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Management and Conservation

A Sightability Model for Correcting Visibility and Availability Biases in Standardized Surveys of Breeding Burrowing Owls in Southwest Agroecosystem Environments

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ABSTRACT Unbiased estimates of burrowing owl populations (*Athene cunicularia*) are essential to achieving diverse management and conservation objectives. We conducted visibility trials and developed logistic regression models to identify and correct for visibility bias associated with single, vehicle-based, visual survey occasions of breeding male owls during daylight hours in an agricultural landscape in California between 30 April and 2 May 2007. Visibility was predicted best by a second-degree polynomial function of time of day and 7 categorical perch types. Probability of being visible was highest in the afternoon, and individuals that flushed, flew, or perched on hay bales were highly visible (>0.85). Visibility was lowest in agricultural fields (<0.46) and nonagricultural vegetation (<0.77). We used the results from this model to compute unbiased maximum likelihood estimates of visibility bias, and combined these with estimated probabilities of availability bias to validate our model by correcting for visibility and availability biases in 4 independent datasets collected during morning hours. Correcting for both biases produced reliable estimates of abundance in all 4 independent validation datasets. We recommend that estimates of burrowing owl abundance from surveys in the southwest United States correct for both visibility and availability biases.

KEY WORDS *Athene cunicularia*, availability bias, burrowing owl, California, Imperial Valley, sightability model, vehicle-based survey, visibility bias.

A fundamental concern when conducting visual surveys for wildlife is that some individuals are not seen by observers (Krebs 2001, White 2005, Diefenbach et al. 2007). Failure to detect all individuals that are available for detection in a sampled area is termed visibility bias, measured as a probability (P_V), and differs from availability bias, which refers to the probability of being available for detection (P_A; Diefenbach et al. 2007). Visibility bias can be a primary source of error in surveys (White 2005), and can vary spatially, temporally, among modes of travel during surveys (e.g., automobile, aircraft, or foot-based surveys), and among observers (Pollock et al. 2002, Diefenbach et al. 2003, Kery and Schmid 2004). Availability bias may also be an important source of error in surveys, and can vary spatially and temporally (Diefenbach et al. 2007). The product of these 2 parameters equates to detection probability (P). When population estimation fails to incorporate variation in visibility and availability, the resulting estimates and inferences based on those estimations will be biased.

Correcting estimates of population size ($\hat{N}$) for visibility and availability biases is vital for studies that compare population densities or abundance across space and time (White 2005, Diefenbach et al. 2007), and is especially important for long-term monitoring of species of conservation concern. The burrowing owl (*Athene cunicularia*) is listed as a Species of National Conservation Concern in the United States due to declines across much of its range, and reliable population estimates are needed to achieve diverse management and conservation objectives (U.S. Fish and Wildlife Service 2002). Because it is listed or being considered for listing as Threatened or Endangered in many western states (James and Espie 1997, Klute et al. 2003), range-wide surveys have been recommended (Holroyd et al. 2001). Guidelines for conducting standardized visual surveys prior to development in an area have been developed by numerous nongovernmental organizations and regulatory agencies across the southwest (California Burrowing Owl Consortium 1997, Arizona Game and Fish Department 2007, New Mexico Department of Game and Fish 2007). Currently, these guidelines do not specify how to account or correct for visibility or availability bias that may occur due to variable environmental conditions associated with habitat, time of day, or weather.

Although factors that affect detection of owls during the breeding season have been reported for populations in the northwest and central United States (Conway et al. 2008), the environmental conditions (i.e., temperature, precipitation,

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and land use) in these regions differ dramatically from other regions such as the southwest, where the largest concentration of owls presently occurs in the agroecosystem of the Imperial Valley, California (DeSante et al. 2004). Consequently, Conway et al. (2008) emphasized that "detection probability of burrowing owls is affected by a variety of extrinsic factors and such variation should be accounted for when designing a survey protocol for a particular region." Methods that estimate and correct detection bias from multiple survey occasions such as capture–recapture (Williams et al. 2002) or point-coordinate capture–recapture (Manning and Goldberg 2010) are available, but multiple survey occasions can be costly and hence constrain the extent of sampling area when attempting to achieve assumptions of population closure required for estimating abundance across large agroecosystems.

Constraining the extent of sampling within large areas such as the Imperial Valley where an estimated 5,600 breeding pairs of owls occur (DeSante et al. 2004) can be problematic. Dense owl populations such as this can extend across a range of environmental conditions that lead to variable rates of visibility bias during a single standardized survey occasion. A single-occasion survey method would allow fewer observers to cover the same sampling area as that required for multi-occasion surveys, or to cover a larger area that incorporates a broader range of environmental conditions. However, a count from a single survey occasion can be fraught with both visibility and availability biases. Fortunately, estimates of availability ($\hat{P}_A$) during owl abundance surveys in southwest agroecosystem environments are available (Manning 2011), and recent methods are available for estimating visibility bias. Thus, models that jointly correct for availability and visibility biases from a single survey occasion in southwest agroecosystems are needed to provide a relatively affordable alternative to multiple survey occasions that can provide broad coverage of these systems for long-term monitoring.

Some of the variation that occurs in visibility of owls can be minimized using skilled observers and standardized protocols so that surveys are conducted under similar conditions, but it is unlikely that these actions would eliminate all visibility bias (Burnham 1981, Johnson 1995). Additionally, analytical methods that estimate visibility bias can be used (e.g., Nichols et al. 2000, Farnsworth et al. 2002, Royle and Nichols 2003), and these can be generalized to incorporate visibility bias of birds counted under different conditions. One method that can be less expensive to apply than others is the development and application of a sightability model, which is based on a 2-stage process. First, a sightability dataset is collected, a model is fit to the data, and probabilities of seeing birds under particular conditions are predicted (Johnson et al. 1989, Giudice 2001, Pearse et al. 2008). Once the model is validated with an independent dataset, subsequent surveys can be conducted in which key variables affecting sightability are recorded and the sighting probabilities are used to account for birds that were available for detection but not seen (Cook and Jacobson 1979, Pollock and Kendall 1987, Buckland et al. 1993). These models have been developed for ungulate and waterfowl surveys (e.g., Samuel et al. 1987, Johnson et al. 1989, Anderson et al. 1998, Giudice 2001, Pearse et al. 2008). The estimation of population size using sightability models assumes that the population is closed, detections are independent, and counts of observed animals are correctly recorded (Steinhorst and Samuel 1989, Giudice 2001). However, the chief advantage of sightability models is that they can account and correct for multiple factors that affect visibility bias.

We developed a sightability model to identify and estimate visibility bias ($\hat{P}_V$) associated with a single, vehicle-based, visual survey occasion of breeding male owls during daylight hours in the Imperial Valley. We investigated factors that affected $\hat{P}_V$ by standardizing those that were controllable by observers and measuring those potential biases that could not be controlled. We estimated availability bias ($\hat{P}_A$) using the empirical model developed for owls in this system by Manning (2011), and combined this with $\hat{P}_V$ to calculate a joint visibility and availability bias correction factor. We validated this joint correction factor by calculating estimates of abundance corrected for biases in visibility and availability, using an independent dataset from a population of known size.

STUDY AREA

We studied burrowing owls throughout the 3,300 km^2 Imperial Valley in Imperial County, California, USA. This area currently supports the largest population of owls in North America (Coulombe 1971, DeSante et al. 2004), with both resident breeding owls and winter migrants. It is a desert environment intensively managed year-round for irrigated agricultural production, with alfalfa (*Medicago sativa*), Sudan grass (*Sorghum bicolor*), Bermuda grass (*Cyondon dactylon*), and wheat (*Triticum* spp.) as the dominant crops (Falkowski and Manning 2011). Within this agricultural landscape, owls nested almost entirely within or along irrigation drains, canals, and ditches (water conveyance structures) that paralleled access roads (Manning 2011).

METHODS

Surveys

We conducted independent visibility trials from sunrise to sunset at randomly selected active owl nests (i.e., each nest received a single trial) between 30 April and 2 May 2007. We chose this period because winter migrants are no longer present and it corresponded with the pre-hatch stage of the nesting cycle, when females incubate and males remain sentinel outside the nest entrance (Martin 1973, Plumpton and Lutz 1993). We balanced survey effort with 12 hr of survey effort per 1-hr survey period over the 3 days.

We surveyed each nest once with 1 observer and 1 driver without the aid of optical equipment in a vehicle that traveled 11 km/hr. The observer and driver both located owls, but the observer usually detected owls. Each trial was preceded by 5–10 min of continuous observations by 1 person with optical equipment in a second vehicle parked at a distance that we believed would not disturb owls (approx. 160 m). To avoid the potential bias of behavioral responses to the parked vehicle, we randomly chose when each trial was started between 5 min and 10 min after continuous observations began, at which time the person in the parked vehicle recorded whether the owl was available for detection (i.e., not in its burrow). If the person in the parked vehicle observed the owl entering a nest burrow prior to and not leaving it during a trial, that owl was considered unavailable for detection by the surveyors; all other owls were considered available for detection, although the visibility of those owls to surveyors in the moving vehicle were expected to vary due to environmental conditions such as perch locations and vegetation cover. Thus, if the person in the parked vehicle observed an owl aboveground that moved behind a barrier (e.g., dense vegetation), that owl was still considered available for detection. The observer and driver of the moving vehicle did not know the location of the nest burrow prior to a trial. We surveyed only owls with locations that were known by the person in the parked vehicle. To avoid problems with overestimating detection due to observers and drivers anticipating the presence of an owl based on the presence of the parked car, we also conducted trials on owls that were not available for detection (e.g., in burrows). Thus, the presence of a parked car was not a reliable cue that an owl was available for detection. We excluded data from these mock-trials from analyses of bias in visibility.

To reduce potential variation in our ability to detect an owl during a trial due to differences in fields of view among types of vehicles, we used the same make and model (Ford Escape), and kept the side windows up. This vehicle afforded good forward and lateral visibility from the driver's and front passenger's seats.

We recorded whether the observer or driver in the survey vehicle saw an owl during each trial. When we saw an owl, we stopped the survey vehicle and recorded data on factors that we believed could affect the visibility of an owl from the vehicle given that it was available for detection. To reduce potential problems associated with variability in continuous predictor variables, we measured some factors according to broad categories. We recorded the number of owls (1 or 2) present that were ≤ 3 m apart, time, type of water conveyance structure closest to the owl (earthen or cement-lined), and percent vegetation cover (0%, 1%–25%, 26%–50%, 51%–75%, or 76%–100%) within a 30° horizontal field of view from where the surveyors first detected the owl (centered on the detected owl). We also recorded if we detected the owl in flight (i.e., flushed or flying) or on a perch (burrow entrance, bare ground, cement liner, fence post or stake, pipe, utility pole, utility or fence wire, farm equipment, irrigation head gate, debris pile, in or on vegetation, in vegetated agricultural field, or hay bales). We recorded the average wind speed (<20 km/hr or >20 km/hr) for 1 min immediately after detection using a Kestrel 3000 Pocket Weather Monitor (Nielsen-Kellerman, Boothwyn, PA) and percent of the sky obstructed by clouds (0%, 1%–25%, 26%–50%, 51%–75, or 76–100%) because others have reported that high wind speeds (>20 km/hr) and cloud cover influence detection of owls (Shyry et al. 2001, Conway et al. 2008). We counted the number of owls present because we anticipated that 2 owls would be more visible than a single owl. We distinguished owls first observed on perches from those detected when they flushed or flew because we anticipated that movement would increase visibility. If an owl was undetected by the surveyors, the person in the parked vehicle recorded the above information from where that person first detected the owl during the trial after the 5–10 min continuous observation period.

Correcting for Visibility and Availability Biases

We used only the data from owls that were available for detection to develop visibility models to avoid the confounding affect of availability and because we did not design our visibility trials to account for variation in availability. To avoid problems with small sample sizes in each perch category (Table 1), we created the following reduced categories: 1) perched at burrow entrance, 2) flushed or flying, 3) perched in agricultural field, 4) perched on bare ground, including cement liner, 5) perched on hay bales, 6) perched on or in nonagricultural vegetation, and 7) perched on post, pipe, pole, wire, irrigation head gate, debris pile, or farm equipment. Although the sample size was small ($n = 11$), we chose to keep agricultural field as a separate perch type given its high prevalence across the landscape, close proximity to most nest burrows, and frequent use by owls in this system (Rosenberg and Haley 2004).

We fit a candidate set of 41 logistic regression models to our visibility data, where each model represented an alternative a priori hypothesis. We modeled P_V of owls as a binomial response (i.e., seen or missed) to either a single, additive, or interactive affect of the discrete and categorical predictor variables. We based the structure of our models on biologically meaningful relationships that we derived from natural history records of owls (Coulombe 1971, Martin 1973, Rosenberg and Haley 2004, Conway et al. 2008). Models that included time of day (hr + min/60) used a second-degree polynomial function of time because detections have been reported to decline during midday in this region (Coulombe 1971). We used Akaike's Information Criterion (AIC) to identify a reduced set of models ($\Delta AIC < 2.0$), used parsimony to select a single model from the competing set (Akaike 1973, Lebreton et al. 1992, Burnham and Anderson 2002), and considered this to be our best predictive model.

We used the area under a receiver operating characteristic (ROC) curve to assess how well the parameters from our best logistic model predicted when owls were seen or missed (Hanley and McNeil 1982, Heagerty et al. 2000). We did this by generating predicted values for our ROC curve by applying a leave-one-out *k*-fold cross validation with our best model (Devijver and Kittler 1982). This validation approach involved using a single observation from the original sample as the validation data, and the remaining observations as the training data. We also used the deviance/df from our best model to assess how well it explained the observed variation

Table 1. Breeding burrowing owl visibility survey results by independent variable from the Imperial Valley, California, USA, 2007.

Variable	≥1 Owl[a] Seen	Missed	Visibility[b]
Number of owls[c]			
1	412	67	0.860
2	73	14	0.839
Time of day			
0630–0729	19	4	0.826
0730–0829	47	12	0.797
0830–0929	51	15	0.773
0930–1029	65	12	0.844
1030–1129	57	4	0.934
1130–1229	35	4	0.897
1230–1329	15	0	1.000
1330–1429	24	2	0.923
1430–1529	46	6	0.885
1530–1629	48	5	0.906
1630–1729	38	4	0.905
1730–1829	34	5	0.872
1830–1929	6	2	0.750
Water conveyance structure			
Cement-lined	187	37	0.835
Earthen	305	48	0.864
Wind speed ($\bar{x}$km/hr)			
0	217	35	0.861
<20	22	6	0.786
>20	252	45	0.848
Cloud cover (%)			
0	68	18	0.791
1-25	279	45	0.861
26-50	47	4	0.922
51-75	48	9	0.842
76-100	49	10	0.831
Vegetation cover (%)			
0	22	5	0.815
1–25	217	28	0.886
26–50	203	32	0.864
51–75	41	17	0.707
76–100	8	4	0.667
Perch or flying			
Flushed or flying	41	3	0.932
At burrow entrance	89	13	0.873
Debris pile	4	0	1.000
In agricultural field	5	6	0.455
In or on vegetation[d]	14	7	0.667
On bare ground	258	42	0.860
On cement liner	6	1	0.857
On farm equipment	3	1	0.750
On fence post	32	1	0.970
On hay bales	17	1	0.944
On head gate	9	1	0.900
On pipe	5	2	0.714
On utility pole	2	0	1.000
On utility wire	1	2	0.333

[a] ≥1 Owl detected in a breeding territory.
[b] Visibility = (no. of owls seen) ÷ (no. of owls seen + no. of owls missed).
[c] Number of owls ≤3 m apart.
[d] In or on vegetation other than agricultural crops.

in P_V, where a model with deviance/df > 1 would suggest over-dispersion (i.e., extra binomial variance).

Based on the concept of sampling weights, where a sample unit's weight is the inverse of its probability of being visible (Lohr 1999), we used the results from our best model to compute unbiased maximum likelihood estimates of P_V ($\hat{P}_{Vi}$) as a devisor to correct for visibility bias (Diefenbach et al. 2007), such that

$$\hat{\theta}_{Vi} = \frac{1}{\hat{P}_{Vi}} = 1 + e^{-x_i'\tilde{\beta} - x_i' \sum x_i/2}$$

where $x_i'\tilde{\beta}$ is a logistic regression function ($\beta_o + \beta_i x_{1i} + \cdots + \beta_{p-1} x_{p-1i}$) and x_i' is the vector of covariates ($x_1, \ldots x_p$) that significantly influence visibility of those owls i with those environmental characteristics, and $\sum x_i$ is the empirically derived variance-covariance matrix (Steinhorst and Samuel 1989).

Because our logistic visibility model is intended for applying to a census of an area rather than a sample of available land units, the estimated variance of $\hat{\theta}_V$ is a reduced version of the variance estimator of (Steinhorst and Samuel 1989), such that

$$\hat{v}ar(\hat{\theta}_V) = \left(\sum_{i=1}^{n} \frac{1-\hat{\theta}_{Vi}}{\hat{\theta}_{Vi}}\right) + \left(\sum_{j}\sum_{j'} b_j \times b_{j'} \times S(\hat{\theta}_{Vj}, \hat{\theta}_{Vj'})\right)$$

where the 2 variance components relate to visibility error and error associated with estimating $\hat{\theta}_V$ (Steinhorst and Samuel 1989), j indexes a group of owls i having a constant level of a given environmental characteristic, $b_j = \sum_{i \in j} m_i$, where m_i is the number of owls in the ith group, and $S((1/\hat{\theta}_{Vj}), (1/\hat{\theta}_{Vj'}))$ is the empirically derived standard error (Steinhorst and Samuel 1989).

We estimated availability bias separately because the probability of being available generally follows a different pattern from the probability of being visible (Diefenbach et al. 2007). To correct for availability bias, we used the mixed effects linear equation by Manning (2011) as a devisor such that

$$\hat{\theta}_{Ai} = \frac{1}{\hat{P}_{Ai}} = \frac{1}{(\sin(2.13 - 0.03 \times \text{temperature}))^2}$$

where temperature was measured in °C. The estimated variance of $\hat{\theta}_A$ is

$$\hat{v}ar(\hat{\theta}_A) = \left(\sum_{i=1}^{n} \frac{1-\hat{\theta}_{Ai}}{\hat{\theta}_{Ai}}\right) + \left(\sum_{j}\sum_{j'} b_j \times b_{j'} \times S(\hat{\theta}_{Aj}, \hat{\theta}_{Aj'})\right)$$

Visibility and availability corrected estimates of population size ($\hat{N}_{VA}$) are computed as

$$\hat{N}_{VA} = \sum_{i=1}^{n} n_i \times (\hat{\theta}_{Vi} \times \hat{\theta}_{Ai})$$

(e.g., 8 owls observed with a $\hat{P}_{Vi}$ of 0.5 and $\hat{P}_{Ai}$ of 0.5 yields an estimate of 32 owls). Given that $\hat{\theta}_V$ and $\hat{\theta}_A$ are independent and their covariance is zero (Goodman 1960, Schreuder et al. 2004), the variance of $\hat{N}_{\mathrm{VA}}$ is

$$\hat{v}ar(\hat{N}_{\mathrm{VA}}) = (\hat{N}_{\mathrm{VA}} \times \bar{\hat{\theta}}_{\mathrm{V}} \times \bar{\hat{\theta}}_{\mathrm{A}})^2 \times \left(\frac{\hat{v}ar(\hat{\theta}_{\mathrm{V}})}{\bar{\hat{\theta}}_{\mathrm{V}}^2} + \frac{\hat{v}ar(\hat{\theta}_{\mathrm{A}})}{\bar{\hat{\theta}}_{\mathrm{A}}^2} \right)$$

Validation

To gauge the performance of our modeled $\hat{\theta}_{\mathrm{V}}$s and validate their use with estimates of $\hat{\theta}_{\mathrm{A}}$ to produce reliable estimates of $\hat{N}_{\mathrm{VA}}$, we used a portion of our study area where abundance was known and independent from that we used to develop the visibility model. The validation site was representative of the study area in terms of the agricultural activities, water conveyance structures, vegetation cover, and other perches found across the study area. We randomly selected a 6.5 km length of irrigation system from a vector layer of all possible 6.5-km segments of irrigation drains and canals (5,385 km) maintained by the Imperial Irrigation District (Imperial, California) in the study area and counted all active burrows that contained sign of owl use (e.g., regurgitated pellets, feathers, nest lining, whitewash, footprints with an absence of cobwebs, or an owl that retreated or flushed from a burrow; Conway et al. 2008). We also captured 22 resident male owls in this area with noose carpets, bal-chatris traps, Havahart traps, and mist nets (Collister 1967, McClure 1984, Bloom 1987, Bloom et al. 2007; Federal Bird Marking and Salvage permit 20431 and California Scientific Collector's Permit 801176-02). Each owl was fitted with metal U.S. Geological Survey and colored plastic, alphanumeric leg bands. We used the apparent absence of brood patches to assign sex to each banded owl, and verified that the male in each territory was banded by revisiting the area 3 times during the subsequent days when we anticipated that females would be incubating eggs in the nest burrow. We used this information and that from counting active nests to derive a true number of active territories; we believe this was sufficient for obtaining true abundance because no new owls or nests were located on the third visit.

We completed 4 separate visibility survey occasions of owls along this length from 0700 hours to 1100 hours between 2 April and 17 April 2007 with surveyors that were independent from those who collected the data used to develop the visibility model. Each visibility survey was conducted on a different day by a different set of surveyors (driver and passenger). We recorded the information required to apply our best visibility model, and calculated $\hat{\theta}_{\mathrm{Vi}}$ and $\hat{\theta}_{\mathrm{Ai}}$ for each group of owls *i* with the same environmental covariates. We used these correction factors to compute $\hat{N}_{\mathrm{VA}}$ for each survey, and compared the associated 90% confidence intervals to the true number of active territories. We computed statistics using R (R Version 2.11.1, www.r-project.org, accessed 31 Mar 2008).

RESULTS

We collected data on 7 factors anticipated to influence visibility while conducting vehicle-based surveys during the pre-hatch stage of the breeding cycle at 567 randomly selected active burrowing owl territories (Table 1). We observed owls perching on bare ground at a higher frequency than any other perch, but there was a marked decrease in the use of this perch type in early afternoon followed by an increase in the late afternoon (Fig. 1). The number of observations at the burrow entrance also followed this pattern, although at lower frequencies. We observed the majority of owls at the burrow entrance or on bare ground away from their nest. The visibility of 2 owls was similar to that of 1 (Table 1); thus, we did not include number of owls in our visibility models.

Factors Influencing Visibility

There were 6 competing models in our candidate set that explained the variation in visibility (Table 2), although the most parsimonious of these hypothesized that visibility was a second-degree polynomial function of time of day and a function of perch type (Fig. 2). We considered this our best model because the inclusion of vegetation type, cloud

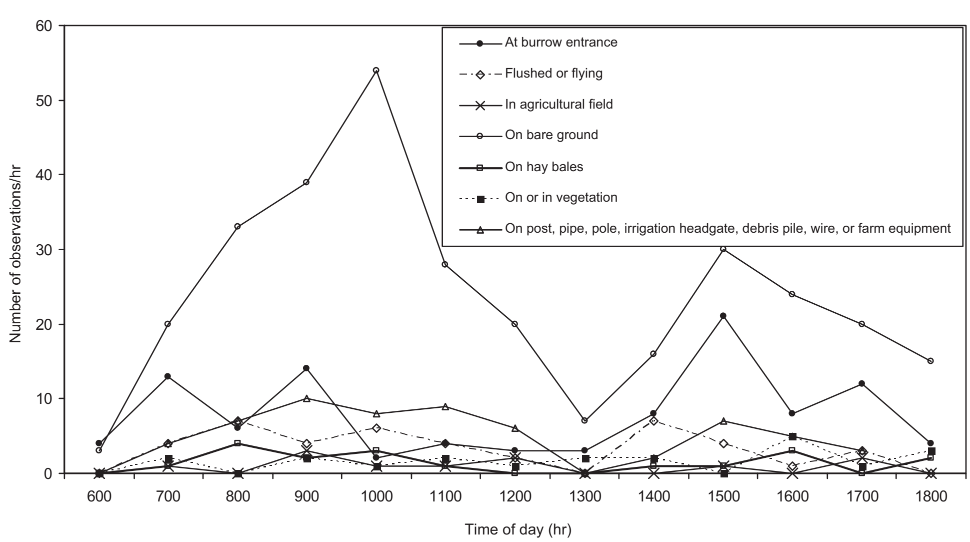

Figure 1. Number of burrowing owl detections on perches and flushed or flying during vehicle-based visual surveys in the pre-hatch stage of the breeding cycle during daylight hours in the Imperial Valley, California, USA, 2007. Survey effort was balanced across all 1-hr periods. Sunrise and sunset were at 0600 and 1922, respectively.

Table 2. Top 20 logistic regression models predicting the probability of a burrowing owl being visible during the pre-hatch stage of the breeding cycle in the Imperial Valley, California, USA, 2007. Models are ranked from best to worst on the basis of the difference in Akaike's Information Criterion (ΔAIC) between a model and that of the model with the lowest AIC, where AIC is based on −2log likelihood and the number of parameters (*K*) in the model.

Model	*K*	ΔAIC
Time + time^2 + perch[a] + vegetation cover[b] + cloud cover[c]	14	0.0
Time + time^2 + perch + cloud cover	11	0.0
Time + time^2 + perch	9	0.3
Time + time^2 + perch + vegetation cover + wind speed[d]	11	1.0
Time + time^2 + perch + water conveyance structure[e]	10	1.3
Perch + vegetation cover + cloud cover	12	1.7
Perch	7	2.1
Time + time^2 + perch + wind speed	11	2.4
Perch + cloud cover	9	2.5
Perch + water conveyance structure	8	2.5
Perch + water conveyance structure + cloud cover	10	3.0
Perch + vegetation cover + wind speed	11	3.1
Perch + wind speed	9	4.9
Perch + water conveyance structure + wind speed	10	5.6
Time + time^2 + vegetation cover	6	7.0
Time + time^2 + vegetation cover + cloud cover	8	7.2
Vegetation cover	4	7.3
Time + time^2 + vegetation cover + wind speed	8	8.0
Vegetation cover + cloud cover	6	8.1
Time + time^2 + vegetation cover + water conveyance structure	7	8.8

[a] Flushed or flying, in agricultural field, on bare ground, on hay bales, on or in vegetation, or on post, pipe, pole, wire, irrigation head gate, debris pile, or farm equipment.
[b] 0%, 1%–15%, 26%–50%, 51%–100%.
[c] 0%, 1%–50%, 51%–100%.
[d] 0 km/hr, <20 km/hr, or >20 km/hr.
[e] Earthen or cement-lined.

cover, wind speed, and type of water conveyance structure in the nested competing models did not significantly improve the fit of our best model (ΔAIC < 2.0), indicating little support for these covariates in that they did not explain additional variation in visibility beyond that accounted for by time of day and perch type. This model was fairly accurate (area under the ROC curve = 0.70), with no evidence of over-dispersion (deviance/df = 0.68), indicating that the independent variables in the model adequately accounted for the observed variation in probabilities of visibility. Parameter estimates indicated that visibility varied by type of perch and throughout the day, with visibility unexpectedly being highest in the afternoon (Table 3, Fig. 2). This was opposite the pattern observed with respect to availability (Manning 2011). We also included the empirically derived covariance matrix of vector covariates used to develop the visibility bias correction model (Appendix). The model predicted that owls observed flushing and flying or perched on hay bales were highly visible (>0.93 and >0.88, respectively) throughout the day, whereas visibility was lowest in agricultural fields (<0.46) and nonagricultural vegetation (<0.72).

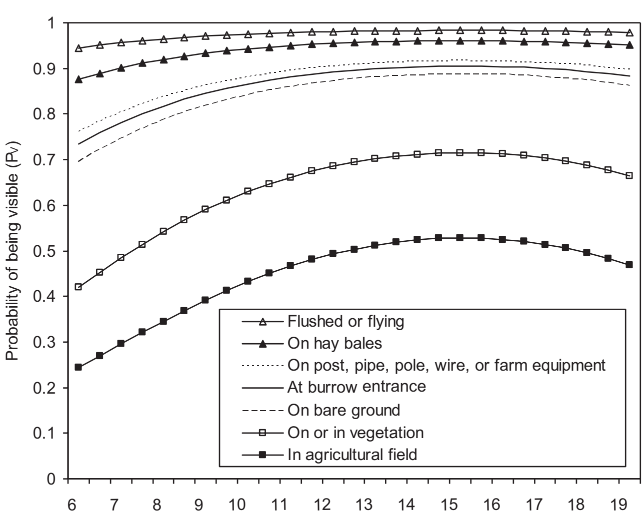

Figure 2. Probability of a burrowing owl being visible as a function of time of day and type of perch during vehicle-based visual surveys estimated by a logistic regression model based on 567 diurnal observations in the pre-hatch stage of the breeding cycle in Imperial Valley, California, USA, 2007.

Model Estimates and Validation

We combined the unbiased maximum likelihood estimates of $\hat{\theta}_V$ derived from our best visibility model with $\hat{\theta}_A$s estimated using the quadratic model by Manning (2011) to compute visibility and availability corrected estimates of $\hat{N}$ from 4 independent surveys of 22 resident male owls conducted between 0700 hours and 1100 hours in our study area. The average of the raw survey counts ($\bar{x} = 17.75$) was biased 18% below the true number of territories, with 90% confidence intervals that did not include the true number. The average of the visibility and availability corrected estimates ($\bar{x} = 22.1$) was unbiased, and the 90% confidence intervals overlapped the true number. All of the 4 corrected estimates had 90% confidence intervals that overlapped the true number of resident males (Fig. 3).

Table 3. Parameter estimates for burrowing owl visibility model (Imperial Valley, California, USA, 2007).

Variable	Estimate	SE	95% CI
Intercept[a]	−1.176	0.568	−2.289 to −0.063
Time	0.456	0.219	0.025–0.886
Time^2	−0.015	0.013	−0.040 to 0.010
Perch type			
Flushed or flying	1.816	1.058	−0.258 to 3.889
Perched in agricultural field	−2.142	0.682	−3.478 to −0.805
Perched on bare ground	−0.188	0.342	−0.858 to 0.483
Perched on hay bale(s)	0.939	1.074	−1.165 to 3.044
Perched on or in nonagricultural vegetation	−1.335	0.558	−2.429 to −0.241
Perched on post, pipe, pole, wire, irrigation head gate, debris pile, or farm equipment	0.144	0.505	−0.845 to 1.133

[a] Intercept is the coefficient that coincides with the at burrow entrance perch type.

DISCUSSION

Our validated results demonstrated that jointly correcting for burrowing owl visibility and availability can produce unbiased estimates of population size. Burrowing owl visibility during single, diurnal, vehicle-based, visual surveys in the pre-hatch stage of the breeding cycle was determined primarily by perch type and a second-degree polynomial function of time of day. Visibility peaked in the afternoon, which was the opposite of that found for availability during the same stage of the breeding cycle in our study area (Manning 2011). Although patterns of availability indicate that owls are least available for detection in the afternoon, the limited numbers that were available were more easily seen by observers. Thus, estimates from a single afternoon count will be relatively precise, but negatively biased, whereas those from morning and late afternoon will be less biased and less precise.

Although there were competing models, the addition of vegetation type, cloud cover, wind speed, and type of water conveyance structure did not significantly improve the fit of our best model (ΔAIC < 2.0), indicating that they did not explain additional variation in visibility beyond that explained by the model with only time of day and perch type (Burnham and Anderson 2002, Arnold 2010). We were surprised that cloud cover and wind speed did not improve model fit because others have found them to be important in estimating P in northern owl populations (Conway et al. 2008). One reason for why the addition of clouds and wind did not significantly improve model fit among the nested competing visibility models may be that they only influenced the P_A component of P. Alternatively, our field measurements associated with these variables may have introduced additional measurement error relative to that associated with recording only time of day and type of perch. However, the ROC curve with the *k*-fold cross validation predicted values from our best model did show that time of day and perch type alone performed fairly well at predicting whether an owl was visible or not.

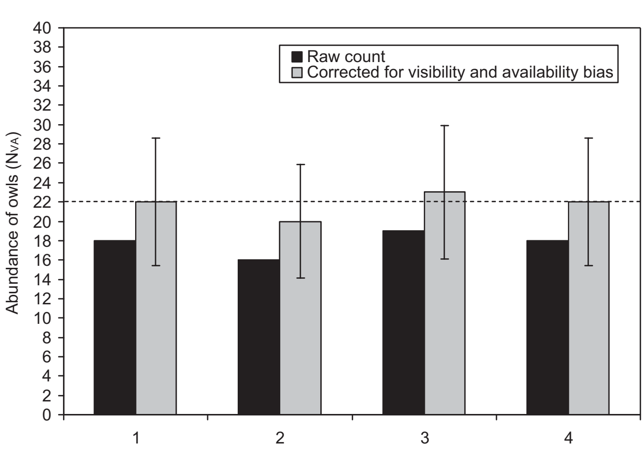

Figure 3. Visibility corrected estimates and raw counts of burrowing owls from a population of known size (dashed line) during vehicle-based visual surveys in the pre-hatch stage of the breeding cycle in the Imperial Valley, California, USA, 2007. The reference perch category was at burrow entrance. Vertical bars are 90% confidence intervals.

Ambient temperature has been reported to affect the detection of owls in the northwestern United States, where temperatures are considerably cooler (Conway et al. 2008). We did not measure temperature because the results from a pilot study suggested that the high temperatures in our study area were not good predictors of detection, and perch selection in our system may be a function of thermoregulatory needs (Coulombe 1971). Owls in the Imperial Valley perch on the ground in the early morning, move to perches elevated several meters above ground in late morning, and use either the shade of their burrow entrance or cooling wind at the top of a utility pole in the afternoon (Coulombe 1971). Although we observed an increase of owls at nest entrances in the late afternoon when temperatures were high, this coincided with an unexpected increase in observations on bare ground, which were not recorded concomitantly with observations at nest entrances. This unexpected increase may have occurred because we assigned small dirt clods (>7.5 cm in diameter) that were frequently used by owls as sentry or secondary perches along the embankments of irrigation ditches as bare ground, but these may have functioned as elevated perches. Another cause may be the increase in activities by owls in late afternoon in preparation for crepuscular and nocturnal foraging. Under laboratory conditions, temperature, and time of day have been shown to influence owl activities (Coulombe 1971), and this suggests that effects of temperature on visibility and availability may be confounded by time of day. Additionally, ambient temperature has been found to interact with wind speed (Conway et al. 2008, Manning 2011).

The external validation consistently demonstrated that our model corrected for visibility and availability biases despite using a validation dataset that was collected 2 weeks earlier during the breeding cycle compared to that used for model development. Although the stage of the breeding cycle has been shown to affect detection probability of burrowing owls (Conway et al. 2008), we did not observe fledglings throughout the 1-month study, indicating that the data used to develop and validate the model represented the early stages of nest phenology (Coulombe 1971, Thomsen 1971, Plumpton and Lutz 1993). Consequently, our validations suggested that our model was robust to slight changes in visibility and/or availability that may have occurred over the 2-week period. However, we caution against applying our model to later stages of nesting phenology when availability is likely to increase due to females and nestlings emerging aboveground (Coulombe 1971, Thomsen 1971, Plumpton and Lutz 1993).

Because probabilities of visibility described here and probabilities of availability reported by Manning (2011) differ throughout the day in the Imperial Valley and likely across the southwest United States, surveying throughout the day will produce biased estimates of population size in southwest agroecosystems if both types of bias are unaccounted for. Our validation showed that single uncorrected counts of burrowing owls conducted prior to the afternoon in our system were negatively biased by approximately 20%. Thomsen (1971) reported that low availability of burrowing owls during mid-afternoon surveys in northern California biased population counts 90% below the known population size. Our joint bias correction factors correct for visibility and availability biases that occur during single diurnal counts conducted throughout the day during the pre-hatch stage of the breeding cycle. Thus, future burrowing owl population data collected under similar sighting conditions throughout the day in the Imperial Valley and like habitats across the southwest as those used to develop our sightability model should provide unbiased owl population estimates. However, as we did not have independent data to validate our visibility and availability bias corrected estimates for times after 1,100, additional external validation should be completed for later hours of the day when environmental conditions such as increased temperature and wind speed may further affect owl detection probabilities.

MANAGEMENT IMPLICATIONS

As burrowing owls increasingly occupy agricultural environments across their range in North America (Rich 1986, Leptich 1994, DeSante et al. 2004), these areas will become increasingly important for conservation and management of this species. Because probabilities of visibility and availability vary throughout the day and seasonally in the dense owl population occupying the agricultural matrix of the Imperial Valley, long-term monitoring that requires reliable estimates of population size necessitate that survey counts in this region be corrected for both types of bias. Our bias correction factors (with the empirically derived covariance matrix of vector covariates in Appendix) provide a method to correct these biases using a single survey occasion that is relatively affordable for long-term monitoring compared to other methods that require multiple survey occasions (e.g., capture–recapture; Williams et al. 2002). This method corrects both types of biases and provides a measure of precision that can be incorporated into guidelines for local and range-wide survey efforts that involve surveying the Imperial Valley and other like habitats across the southwest. The efficacy of applying these joint bias correction factors to other areas can easily be assessed by replicating our validation approach where owl abundance is known.

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APPENDIX. COVARIANCE MATRIX OF VECTOR COVARIATES

Empirically derived covariance matrix of vector covariates ($\sum x_i$) used to develop a visibility bias correction model with unbiased maximum likelihood estimates of visibility for burrowing owls (Imperial Valley, California, USA, 2007).

Parameter	Intercept	Time	Time^2	Flushed or flying	Perched in agricultural field	Perched on bare ground	Perched on hay bale(s)	Perched on or in nonagricultural vegetation	Perched on post or other[a]
Intercept[a]	0.323	−0.288	0.023	−0.023	0.020	−0.020	−0.063	−0.033	0.005
Time	−0.288	0.048	−0.004	−0.013	−0.019	−0.013	−0.006	−0.008	−0.017
Time^2	0.023	−0.004	0.000	0.001	0.001	0.001	0.000	0.000	0.001
Flushed or flying	−0.023	−0.013	0.001	1.119	0.092	0.092	0.091	0.088	0.093
Perched in agricultural field	0.020	−0.019	0.001	0.092	0.465	0.092	0.091	0.091	0.093
Perched on bare ground	−0.020	−0.013	0.001	0.092	0.092	0.117	0.091	0.090	0.092
Perched on hay bale(s)	−0.063	−0.006	0.000	0.091	0.091	0.091	1.153	0.089	0.091
Perched on or in nonagricultural vegetation	−0.033	−0.008	0.000	0.088	0.091	0.090	0.089	0.311	0.089
Perched on post or other[b]	0.005	−0.017	0.001	0.093	0.093	0.092	0.091	0.089	0.255

[a] Intercept is the coefficient that coincides with the at burrow entrance perch type.
[b] Pipe, pole, wire, irrigation head gate, debris pile, or farm equipment.