Association of Sex, Fledging Date, and Sibling Relationships with Post-Fledging Movements of Burrowing Owls in a Nonmigratory Population in the Imperial Valley, California

ASSOCIATION OF SEX, FLEDGING DATE, AND SIBLING RELATIONSHIPS WITH POST-FLEDGING MOVEMENTS OF BURROWING OWLS IN A NONMIGRATORY POPULATION IN THE IMPERIAL VALLEY, CALIFORNIA

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Abstract.—Natal dispersal is an important driver of population and colonization dynamics, yet factors that affect timing and distance of post-fledging movements are poorly understood. We studied post-fledging movements of 34 (12 male and 22 female) juvenile Burrowing Owls (*Athene cunicularia*) between June 2002 and April 2003, in a nonmigratory population in the Imperial Valley, California. We found high variation in movement patterns among individuals. Juvenile Burrowing Owls left their nest throughout the year, with two females (6%) remaining within 100 m of their natal burrow until the beginning of the following year's breeding season. Juvenile Burrowing Owls moved up to 11.7 km (males: 397 ± 124 m; females 1762 ± 630 m) between emergence from the nest to the following breeding season. Those that fledged early in the season remained closer to their nests for a longer period than those that fledged later in the season. Female Burrowing Owls remained ≤100 m from their natal nests for a longer duration than males. Members of male–female, but not male–male, sibling pairs were more likely to be within 100 m of one another than members of female–female sibling pairs. After members of sibling pairs were >100 m apart, distance between members of sibling pairs was related only to time since fledging. Our study, conducted in a highly simplified agricultural environment, provides evidence that sex, fledging date, and sibling relationships can be responsible for the high individual variation in post-fledging movements of Burrowing Owls that has often been attributed to environmental variation.

Key Words: *Burrowing Owl*; Athene cunicularia; *California*; *Imperial Valley*; *natal dispersal*; *post-fledging movements*; *sibling behavior.*

ASOCIACIÓN DEL SEXO, LA FECHA DE EMPLUMAMIENTO Y LAS RELACIONES ENTRE HERMANOS CON LOS MOVIMIENTOS POSTERIORES AL EMPLUMAMIENTO DE *ATHENE CUNICULARIA* EN UNA POBLACIÓN NO MIGRATORIA EN EL VALLE IMPERIAL, CALIFORNIA

Resumen.—La dispersión natal es un impulsor importante de las dinámicas poblacionales y de colonización, sin embargo se conoce muy poco sobre los factores que afectan los tiempos y la distancia de los movimientos post abandono del nido. Estudiamos los movimientos posteriores al emplumamiento de 34 (12 machos y 22 hembras) individuos juveniles de *Athene cunicularia* entre junio del 2002 y abril del 2003, en una población no migratoria en el Valle Imperial, California. Encontramos una elevada variación en los patrones de movimiento entre individuos. Los juveniles de *A. cunicularia* dejaron sus nidos a lo largo del año, con dos hembras (6%) que permanecieron a menos de 100 m de su madriguera hasta el comienzo de la próxima época reproductiva. Los juveniles de *A. cunicularia* se movieron hasta 11.7 km (machos: 397 ± 124 m; hembras: 1762 ± 630 m) desde la emergencia del nido hasta la próxima estación reproductiva. Aquellos individuos que dejaron el nido a comienzos de la temporada permanecieron más cerca de sus nidos por un periodo más prologado que aquellos que abandonaron el nido más tarde en la temporada. Las hembras de *A. cunicularia* permanecieron ≤100 m de sus nidos natales durante más tiempo que los machos. Fue más probable encontrar a miembros de pares de hermanos macho–hembra, pero no

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macho–macho, a menos de 100 m el uno del otro que miembros de pares de hermanos hembra–hembra. Después de que los miembros de pares de hermanos estuvieron separados por >100 m la distancia entre los miembros de un par de hermanos estuvo relacionada sólo con el tiempo transcurrido desde la partida del nido. Nuestro estudio, realizado en un ambiente agrícola altamente simplificado, proporciona evidencia de que el sexo, la fecha del emplumamiento y las relaciones entre hermanos pueden ser responsables de la alta variación individual de los movimientos posteriores al emplumamiento de individuos de *A. cunicularia*, que a menudo ha sido atribuida a la variación ambiental.

[Traducción del equipo editorial]

Natal dispersal, or the movement of an individual from birthplace to the place of its first breeding attempt (Matthysen 2012), has received a great deal of attention as an important life-history characteristic. Understanding natal dispersal is central to predicting the consequences of environmental change because of natal dispersal's influence on the dynamics of populations and the colonization dynamics of unoccupied patches (Clobert et al. 2009). Simplifying natal dispersal into a single event, which has often been the case in studies of dispersal, neglects the complex nature of animal movement. Natal dispersal in birds is often more complicated than a single move (Morton 1992, Wiens 2001, Forsman et al. 2002, Morrison and Wood 2009, Delgado et al. 2010, Cox and Kesler 2012). This understanding, as well as the improvement of tracking methods, has led to an increasing number of studies of the components of natal dispersal in birds, and in particular, post-fledging movements (Belthoff and Ritchison 1989, Vega Rivera et al. 1998, O'Toole et al. 1999, Powell et al. 2002, Cox and Kesler 2012).

Several factors have been posed to explain what post-fledging movements represent: the beginning stages of migration (Vega Rivera et al. 1998), social interactions (Morton 1992, Vega Rivera et al. 1998), exploration for breeding sites (Baker 1993, Vega Rivera et al. 1998, Delgado et al. 2010, Cox and Kesler 2012) or overwintering sites (Baker 1993), and searching for food sources (Vega Rivera et al. 1998). Because post-fledging movement is a precursor to and component of both natal dispersal and migration (Morton 1992, Morrison and Wood 2009), examining its features may aid in explaining these two important yet poorly understood phenomena.

Post-fledging movements of siblings may not be independent of each other (Alberico et al. 1992, Massot et al. 1994, Overskaug et al. 1999), which may indicate that dispersal tendencies are heritable traits (Schroeder and Boag 1988, Dingemanse et al. 2003, Charmantier et al. 2011) or a result of a common environment (Clobert et al. 2001). Studies of natal behavior often avoid using multiple young from a single nest to avoid statistical issues of non-independence (King and Belthoff 2001, Todd 2001, Todd et al. 2003), but choosing a single individual may mask important patterns (Massot et al. 1994) and behavioral associations (O'Toole et al. 1999). Examining relationships among siblings through the post-fledging period may provide insights on factors affecting movement patterns (Belthoff and Ritchison 1989, O'Toole et al. 1999, Forsman et al. 2002).

We evaluated the role of sex, fledging date, and sibling relationships on post-fledging movements in a nonmigratory population of Burrowing Owls (*Athene cunicularia*) that encounter similar environmental conditions in an expansive agricultural landscape. Burrowing Owls are small, ground-dwelling owls distributed across western North America, parts of Central and South America, Florida, and the Caribbean islands (Poulin et al. 2011). Populations of Burrowing Owls may be migratory (King and Belthoff 2001, Todd 2001), nonmigratory (Rosenberg and Haley 2004, LaFever et al. 2008), or include individuals that display either strategy (Conway et al. 2006). Studies of Burrowing Owl post-fledging movements have focused on migratory populations (King and Belthoff 2001, Todd 2001, Davies and Restani 2006, Todd et al. 2007). How post-fledging movements in a nonmigratory population differ from those in migratory populations of the same species is unknown, and provides an opportunity for contrasting movement patterns within a species that has a range of migratory strategies.

Study Area

We conducted our study in the Imperial Valley, California, south of the Salton Sea, approximately 40 km north of El Centro, California (33°07′N, 115°31′W). The study area was centered within an 11.7-km² core area where we trapped juvenile Burrowing Owls at their nest burrows. We searched for radio-tagged Burrowing Owls within approximately 25 km from the center of the study site. The entire study area was characterized by intensive agriculture

and a high density of Burrowing Owls (Rosenberg and Haley 2004). The agricultural system on our study area consisted of a network of cement drains and canals, as well as earthen drains, all of which provided nesting sites either in natural nests or nest boxes (Rosenberg and Haley 2004). Although Burrowing Owls selectively foraged in, or nested near, some crop types more often than in others in the Imperial Valley (Rosenberg and Haley 2004, Bartok and Conway 2010), the study area was a relatively homogeneous mix of nesting and foraging areas because of the highly managed nature of this agricultural area (Rosenberg and Haley 2004).

METHODS

Radio-tagging of Juvenile Owls. From 9 June to 20 July 2002, we captured and radio-tagged 34 (22 female, 12 male) juvenile Burrowing Owls. To capture young Burrowing Owls we selected natural nests based on the presence of emerged young, and randomly selected nest boxes. We searched for nests in early April, during the egg-laying period. We observed nests weekly for signs of emerging young. We captured young within a week of when we first observed them outside of nest burrows or within the mouth of the burrow. We captured Burrowing Owls using two-way burrow traps (Catlin and Rosenberg 2008) and by opening nest boxes. Burrowing Owls frequently occupy nest boxes (Belthoff and Smith 2003), and the nest boxes used in this study were within 100 m of naturally occurring nest and non-nest burrows. Burrowing Owl reproductive success and movement patterns of adults was similar between those nesting in natural nests and nest boxes (Rosenberg and Haley 2004; D. Rosenberg unpubl. data). Previous studies of post-fledging movements that included both natural nests and nest boxes have not reported differences in movement patterns (Clayton and Schmutz 1999, King and Belthoff 2001, Todd et al. 2003), but sample sizes were small. We assumed nest type did not bias our assessment of factors associated with post-fledging movements of Burrowing Owls.

We fitted juvenile Burrowing Owls with radio transmitters that had a ca. 400-d battery life (American Wildlife Enterprises, Monticello, Florida, U.S.A.) using a backpack harness mount and 5.08 ± 0.02 g (mean $\pm$ 1 SE) total assembly mass. Burrowing Owls generally have a mass of 135–150 g (King and Belthoff 2001) at the time of fledging; we only attached radio transmitters to juvenile Burrowing Owls with a mass $\geq$120 g to minimize negative

effects. We attempted to capture Burrowing Owls that recently fledged; therefore, the number of weeks since tagging represented the number of weeks since fledging. We removed one breast feather to determine sex through genetic analysis conducted by Avian Biotech International (Tallahassee, Florida, U.S.A.).

Tracking of Radio-tagged Young. We used ground and aerial surveys to locate radio-tagged Burrowing Owls from June 2002 to April 2003. During ground surveys, we used two 4-element Yagi antennae (Cushcraft Corp., Manchester, New Hampshire, U.S.A.) joined by a null combiner (Telonics, Inc., Mesa, Arizona, U.S.A.) and mounted to the bed of a truck (Gervais et al. 2003). Ground surveys started at the last known location of each radio-tagged Burrowing Owl, but if we were unable to locate a radio-tagged Burrowing Owl near that location, we covered a 1-km-diameter circle, checking at 500-m increments in each of the four cardinal directions around the last known location. We attempted to minimize our effect on a radio-tagged Burrowing Owl's behavior by scanning from $\geq$100 m from their last known location. Moreover, Burrowing Owls in our study area were habituated to humans in vehicles making frequent stops to check irrigation equipment, which reduced the likelihood that they would react to our presence. We conducted ground surveys weekly (June–August, 2002) or biweekly (September 2002 to April 2003), except between 29 August and 21 September 2002. After we located a Burrowing Owl via radiotelemetry, we attempted to confirm whether it was alive or dead. We used an infrared probe (Sandpiper Technologies, Mateca, California, U.S.A.) for belowground inspections to determine status, if necessary.

Aerial surveys consisted of north–south aerial transects with 5-km spacing. We conducted aerial surveys 16 times from a fixed-wing aircraft to search for radio signals from radio-tagged Burrowing Owls that were not detected during ground surveys. We consistently searched an area of approximately 2250 km², allowing us to detect Burrowing Owls that moved up to 23–27 km from their nests. In the last week of our study, we searched for missing radio-marked Burrowing Owls during two surveys during daylight hours and a single survey during the night of each of the north–south roads within the core study area (daylight) or within the core area and 1.6 km beyond (nighttime). Although these methods resulted in a variable number of missing Burrowing Owls throughout the study, only

three Burrowing Owls (9%) were unaccounted for at the end of the study.

Analysis of Telemetry Data. We classified a Burrowing Owl juvenile as independent if at any point during a given sampling interval (defined below) it was >100 m from its nest, regardless of previous or subsequent classifications. Our operational criterion of 100 m was approximately the median nearest-neighbor distance for active Burrowing Owl nests at our study area (Rosenberg and Haley 2004). This distance defined the area around a nest that typically includes satellite burrows for juveniles and the breeding pair (Desmond and Savidge 1999, Ronan 2002) and the distance between neighboring pairs of Burrowing Owls where territorial interactions occur (Green and Anthony 1989, Moulton et al. 2004). We considered Burrowing Owls that we did not locate via radiotelemetry to be >100 m from their nest because we would have detected the signal otherwise.

We assumed that each of the juvenile Burrowing Owls in our samples was approximately the same age when we equipped them with a radio transmitter. We defined time of capture as ''fledging.'' Although fledging is difficult to define for burrow nesters, all Burrowing Owls that we radio-tagged had emerged from their nests, weighed more than 120 g, and were generally capable of at least short flights.

Statistical Analyses. We divided the radiotelemetry data collected throughout the year into 23 time intervals (based on an individual's fledging date) that approximated weekly intervals for the first 10 wk, biweekly intervals for weeks 11–34 (12 intervals), and a single interval for the final 2 mo of the study, which coincided with the initiation of the following year's breeding season. For all analyses, we used the 23 intervals as the time since fledging, which we treated as a continuous covariate in the regression models described below.

For analyses of independence from the nest, we calculated the proportion of individuals that were >100 m from their nest during each of the 23 intervals separately for male and female Burrowing Owls, and for Burrowing Owls that fledged early and late in the season, defined by the median capture date (25 June 2002). For analyses of the maximum distance moved from the nest, given that it was >100 m, we calculated the average maximum distance for each of the 23 sampling intervals separately for each sex and fledging period (early or late).

We examined independence and maximum distance moved with multiple linear regression models that included as explanatory variables (1) time since fledging (log transformed), (2) an indicator variable for sex, (3) an indicator variable for early or late fledging date, and (4) interaction between the indicator variables and time since fledging (log transformed). The interaction terms allowed us to examine differences between the sexes and between early and late fledging date with respect to time since fledging. For analyses of independence, the response variable was the arcsine square-root of the proportion of juvenile Burrowing Owls >100 m away from their nest for a given interval. For analyses of maximum distance from the nest, given they were >100 m away, the response variable was the log-transformed average maximum distance for a given interval. We performed all transformations to meet assumptions of normality and constant variance for linear regression. Because mortality reduced the sample size of radio-tagged juvenile Burrowing Owls as the study progressed, we used weighted multiple regression and used the number of Burrowing Owls in each interval as the weight.

We compared post-fledging movements relative to the type of sibling relationship based on sex (i.e., male–male, female–female, or female–male). The 34 Burrowing Owls that we fitted with radio transmitters came from 16 nests. We tagged multiple juveniles at 10 of these nests, where we radio tagged two (five nests), three (three nests), four (one nest), and five (one nest) juveniles. We investigated independence and distance between members of sibling pairs for each of the 23 sampling intervals. When there was more than a single pair of a particular type (male–male, female–male, female–female) from a single brood, we calculated distances for each combination without replacement. These pairs were then included in the average (distance or proportion within 100 m) for the sampling interval for each type of sibling relationship.

For analyses of movements between members of sibling pairs, the explanatory variables included time since fledging (log transformed), an indicator variable for the type of sibling relationship, and an interaction between time since fledging (log transformed) and the type of sibling relationship. The interaction represented the difference in the rate of separation between members of sibling pairs. For analyses of independence of members of sibling pairs, the response variable was the arcsine

square-root of the proportion of members of sibling pairs >100 m from one another. For comparing factors associated with the distance between members of sibling pairs when >100 m from one another, we related the explanatory variables described above to the natural log transformation of the average distance between members of sibling pairs (response variable). The response variable in both models was based on the average value (proportion or maximum distance) for each of the 23 sampling intervals partitioned by the type of sibling relationship. We weighted both models by the number of sibling pairs used in the average for each sampling interval. We transformed variables to meet the assumptions of normality and constant variance for linear regression.

We mean-centered the time since fledging (log transformed) for all analyses because the introduction of an interaction term complicates the interpretation of indicator variables (Aiken and West 1991). After centering around mean time since fledging, the parameter estimates for sex (β_{sex}) and for early or late (β_{early}) fledging is the difference between parameter estimates for the observed time since fledging and the average time since fledging.

We report means ± 1 SE unless otherwise specified, and 95% confidence intervals around regression coefficients. We present untransformed β estimates.

RESULTS

We captured and radio-tagged 22 female and 12 male juvenile Burrowing Owls. The average mass of juvenile Burrowing Owls that received transmitters was 134 ± 9 g (mean ± 1 SD, range: 120–157 g, n = 22) for females and 132 ± 9 g (mean ± 1 SD, range: 121–149 g, n = 12) for males. All radio-marked male Burrowing Owls were found dead by 13 wk since fledging (5.9 ± 4.6 wk [mean ± 1 SD]; range: 1–13 wk, n = 12). Seventeen of 22 radio-marked female Burrowing Owls were found dead by 43 wk since fledging (18.5 ± 11.4 wk [mean ± 1 SD]; range: 2–43 wk), and the remaining five radio-marked female Burrowing Owls survived the entire study period.

Independence from Nest. All radio-marked juvenile Burrowing Owls moved >100 m from their nest prior to or early in the following year's nesting season. The date when juvenile Burrowing Owls were first located >100 m from nests was associated with time since fledging and sex. The average date that male Burrowing Owls were last seen within 100 m of their nest was 21 July 2002 ± 7 d (range: 20 June 2002 to 25 August 2002, n = 12), or 3.4 ± 0.8 wk (range: 1–8 wk) post-fledging. Females remained at their nest area on average 8 wk longer than males, being last seen, on average, within 100 m from the nest burrow on 10 September 2002 ± 19 d (range: 12 June 2002 to 8 April 2003, n = 22), or 11.8 ± 2.6 wk (range: 1–40 wk) post-fledging. Two of these females remained at their nest until the following April, when Burrowing Owls on our study area typically initiate egg-laying (Rosenberg and Haley 2004). The proportion of juvenile Burrowing Owls that were independent increased with time since fledging (β_{time} = 0.43, 95% CI: 0.26–0.60; Fig. 1). At the average time since fledging, a lower proportion of Burrowing Owls that fledged early in the season were independent (β_{early} = −0.17, 95% CI: −0.29–−0.05) but this proportion increased more rapidly with time ($\beta_{early \times time}$ = 0.13, 95% CI: 0.01–0.24; Fig. 1) for juveniles that fledged early than for those that fledged later in the season. The proportion of male and female juvenile Burrowing Owls independent from their nests was similar at the average time since fledging (β_{sex} = 0.04, 95% CI: −0.11–0.19) but the proportion of female Burrowing Owls that became independent over time increased more slowly than the proportion of male Burrowing Owls ($\beta_{sex \times time}$ = −0.22, 95% CI: −0.39–−0.04; Fig. 1). However, because no male Burrowing Owls lived longer than 13 wk post fledging, interpretation of sex-related parameters is limited to the early post-fledging period.

Distance from Nest. Distance juvenile Burrowing Owls moved away from their nests was related to timing of fledging and time since fledging. Distances >100 m from the nest ranged from 108 to 11 700 m. Of the 29 Burrowing Owls that we classified as independent and for which we knew locations, distances moved by males (397 ± 124 m, n = 8) and females (1762 ± 630 m, n = 21) had high individual variation but we detected no differences between sexes (β_{sex} = 0.03, 95% CI: −0.49–0.54; $\beta_{sex \times time}$ = 0.53, 95% CI: −0.31–1.37; Fig. 2). Burrowing Owls that fledged earlier in the season remained closer to their natal burrows (β_{early} = −0.51, 95% CI: −0.92–−0.11) and moved away more slowly with respect to time since fledging ($\beta_{early \times time}$ = −0.51, 95% CI: −0.99–−0.03) than those that fledged later in the season (Fig. 2). There was only weak support that distance from the nest was related to time since fledging (β_{time} = 0.57, 95% CI: −0.23–1.36; Fig. 2).
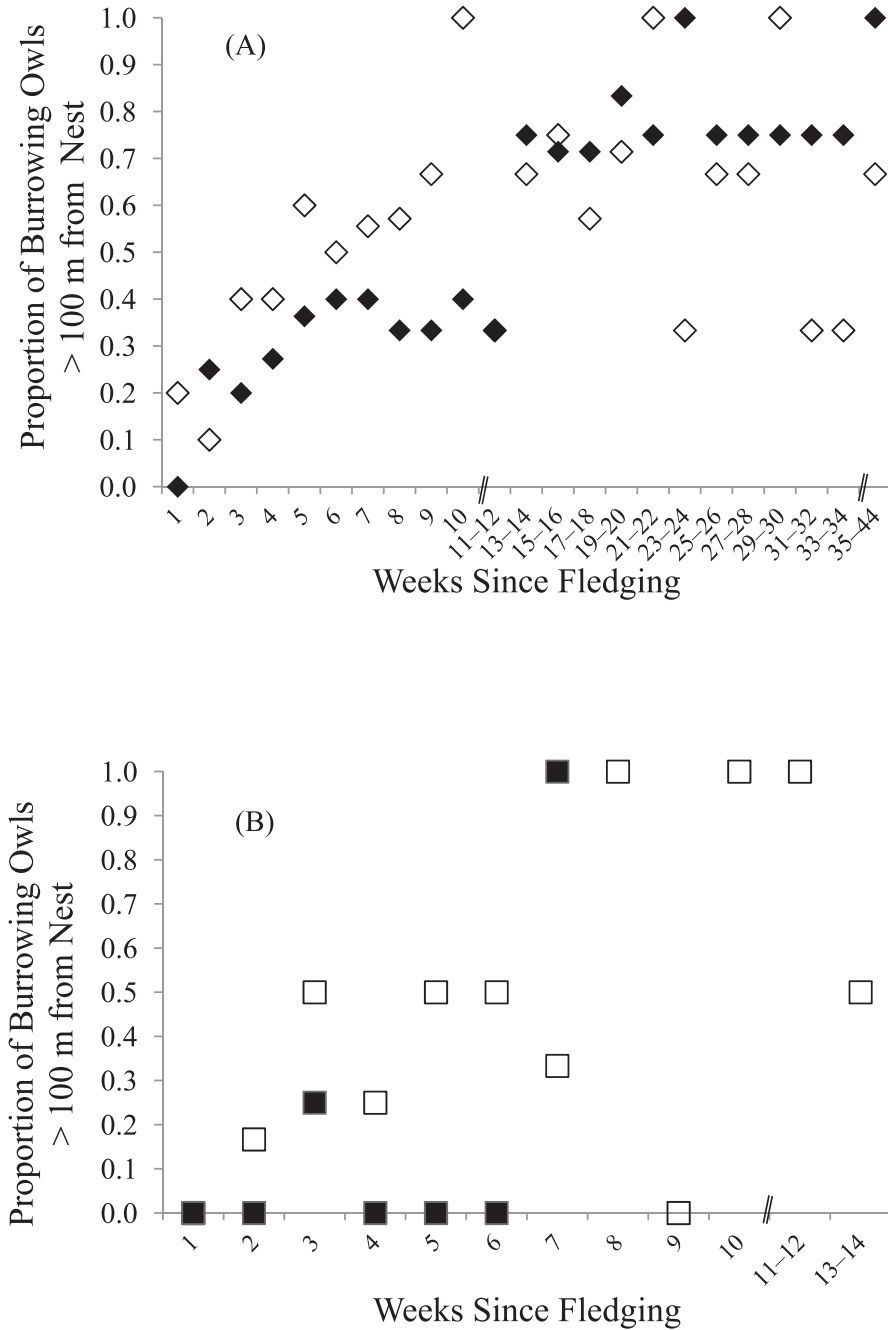
Figure 1.   Proportion of juvenile Burrowing Owls found >100 m from their nest between June 2002 and April 2003, in a nonmigratory population in the Imperial Valley, California. Data are presented for (A) female Burrowing Owls [$n = 22$ (initial sample size)] fledging early in the season (before 25 June; filled diamonds, $n = 12$) and late in the season (after 25 June; open diamonds, $n = 10$), and (B) male Burrowing Owls ($n = 12$) fledging early in the season (filled squares, $n = 5$) and late in the season (open squares, $n = 7$). Burrowing Owls not located via radiotelemetry were assumed to be >100 m from the nest. Burrowing Owls that returned within 100 m of their nest in subsequent weeks were reclassified for that interval, but earlier designations were not changed. Burrowing Owls that died were removed from the proportion such that the sample size decreased with weeks since fledging.
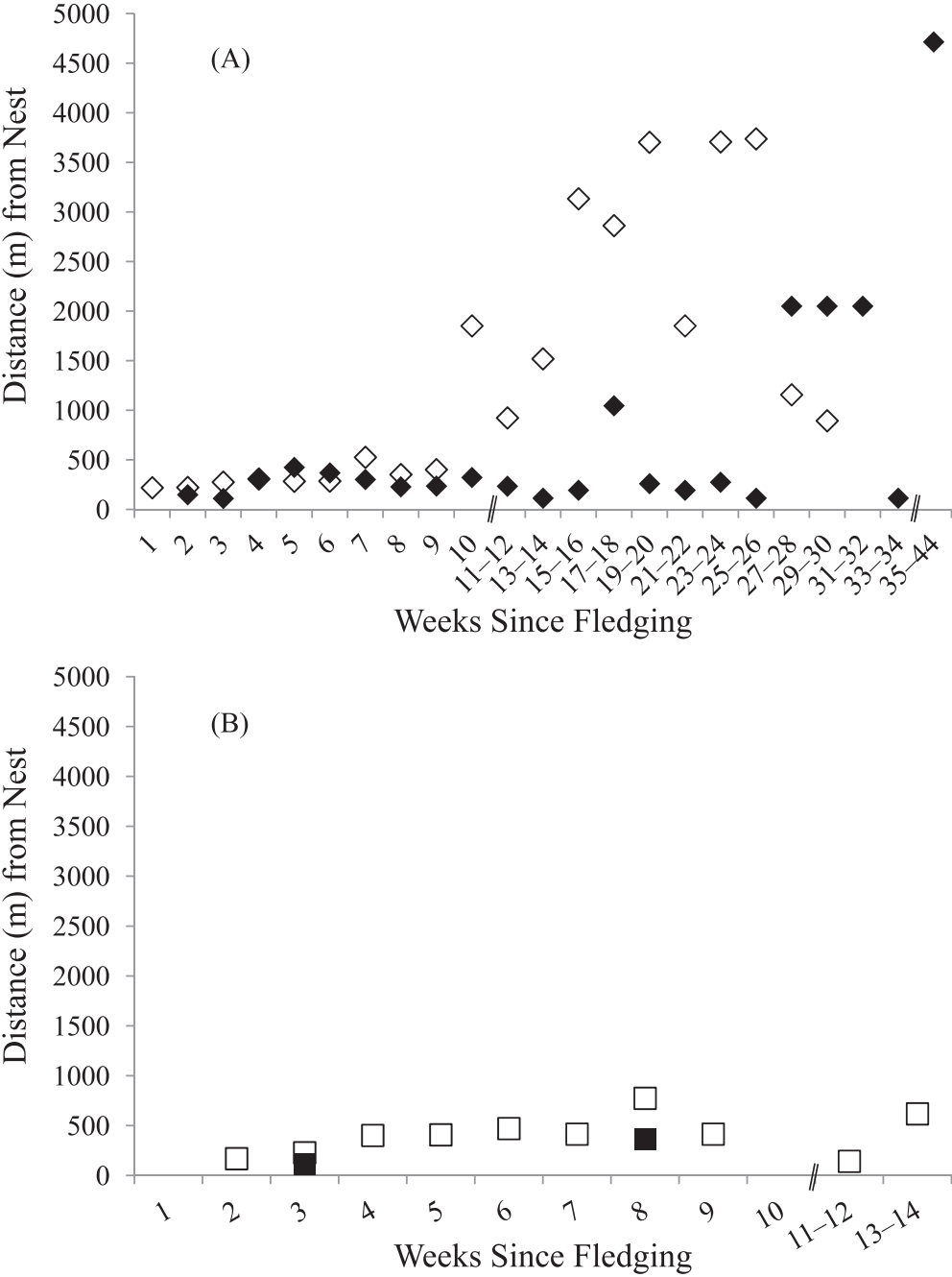
Figure 2. Average maximum distance for juvenile Burrowing Owls that moved >100 m from their nest between June 2002 and April 2003, in a nonmigratory population in the Imperial Valley, California. Data are presented for (A) female Burrowing Owls [$n = 22$ (initial sample size)] fledging early in the season (before 25 June; filled diamonds, $n = 12$) and late in the season (after 25 June; open diamonds, $n = 10$), and (B) male owls ($n = 12$) fledging early in the season (filled squares, $n = 5$) and late in the season (open squares, $n = 7$).
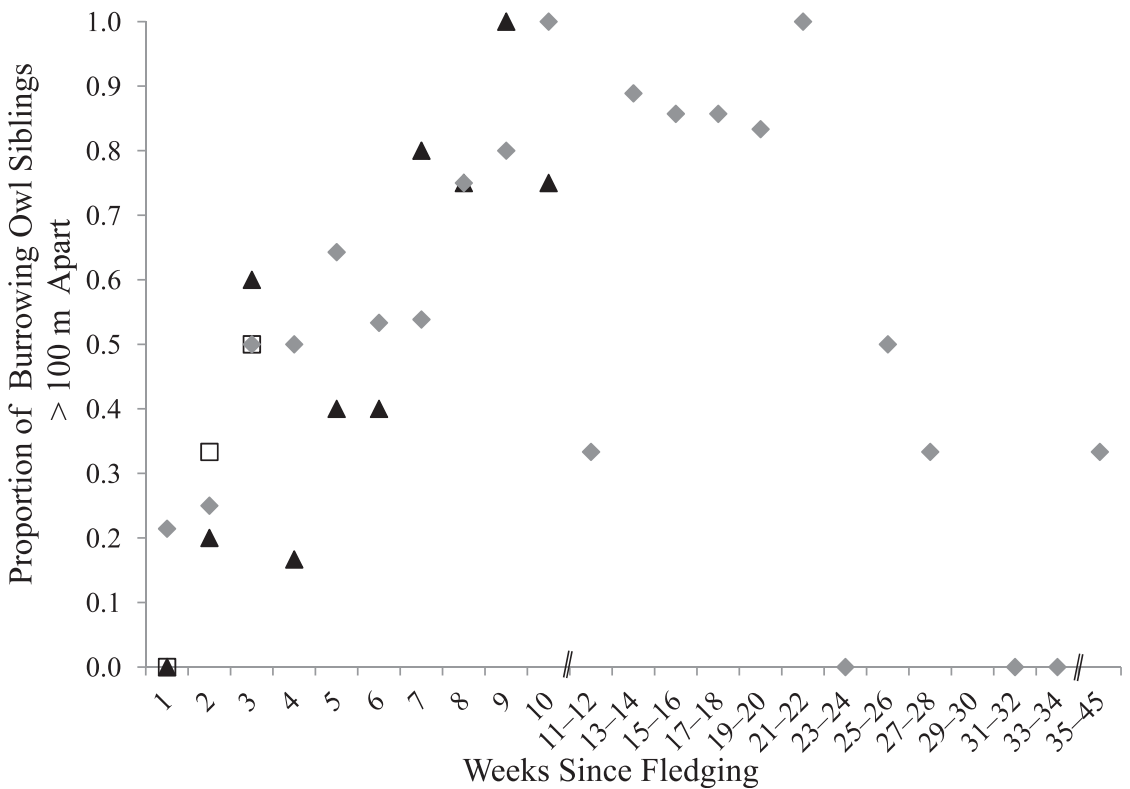
Figure 3. Proportion of juvenile Burrowing Owls found >100 m from their siblings following fledging between June 2002 and April 2003, in a nonmigratory population in the Imperial Valley, California. Proportions were calculated as the number of sibling pairs whose members were >100 m apart divided by the total number of sibling pairs for each time interval and type of sibling relationship: female–female sibling pairs [gray diamonds, $n = 16$ pairs (initial sample size)], male–male sibling pairs (open squares, $n = 3$ pairs), and mixed sibling pairs (black triangles, $n = 10$ pairs). In cases of multiple pairs within a brood, we calculated distances for each combination without replacement and included these pairs in the average proportion for each time interval. Burrowing Owls that were not located via radiotelemetry were considered >100 m from their siblings. Burrowing Owls that returned within 100 m of a sibling in subsequent weeks were reclassified for that interval, but earlier designations were not changed. Pairs in which one or both Burrowing Owls died were removed from the proportion such that the sample size decreased with weeks since fledging.

Sibling Behavior. The proportion of sibling pairs whose members were >100 m from one another was related to the type of sibling relationship and time since fledging. Members of mixed–sex sibling pairs were >100 m from one another less frequently than members of female–female sibling pairs ($\beta_{mixed} = -0.27$, 95% CI: -0.55–0.01), whereas the proportion of male-male siblings >100 m apart did not differ from female-female sibling pairs ($\beta_{male} = -0.16$, 95% CI: -0.66–0.33). The proportion of members of mixed-sex sibling pairs that were >100 m apart increased more rapidly than for female-female sibling pairs as time since fledging increased ($\beta_{mixed \times time} = 0.28$, 95% CI: 0.03–0.53),

but there was no clear pattern for male-male sibling pairs relative to female-female sibling pairs ($\beta_{male \times time} = 0.55$, 95% CI: -0.49–0.16). Regardless of the type of sibling relationship, the proportion of members of sibling pairs that were >100 m apart increased through time ($\beta_{time} = 0.19$, 95% CI: 0.07–0.32; Fig. 3).

After siblings were >100 m apart from one another, the mean distance between members of sibling pairs was not related to the type of sibling relationship, only to time since fledging. Distances between members of both mixed-sex and male–male sibling pairs were not different than between members of female–female sibling pairs at the average time

since fledging (β_{mixed} = 0.03, 95% CI: −1.15–1.20; β_{male} = −0.04, 95% CI: −2.11–2.03). Regardless of time since fledging, the distance between members of male–male pairs ($\beta_{male \times time}$ = 0.16, 95% CI: −9.70–10.01) and between members of mixed-sex pairs ($\beta_{mixed \times time}$ = −0.44, 95% CI: −1.75–0.87) was not different from that of female–female pairs. However, as the time since fledging increased, the distance between members of sibling pairs also increased (β_{time} = 0.82, 95% CI: 0.30–1.34).

DISCUSSION

Our study is the first to report on post-fledging movements for a nonmigratory population of Burrowing Owls. Although factors such as sex, sibling relationships, time since fledging, and timing of fledging were related to post-fledging movements of Burrowing Owls, individuals exhibited considerable variation in their movement patterns not related to these factors. Movement patterns were generally similar for the two components of post-fledging movements we examined: initial independence from the nest area, which we operationally defined as >100 m from the nest burrow, and maximum distance moved during the period from independence until either mortality or the beginning of the following breeding season.

Time since fledging, timing of fledging, and sex differed in magnitude as factors related to initial independence and maximum distance moved. Males, on average, achieved independence more quickly than female Burrowing Owls. Females remained near the nest much longer. There was very high variation of maximum distance moved among individuals and sampling intervals, resulting in no apparent relationship with sex and only a weak relationship with time since fledging. Our estimates of the relationship of sex and distance moved were limited to the earlier portion of the study because of the early mortality of males. Mortality was due, in part, to transmitter effects (Gervais et al. 2006), and generally low survival of juvenile Burrowing Owls at our study site (Rosenberg and Haley 2004) and throughout their range (Todd et al. 2003, Davies and Restani 2006, Gervais et al. 2006, Barclay et al. 2011).

Timing of fledging was the only factor that was clearly related to both independence and maximum distance moved. Owls that fledged later in the season gained independence and distance from the natal burrow at a younger age than owls that fledged early in the season. This may be a response by later-fledged young to increase their opportunities to establish territories and pair bonds before the next breeding season. Contrary to our results, the age of independence for juvenile Wood Thrush (*Hylocichla mustelina*) was not related to the timing of fledging but Wood Thrushes that were from clutches later in the season dispersed from the study area at a younger age than those from earlier clutches (Vega Rivera et al. 1998). Timing of fledging was not consistently associated with departure from the natal area for Bald Eagles (*Haliaeetus leucocephalus*, Wood et al. 1998) or in other Burrowing Owl populations (Garcia 2005). The complexities of factors affecting timing of dispersal contribute to high variation among individuals (Forsman et al. 2002, Ausprey and Rodewald 2013). For example, juvenile Burrowing Owls that were treated with insecticides to remove ectoparasites initiated dispersal an average of 15 d earlier than nontreated owls (Garcia 2005). The effect of ectoparasite removal on initiation of dispersal was year-dependent (Garcia 2005), suggesting an influence of physiological condition.

Few studies of post-fledging movements or dispersal have investigated movement patterns of siblings related to sex. Movements of siblings in our study demonstrated that they quickly gained independence from one another and that independence from one another was related to sex of members of sibling pairs. However, distance moved between members of sibling pairs, once >100 m apart, was related to time since fledging and not the type of sibling relationship.

Our nonmigratory population of juvenile Burrowing Owls displayed post-fledging movements both similar to and different from those of migratory populations. Todd (2001) described and observed three patterns of post-fledging movements of migratory Burrowing Owls in her studies of a population in the northern extent of their range in western Canada. These included (1) nest-centered: juveniles remained near the nest until abruptly departing the area when initiating migration; (2) single-roost: juveniles departed the natal area but remained at a new location until migration, and (3) multiple-roost: juveniles moved progressively farther from the nest until departure for migration. Todd (2001) observed all three patterns in approximately equal proportions, whereas the multiple-roost strategy and nest-centered strategy best described the patterns reported in migratory populations in Idaho (King and Belthoff 2001) and North Dakota (Davies and Restani 2006), respectively. Nest-centered

dispersal patterns were most evident when the nest was within isolated habitat patches (Todd 2001, Todd et al. 2007), which Davies and Restani (2006) believed was analogous to their study area where nesting occurred within black-tailed prairie-dog (*Cynomys ludovicianus*) colonies. The multiple-roost strategy best described post-fledging movements in the nonmigratory Burrowing Owl population we studied. In our study area, the landscape pattern of drains and canals provided a relatively homogeneous landscape, as evidenced by rather continuous nesting habitat, albeit in a linear arrangement (Rosenberg and Haley 2004).

Timing of movements away from the nest in our nonmigratory population was also similar to that observed in migratory populations. At two study areas with migratory populations, juvenile Burrowing Owls typically stayed within 300 m of the nest an average of <60 d post-hatch (King and Belthoff 2001, Todd 2001). In North Dakota, where Burrowing Owls displayed only nest-centered movements, juveniles remained near the nest until the onset of migration at an average age of approximately 83 d post-hatch (Davies and Restani 2006). At all four study areas with migratory populations (Clayton and Schmutz 1999, King and Belthoff 2001, Todd 2001, Davies and Restani 2006), juveniles initiated migration by mid- to late-summer. Relatively long-distance movements were observed prior to migration in the two populations with single- and multiple-roost movement patterns (King and Belthoff 2001, Todd 2001). In populations exhibiting single- and multiple-roost movement patterns, there was some variation in maximum distance moved among individuals, ranging from 0.5–9.4 km (2.1 ± 0.9 km) in Idaho (King and Belthoff 2001), 1.3 ± 0.53 km (no range provided) in western Canada (Todd 2001), and averaging 5.5 km prior to migration in a continuous grassland in western Canada (Clayton and Schmutz 1999). Similarly, most of the juvenile Burrowing Owls in our study area left their natal area by late summer and early fall, with several notable exceptions, including two females that spent nearly the entire year at their nest before dispersing. Thus, our nonmigratory population displayed similar movement patterns as migratory populations up until the time of migration (for populations within continuous habitat).

Individual variation in natal dispersal (Roff and Fairbairn 2001, Chelgren et al. 2008, Clobert et al. 2009) is increasingly being recognized as key to understanding population dynamics in real landscapes. Many intrinsic factors may lead to high individual variation in post-fledging movements, but such variation has often been attributed to heterogeneous environments (Wiens 2001, Delgado et al. 2010, Ausprey and Rodewald 2013). Although we did not measure micro- or macro-environmental characteristics, nests in our study were from a relatively small area (11.7 km²) within a highly managed, agricultural landscape with low complexity. Our results suggest that environmental variation may not be solely responsible for individual variation in dispersal. Most studies of Burrowing Owls have reported high variation in post-fledging movements that was only partially attributable to habitat or landscape variation (reviewed in Todd et al. 2007). Rather, intrinsic factors, such as variable behavioral responses to environmental factors (Clobert et al. 2009), may also explain the high variation we observed in post-fledging movement patterns.

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