



WHAT CONSTITUTES A NESTING ATTEMPT? VARIATION IN CRITERIA CAUSES BIAS AND HINDERS COMPARISONS ACROSS STUDIES

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ABSTRACT.—Because reliable estimates of nesting success are very important to avian studies, the definition of a “successful nest” and the use of different analytical methods to estimate success have received much attention. By contrast, variation in the criteria used to determine whether an occupied site that did not produce offspring contained a nesting attempt is a source of bias that has been largely ignored. This problem is especially severe in studies that deal with species whose nest contents are relatively inaccessible because observers cannot determine whether or not an egg was laid for a large proportion of occupied sites. Burrowing Owls (*Athene cunicularia*) often lay their eggs ≥ 3 m below ground, so past Burrowing Owl studies have used a variety of criteria to determine whether a nesting attempt was initiated. We searched the literature to document the extent of that variation and examined how that variation influenced estimates of daily nest survival. We found 13 different sets of criteria used by previous authors and applied each criterion to our data set of 1,300 occupied burrows. We found significant variation in estimates of daily nest survival depending on the criteria used. Moreover, differences in daily nest survival among populations were apparent using some sets of criteria but not others. These inconsistencies may lead to incorrect conclusions and invalidate comparisons of the productivity and relative site quality among populations. We encourage future authors working on cavity-, canopy-, or burrow-nesting birds to provide specific details on the criteria they used to identify a nesting attempt. Received 6 December 2006, accepted 15 June 2008.

Key words: *Athene cunicularia*, Burrowing Owl, cavity nesting, daily nest survival, nest monitoring, nesting attempt, nesting success.

¿Qué Define un Intento de Anidación? La Variación en los Criterios Causa Sesgo y Dificulta las Comparaciones entre Estudios

RESUMEN.—Debido a que las estimaciones confiables de éxito de anidación son importantes en los estudios de aves, la definición de un “nido exitoso” y el uso de diferentes métodos analíticos para estimar el éxito, han recibido mucha atención. En contraste, la variación en los criterios usados para determinar si un sitio ocupado que no produjo descendencia constituye un intento de anidación es una fuente de sesgo que ha sido largamente ignorada. Este problema es particularmente severo en los estudios de especies cuyos contenidos de los nidos son relativamente inaccesibles y en los que en una gran proporción de los sitios ocupados los observadores no pueden determinar si se puso o no un huevo. *Athene cunicularia* comúnmente pone sus huevos ≥ 3 m por debajo del suelo, por lo que los estudios previos de esta especie han usado una variedad de criterios para determinar si se ha iniciado un intento de anidación. Realizamos una búsqueda en la literatura para documentar la magnitud de esta variación y para examinar cómo esta variación influyó las estimaciones de supervivencia diaria de los nidos. Encontramos 13 sets diferentes de criterios usados por autores en estudios anteriores y aplicamos cada uno de estos criterios a nuestro set de datos de 1,300 madrigueras ocupadas. Encontramos una variación significativa en las estimaciones de supervivencia diaria de los nidos dependiendo del criterio usado. Más aún, aparecieron diferencias en la supervivencia diaria de los nidos entre las poblaciones usando algunos sets de criterios, pero no usando otros. Estas inconsistencias pueden conducir a conclusiones incorrectas e invalidar las comparaciones de productividad y de calidad relativa de los sitios entre las poblaciones. Recomendamos a los futuros autores que trabajan con aves que anidan en cavidades, en el dosel o en madrigueras a brindar detalles específicos sobre los criterios usados para identificar un intento de anidación.

IN BIRDS, MANY life-history traits are associated with nesting (Stearns 1992), and reliable estimation of reproductive parameters requires locating and monitoring large numbers of nests. Additionally, one of the routine ways we evaluate the effects of

management actions on birds is to measure how these actions affect reproductive parameters (e.g., Larison et al. 2001, Monroe and Ritchison 2005). Hence, locating and monitoring nests to estimate nesting success and other reproductive parameters is common in

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studies designed to examine the evolution of life-history traits as well as in those designed to evaluate the effects of management actions on birds.

Because estimating nesting success is very important, the analytical methods used to estimate nesting success have received much attention (Johnson 2007a). However, another possible source of bias in accurately estimating nesting success has been largely ignored. Before determining which analytical method will be used to estimate nesting success, a researcher must first determine whether a nesting attempt occurred at each site that was monitored (i.e., which data to include in the analysis). For species of birds that build open-cup nests, determining when a nesting attempt has been initiated is straightforward and requires only that field personnel confirm whether ≥ 1 egg was laid. Looking into nests is much more difficult with cavity-nesting birds (e.g., woodpeckers [Picidae] and nuthatches [Sittidae]), burrow-nesting birds (e.g., storm-petrels [Hydrobatidae] and puffins [*Fratercula* spp.]), cliff-nesting birds (e.g., falcons [Falconidae]), and canopy-nesting birds (e.g., many warblers). Accordingly, many researchers have used mirrors or video probes to look into possible nests to determine when (and whether) nesting attempts have been initiated. However, field personnel can seldom use these devices on every nest monitoring visit or gain access to all possible nests, even with these devices (Conway et al. 2006). When some cavities or burrows are probed and no eggs or juveniles are observed, it is often impossible (without destroying the structure) to determine whether eggs are (1) not present or (2) present but not visible. Therefore, these field methods can confirm that a nesting attempt has occurred, but they often cannot confirm that a nesting attempt has not occurred.

In some species whose nest contents are difficult to see, the number of occupied sites where observers cannot determine whether a nesting attempt occurred may represent a significant portion of all the occupied sites. One approach to dealing with this problem has been to estimate reproductive parameters based on a subset of readily accessible nests (Monterrubio et al. 2002). However, estimates of reproductive parameters based on this subset of nests may be biased because nest accessibility is often correlated with breeding productivity (Steenhof 1987). Knowing this, researchers often attempt to include at least some inaccessible nests in their sample by making a decision as to whether or not a nesting attempt was initiated at these inaccessible nest sites. However, the criteria used to make these decisions may vary greatly among researchers.

Such is the case with many Burrowing Owl (*Athene cunicularia*) studies. Burrowing Owls typically lay eggs in nest chambers that are often ≥ 3 m below ground, and many burrows have tortuous tunnels (Haug et al. 1993, Lantz et al. 2007). Thus, even infrared probes pushed underground do not allow field personnel to see into every nest chamber (Conway et al. 2006). Western Burrowing Owls (*A. c. hypugaea*) typically lay their eggs in burrows created by fossorial mammals (Haug et al. 1993), but nonbreeding owls also roost in burrows (Butts 1976, Haug et al. 1993). Therefore, the presence of adult owls standing at the entrance to a burrow does not necessarily indicate that eggs or young are below. Moreover, observing only one adult on repeated visits to a burrow (i.e., not observing a pair) does not necessarily indicate that a nesting attempt has not been initiated because incubating females are often not seen above ground for weeks at a time (C. Conway unpubl. data).

Burrowing Owls are not territorial (Haug et al. 1993) and often use numerous burrows during the breeding season (Winchell 1994). The combination of these traits make decisions about whether a nesting attempt has or has not been initiated particularly difficult with regard to Burrowing Owls. Successful nesting attempts become obvious once juveniles emerge from the burrow, but distinguishing failed nesting attempts from occupied burrows that never contained eggs is more challenging. To estimate nesting success, researchers must subjectively decide whether a nesting attempt was or was not initiated at each burrow occupied by owls.

To deal with this problem, researchers who have worked on Burrowing Owls have devised a variety of criteria to determine whether a nesting attempt was initiated at a burrow. These criteria range from asking field personnel to judge (on the basis of experience) whether eggs were laid at each burrow to establishing a subjective checklist of criteria that, if met, would qualify the burrow as a nest where eggs were presumably laid. However, we currently lack consensus regarding which criteria should be used for identifying a nesting attempt in Burrowing Owls (and other cavity-, burrow-, or high-canopy-nesting birds). To make matters worse, many studies do not explicitly state the criteria used. This lack of consensus hinders our ability to make comparisons across studies, years, or management treatments. Reliably estimating reproductive parameters is especially important for Burrowing Owls because they are decreasing in many parts of their breeding range and are federally endangered in Canada (Wellicome and Haug 1995, Klute et al. 2003). Comparable estimates of reproductive parameters across regions and years are needed to help determine which demographic parameters are most symptomatic of population declines.

The difficulties of estimating nesting success (Lehman et al. 1998) and number of offspring produced per successful nest (Gorman et al. 2003) in Burrowing Owls and other species have been addressed elsewhere. The benefits and drawbacks of the different analytical methods for estimating nesting success have also received much attention (Johnson 2007a). By contrast, variation among researchers in the criteria used to determine whether a nesting attempt was initiated at an occupied site has been completely ignored. We examined the extent of this potential problem in Burrowing Owls by documenting variation among past studies in the criteria used to determine whether a nesting attempt has been initiated. We then used our data set of 1,300 occupied burrows collected across five study areas to determine how variation in the criteria used to identify a nesting attempt influenced estimates of daily nest survival given the same data set (i.e., we subjected each set of published criteria to the same data set of 1,300 potential nesting attempts).

METHODS

We searched journal articles, theses, and reports that contained estimates of demographic or reproductive parameters of Burrowing Owls. We searched the database Wildlife and Ecology Studies Worldwide for the years 1990–2006, using the term “Burrowing Owl.” We also searched articles and reports we had in our files or that were cited in papers identified in our initial search. For each study, we recorded the set of criteria the author(s) used to determine whether a burrow occupied by ≥ 1 owl was considered a nest

containing a nesting attempt and therefore included in estimates of parameters. We deconstructed each set of criteria so that each consisted of a list of cues or behaviors (and the frequency of each) that had to be observed for the occupied burrow to be considered a nesting attempt (and, hence, included in the author's analysis).

Although many of the sets of criteria were clear and explicit, others required that we assign frequencies for cues. For example, one paper included the statement "if owls were observed to frequent the burrow." To interpret unclear criteria such as this, we each independently interpreted what the original authors likely intended by the statement and used a compromise when our interpretations differed. For example, we interpreted the above statement as requiring one or two owls to have been observed at the burrow ≥ 5 times during the breeding season. We were unable to use a few criteria that we found (e.g., presence of feces, owls reluctant to flush, increase in aggressive behavior) because the criteria were too vaguely defined or because we did not have the relevant information in our data set.

After identifying the different criteria used in past studies, we then used our own Burrowing Owl data to estimate daily nest survival after subjecting our data to each set of criteria found in the literature. That is, we used each set of published criteria on the same (our own) data set. Each set of published criteria led to the exclusion of a different subset of our 1,300 occupied sites because they did not qualify as nesting attempts under that set of criteria. We then estimated daily nest survival for each set of nesting attempts identified by each set of criteria. Differences among these estimates of daily nest survival cannot be based on anything other than differences in the criteria used to define a nesting attempt because each estimate was based on the same data from the same set of occupied sites.

We collected data on Burrowing Owls at five study areas: southeastern Arizona (Conway and Ellis 2004), central Arizona (Conway et al. 2005b), northeastern Wyoming (Lantz et al. 2007), southeastern Washington (Conway et al. 2006), and central Washington (Conway et al. 2006). We located occupied burrows in each study area by talking to landowners and wildlife officials, by incidental observations, and by conducting standardized point-count surveys (Conway and Simon 2003). We monitored burrows from 2002 to 2004 in each study area during weekly or semiweekly visits in which we recorded the presence of (1) adults, (2) juveniles, (3) shredded material such as cow dung or grass, (4) prey items, (5) nest decorations, (6) eggshells, and (7) any other common sign of burrow occupancy or nesting reported in Burrowing Owls. We used a total of 1,300 occupied burrows (i.e., potential nesting attempts) for our evaluation. Each of these 1,300 occupied burrows either did or did not qualify as a nesting attempt according to each set of published criteria used by previous authors. We estimated daily nest survival using all the occupied burrows that qualified as nesting attempts for each set of criteria. We also examined how the 13 sets of published criteria used to identify a nesting attempt affected the ability to detect differences in daily nest survival among three of our study areas in two years (central Arizona in 2004, central Washington in 2002 and 2004, and Wyoming in 2004).

We used the Mayfield method (Mayfield 1961, 1975) to estimate daily nest survival and calculated 95% confidence intervals (CI) for each estimate (Johnson 1979, Hensler and Nichols 1981). We chose the Mayfield method because the question we sought to answer does not require the more parameterized models that

allow observers to include covariates. Our goal was not to provide estimates of nest survival that take into account changes over time and other covariates for each of our study areas but, rather, to point out a novel source of significant bias that has previously been ignored. The Mayfield method continues to be used for many applications in which explanatory variables are not of interest (e.g., Buehler et al. 2007, Podolsky et al. 2007) and was appropriate for this type of question (Johnson 2007a). The main criticisms of the Mayfield method are (1) that it assumes that daily nest survival is the same for all days and all nests and (2) that its estimates are not as precise as those derived from the newer approaches (Shaffer and Thompson 2007). However, these criticisms were not relevant to our analysis because (1) we are using the exact same data set from the same occupied sites to compare among the 13 different sets of criteria for determining whether eggs were laid at those occupied sites and (2) comparing estimates of daily nest survival among treatments or populations is not our main objective here. We are merely trying to demonstrate that these 13 different sets of criteria that have been used to define a nesting attempt will produce very different estimates even when used on the same data set. Moreover, logistic regression and the Mayfield method yielded very similar estimates when we used both to estimate nest success for our Wyoming study area (Lantz and Conway 2009).

For each of the 13 sets of criteria, we counted the number of days each nesting attempt was under observation from initiation of the nesting attempt (or the time the nesting attempt was found) until the nesting attempt failed or juveniles reached 30 days old. We included the pre-laying stage as part of the nesting cycle because many of the 13 sets of published criteria included an occupied site as a nesting attempt in their analysis even if no evidence of eggs was observed. However, only burrows that were occupied between the date the first egg was laid and the date the last clutch hatched at each study area in each year were included in the analysis. That is, although we included the pre-laying stage, burrows that were occupied only before any eggs were laid (i.e., before the first egg date for our sample of that population) were not included. We considered a nesting attempt to have failed during the pre-laying stage if an owl occupied a burrow but we never detected evidence of eggs, and the burrow still qualified as a nesting attempt for that set of criteria.

We used our 13 estimates of daily nest survival (one for each of the 13 sets of criteria) to estimate overall nesting success based on the following formula: nesting success = daily nest survival^(average length of the nesting cycle). The average length of the nesting cycle for a successful nesting attempt across all 13 sets of criteria was 80 days (pre-laying = 18.4 days, laying = 5.3 days, incubation = 26.2 days, nestling stage = 30 days). We calculated nesting success to provide added context for our estimates of daily nest survival. However, the estimates and 95% CIs that appear in the figures are based on daily nest survival, not nesting success. We considered daily nest survival estimates to be statistically different from each other if their 95% CIs did not overlap.

RESULTS

We could not identify the criteria used to define a nesting attempt in 6 of 29 papers that reported estimates of Burrowing Owl reproductive parameters (Gleason and Johnson 1985; Botelho and

Arrowood 1996, 1998; Desmond and Savidge 1999; Desmond et al. 2000; Rosier et al. 2006). In another six papers, the criteria were not explicit enough for us to apply them to our own data set (Thomsen 1971, Green 1983, Green and Anthony 1989, Mealey 1997, Holmes et al. 2003, Rosenberg and Haley 2004). These sets of criteria could not be applied to our data because, even after checking the references provided for their criteria, we could not determine exactly what behaviors, evidence, activities, or length of occupancy (or frequency of these cues) were required to classify an occupied burrow as a nesting attempt. We found either explicit sets of criteria or sets of criteria that required minimal interpretation to classify occupied burrows as nesting attempts in the remaining 17 papers (Appendix). Each set of criteria involved observing some combination of the following cues a given number of times: (a) single owl, (b) pair of owls, (c) nest lining, (d) nest decorations, (e) eggshell fragments, (f) prey items, and (g) juveniles. Among these 17 papers, we found 13 different sets of criteria for determining whether a nesting attempt had been initiated at an occupied site.

The number of the 1,300 occupied burrows included as nesting attempts using each set of criteria varied from 370 to 1,172 (Appendix). The use of more conservative criteria (i.e., criteria nos. 12 and 13) likely excluded many failed nesting attempts that were included in the more liberal criteria (i.e., criteria nos. 1–6). However, the more liberal criteria likely classified some occupied burrows at which eggs were never laid as failed nesting attempts. Because of these differences, estimates of daily nest survival based on our data set differed depending on the set of criteria used to determine whether a nesting attempt had been initiated (Fig. 1).

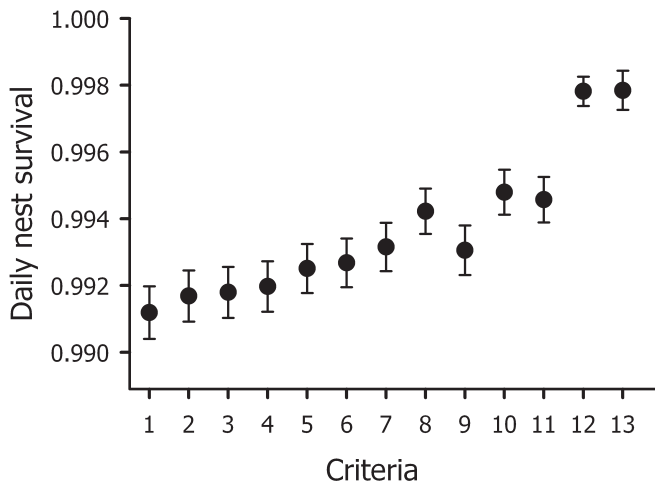


FIG. 1. Estimates of daily nest survival (\pm 95% confidence interval) of Burrowing Owl nesting attempts based on each of 13 sets of criteria for determining whether a nesting attempt had been initiated at an occupied site. Estimates were based on pooled data collected at five study areas (central Washington, southeastern Washington, northeastern Wyoming, central Arizona, and southeastern Arizona) from 2002 to 2004. See Appendix for explanation of the 13 sets of criteria and for how many of the 1,300 occupied sites qualified as nesting attempts under each set of criteria.

These differences in the subset of occupied burrows that were considered actual nesting attempts also affected our ability to detect differences in daily nest survival among study areas and years (Fig. 2). Daily nest survival in central Arizona in 2004 differed from that in Wyoming in 2002 under criteria 1–9 and 11–12, but not under 10 or 13. Daily nest survival in central Washington in 2002 differed from that in central Washington in 2004 under criteria 1–2, 4–6, 9, and 11, but not under 3, 7–8, 10, or 12–13. Daily nest survival in central Washington in 2002 differed from that in Wyoming in 2004 under criteria 1–11 and 13, but not under 12. We did not find a difference in daily nest survival between central Arizona in 2004 and central Washington in 2004 for all sets of criteria except number 6 (Fig. 2).

DISCUSSION

Different sets of criteria for determining which sites occupied by Burrowing Owls were considered nesting attempts yielded estimates of nesting success from the same data set that varied from 49% to 84% (Fig. 1 and Appendix). This range of variation is very similar to the range of variation among published studies (Green and Anthony 1989, James et al. 1997, Lehman et al. 1998, Lutz and Plumpton 1999, Holmes et al. 2003, Conway et al. 2006, Griebel and Savidge 2007). Many of the published studies that report estimates of Burrowing Owl nesting success did not use video probes to view nest chambers (or were unable to reach all the nest chambers) and, hence, had to use cues to identify nesting attempts. Therefore, the lack of a standardized set of criteria for determining whether a nesting attempt has been initiated affects our ability to make comparisons among populations.

The criteria for defining a successful nest have been well developed (Martin et al. 1997). Several analytical methods for estimating daily nest survival account for the bias associated with the higher detection probability of successful nesting attempts, including the fact that nests found later in the nesting cycle are more likely to be successful (Johnson 2007b). However, no matter which analytical method one uses, one still must decide which occupied sites constitute a nesting attempt and are to be included in the analysis. This issue is also relevant for other species whose nest contents are not readily visible and in situations where field personnel must decide whether eggs were laid on the basis of observations of adult behavior and the presence of nesting cues and field sign (e.g., Cox and Slater 2007, Saab et al. 2007). Future studies should examine the extent of this problem in other cavity-, burrow-, and high-canopy-nesting birds.

Our results illustrate an important source of bias that has previously been ignored, but we currently do not know which set of criteria yields the most accurate estimates of daily nest survival in Burrowing Owls. One possible way to remedy this problem would be to develop a model that uses a variety of cues to classify each occupied site as either containing a nesting attempt or not containing a nesting attempt. This model-based approach may prove very useful and we encourage future researchers to explore this possibility, with the following caveats. (1) A model that estimates the probability that an occupied site constitutes a nesting attempt would have to be based on a subset of sites at which eggs were observed early in the nesting cycle (i.e., during the laying period) to ensure that the model contains the information to identify nests that fail early. However, using

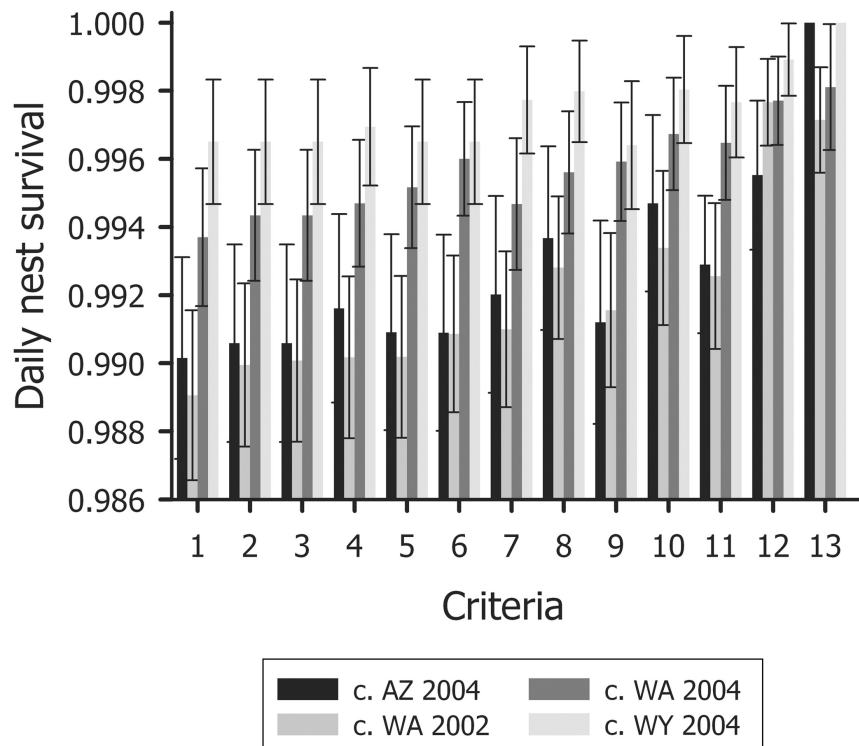


FIG. 2. Estimates of daily nest survival (\pm 95% confidence interval) for Burrowing Owls in central Arizona in 2004, central Washington in 2002 and in 2004, and Wyoming in 2004, based on each of 13 sets of criteria for determining whether a nesting attempt had been initiated at an occupied site. Daily nest survival differed among study areas under some sets of criteria, but we did not find differences among those study areas under other sets of criteria. See Appendix for explanation of the 13 sets of criteria. Sample sizes, from left to right: 103, 101, 101, 96, 99, 99, 82, 74, 86, 65, 70, 75, 23 (central Arizona 2004); 142, 136, 135, 134, 134, 128, 128, 114, 118, 108, 111, 82, 66 (central Washington 2002); 117, 113, 113, 109, 108, 94, 101, 95, 85, 76, 76, 88, 31 (central Washington 2004); 70, 70, 70, 67, 70, 70, 57, 56, 67, 46, 55, 60, 13 (Wyoming 2004).

a subset of sites at which eggs were observed could introduce a source of bias. For example, if we used the subset of burrows at which we observed eggs in the present study, we could include only those burrows at which we reached the nest chamber with our video probe (i.e., the most accessible nests), and daily nest survival often differs between accessible and inaccessible nests (Steenhof and Newton 2007). (2) Some of the cues used to identify nesting attempts—and, hence, used as explanatory variables in the model—may be correlated with daily nest survival (e.g., nest lining could be present at all successful nests and present at some, but not all, failed nests). Therefore, any variables included in the model would have to be checked for correlation to daily nest survival and other parameters of interest. And (3) the predictive ability of some cues likely varies among regions, and the likelihood of detecting many of the cues is dependent on the frequency of monitoring visits (i.e., effort). Therefore, a model developed in one region or with one set of field protocols may not be applicable in another region or under a different set of protocols. Despite these caveats, a model-based approach for determining whether eggs were laid at each occupied site is the next logical step in resolving this dilemma.

Whether an occupied site is included as a nesting attempt is affected by the frequency of monitoring visits because field personnel

may not observe some of the cues that define a nesting attempt (and, therefore, will miss some failed nesting attempts) if occupied sites are visited infrequently. Some published studies did not report the frequency of nest visits (eg., Green and Anthony 1989, James et al. 1997), and visit frequency varied in those that did (Johnson et al. 1997, Lehman et al. 1998, Lutz and Plumpton 1999). Studies in which occupied sites were visited less frequently will yield estimates of daily nest survival that are biased high because a higher proportion of the failed nests will be excluded from the sample. Some sets of criteria will be more robust to variation in the frequency of monitoring visits than others. For example, a set of criteria that requires that a pair be observed only once (Restani et al. 2001) will include (almost) the same occupied sites regardless of whether visits occurred every 5 or every 10 days. By contrast, a set of criteria that requires a pair of owls to be observed multiple times (Machicote et al. 2004) will likely include many more occupied sites if visits occurred every 5 rather than every 10 days. This issue could possibly be addressed with a model-based approach that includes the frequency of monitoring visits (as well as other variables) in the model.

The effectiveness of different criteria in distinguishing a nesting attempt also depends on how early in the breeding season potential nest sites are monitored and how the breeding season is defined. If monitoring starts after most birds begin laying eggs, researchers will

miss some nesting attempts that fail early, regardless of which set of criteria they use (Mayfield 1961, 1975; Steenhof 1987). By contrast, if monitoring begins well before eggs are laid, some occupied sites will qualify as nesting attempts using some sets of criteria (e.g., criteria no. 1, Appendix) even though a nesting attempt never occurs at that site. Most of the published Burrowing Owl studies reported when field work began, but few reported how these dates related to the local nesting cycle (i.e., the range of dates when nests were initiated; Gleason and Johnson 1985, Rodriguez-Estrella 1997). Studies using artificial nest boxes may help determine which criteria are most accurate because the true nest status is known on every visit.

Our goal in the present study was not to determine the most accurate criteria, nor to report accurate estimates of daily nest survival for Burrowing Owls. Rather, our goal was to highlight the lack of standardization in the criteria used to identify a nesting attempt across studies and the extent of bias caused by this lack of consensus. Estimates of nesting success based on the same data set varied from 49% to 84% depending on the criteria used. Standardization alone does not ensure unbiased estimates. However, until we develop a model that reliably estimates which occupied sites likely contain eggs, we can make comparisons more meaningful if we report estimates of daily nest survival based on a standardized criteria for determining when a nesting attempt has been initiated (e.g., Dudley and Saab 2003).

In Burrowing Owls (and probably other species), the ideal set of criteria for determining whether a nesting attempt occurred will differ depending on the question being asked and may not be the same for each population or study area because detection probability likely differs among study areas (Conway et al. 2008). For example, adult owls are more conspicuous in flat landscapes with little vegetation and in areas with substantial human activity. These factors likely affect the number of visits required to detect a nesting attempt (C. Conway pers. obs.). Moreover, the adaptive function of some cues that are often referred to as “nest lining” (e.g., cow manure) or “nest decorations” (e.g., bits of trash present at the nest entrance) are still not clear (Smith and Conway 2007), and their presence at a burrow may depend on their availability in the landscape. Hence, the presence of manure may be a reliable cue for identifying a nesting attempt in some, but not all, locations.

On the basis of our results, we developed two sets of recommendations: one set specific to future studies of Burrowing Owls and another set applicable to all species whose nests are inaccessible. We recommend that studies of Burrowing Owls report two estimates of daily nest survival (and other reproductive parameters) by identifying nesting attempts using each of the following two criteria: (1) burrows occupied by ≥ 1 adult owl on ≥ 2 visits (criteria no. 4; Appendix) and (2) burrows occupied by a pair on ≥ 1 visit (criteria no. 8; Appendix) (Steenhof 1987, Lehman et al. 1998). The first set of criteria would yield the proportion of burrows where a single owl was observed standing at a burrow at least twice during the breeding season (excluding use of satellite burrows by owls known to be occupying other burrows) that produced ≥ 1 fledgling. The second set of criteria would yield the proportion of burrows where a pair of owls was observed at least once during the breeding season that produced ≥ 1 fledgling. These two sets of criteria each include different biases with respect to the true proportion of successful nesting attempts. Researchers can always include estimates of nesting success based on additional criteria if those criteria better suit their question. If all researchers report estimates

based on these same criteria for identifying a nesting attempt, the data generated will provide greater inferences when making comparisons across studies and will greatly improve our ability to compare demographic parameters across geographic regions.

For future studies on cavity-, burrow-, and canopy-nesting birds with inaccessible nests (including Burrowing Owls), we suggest that authors report the following information: (1) the explicit criteria used for identifying a nesting attempt (i.e., the cues that determined which occupied sites were included or excluded from parameter estimates [Dudley and Saab 2003, Daw et al. 2004], and the frequency of observing those cues), (2) dates or spans of time during which the criteria had to be observed for an occupied site to qualify as a nesting attempt, (3) how frequently field personnel visited potential and occupied nest sites and when they initiated monitoring visits in relation to the earliest nest-initiation dates for their population, and (4) the average number of fledglings produced per successful pair (Steenhof 1987, Gorman et al. 2003). By focusing on successful nesting attempts only, the number of fledglings produced per successful pair circumvents biases associated with different criteria used to identify a nesting attempt and, therefore, can be compared across studies regardless of how nesting attempts were identified in each study (but this approach does not provide estimates of nesting success). We also recommend that all potential nest sites in the study area be visited approximately the same number of times, and that all occupied sites be monitored with the same frequency. If logistics prevent standardization in frequency of monitoring visits, we recommend that authors report the extent of variation in frequency so that factors that are influenced by nest-site accessibility are not confounded by frequency of visits. Following these recommendations should allow more meaningful comparisons of reproductive parameters across studies.

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APPENDIX. Thirteen sets of criteria used in past studies to determine whether a nesting attempt had been initiated at a burrow occupied by Burrowing Owls. The following cues were listed as criteria: (a) single owl, (b) pair of owls, (c) nest lining, (d) nest decorations, (e) eggshell fragments, (f) prey remains, and (g) juveniles. The combination of cues required to classify an occupied burrow as a nesting attempt for inclusion in estimates of reproductive parameters is listed according to our interpretation of each set of criteria. For example, $(2 \times a) + (1 \times c)$ indicates that item (a), a single owl, must be seen on ≥ 2 occasions and, in addition, item (c), nest lining, must be seen at least once for an occupied burrow to constitute a nesting attempt. The number of the 1,300 occupied burrows from our own data set that qualified as nesting attempts (n) and the estimate of nesting success are listed for each set of criteria. Estimates were based on data collected at five study areas (central Washington, southeastern Washington, northeastern Wyoming, central Arizona, and southeastern Arizona) from 2002 to 2004. The text for each set of criteria was taken directly from the source.

Source ^a	Stated criteria used to identify a nesting attempt	Our interpretation	n	Nesting success
1	"If ≥ 1 adult was seen on ≥ 2 visits, or ≥ 2 adults were seen on ≥ 1 visit, or ≥ 1 adult was seen on ≥ 1 visit and nest lining was observed, or ≥ 1 adult was seen on ≥ 1 visit and prey remains were observed, or ≥ 1 adult was seen on ≥ 1 visit and juveniles were observed."	$(2 \times a)$ or $(1 \times b)$ or $(1 \times c) + (1 \times a)$ or $(1 \times f) + (1 \times a)$ or $(1 \times g) + (1 \times a)$	1,172	49%
2	"...one or more of the following criteria: 1) pair of owls seen at burrow, 2) nest decorations present, 3) egg shells present at burrow entrance, 4) chicks seen, 5) owls' behavior at burrow during disturbance a) alarm call given upon human approach, b) owl reluctant to flush, allows close approach, c) behaves defensively (aggression toward human), d) owl retreats into burrow."	$(1 \times b)$ or $(1 \times c) + (1 \times a)$ or $(1 \times d) + (1 \times a)$ or $(1 \times e) + (1 \times a)$ or $(1 \times g) + (1 \times a)$	1,142	51%
3	"...a pair of adult owls, a single adult with young, or nesting behaviors such as burrow excavation or collection of lining materials...."	$(1 \times b)$ or $(1 \times g) + (1 \times a)$ or $(1 \times c) + (1 \times a)$	1,136	52%
4	"If ≥ 1 adult Burrowing Owl was present on ≥ 2 visits between the dates the first egg was laid and the last egg hatched."	$(2 \times a)$ or $(2 \times b)$	1,118	53%
5	"...the area within 88 m of a burrow where a breeding attempt occurred, or where a single adult Burrowing Owl not known to be breeding elsewhere was seen on 3 or more occasions during the breeding period.... Nest sites attended by ≥ 1 adult owls or decorated with shredded paper and grass... were considered occupied."	$(3 \times a)$ or $(3 \times b)$ or $(1 \times c) + (1 \times a)$ or $(1 \times e) + (1 \times a)$ or $(1 \times g) + (1 \times a)$	1,092	55%
6	"...if owls were observed to frequent the burrow and or [sic] if there was some sign of use such as mute (feces), prey items, or signs of incubation (materials lining the nest entrance)."	$(5 \times a)$ or $(5 \times b)$ or $(1 \times f) + (1 \times a)$ or $(1 \times c) + (1 \times a)$	1,056	56%
7	"Pairs of owls occupying a burrow and exhibiting mating behavior, such as food exchange, mutual preening, and copulation were considered mated pairs. No unmated birds were observed on the study areas."	$(1 \times b)$	990	58%
8a	"We assumed every owl pair attempted to breed (i.e., laid eggs)."	$(1 \times b)$, only one attempt per pair per burrow is counted	925	63%
8b	"...estimates of Burrowing Owl success were based on pairs instead of nesting attempts, and we may have included non-laying pairs...."	$(1 \times b)$, only one attempt per pair per burrow is counted	925	63%
8c	"Each nesting pair was counted as one nest attempt..."	$(1 \times b)$, only one attempt per pair per burrow is counted	925	63%
9	"...burrows are located by observing sentry owls and confirmed as active nests by the presence of nesting material...."	$(1 \times c) + (1 \times a)$ or $(1 \times c) + (1 \times b)$	918	57%
10a	"...had to detect both the male and the female at the burrow on at least two visits."	$(2 \times b)$	802	66%
10b	"An occupied burrow was classified a 'nest' if ≥ 2 Burrowing Owls were present on ≥ 2 visits during the breeding season. Unpaired males that failed to attract a mate occupied some burrows; these constituted 'occupied' burrows but not 'nests.'"	$(2 \times b)$	802	66%
10c	"Pairs regularly observed.... Only birds seen on more than one occasion were counted."	$(2 \times b)$	802	66%

(Continued)

APPENDIX. Continued.

Source ^a	Stated criteria used to identify a nesting attempt	Our interpretation	<i>n</i>	Nesting success
11	"...monitored every burrow which appeared to be occupied by a pair, as indicated by the fresh lining of livestock or coyote dung around the entrance."	$(1 \times b) + (1 \times c)$	795	65%
12	"...a burrow site where young owls were detected photographically with two exceptions: 1) burrows at which older young were first detected photographically late in the breeding season were not considered nest burrows because it was assumed that these young owls moved to these burrows from other areas and..."	$(1 \times g) + (1 \times a)$ or $(1 \times g) + (1 \times b)$; juveniles must be <40 days old when first seen	759	84%
13	"...when a pair was seen at least five times and a burrow showed signs that a breeding attempt occurred (Millsap and Bear 2000)."	$(5 \times b) + (1 \times c)$ or $(5 \times b) + (1 \times e)$ or $(5 \times b) + (1 \times g)$	370	84%

^a1 = Garcia et al. 2007:21–22; 2 = Rosenberg et al. 1998:18; 3 = Estabrook and Mannan 1999:9; 4 = Conway et al. 2004:6, 2005a:7, 2006:282; 5 = Millsap and Bear 2000:34–35; 6 = Johnson et al. 1997:5; 7 = Desmond et al. 1995:1376; 8a = Restani et al. 2001:297; 8b = Lehman et al. 1998:249; 8c = James et al. 1997:34; 9 = Winchell 1994:84; 10a = Lantz 2005:7; 10b = Conway et al. 2003:4; 10c = Trulio 1997:87; 11 = Rodriguez-Estrella 1997:100; 12 = Hall et al. 2003:23; 13 = Machicote et al. 2004:529.