain and often are not determined during population surveys (California Burrowing Owl Consortium 1997, Arizona Game and Fish Department 2007). Not distinguishing among the early nesting stages during this brief period may have added additional variation among sites, but I believe this variation did not influence the general pattern in detection probability I found because the same model and shape of the detection response surface was consistent among the 4 site categories that were confounded by the timing of surveys and average nesting stage among sites.

Surveying only during this stage of the breeding cycle also helped minimize risk of double counting activity centers in this dense population while conducting PCCR surveys of unmarked owls (Manning and Goldberg 2010). Additionally, although nest failure or mate loss may instigate dispersal (Catlin et al. 2005), I assumed it did not occur during the 11 consecutive 1-hr PCCR survey occasions at each site. Lastly, the continued increase in detection probability I found at high temperatures and wind speeds may be an artifact of the small sample of PCCR survey occasions when temperatures and wind speeds were high ($>34^\circ$ C and >20 km/hr; $n = 9$ of 132 survey occasions). When I removed these 9 activity centers in an ad hoc analysis, the same saddle-shape in detection probability was present, but the overall predicted slope in detection above these temperatures and wind speeds declined. Thus, I caution against using the detection probabilities estimated from my model when both ambient temperature and wind speed are high until studies with a larger sample of surveys under these conditions can validate that portion of the pattern in detection probability.

MANAGEMENT IMPLICATIONS

My results identify some of the sources of variation in detection probability and the probability of being available for detection in southwest agroecosystem environments, and indicate the importance of being available for detection as a source of variation in detection probability during standardized surveys. Ambient temperature and wind speed affected detection probability of burrowing owls in this southwest agroecosystem differently than in the owl's northern breeding range, and these factors should be accounted for when developing survey protocols in these southwest environments. The relationship between detection probability, ambient temperature, and wind speed (Fig. 1B) can be used to improve detection probability during visual surveys and can be used to provide guidance in the timing of future surveys in these environments. The timing of surveys should lie within the range of temperatures and wind conditions associated with average detection probabilities >0.5 to avoid problems with low detection probabilities that can lead to unreliable model-based estimators of population size (Otis et al. 1978, Rosenberg et al. 1995). To increase detection probability, investigators should avoid conducting surveys when temperatures are $>33^\circ$ C with concomitant wind speeds <8 km/hr and when temperatures are $<21^\circ$ C with concomitant wind speeds >4 km/hr. Survey designs intended to estimate abundance of owls should incorporate methods to estimate and correct for variation in detection probability that include measurements of ambient temperature and wind speed for use as covariates. Lastly, future range-wide and local survey efforts should incorporate methods to account for detection and availability biases.

ACKNOWLEDGMENTS

This work evolved from a larger project studying burrowing owls in the Imperial Valley, and I thank D. Bittner, B. Dirksen, D. Kamada, J. Konecny, J. Lincer, J. Luttrell, D. McGraw, W. Meno, A. Musante, and S. Thomas for their extensive efforts observing owls. Helpful were P. Bloom's, D. Bittner's, J. Lincer's, J. Groom's, and others' enthusiastic discussions during the initial stages of this project. N. Kidd helped in procuring equipment, Bloom Biological, Inc. administered support, and the Wildlife Research Institute, Inc. hired selected field biologists. Discussions with C. Conway, P. Bloom, and D. Rosenberg on owls and comments and reviews from C. Goldberg, D. Catlin, J. Baumgardt, 2 anonymous reviewers, and the Associate Editor on earlier drafts greatly improved the manuscript. Field activities were funded by the Imperial Irrigation District's Water Transfer Project Joint Powers Authority.

LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. Petran and F. Csaki, editors. International Symposium on Information Theory. Second edition. Akademiai Kiado, Budapest, Hungary.

Anderson, D. E. 2007. Raptor survey techniques. Pages 89–100 *in* D. M. Bird and K. L. Bildstein, editors. Rapture research and management techniques. Hancock House Publishers, Blaine, Washington, USA.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Arizona Game and Fish Department. 2007. Burrowing owl management guidelines for municipalities in Arizona. Arizona Game and Fish Department, Phoenix, USA.

Bailey, R. G. 1994. Ecological classification for the United States. USDA Forest Service, Washington, D.C., USA.

Bartok, N. D., and C. J. Conway. 2010. Factors affecting the presence of nesting burrowing owls in an agricultural landscape. Journal of Raptor Research 44:286–293.

Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton, New Jersey, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, Inc., New York, New York, USA.

California Burrowing Owl Consortium. 1997. Burrowing owl survey protocol and mitigation guidelines. Raptor Research Report 9:171–177.

Catlin, D. H., D. K. Rosenberg, and K. L. Haley. 2005. The effects of nesting success and mate fidelity on breeding dispersal in burrowing owls. Canadian Journal of Zoology 83:1574–1580.

Caughley, G. 1977. Analysis of vertebrate populations. The Blackburn Press, Caldwell, New Jersey, USA.

Cochran, W. G. 1977. Sampling techniques. Third edition. John Wiley and Sons, New York, New York, USA.

Conway, C. J., and J. Simon. 2003. Comparison of detection probability associated with burrowing owl survey methods. Journal of Wildlife Management 67:501–511.

Conway, J. C., V. Garcia, M. D. Smith, and K. Hughes. 2008. Factors affecting detection of burrowing owl nests during standardized surveys. Journal of Wildlife Management 72:668–696.

Cooch, E. G., and G. C. White. editors. 2007. Program MARK: a gentle introduction. <http://www.phidot.org/software/mark/docs/book>. Accessed 29 Apr 2010.

Coulombe, N. H. 1970. Physiological and physical aspects of temperature regulation in the burrowing owl, *Speotyto cunicularia*. Comparative Biochemistry and Physiology 35:304–335.

Coulombe, N. H. 1971. Behavior and population ecology of the burrowing owl, *Speotyto cunicularia*, in the Imperial Valley. California. Condor 73:162–176.

Crowe, D. E., and K. M. Longshore. 2010. Estimates of density, detection probability, and factors influencing detection of burrowing owls in the Mojave Desert. Journal of Raptor Research 44:1–11.

Diefenbach, D. R., D. W. Brauning, and J. A. Mattice. 2003. Variability in grassland bird counts related to observer differences and species detection rates. Auk 120:1168–1179.

Diefenbach, D. R., M. R. Marshall, J. A. Mattice, and D. W. Brauning. 2007. Incorporating availability for detection in estimates of bird abundance. Auk 124:96–106.

Desante, D. F., E. D. Ruhlen, and D. K. Rosenberg. 2004. Density and abundance of burrowing owls in the agricultural matrix of the Imperial Valley, California. Studies in Avian Biology 27:116–119.

Dobson, A. J. 2002. An introduction to generalized linear models. Second edition. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Falkowski, M. J., and J. A. Manning. in press. Parcel-based classification of agricultural crops via multi-temporal Landsat imagery in support of habitat availability monitoring for western burrowing owls in the Imperial Valley agro-ecosystem. Canadian Journal of Remote Sensing.

Garcia, V., and C. J. Conway. 2009. What constitutes a nesting attempt? Variation in criteria causes bias and hinders comparisons across studies. Auk 126:31–40.

Haug, E. A., and A. B. Didiuk. 1993. Use of recorded calls to detect burrowing owls. Journal of Field Ornithology 64:188–194.

Holroyd, G. L., R. Rodríquez-Estrella, and S. R. Sheffield. 2001. Conservation of the burrowing owl in western North America: issues, challenges, and recommendations. Journal of Raptor Research 35:399–407.

James, P. C., and R. H. M. Espie. 1997. Current status of the burrowing owl in North America: an agency survey. Raptor Research Report 9:3–5.

Kery, M., and H. Schmid. 2004. Monitoring programs need to take into account imperfect species detectability. Basic and Applied Ecology 5:65–73.

Klute, D. S., L. W. Ayers, M. T. Green, W. H. Howe, S. L. Jones, J. A. Shaffer, S. R. Sheffield, and T. S. Zimmerman. 2003. Status assessment and conservation plan for the western burrowing owl in the United States. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical, Publication FWS/BTP-R6001-2003, Washington, D.C., USA.

LaFever, D. H., K. E. LaFever, D. H. Catlin, and D. K. Rosenberg. 2008. Diurnal time budget of burrowing owls in a resident population during the non-breeding season. Southwestern Naturalist 53:29–33.

Lebreton, J., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 61:67–118.

Lindstrom, M. J., and D. M. Bates. 1990. Nonlinear mixed effects models for repeated measures data. Biometrics 46:673–687.

Manning, J. A., and R. S. A. Kaler. 2011. Effects of survey methods on burrowing owl behaviors. Journal of Wildlife Management 75:525–530.

Manning, J. A., and C. S. Goldberg. 2010. Estimating population size using capture-recapture encounter histories created from point-coordinate locations of animals. Methods in Ecology and Evolution 1:389–397.

McFadden, D. 1973. Conditional logit analysis of qualitative choice behavior. Pages 105–142 *in* P. Zarembka, editor. Frontiers in econometrics. Academic Press, New York, New York, USA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. Wildlife-habitat relationships: concepts and applications. Second edition. University of Wisconsin Press, Madison, USA.

Moulton, C. E., R. S. Brady, and J. R. Belthoff. 2006. Association between wildlife and agriculture: underlying mechanisms and implications for burrowing owls. Journal of Wildlife Management 70:708–716.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Hegund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117:393–408.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1–135.

Pearse, A. T., P. D. Gerard, S. J. Dinsmore, R. M. Kaminski, and K. J. Reinecke. 2008. Estimation and correction of visibility bias in aerial surveys of wintering ducks. Journal of Wildlife Management 72:808–813.

Plumpton, D. L., and R. S. Lutz. 1993. Influence of vehicular traffic on time budgets of nesting burrowing owls. Journal of Wildlife Management 57:612–616.

Pollock, K. H., and W. L. Kendall. 1987. Visibility bias in aerial surveys: a review of estimation procedures. Journal of Wildlife Management 51:502–510.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth: a course in method of data analysis. Second edition. Duxbury Press, Belmont, California, USA.

Rosenberg, D. K., W. S. Overton, and R. G. Anthony. 1995. Estimation of animal abundance when capture probabilities are low and heterogeneous. Journal of Wildlife Management 59:252–261.

Rosenberg, D. K., and K. L. Haley. 2004. The ecology of burrowing owls in the agroecosystem of the Imperial Valley. California. Studies in Avian Biology 27:120–135.

Royle, J. A., D. K. Dawson, and S. Bates. 2004. Modeling abundance effects in distance sampling. Ecology 85:1591–1597.

Sauer, J. R., J. E. Hines, and J. Fallon. 2008. The North American breeding bird survey, results and analysis 1966–2007. Version 5.15.2008. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA: <http://www.mbr-pwrc.usgs.gov/bbs/>. Accessed 26 Apr 2010.

Shyry, D. T., T. I. Wellicome, J. K. Schmutz, G. L. Erickson, D. L. Scobie, R. F. Russell, and R. G. Martin. 2001. Burrowing owl population-trend surveys in southern Alberta: 1991–2000. Journal of Raptor Research 35:310–315.

Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. Auk 119:18–25.

Thomsen, L. 1971. Behavior and ecology of burrowing owls on the Oakland Municipal Airport. Condor 73:177–192.

Wellicome, T. I., and G. L. Holroyd. 2001. The second international burrowing owl symposium: background and context. Journal of Raptor Research 35:269–273.

Western Regional Climate Center. 2010. Historical climate information. Western Regional Climate Center, Reno, Nevada, USA: <http://www.wrcc.dri.edu/inventory/sodca.html>. Accessed 29 Apr 2010.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement): 120–138.

Williford, D. L., M. C. Woodin, M. K. Skoruppa, and G. C. Hickman. 2007. Characteristics of roost sites used by burrowing owls (*Athene cunicularia*) wintering in southern Texas. Southwest Naturalist 52: 60–66.

Associate Editor: Kevin McKelvey.