

Intraspecific variation in reproductive traits of burrowing owls

Meaghan Conway · Christopher P. Nadeau ·
Courtney J. Conway

Received: 31 August 2011 / Accepted: 16 May 2012 / Published online: 24 June 2012
© Japan Ethological Society and Springer 2012

Abstract Reviews of hatching asynchrony in birds recommended more studies on intraspecific variation in the extent of hatching asynchrony. We examined intraspecific variation in clutch size, laying chronology, onset of incubation, incubation period, and hatching asynchrony in burrowing owls (*Athene cunicularia*) in the Imperial Valley of California. Mean clutch size was 7.4 eggs and owls averaged 0.5 eggs laid per day. Females varied considerably in laying interval and onset of incubation (range = 1st to 9th egg in the clutch). The mean incubation period was 21.9 days. Hatching interval also varied greatly among females ($\bar{x} = 0.8$, range 0.1–2.0 days between successively hatched eggs). Past burrowing owl studies have largely overlooked the substantial intraspecific variation in these traits or have reported estimates that differ from ours. Future studies designed to identify the environmental factors that explain the large intraspecific variation in these traits will likely provide insights into the constraints on local abundance.

Keywords *Athene cunicularia* · Burrowing owl · Clutch size · Hatching asynchrony · Laying chronology · Onset of incubation

Introduction

Many species of birds hatch their young asynchronously, often over a period of several days or weeks (Stoleson and Beissinger 1995). The time span between the first and last hatched eggs in a bird's clutch (i.e., the degree of hatching asynchrony) can be large enough to cause size discrepancies among offspring within a brood that are often detrimental to the youngest brood members (Beissinger and Waltman 1991; Kim et al. 2010). This hatching pattern seems maladaptive, yet many species of birds exhibit a high degree of hatching asynchrony. For this reason, hatching asynchrony in birds has been the subject of much research. Twenty alternative hypotheses have been proposed to explain the adaptive function of hatching asynchrony and hundreds of studies have tested one or more of these 20 hypotheses (Clark and Wilson 1981; Magrath 1990; Stoleson and Beissinger 1995; Stenning 1996; Ricklefs 1997).

The majority of studies that have examined hatching asynchrony in birds have experimentally manipulated hatching span to measure its effects on fledging success or body mass (Slagsvold et al. 1992; Nilsson 1995; Stenning 1996; Szollosi et al. 2007), focusing on the brood rearing stage while ignoring constraints acting during laying and incubation. In contrast, only a few studies have measured intraspecific variation in the extent of hatching asynchrony (Slagsvold and Lifjeld 1989; Wellicome 2005; Wang and Beissinger 2009; Kim et al. 2010; Kontiainen et al. 2010) or examined the factors that influence that variation (Stenning 1996). In fact, many studies have classified species as either synchronous or asynchronous (Clark and Wilson 1981; Ricklefs 1993), ignoring intraspecific variation in hatching asynchrony (Stoleson and Beissinger 1995). Indeed, most hypotheses proposed to explain

M. Conway (✉) · C. P. Nadeau
Arizona Cooperative Fish and Wildlife Research Unit,
School of Natural Resources and the Environment,
University of Arizona, 325 BioSciences East,
Tucson, AZ 85721, USA
e-mail: Mconway1@email.arizona.edu

C. J. Conway
U.S. Geological Survey, Idaho Cooperative Fish and Wildlife
Research Unit, Department of Fish and Wildlife Sciences,
University of Idaho, 975 W. 6th St., Moscow,
ID 83844-1141, USA

hatching asynchrony in birds do not adequately explain intraspecific variation (Wiebe 1995). For these reasons, two major reviews of hatching asynchrony have urged that more studies focus on intraspecific variation (Stoleson and Beissinger 1995; Stenning 1996).

Although onset of incubation is often assumed to be the proximate mechanism that affects variation in hatching asynchrony, variation in clutch size (Wellicome 2005; Kontiainen et al. 2010), incubation length, development times of eggs, and laying pattern may also cause variation in hatching asynchrony (Astheimer 1985; Viñuela 1997; Wang and Beissinger 2009; Kontiainen et al. 2010). Species that lay large clutches and have large intraspecific variation in all of these reproductive traits could be useful study species to better elucidate the proximate factors that cause variation in hatching asynchrony.

Burrowing owls are ideal for examining intraspecific variation in hatching asynchrony because they lay large clutches ($\bar{x} = 6.5$ eggs; Haug et al. 1993) and the following traits all appear to have large intraspecific variation: clutch size (3–12 eggs), length of the laying period (8–17 days), and the extent of hatching asynchrony (1–7 day hatching span; Haug et al. 1993; Rosenberg and Haley 2004; Wellicome 2005). However, previous studies have not reported the extent of intraspecific variation in laying interval or the onset of incubation in burrowing owls, few have reported information on the extent of intraspecific variation in hatching span (Rosenberg and Haley 2004; Wellicome 2005), and only Wellicome (2005) has documented the length of the laying period (and only for a population at the northern edge of the species' breeding range). Here, we describe intraspecific variation in clutch size, laying interval, incubation period, onset of incubation, and hatching asynchrony in burrowing owls at a site in the southern portion of their breeding range in the United States. We use this information to suggest how each trait may influence intraspecific variation in hatching asynchrony. This work provides insight into potential proximate causes of intraspecific variation in hatching asynchrony other than the onset of incubation.

Quantifying the extent of intraspecific variation in clutch size, laying interval, incubation period, onset of incubation, and hatching asynchrony in burrowing owls is also useful for more practical reasons. Reliable estimates of these traits are important for determining the most vulnerable stage(s) during the nesting cycle and to evaluate the factors that contribute to nest failure. Furthermore, knowledge of laying dates and the length of nesting stages are essential components of modern analytical methods for estimating nest survival (Mayfield 1961; Dinsmore et al. 2002). Investigators who wish to model nest survival in burrowing owls are often forced to make assumptions about these traits based on previous studies (Garcia and Conway 2009;

Lantz and Conway 2009). Hence, our ability to more accurately estimate nesting success (and to use modern nest survival models) in burrowing owls is hindered because we do not have good estimates of most reproductive traits. Estimates of nest survival are important because burrowing owls are thought to be declining in many portions of their range, and consequently, the species is currently listed as endangered in Canada, a species of national conservation concern in the United States, and is declining or a species of concern in many US states (Haug et al. 1993; James and Espie 1997; Holroyd et al. 2001; Wellicome and Holroyd 2001; Klute et al. 2003; Conway and Pardieck 2006).

Methods

Study area

We monitored burrowing owls nesting in artificial nest boxes on the southern portion of the Sonny Bono Salton Sea National Wildlife Refuge and adjacent lands in Imperial County, California between 2005 and 2007. California has one of the largest populations of resident and migratory burrowing owls, with the Imperial Valley supporting a particularly high density of nesting owls (Coulombe 1971; Sheffield 1997; DeSante et al. 2004; Rosenberg and Haley 2004). The area has little native vegetation and is dominated by year-round agricultural production with cultivated fields bordered by irrigation structures. Artificial nest boxes were buried approximately 30–90 cm below the ground and had a removable lid which allowed us to view the nest contents. Nest boxes were located adjacent to dirt roads, usually situated between a road and a water delivery canal.

Nest monitoring

We monitored 123 clutches at 53 artificial nest boxes from March to July of 2005 through 2007. The date of our initial visit to the nest boxes differed slightly among the 3 years: 24 March–20 April in 2005, 13–30 March in 2006, and 4–20 March in 2007. We visited all occupied nest boxes every 1–14 days prior to finding eggs in the nest. We considered a nest box occupied by owls if we saw either an owl or sign of an owl (e.g., whitewash, pellets, manure, or other lining materials) at the nest burrow entrance. We opened each nest box after observing owls or sign of owls at the entrance for two consecutive visits. If we did not find eggs, we continued to monitor the nest until we found eggs. Once we found eggs in a nest box for the first time, we used an assumed laying pattern of 110110 (where a 1 represents a day in the laying pattern on which an egg was laid, and 0 represents a day on which no eggs were laid; Olenick 1990)

to estimate the lay date of the 8th egg. We did not open the nest box again until the estimated lay date of the 8th egg to minimize disturbance to the laying female. Our experience suggested that opening the nest box prior to this time could cause nest abandonment. After the estimated lay date of the 8th egg, we continued to open the nest box every other day (every 2–4 days in 2007) until all juveniles left the burrow or until the nest failed. We opened a subset of nest boxes less frequently (every 2–19 days, \bar{x} = every 5 days, $n = 53$ clutches) after finding eggs, due to logistical constraints early in the season (March and April of all 3 years). In 2006, we opened a subset of six nest boxes every 2–3 days after the first visit that we observed eggs (i.e., we did not wait until the estimated lay date of the 8th egg) to gain more observations during the laying stage, which allowed us to calculate more precise estimates of the laying pattern.

We recorded the number of eggs and juveniles present in the nest chamber and touched the eggs to determine if they were warm (i.e., if incubation had begun) each time we opened a nest box. We identified individual nestlings by marking unique combinations of toes with indelible ink. We reapplied markings each time we opened a nest box so that individuals could be reliably identified until they could be fitted with a US Geological Survey leg band. We assumed that new nestlings with wet or damp down feathers had hatched earlier that day and that new nestlings with dry down feathers had hatched the day prior (Wellcome 2005).

Clutch size

We defined clutch size as the maximum number of eggs observed during any one visit to a nest. We did not include nests that were depredated or abandoned prior to clutch completion ($n = 30$ clutches) in our summary of intraspecific variation in clutch size. We assumed that the female had completed a clutch when the egg count remained constant for at least 6 days. We considered a nest to be abandoned if we consistently found cold, buried, or scattered eggs, or if owls and other signs of nest box occupancy disappeared.

Laying pattern

We created a timeline of egg lay dates based on the number of eggs observed on each nest visit and compared these to eight a priori laying patterns (Table 1) to determine which pattern(s) most closely matched our observations for each nest. We only used nests where we recorded the number of eggs present at least twice during the laying period. We also only used nests with a final clutch size of >3 eggs, because laying patterns are

Table 1 Comparison of observed information on laying patterns at 45 burrowing owl nests to eight laying patterns based on data from periodic nest visits

Pattern	Laying pattern	Number of days to lay eight eggs	Percent of nests that fit pattern ($n = 45$)
1	110110110	11	31
2	101010101	15	73
3	111111111	8	13
4	101101011	13	42
5	110101101	12	47
6	100100100	22	27
7	110011001	14	49
8	100010001	29	9
9	Other	13–21 ($\bar{x} = 17$)	13

We only included nests at which we had opened nest boxes and counted eggs on ≥ 2 dates during the laying period. Data from most nests fit >1 possible laying pattern. Hence, the percentages of nests that fit each laying pattern do not sum to 100%. We present the number of days required to lay eight eggs (median clutch size of burrowing owls in our population) to aid comparisons among the laying patterns and highlight the resultant variation in the length of the laying period

difficult to estimate for clutches of ≤ 3 eggs. We selected the eight laying patterns that were most similar to the laying interval of 1.5 days reported in the literature (typically laid in a pattern of 110110110, where females lay 1 egg on each of 2 consecutive days, followed by a day on which no eggs are laid; Olenick 1990; Wellcome 2005). We chose eight patterns because we thought they would be sufficient to capture the amount of intraspecific variation. We compared our observations of egg-laying behavior to these eight combinations of 1 and 0 (where 1 represents a day on which a female laid 1 egg, and 0 represents a day on which no eggs were laid) in order to document possible variation in laying behavior among females. We identified the laying pattern(s) that best matched the observations at each nest to estimate the day that the female laid the first and last egg. Most nests matched >1 possible laying pattern because most of our eight a priori laying patterns only differed slightly from one or more of the other patterns and we did not open nest boxes daily. Hence, we used the midpoint of the earliest and latest possible lay dates for the first and last egg in the clutch to calculate the mean laying interval (i.e., the average number of days between two consecutive eggs in the laying pattern) across all clutches.

Onset of incubation and incubation period

We recorded the egg number in the clutch on which the female initiated full incubation by taking the midpoint

between the number of eggs on the last nest visit when the eggs felt cold (or there were no eggs) and the number of eggs on the first nest visit when the eggs felt warm. We included nests where no more than four eggs were laid between the nest visit with no or cold eggs and the nest visit with warm eggs (i.e., we did not include nests that were visited infrequently during the laying period). This restriction allowed us to calculate the egg on which incubation began to within ± 1 egg for 52 % of nests, and a maximum of ± 2 eggs for all nests included in this analysis ($n = 33$). Although many birds often initiate partial incubation before the clutch is complete, our approach still provides the best available insight into the extent of intraspecific variation in the onset of incubation for a bird that lays its eggs in narrow burrows deep underground.

We used two approaches to calculate the length of the incubation period: (1) the interval between the onset of incubation and the day the first egg hatched, and (2) the interval between the day the last egg was laid and the day the last egg hatched. We used the laying pattern(s) that best matched the observations at each nest to estimate the day that the female laid the last egg, and the egg on which incubation began. We used the midpoint of the earliest and latest possible lay dates of each egg at nests that fit >1 laying pattern. We visited all nests used in this analysis frequently enough to ensure that the interval between the earliest and latest estimated dates the female laid the last egg was <7 days.

Hatching asynchrony

We estimated the hatching span (i.e., the number of days between the first and last hatched eggs) for each nest based on the estimated hatch dates for each nestling. We then calculated the hatching interval (average number of days between sequentially hatched eggs in a clutch) as a metric of hatching asynchrony. Hatching interval allowed us to quantify intraspecific variation in hatching asynchrony after controlling for variation in clutch size. Previous authors have used hatching span as their metric of the extent of hatching asynchrony, but this metric is problematic for species that have intraspecific variation in clutch size or those that commonly have infertile eggs due to the strong correlation between hatching span and brood size at hatch (Kontiainen et al. 2010). Hatching interval is an alternative metric that is less affected by variation in clutch size or infertility of eggs. We included only those nests where ≥ 2 eggs hatched (because we could not quantify the extent of asynchrony in a nest with only one hatchling; Kontiainen et al. 2010) and those nests that we visited within 1 day of hatching.

Results

Mean clutch size was 7.4 eggs (SD = 1.9 eggs), with a range of 2–12 eggs ($n = 92$). The mean clutch size was 8.1 in 2005 (SD = 1.6, range 5–11, $n = 27$), 7.1 in 2006 (SD = 2.0, range = 3–12, $n = 40$), and 7.1 in 2007 (SD = 1.8, range = 2–10, $n = 25$). The mean laying interval between consecutively laid eggs was 2.0 days (SD = 0.4, range 1.5–3.6 days, $n = 45$). We found substantial variation in egg-laying behavior and the most common laying pattern differed from that reported in the literature. Seventy-three percent (33 of 45) of clutches matched a laying pattern of 101010101, which equates to a laying span of 15 days to lay an 8-egg clutch (Table 1). Among the 12 clutches that did not match the 101010101 laying pattern, six did not match any of the eight a priori patterns we examined and had laying spans that equated to 13–21 days ($\bar{x} = 17$ days) to lay an 8-egg clutch. Four of the 12 aberrant laying patterns followed patterns with longer laying intervals; three of which laid in a pattern that most closely resembled 100100100, and one which resembled 100010001. The remaining two resembled slightly shorter laying patterns of 110110110, 101101011, or 110101101 (laying spans that require 12–14 days to lay an 8-egg clutch).

Burrowing owls in our study area varied considerably in the relative time within the laying period when they started incubating. The egg on which incubation began ranged from the 1st to 9th egg ($\bar{x} = 5$ th egg in the clutch, SD = 2.5, $n = 33$). The mean egg on which females initiated incubation was 5.0 in 2005 (SD = 0.7, $n = 4$), 5.2 in 2006 (SD = 2.4, $n = 20$), and 2.8 in 2007 (SD = 2.5, $n = 9$). Females initiated incubation when 69.8 % (SD = 20.2 %), 73.7 % (SD = 22.7 %), and 39.4 % (SD = 23.6 %) of the clutch had been laid in 2005, 2006, and 2007, respectively. Although clutch sizes were similar between 2006 and 2007, females incubated earlier relative to clutch completion in 2007 suggesting that annual differences in clutch size were not entirely responsible for the observed annual differences in onset of incubation.

The interval between the date the female laid the last egg and the date the last egg hatched ranged from 19 to 26 days ($\bar{x} = 21.9$ days, SD = 1.8, $n = 39$). Our estimate for length of the incubation period was 1 day longer when we only included nests where all the eggs hatched ($\bar{x} = 23.1$, SD = 1.4, $n = 11$). The interval between the onset of incubation and the date the first egg hatched ranged from 16 to 38 days ($\bar{x} = 23.0$ days, SD = 4.9, $n = 21$).

Hatching span varied greatly among clutches, from 1 to 8 days ($\bar{x} = 4.5$ days, SD = 1.6, $n = 58$). One nest hatched all nine eggs on the same day, and three nests (where 0 of 3 eggs, 1 of 3 eggs, and 2 of 5 eggs failed to hatch)

hatched only one egg per day. The hatching interval varied from 0.1 to 2 days between successively hatched eggs ($\bar{x} = 0.8$ days, $SD = 0.34$, $n = 58$). The maximum number of eggs that hatched on any one day occurred on the first hatch day at 59 % of nests, on the 2nd hatch day at 24 % of nests, on the 3rd hatch day at 12 % of nests, and on the 4th or 5th hatch day at 5 % of nests.

Discussion

We observed substantial intraspecific variation in all of the reproductive traits measured within this population of burrowing owls. Moreover, our results differed from those reported in several past studies that reported estimates of burrowing owl reproductive traits. For example, clutch size was slightly higher and had higher intraspecific variation compared to other estimates of burrowing owl clutch size in California ($\bar{x} = 7.0$, range 1–11 eggs, Landry 1979; $\bar{x} = 6.7$, range 4–8 eggs, Rosenberg and Haley 2004). Earlier lay dates in some years could explain why our mean clutch size was higher than estimates reported by Rosenberg and Haley (2004); seasonal declines in clutch size have been well documented in birds (Newton 1976; Newton and Marquiss 1984; Pietiainen 1989; Wellicome 2000; Decker et al. 2012). Numerous hypotheses have been proposed to explain variation in avian clutch size and many of these hypotheses rely on seasonal changes in food availability (Newton 1976; Drent and Daan 1980; Newton and Marquiss 1984; Decker et al. 2012). Furthermore, age and individual quality are correlated with both nest initiation date and clutch (or brood) size in many birds (Hussell 1972; Newton et al. 1983; Newton and Marquiss 1984; Pietiainen 1989; Wellicome 2000; Boal 2001), which could further explain variation in clutch size. Burrowing owls may reduce their clutch size when re-nesting after a depredation event (Catlin and Rosenberg 2008). Hence, variation in predation rates could provide another possible explanation for annual variation (and the large intraspecific variation) in clutch size.

Most burrowing owls in our study exhibited a long laying period and laid approximately one egg every other day (i.e., laying interval of 2.0 days); however, the laying interval varied greatly among individuals. In contrast, burrowing owls reportedly laid eggs at intervals of 1.5 days in Idaho and Saskatchewan (Olenick 1990; Wellicome 2005). For birds that lay large and variable clutches, an additional half day laying interval could increase the laying period by several days. It is possible that this difference may reflect some latitudinal variation, but few studies have reported laying intervals for burrowing owls across their geographic range. Intraspecific brood parasitism has not been documented in burrowing owls. However, this could possibly

explain some of the unexpected laying patterns we observed. One study documented a case of brood usurpation in Lanyu scops owls (*Otus elegans botelensis*), a small cavity-nesting owl (Hsu et al. 2006). We suggest that future studies examine whether intraspecific brood parasitism occurs in burrowing owls. We also observed intraspecific variation in the onset of incubation, and our estimates of this trait also differed from past indirect accounts. This is an important result of our study because past studies have assumed no intraspecific variation in this trait when estimating nesting success or estimating the extent of hatching asynchrony. Our estimates are not without error because females initiate partial incubation before the clutch is complete in many species of birds (Wang and Beissinger 2009). However, our two estimates of length of incubation (one that relied on our estimate of onset of incubation and one that did not) were similar, suggesting that our approach for estimating onset of incubation was accurate. Moreover, our study is the first to estimate the onset of incubation in wild burrowing owls directly, rather than indirectly based on the extent of hatching asynchrony or the resulting size disparity in nestlings. One past study suggested that incubation began with the first-laid egg based on behavioral patterns of incubating females and apparent size differences among brood members (Thomsen 1971), but clutches of cold (presumably unincubated) eggs have been reported by others (Henny and Blus 1981; Haug 1985). Two previous authors suggested that burrowing owls typically start incubating on the 5th egg (Olenick 1990) or midway through the laying pattern (Wellicome 2005) based on the extent of hatching asynchrony observed in nest boxes. The few studies that have examined intraspecific variation in the onset of incubation in other species of birds have reported substantial intraspecific variation (Wang and Beissinger 2009). Future studies that report estimates of the onset of incubation should measure it directly (rather than inferring onset based on hatching asynchrony or nestling size disparities). Direct observations of the onset of incubation will help elucidate factors acting as constraints during laying and incubation and provide a better understanding of the relationship between the onset of incubation and hatching patterns.

Our estimate of the duration of the incubation period is shorter than other reported estimates for burrowing owls: 28–30 days (Thomsen 1971; Zarn 1974; Henny and Blus 1981; Haug et al. 1993). Early studies relied on behavioral observations of females to determine when incubation began (Thomsen 1971), but time spent in the nest cavity is not always indicative of incubation (Porter and Wiemeyer 1972; Bortolotti and Wiebe 1993; Kontiainen et al. 2010). Other studies did not include an explanation of the methods used to calculate the length of the incubation period. Estimates of the length of the incubation period in birds with asynchronous hatching can vary substantially

depending on how incubation period is calculated. For example, estimates of the length of the incubation period in burrowing owls ranged from 17 to 32 days in Idaho depending on assumptions of when incubation began based on synchronous or asynchronous hatching patterns (Olenick 1990). Calculating the length of the incubation period as the interval between the onset of incubation and the date the first egg hatches relies on correctly estimating the onset of incubation. Alternatively, calculating the length of the incubation period as the interval between the last-laid to the last-hatched egg may underestimate the incubation period because the last-laid eggs in a clutch sometimes fail to hatch. Hence, some of the differences between our estimates of the length of the incubation period and those of past studies may be due to differences among studies in how the incubation period was defined. Both of our estimates of the length of the incubation period were very similar, which lends confidence to the accuracy of our estimates. Indeed, our estimates are very similar to the incubation period of 22–24 days reported for burrowing owl eggs under artificial conditions (Haug 1985) and 23.9 days for wild burrowing owls in Idaho (which was based on the time between the onset of incubation and the first egg hatched; Olenick 1990).

We also observed a substantially greater degree of intraspecific variation in the extent of hatching asynchrony within this population of burrowing owls than found in past studies. Our estimate of hatching span ($\bar{x} = 4.5$ days, $SD = 1.6$, range 1–8 days) was slightly higher and had higher intraspecific variation compared to other estimates for burrowing owls in California ($\bar{x} = 3.3$, $SD = 1.1$, range 1–6 days in 1999, $\bar{x} = 4.3$, $SD = 0.6$, range 3–7 days in 2000; Rosenberg and Haley 2004) and Saskatchewan ($\bar{x} = 3.8$, range 1–7 days; Wellicome 2005).

Most studies of hatching asynchrony have assumed that onset of incubation is the sole proximate cause of variation in hatching asynchrony; however, various other factors are thought to influence hatching asynchrony (Stoleson and Beissinger 1995). Although the onset of incubation may be one of the primary factors influencing hatching asynchrony, the large variation in other traits should not be ignored. For example, some owls may adjust the onset of incubation differentially according to clutch size (Wellcome 2005, Kontiainen et al. 2010). However, larger clutches may be difficult for small-bodied females to incubate effectively, resulting in unexpected hatching patterns (Bortolotti and Wiebe 1993). In addition, both weather conditions and clutch size can affect incubation patterns (Wang and Beissinger 2009). Moreover, increases in temperature can shorten incubation periods, reduce hatching success, and increase hatching asynchrony in birds (Veiga and Viñuela 1993; Stoleson and Beissinger 1999; Ardia et al. 2006). Variation in laying interval and

variation in development times of individual eggs within a clutch may also serve as mechanisms to adjust the degree of hatching asynchrony (Astheimer 1985; Viñuela 1997; Wang and Beissinger 2009). These studies suggest that multiple factors may influence the degree of hatching asynchrony within a clutch. We demonstrated substantial intraspecific variation in many reproductive traits within a population of burrowing owls: laying interval, onset of incubation, incubation period, and hatching asynchrony. Additional studies focusing on species such as burrowing owls that lay large clutches and have substantial intraspecific variation in the reproductive traits that affect hatching interval may provide further insights into the proximate and ultimate causes of hatching asynchrony and elucidate the relative importance of different selective constraints.

Estimates of reproductive traits of burrowing owls are also important for applied reasons. Since nest survival estimates are based on probability of survival over a specified period of time, the amount of error can vary according to the number of days the nest was not under observation (Mayfield 1975). Therefore, assumptions regarding the timing of nesting events due to the unique limitations associated with monitoring subterranean nests can introduce bias. The large individual variation documented in this study further complicates our ability to compare demographic traits across studies because the amount of individual variation in these traits could differ by geographic region. Future demographic studies in burrowing owls should seek to accurately estimate laying interval, onset of incubation, and hatching asynchrony to help improve our ability to understand behavioral choices that confront breeding birds.

Acknowledgments The Sonny Bono Salton Sea National Wildlife Refuge provided housing and logistical support and A. Kalin facilitated our work on private lands. Many technicians assisted with data collection, especially N. Bartok and J. Mohlmann.

References

- Ardia DR, Cooper CB, Dhondt AA (2006) Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in tree swallows, *Tachycineta bicolor*, at the extremes of their range. *J Avian Biol* 37:137–142
- Astheimer LB (1985) Long laying intervals: a possible mechanism and its implications. *Auk* 102:401–409
- Beissinger SR, Waltman JR (1991) Extraordinary clutch size and hatching asynchrony of a neotropical parrot. *Auk* 108:863–871
- Boal C (2001) Nonrandom mating and productivity of adult and subadult cooper's hawks. *Condor* 103:381–385
- Bortolotti GR, Wiebe KL (1993) Incubation behaviour and hatching patterns in the American kestrel *Falco sparverius*. *Ornis Scand* 24:41–47
- Catlin D, Rosenberg DK (2008) Breeding dispersal and nesting behaviors of burrowing owls following experimental nest predation. *Am Midl Nat* 159:1–7

- Clark AB, Wilson DS (1981) Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q Rev Biol* 56:253–277
- Conway CJ, Pardieck KL (2006) Population trajectory of burrowing owls in eastern Washington. *Northwest Sci* 80:292–297
- Coulombe HN (1971) Behavior and population ecology of the burrowing owl, *Speotyto cunicularia*, in the Imperial Valley of California. *Condor* 73:162–176
- Decker K, Conway CJ, Fontaine JJ (2012) Nest predation, food, and female age explain seasonal declines in clutch size. *Evol Ecol* 26:683–699
- DeSante DF, Ruhlen ED, Rosenberg DK (2004) Density and abundance of burrowing owls in the agricultural matrix of the Imperial Valley, California. *Stud Avian Biol* 27:116–119
- Dinsmore SJ, White GC, Knopf FL (2002) Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488
- Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252
- Garcia V, Conway CJ (2009) What constitutes a nesting attempt? Variation in criteria causes bias and hinders comparisons across studies. *Auk* 126:31–40
- Haug EA (1985) Observations on the breeding ecology of burrowing owls in Saskatchewan [thesis]. University of Saskatchewan, Saskatoon
- Haug EA, Millsap BA, Martell MS (1993) Burrowing owl (*Athene cunicularia*). In: Poole A, Gill F (eds) *The birds of North America*. The Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Washington, DC
- Henny CJ, Blus LJ (1981) Artificial burrows provide new insight into burrowing owl nesting biology. *J Raptor Res* 15:82–85
- Holroyd GL, Rodriguez-Estrella R, Sheffield SR (2001) Conservation of the burrowing owl in western North America: issues, challenges and recommendations. *J Raptor Res* 35:399–407
- Hsu Y, Li S, Lin Y, Philippart MT, Severinghaus LL (2006) High frequency of extra-pair copulation with low level of extra-pair fertilization in the Lanyu scops owl *Otus elegans botelensis*. *J Avian Biol* 37:36–40
- Hussell DJT (1972) Factors affecting clutch size in arctic passerines. *Ecol Monogr* 42:317–364
- James PC, Espie RHM (1997) Current status of the burrowing owl in North America: an agency survey. *J Raptor Res* 9:3–5
- Kim M, Furness RW, Nager RG (2010) Hatching asynchrony is constrained by parental nest attendance during laying. *Behav Ecol Sociobiol* 64:1087–1097
- Klute DS, Ayers LW, Green MT, Howe WH, Jones SL, Shaffer JA, Sheffield SR, Zimmerman TS (2003) Status assessment and conservation plan for the western burrowing owl in the United States. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication FWS/BTP-R6001-2003, Washington, D.C.
- Kontiaainen P, Pietiainen H, Karell P, Pihlaja T, Brommer JE (2010) Hatching asynchrony is an individual property of female Ural owls which improves nestling survival. *Behav Ecol* 21:722–729
- Landry RE (1979) Growth and development of the burrowing owl (*Athene cunicularia*) [thesis]. California State University, Long Beach
- Lantz S, Conway CJ (2009) Factors affecting daily nest survival of burrowing owls within black-tailed prairie dog colonies. *J Wildl Manag* 73:232–241
- Magrath RD (1990) Hatching asynchrony in altricial birds. *Biol Rev* 65:587–622
- Mayfield HF (1961) Nesting success calculated from exposure. *Wilson Bull* 73:255–261
- Mayfield HF (1975) Suggestions for calculating nest success. *Wilson Bull* 87:456–466
- Newton I (1976) Breeding of sparrowhawks (*Accipiter nisus*) in different environments. *J Anim Ecol* 45:831–849
- Newton I, Marquiss M (1984) Seasonal trend in the breeding performance of sparrowhawks. *J Anim Ecol* 53:809–829
- Newton I, Marquiss M, Village A (1983) Weights, breeding and survival in European sparrowhawks. *Auk* 100:344–354
- Nilsson JA (1995) Parent-offspring interaction over brood size: cooperation or conflict? *J Avian Biol* 26:255–259
- Olenick BE (1990) Breeding biology of burrowing owls using artificial nest burrows in southeastern Idaho [thesis]. Idaho State University, Pocatello
- Pietiainen H (1989) Seasonal and individual variation in the production of offspring in the Ural owl *Strix uralensis*. *J Anim Ecol* 58:905–920
- Porter SN, Wiemeyer N (1972) Reproductive patterns in captive American kestrels (sparrow hawks). *Condor* 74:46–53
- Ricklefs RE (1993) Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds. In: Power DM (ed) *Current ornithology*, vol 11. Plenum Press, New York, pp 199–276
- Ricklefs RE (1997) Hatching asynchrony in birds. *Trends Ecol Evol* 12:229
- Rosenberg DK, Haley KL (2004) The ecology of burrowing owls in the agroecosystem of the Imperial Valley, California. *Stud Avian Biol* 27:120–135
- Sheffield SR (1997) Current status, distribution, and conservation of the burrowing owl (*Speotyto cunicularia*) in Midwestern and western North America. In: Duncan JR, Johnson DH, Nicholls TH (eds) *Biology and conservation of owls of the northern hemisphere*, second international symposium. U.S. Forest Service General Technical Report NC-GTR-190, North Central Forest Experiment Station St. Paul, MN, pp 399–407
- Slagsvold T, Liffeld JT (1989) Constraints on hatching asynchrony and egg size in pied flycatchers. *J Anim Ecol* 58:837–845
- Slagsvold T, Husby M, Sandvik J (1992) Growth and sex ratio in two species of crows: how important is hatching asynchrony? *Oecologia* 90:43–49
- Stenning MJ (1996) Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. *Trends Ecol Evol* 11:243–246
- Stoleson SH, Beissinger SR (1995) Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? In: Power DM (ed) *Current ornithology*, vol 12. Plenum Press, New York, pp 191–270
- Stoleson SH, Beissinger SR (1999) Egg viability as a constraint on hatching asynchrony at high ambient temperatures. *J Anim Ecol* 68:951–962
- Szollosi E, Rosivall B, Torok J (2007) Is hatching asynchrony beneficial for the brood? *Behav Ecol* 18:420–426
- Thomsen L (1971) Behavior and ecology of burrowing owls on the Oakland Municipal Airport. *Condor* 73:177–192
- Veiga JP, Viñuela J (1993) Hatching asynchrony and hatching success in the house sparrow: evidence for the egg viability hypothesis. *Ornis Scand* 24:237–242
- Viñuela J (1997) Laying order affects incubation duration in black kites (*Milvus migrans*): counteracting hatching asynchrony? *Auk* 114:192–199
- Wang JM, Beissinger SR (2009) Variation in the onset of incubation and its influence on avian hatching success and asynchrony. *Anim Behav* 78:601–613
- Wellicome TI (2000) Effects of food on reproduction in burrowing owls (*Athene cunicularia*) during three stages of the breeding season [dissertation]. University of Alberta, Calgary
- Wellicome TI (2005) Hatching asynchrony in burrowing owls is influenced by clutch size and hatching success but not by food. *Oecologia* 142:326–334

- Wellicome TI, Holroyd GL (2001) The second international burrowing owl symposium: background and context. *J Raptor Res* 35:269–273
- Wiebe KL (1995) Intraspecific variation in hatching asynchrony: should birds manipulate hatching spans according to food supply? *Oikos* 74:453–462
- Zarn M (1974) Habitat management series for unique or endangered species. Bureau of Land Management Technical note T-N-250, Denver Service Center, Bldg. 50, DFC-Denver, CO