ESTIMATION OF REPRODUCTIVE RATES OF BURROWING OWLS

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Abstract: Obtaining reliable estimates of absolute and relative reproductive rates is challenging for avian species whose nests are difficult to observe, such as the burrowing owl (*Athene cunicularia*). We compared methods for estimating reproductive rates of burrowing owls, defined as the number of 21- to 28-day-old young per successful nest. We compared observations using (1) the mean and (2) the maximum number of young observed during 5 30-min observation periods, and (3) the maximum number of young videotaped during 2-hr video surveillance. We evaluated the reliability of these methods with the known number of young present in nest boxes. All 3 methods performed poorly as estimators of absolute reproductive rates (absolute bias >23%, root mean square error [RMSE] >42%). Video surveillance performed most poorly of the 3, with a high incidence of failing to detect any young at successful nests. The maximum number of young observed from direct nest observations was correlated with the known number of young ($r = 0.82 \pm 0.13$, $n = 21$) and provided more reliable estimates of relative than absolute reproductive rates. The mean number of young observed from direct observations was correlated with the known number of young ($r = 0.64 \pm 0.18$, $n = 21$), but had both higher bias and lower precision than the maximum number observed for estimation of relative reproductive rates. Our results suggest that using counts of young observed outside of the nest burrow may lead to incorrect conclusions on factors affecting reproductive rates. When counts are the basis of inference, the effort researchers use at each nest should be standardized and reported. Further work on field methods that allow estimation of detection probability, or ensuring that all young are observed, will be imperative in providing reliable estimates.

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As an essential component of recruitment, estimation of reproductive rates is central to understanding population dynamics of birds. The number of young per female often is used as the measure of reproductive rate and usually is assumed to be a known parameter (i.e., without sampling error; e.g., Franklin et al. 1996). Although this assumption often is incorrect for species with inaccessible nests, such as burrowing owls, the issue largely has been ignored. In such cases, identifying and evaluating methods to estimate reproductive rates using estimators with low bias and high precision is important.

The estimation and comparison of reproductive rates of burrowing owls have been problematic because their nests are underground, and thus the number of young are not easily counted accurately. Natural nests cannot be sampled without destructive excavation, and young are not easily detected visually because they spend significant time in burrows. Therefore, mark–recapture methods (e.g., Otis et al. 1978) have been problematic to apply. Instead, reproductive rates have been estimated based on counts of young seen above ground (reviewed in Haug et al. 1993) or in nest boxes (Henny and Blus 1981, Rosenberg and Haley 2003). The former is likely to result in underestimation of reproductive rates and potentially lead to invalid inferences on tem-

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poral and spatial patterns of relative reproductive rates. Although nest boxes provide a reliable means of determining reproductive rates, they are not always available and used by owls under study.

Little attention has been given to issues related to biases in estimating burrowing owl reproductive rates. Because counts obtained from varying levels of effort to observe and/or trap young at nests would be expected to have different probabilities of encountering young, meaningful comparisons among studies have been limited. Indeed, most studies (e.g., Thomsen 1971, Lutz and Plumpton 1999, Millsap and Bear 2000) do not report the observation effort at each nest. Even among studies that use similar methods, different survey timing relative to the age of young confounds comparisons of reproductive rates with survival and behavior. For example, surveys during early brood-rearing are likely to result in positively biased estimates relative to later counts due to mortality between emergence and fledging. At sites where broods are split between multiple burrows (Desmond and Savidge 1999, Ronan 2002), bias may increase with the age of young due to the difficulty of observing and identifying complete broods. Such biases also are likely to result in invalid conclusions on comparisons of reproductive rates.

Unequal observation effort and differences in sighting probability among nests introduces bias to estimates of relative reproductive rates. Thus, comparisons of reproductive rates with factors such as morphology (Plumpton and Lutz 1994), habitat characteristics and space use (Botelho and Arrowood 1998, Ronan 2002, Gervais et al. 2003), and prey abundance (Gervais et al. 2003) could be confounded with unequal detection rates. Despite the predominant use of counts in assessing relative reproductive rates of burrowing owls, evaluation of such methods remains unexplored.

We addressed these issues by comparing estimates of burrowing owl reproductive rates using visual observations and video surveillance. We compared these estimates with the known number of young from nest boxes to estimate the reliability of absolute and relative measures of burrowing owl reproductive rates.

STUDY AREA

We conducted our fieldwork during May–June in 1998 and 1999 at 3 sites in California: Carrizo Plain National Monument (Carrizo), Naval Air Station Lemoore (Lemoore), and Sonny Bono Salton Sea National Wildlife Refuge (Salton Sea). The Carrizo site is a semi-desert grassland located 100 km west of Bakersfield. Lemoore, located 50 km southwest of Fresno in the San Joaquin Valley, consists of small patches of grasslands surrounded by intensively farmed fields. In the Salton Sea site, located 40 km north of El Centro, owls nested along edges of agricultural fields within and adjacent to the Sonny Bono Salton Sea National Wildlife Refuge.

METHODS

Field Techniques

We evaluated reproductive rates by estimating brood size of successful (i.e., ≥1 young) nests. We use the term reproductive rate throughout because this is the parameter we are interested in estimating. As used here, reproductive rate is the number of 21- to 28-day-old young per successful nest. We evaluated direct observations using 5 30-min observation periods initiated after young were detected above ground and were approximately 21–28 days post hatch, based on feather development and behavior (Priest 1997). This allocation of total effort reflected our goal of providing a logistically feasible method when numerous nests are under study. We restricted the observations to a narrow range of age of young so that any confounding of mortality with comparisons of reproductive rates would be minimal. This also is the nestling stage when young are most easily counted—young are active above ground but remain close to the nest burrow (Haug et al. 1993). We observed 37 nests with binoculars or spotting scopes from vehicles typically 30–100 m from the nest, but up to 500 m when nests were in clear view and would otherwise be disturbed. We conducted observations ≤2 times per day with ≥6 hr between observation periods. Observations typically were conducted within 3 hr of sunrise or sunset. All observations at a nest were completed within 7 days of initial observation.

We evaluated video surveillance by videotaping nests on a single occasion for a 2-hr period at Lemoore and Carrizo (Table 1). A video camera

Table 1. Number of nests sampled for each comparison of reproductive rate estimates of burrowing owls at Carrizo Plain National Monument, Naval Air Station Lemoore, and Sonny Bono Salton Sea National Wildlife Refuge, California, USA, May–Jun 1998 and 1999.

Study site	Direct observation vs. video	Direct observation vs. known no.	Direct observation vs. video vs. known no.
Carrizo	16	–	–
Lemoore	7	7	7
Salton Sea	–	14	–

was mounted on a tripod 20–100 m from the nest and positioned to best view the burrow entrance and an area of ≥3 m on either side. At Carrizo, we left the tripod near the nest for 1 to 2 days before videotaping to acclimate owls to its presence. This was not done at Lemoore, where farm equipment and other disturbances frequently modified the environment adjacent to burrows and likely resulted in the owls' lack of a response to our video equipment (V. Franke, personal observation).

We evaluated the performance of direct (maximum and mean of counts) and video surveillance by comparing estimates between these methods and by estimating their bias and precision from nests with known number of young. We determined the number of young by opening nest boxes at Lemoore and Salton Sea (Table 1). Nests that were in artificial burrows were opened either 1 day prior to initiation of the observations or immediately after observations were completed; we assumed no mortality during the observation period (≤7 days). We computed bias and RMSE of direct observations from 21 nests (Table 1) during 1998 and 1999. Root mean square error incorporates bias and precision and is a useful summary of the performance of an estimator (Williams et al. 2001:45). We conducted both direct observations and video surveillance at nest boxes only at Lemoore (Table 1); comparisons of bias between these methods are thus restricted to nests at Lemoore. We did not use video surveillance at Salton Sea. At Carrizo, where all nests were within natural burrows, direct observations and video surveillance were conducted in 1999 (Table 1).

Statistical Analysis

We compared estimates from direct observation and video surveillance by first comparing the maximum number of young observed to the maximum number videotaped from nests at which both methods were conducted (Table 1). We used Pearson's correlation coefficient to quantify the relationship between these estimates. To compare bias and RMSE between direct observations and video surveillance as estimates of absolute reproductive rate, we used only nests at Lemoore, all of which were from nest boxes where we knew the number of young.

To evaluate the reliability of direct observations as an estimator of absolute reproductive rate, we used data from nest boxes at Lemoore and Salton Sea (Table 1). We calculated the mean percent relative bias (MPRB) as:

$$\text{MPRB} = \left(\frac{1}{n}\sum_{i=1}^{n}\left[\frac{\hat{N}i - N_i}{N_i}\right]\right)100,$$

where n is the number of nests, $\hat{N}_i$ is the maximum number of young observed together at nest i during either direct observations or video surveillance, and N_i is the true number of young per nest. We estimated RMSE as:

$$\text{RMSE} = \left(\frac{1}{n}\sum_{i=1}^{n}[\hat{N}_i - N_i]^2\right)^{\frac{1}{2}}$$

In addition to the evaluation of absolute measures of reproductive rates, we evaluated the reliability of the mean and the maximum number of young observed per nest from direct observations as estimators of relative reproductive rates among nests. Although the maximum number observed is clearly a less biased estimator of absolute reproductive rates, the mean of counts from 5 30-min direct observations could be a more reliable estimator of relative reproductive rates if the maximum number counted has high variance relative to the variance of the mean. To evaluate and compare the reliability of maximum and mean counts, we constructed a matrix of pairwise comparisons among all unique combinations of nest boxes for which number of young were known. For each estimator (N_{mean} and N_{max}), we estimated the relative reproductive rate as the mean ratio (MR):

$$\hat{\text{MR}} = \frac{1}{R}\sum_{r=1}^{R}\left|(\hat{N}_{xr}/\hat{N}_{yr})\right|,$$

where R is the number of combinations of nests (R = 210), and $\hat{N}_{xr}$ and $\hat{N}_{yr}$ are the estimated number of young per nest for each rth comparison ($x \neq y$) of nests. We then compared mean ratio percent relative bias (MRPRB) and RMSE of the ratio (RRMSE) among estimators. We estimated MRPRB as:

$$\text{MRPRB} = \left(\frac{\hat{\text{MR}} - \text{MR}}{\text{MR}}\right)100,$$

where MR is the true mean ratio between pairs of nests. We estimated RMSE of relative reproductive rates as:

$$\text{RRMSE} = \left\{\left[\frac{1}{R}\sum_{r=1}^{R}\left[(\hat{N}_{xr}/\hat{N}_{yr}) - (N_{xr}/N_{yr})\right]^2\right\}^{1/2},$$

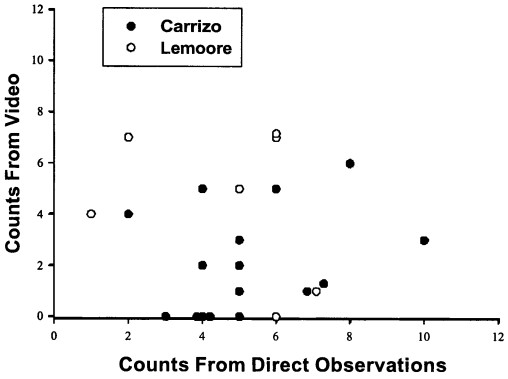

Fig. 1. Relationship between number of young per nest as estimated with counts from the maximum number of young observed during videotaping and direct observations. Counts were made at nest boxes at Lemoore Naval Air Station (n = 7) and from natural burrows at Carrizo Plain National Monument (n = 16), California, USA, May–Jun 1999. We found no apparent relationship between counts made from videotaping vs. direct observation (r = 0.01 ± 0.22).

with N and N greater than zero, as was the case in all comparisons.

Because of the small number of possible ratios that arise from the limited number of possible reproductive outcomes, we used known ratios to estimate a null expectation for RRMSE and thus facilitate comparison of estimator performance. We estimated the null expectation (i.e., no relationship of the number of young between pairwise comparisons of nests) by constructing 2 sets of ratios of reproductive rates that were randomized relative to one another.

RESULTS

Direct observations were more effective than video surveillance as an estimator of absolute reproductive rates. While at least 1 young was always observed at successful nests with direct observations, we failed to observe young at 25% of these nests from video surveillance (Fig. 1). From the sample of 23 nests for which both direct observations and video surveillance were used, 2.3 ± 0.7 more young per nest were estimated with the maximum number observed than with video surveillance. Differences between the 2 methods tended to be greater at Carrizo (3.3 ± 0.6 young/nest, n = 16) than at Lemoore (0.3 ± 1.6 young/nest, n = 7), although the imprecision of the Lemoore estimates resulted in overlapping 95% confidence intervals. The coefficient of variation of the maximum number of young was greater for video surveillance than for direct observations (maximum counted) at Carrizo (109.0 vs. 38.7%) and Lemoore (66.3 vs. 48.4%), respectively. We found no apparent relationship between the numbers of young estimated with the 2 methods (r = 0.01, n = 23; Fig. 1).

Neither direct observations nor video surveillance provided reliable estimates of absolute reproductive rates at the levels of effort used in this study. Precision was poor for both methods, particularly for video surveillance (Table 2). The large RMSE of both estimators resulted from a few nests in which ≤1 young was observed (Fig. 2). These results, which were based on the sample of 7 nests (Lemoore; Table 1) for which number of young was known as well as estimated from direct observations and video surveillance, suggest neither method provided reliable estimates of the number of young. Bias and precision of the maximum number of young counted, as estimated from nest boxes at Salton Sea and Lemoore, was considerably better than represented from the comparison of only the 7 Lemoore nests (Table 2), but bias and RMSE remained reasonably high.

Table 2. Performance of the maximum number of young observed per nest during visual observations and video surveillance as estimators of the reproductive rates of burrowing owls at nest boxes at Naval Air Station Lemoore and Sonny Bono Salton Sea National Wildlife Refuge, California, USA, May–Jun 1998 and 1999.

	Known no. young		Video				Direct observation			
	Mean (range)	SE	Mean (range)	SE	Mean percent relative bias	Root mean square error	Mean (range)	SE	Mean percent relative bias	Root mean square error
Direct observations and video surveillance (n = 7 nests)[a]	7.0 (4–9)	0.7	4.4 (0–7)	1.1	–31.5	4.2	4.7 (1–7)	0.9	–33.0	3.0
Direct observation (n = 21 nests)[b]	4.5 (1–9)	0.6					3.2 (1–7)	0.4	–23.0	1.9

[a] Direct observations and video surveillance were conducted at nest boxes only at Lemoore.
[b] Pooled from Salton Sea (n = 14 nests) and Lemoore (n = 7 nests).

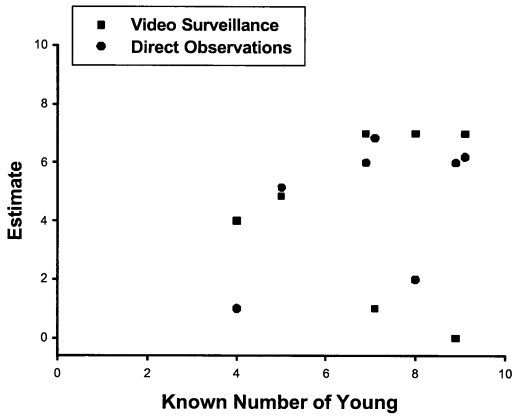

Fig. 2. Number of young in nest boxes (n = 7) estimated by the maximum counted during 5 30-min observation periods and during a 2-hr videotaping of the nest compared to the known number of young, Lemoore Naval Air Station, California, USA, May–Jun 1999.

Direct observations were more reliable as an estimator of relative than absolute reproductive rates. However, of the 2 direct counts, the mean number of young observed during the 5 30-min observation periods performed poorly whereas the maximum number observed performed reasonably well as a measure of relative reproductive rates (Table 3, Fig. 3). We found a stronger relationship between the known number of young and the maximum number counted ($r = 0.82 \pm 0.13$, $n = 21$) than with the mean number counted ($r = 0.64 \pm 0.18$, $n = 21$; Fig. 3). Similarly, our comparison among all unique combinations of nests demonstrated a stronger relationship between known and estimated relative reproductive rates for the maximum ($r = 0.79 \pm 0.03$, $n = 210$) than the mean ($r = 0.35 \pm 0.06$, $n = 210$) number of young counted. Although we found strong positive relationships between true ratios and those estimated with the mean and the maximum number counted, the imprecision of the number counted led to relatively high RRMSE (Table 3). The performance of the randomized comparisons demonstrated that the relationship we found with the maximum number counted was not due to the chance events of few possible outcomes (Table 3). The mean number observed, however, did not provide any improvement in estimation of relative reproductive rates over the null model. The poorer performance of the mean than the maximum as an estimator of relative abundance probably was due to the higher variance of the mean (VAR = 9.1) than the maximum (VAR = 1.8) counted.

DISCUSSION

Obtaining unbiased estimates of burrowing owl reproductive rates is a challenge because of the difficulty of observing complete broods outside of the burrow and the difficulty of obtaining mark–recapture data for model-based estimators. Burrowing owl broods are not often completely observed with count methods, as we demonstrated with our sampling methods. Whenever sighting probability is <1, enumeration leads to a negatively biased estimator of absolute reproductive rate, as discussed by Nichols (1986) for estimation of population size. While the importance of using model-based estimators rather than enumeration techniques in estimating population size is well accepted (Otis et al. 1978, Nichols and Pollock 1983, Nichols 1986), the importance has not been as widely noted when estimating reproductive rates other than nest success (e.g., Mayfield-based methods; Hensler and Nichols 1981). Complete broods can easily be observed in many avian species, and number of young can often be treated as a known parameter (e.g., Franklin et al. 1996). However, this must be estimated for species with inaccessible nests or precocial young that are mobile prior to fledging.

Table 3. Comparison of the performance of the mean and the maximum number of young observed (direct observations) as estimators of relative reproductive rates of burrowing owls at nest boxes at Naval Air Station Lemoore and Sonny Bono Salton Sea National Wildlife Refuge, California, USA, May–Jun 1998 and 1999. We used estimates and known number of young from 21 nests to construct a matrix of 210 estimates of relative abundance between all unique pairwise comparisons of 2 nests.

	Estimated ratio[b]			
Estimator[a]	Mean (range)	SE	Mean ratio percent relative bias (MRPRB)	Root mean square error of the relative reproductive rates (RRMSE)
Null[c]	1.0 (0.1–7.0)	0.1	0	1.6
Maximum number observed	1.1 (0.1–5.0)	0.1	16.3	0.8
Mean number observed	1.8 (0.1–21)	0.2	81.6	2.9

[a] Maximum and mean number counted from 5 30-min observation periods.

[b] Estimated ratio was the relative reproductive rate computed as the ratio between the estimated number of young per nest for each unique pair-wise comparison of 2 nests.

[c] We estimated a null expectation (i.e., the results if no relationship was found between pair-wise comparisons of nests) by constructing 2 sets of known ratios of reproductive rates that were randomized relative to one another.

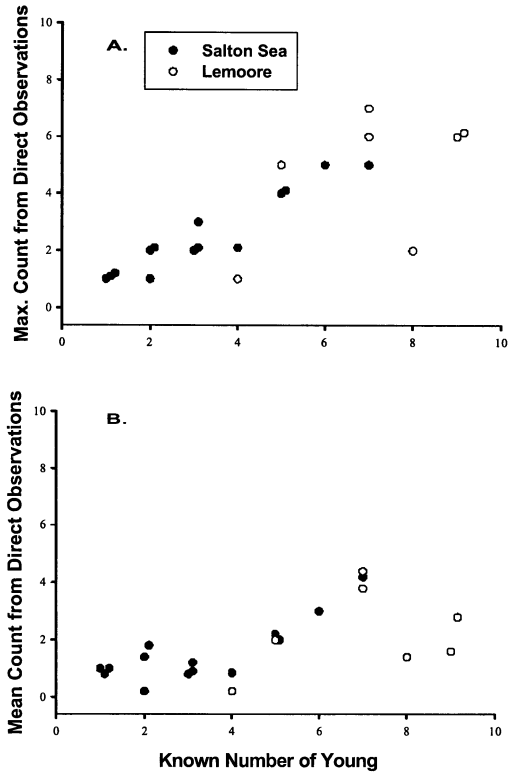

Fig. 3. Relationship of the (A) maximum and (B) mean number of young counted during 5 30-min observation periods of nest boxes with the known number of young, Salton Sea National Wildlife Refuge (n = 14) and Naval Air Station Lemoore (n = 7), California, USA, May–Jun 1998 and 1999. The relationship was stronger for the maximum (r = 0.82 ± 0.13) than the mean (r = 0.64 ± 0.18) number counted.

Mark–resight methods provide a strong theoretical basis for estimating population size (Otis et al. 1978, Skalski and Robson 1992) and thus the number of young at nests. However, logistical constraints have hindered the use of mark–resight for estimating burrowing owl reproductive rates. For example, bands on young are difficult to observe (D. K. Rosenberg, personal observation). Capturing owls on several occasions may be effective (Botelho and Arrowood 1998, Winchell 1999); however, this may be disruptive as well as result in low recapture rates and thus poor estimation (D. K. Rosenberg and J. A. Gervais, unpublished data). Thus, rather than using model-based estimators, most researchers have estimated reproductive rates of burrowing owls using counts of young (Thomsen 1971, Lutz and Plumpton 1999, Desmond et al. 2000, Millsap and Bear 2000), a putative index to reproductive rates (Haug et al. 1993). Our study presents the first assessment of the reliability of such methods.

We found that none of the standardized methods we tested provided reliable estimates of absolute reproductive rates. The difference in the number of young observed between direct observations and video surveillance might have been an artifact of sampling on a single occasion (video surveillance) rather than multiple observation periods (direct observations). In addition, we believe that video surveillance caused greater disturbance at the nest. Owls at Carrizo were observed on videotape giving alarm calls to young in the presence of the camera, thus discouraging young from emerging from burrows. Also, the frequent use of satellite burrows at Carrizo (Ronan 2002) made detection of young by video surveillance difficult and probably contributed to the poor performance of this method as an estimator of absolute and relative reproductive rates.

Despite bias in the estimators of absolute reproductive rate, enumeration should lead to biased estimates of relative reproductive rate only if sighting probability varies, either spatially or temporally (Skalski and Robson 1992). We found direct observations more reliable for estimating relative reproductive rates than video surveillance and the maximum counted more reliable than the mean number of young seen over the 5 30-min observation periods. Although the mean number of young observed could theoretically have been a better estimator of relative reproductive rates, the maximum number observed performed better. This likely was due to the frequent observations of no young at the nest, resulting in a very high variance of the mean number of young observed. Our results suggest that the maximum number of young counted at a given age provided a useful estimate of relative reproductive rates under the conditions that existed during our study. The repeated nature of direct observations will allow precision to be estimated through bootstrap methods (Manly 1991). Providing a variance estimator will improve the ability to separate sampling from process variation (e.g., Burnham et al. 1987) and will thus lead to greater biological insight into factors affecting reproductive rates.

Additional evaluations using more intensive effort per nest is warranted. However, during earlier studies, we found that longer observation periods (e.g., 2 hr/visit) often resulted in few young observed (D. K. Rosenberg, unpublished data). Further, in a study using identical protocols to

those described here, the maximum number of young that were observed typically were seen during the first 10 min of the 30-min observation period (45% of observations; L. Trulio and D. Chromczak, San Jose State University, unpublished data). This probably occurred because of the difficulty of observing the entire brood due to visual obstructions as well as the likelihood that some young return to the burrow when others leave. If so, repeated observations of the nest burrow for short durations will be more effective than fewer but longer observations. In most demographic studies, large sample sizes of nests are required and thus obtaining numerous long-duration visits is logistically difficult. The same arguments likely are true for longer periods of videotaping of nests. Indeed, the single 2-hr videotaping we conducted probably performed poorly in part because of the single observation period.

Using consistent methods may reduce bias in estimators of absolute and relative reproductive rates, although consistency is not necessarily sufficient. Although standardized direct observations provided useful results, enumeration methods will always be sensitive to factors that affect detection probability, thus limiting the strength of inference. Few studies have quantified effort expended on nest observations or trapping. Further, most studies have failed to identify a specific age of young. This results in an inability to account for the influence of mortality on the estimated number of young and on age-specific behaviors that affect detection probabilities. The age of young when reproductive rates are estimated should reflect the specific research question as well as the ability to detect young. Attention to timing of counts (age of young) and sighting probability are needed for rigorous comparisons within or among studies.

Further work on field methods is needed to allow model-based estimators to be used effectively. Tagging methods that do not require recapture or resighting, such as passive integrated transponders (Boarman et al. 1998), offer 1 such strategy for collecting mark–recapture data. We recommend that researchers estimate detection probability of young or demonstrate that it is the same among all comparisons if relative reproductive rates are desired (Skalski and Robson 1992). If that is not possible, we suggest that researchers use a standardized effort that is thoroughly described in resulting publications. Without the reporting of this effort, comparing reproductive rates across studies or evaluating the adequacy of comparisons made within studies will remain impossible. Finally, nest boxes do offer the best means of estimating reproductive rates of burrowing owls, and when possible, such methods should be considered in study design.

MANAGEMENT IMPLICATIONS

Reproductive rates often are compared across time and space to provide guidance to the management or monitoring of wildlife populations. The most common practice of estimating reproductive rates of burrowing owls is through counts of young observed outside of their burrows. Our findings suggest caution in using such counts as an index to reproductive rates. If accurate estimates of either absolute or relative reproductive rates of this species are used as a criterion for management or monitoring, we suggest that either nest boxes be considered as a tool to facilitate obtaining reliable estimates (e.g., Henny and Blus 1981) or that careful attention to detection probabilities be used in establishing survey protocols. Nest boxes offer the most reliable means of estimating reproductive rates of burrowing owls. They are particularly useful in environments where natural burrows are limited. In these environments, burrowing owls are easily enticed into using nest boxes (D. K. Rosenberg, personal observation). In large grasslands with high densities of natural burrows, ensuring that nest boxes are used repeatedly through time will be more difficult. In such cases, counts of young from natural burrows may be the only feasible method. When counts must be used, our findings demonstrate the importance of developing protocols that ensure similar detection probabilities across time and space.

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