FACTORS INFLUENCING MIGRATORY DECISIONS OF WESTERN BURROWING OWLS

by

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DEDICATION

I wish to dedicate this thesis to my parents, Matthew S. and Angela T. Ogonowski, for love and support too profound to define or properly repay;

To my grandparents, Josephine and Peter Tomaselli and Adelaide and Matthew Ogonowski, Sr., for their connection to nature and their open love of life;

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To all those individuals and organizations endeavoring to secure a future for wild lands and their occupants amidst the often mindless advance of the human species;

And to the wildlife, in hopes that any inconvenience caused them by this research contributes in some small way to their persistence on the arid lands of the American West.

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ABSTRACT

Migratory patterns of many birds have changed in recent decades, presumably due to environmental changes linked to altered climate and land-use. We used experimental food supplementation to determine if food abundance affects migratory tendency of individual western burrowing owls (*Athene cunicularia hypugaea*) at two study sites in southern Arizona. We analyzed the effect of food, annual fecundity, burrow availability, and intrinsic factors on migratory tendency with logistic regression. Food-supplemented males were slightly less likely to migrate but food-supplemented females were significantly more likely to migrate than controls. Annual fecundity was negatively related to migratory tendency for owls fledging at least 1 owlet. Owls were less migratory at the agricultural site, females were more likely to migrate than males at the urban site, and migratory tendency was negatively related to body size. We also used logistic regression to examine the association between the migratory tendency of parents and their offspring, and found that variation in migratory tendency was likely due to 1) environmental factors, or 2) a combination of environmental factors and non-additive genetic variation. Our study demonstrates that environmental factors can alter the migratory behavior of individual burrowing owls.

INTRODUCTION AND LITERATURE REVIEW

Avian migration entails a coordinated sequence of morphological, physiological, and behavioral changes. Due to the integrated and complex nature of the biological processes involved, a number of early authors assumed that migratory behaviors were largely resistant to change (Rowan 1925, Farner 1955). However, changes in migratory behavior have been observed in populations of over 200 avian taxa in the past several decades (Fiedler 2001a), including changes in: 1) timing of migration (Root 1997, Bradley et al. 1999); 2) migratory distance (James et al. 1987, Fiedler 2001b); 3) migratory routes (Berthold et al. 1992, Berthold 1995, Svazas 2001); and 4) migratory tendency (i.e., whether individuals migrate or overwinter; Heyder 1955, Schwabl 1983, Able and Belthoff 1998, Rivalan et al. 2007). These recent studies suggest that many of the behaviors associated with avian migration are more malleable than previously thought, and have been cited by some ecologists as evidence that human alteration of earth’s climate is already influencing biological systems (Root 1997, Bradley et al. 1999, Hughes 2000, Inouye 2000).

The extent to which changes in migratory behavior result from behavioral plasticity of individuals, or from generational changes resulting from modifications in the selective landscape (“microevolution”) is unknown. Rappole (1995) suggested that natural selection should be expected to act quickly on avian migratory behaviors, proposing that “(m)igration is a dynamic process, surely subject to rapid evolutionary change.” Moreover, artificial selection experiments with blackcap warblers (*Sylvia atricapilla*) demonstrated that migratory restlessness (*zugunruhe*) and compass orientation are heritable traits, and that changes in the frequency of different genotypes can be produced after a few generations of selective breeding (Biebach 1983, Berthold et al. 1990, Helbig 1991, Berthold and Helbig 1992, Pulido et al. 1996, Berthold 2001). In contrast, Lundberg (1988) argued that behavioral phenotypes exhibited by genetically different individuals (i.e., individuals that inherit either the tendency to migrate or the tendency to overwinter) may be proximately governed by environmental conditions and competitive interactions. Indeed, songbirds exposed to manipulated photoperiods significantly advanced the onset of spring migratory activity and testicular development (Coppack et al. 2003). Hence, individual birds might exhibit what Lundberg termed "condition-dependence" and elect either to migrate or remain year-round at their breeding site depending on local conditions (see also Cristol et al. 1999). Despite the appreciation that many migratory behaviors are likely influenced by both genetic and environmental components, few studies have sought to quantify the importance of each. More information is needed about the extent to which migratory behaviors are genetically or environmentally controlled to better understand the causes of observed changes in avian migratory patterns. Determining whether individual birds are able to alter their migratory behavior will also prove critical for predicting how migratory birds will respond to climate change and for assessing the probability of persistence in the face of such changes (Coppack and Both 2002, Winkler et al. 2002, van Noordwijk et al. 2006).

Regardless of whether observed changes in migratory behaviors are caused by phenotypic plasticity of individuals or by genotypic changes across generations due to alterations in the suite of selective pressures, the ultimate causes are presumably environmental (Berthold 2001, Fiedler 2001a). At present, the ecological factors underlying the observed changes in avian migratory behaviors remain unknown. Most hypotheses that have been proposed point to anthropogenic changes, such as changes in land use or human-induced climate change (Root 1997, Bradley et al. 1999, Inouye 2000, Fiedler 2001a). Land-use practices such as urbanization, grazing, and agricultural conversion may create new foraging and roosting opportunities or lead to milder temperatures associated with urban “heat islands.” For example, large numbers of bird feeders in urban areas may increase food availability above some critical threshold that allows birds to overwinter in their temperate breeding areas (Berthold 1995, Lepczyk et al. 2004). Climate change is expected to alter ambient temperature, precipitation, and wind and these changes may affect migratory behavior by altering physiological limits (e.g., through elevated winter temperatures) or by causing changes in food, habitat, competitors, predators, parasites, or diseases (Fiedler 2001a). Importantly, climate and land-use changes could adversely affect migratory birds through decoupling of the proximate cues and the ultimate resources that affect migratory decisions (Coppack and Both 2002, Gienapp and Visser 2006). For example, altered climatic factors may cause some birds to arrive earlier to breed, but earlier arrival times may not correspond to an advanced peak in food availability. Spring arrival and other aspects of avian breeding phenology no longer coincide with peak resource availability in some species and these changes have fitness consequences (Both et al. 2006, Visser et al. 2006). Alternatively, some species may exhibit relatively limited capacity for a behavioral response, whether through phenotypic plasticity or genetic variation (Sutherland 1998, Fiedler 2001a). We need to understand the various ways in which migrant birds respond behaviorally to environmental change at both the individual and population level so that we can predict how future environmental changes will affect species' persistence.

Despite the many hypotheses proposed to explain observed changes in migratory behavior, empirical studies to establish causality and to determine the extent of phenotypic plasticity in migratory tendency are lacking. The need for such studies is urgent given the magnitude of climate and land-use changes with their uncertain consequences for migratory birds and the communities to which they belong (Coppack and Both 2002, Winkler et al. 2002, Archaux 2003, World Wide Fund for Nature 2006). Species that exhibit partial migration are ideal for identifying the ecological factors that affect avian migratory tendency because all individuals in a population breed in the same location and yet some migrate but others do not.

Breeding populations of western burrowing owls (*Athene cunicularia hypugaea*) in southern Arizona are particularly well-suited for examining factors that influence migratory tendency. Populations throughout the western United States vary in the proportion of individuals that migrate (Haug et al. 1993, Klute et al. 2003) and past surveys suggest that southern Arizona populations are partially migratory (Conway et al. 2005, Conway and Ogonowski 2005, Ogonowski and Conway 2006). Burrowing owls exhibit high site and burrow fidelity (Haug et al. 1993), often perch at the entrance to their nest burrow during daylight hours, and color-banded owls are relatively easy to resight. Many burrowing owl populations at the northern and eastern periphery of their breeding range have declined (Desmond et al. 2000, Holroyd et al. 2001, Conway and

Pardieck 2006), but populations in some urban and agricultural areas remain stable or have increased (Coulombe 1971, DeSante et al. 2004, Rosenberg and Haley 2004). Causes of these trends are poorly understood, but declines are generally attributed to habitat loss and eradication of burrowing mammals. An alternative hypothesis (the altered migration hypothesis) suggests that population declines observed in northern latitudes reflect changes in migratory tendency. In this scenario, owls that formerly migrated to the northern United States and southern Canada to breed have become year-round residents in human-altered landscapes in more southern latitudes with artificially-elevated food abundance, effectively leading to a latitudinal redistribution of individuals.

We tested 2 key assumptions of the altered migration hypothesis. First, we examined whether observed variation in migratory tendency of burrowing owls was due to genetic variation among individuals by 1) using logistic regression to estimate the strength of association between the migratory tendency of parents and their offspring, and 2) examining the consistency of individuals' migratory tendency in successive years. Second, we provided supplemental food at a subset of burrowing owl nests to examine whether food abundance influences an owl's decision to migrate (i.e., leave the breeding area during the winter). We also examined the effect of other ecological factors on migratory tendency: the number of additional (satellite) burrows surrounding the nest, annual fecundity, nesting success, breeding density, and burrow or mate loss. The density of burrows in an area is often considered an indicator of habitat quality for burrowing owls (Klute et al. 2003, Lantz et al. 2007) and is positively correlated with the probability of nesting success (Desmond and Savidge 1999). Hence, we predicted that adult owls nesting at burrows with greater numbers of satellite burrows would be less likely to migrate to avoid losing a high-quality nest site to a resident competitor. We considered that owls might use annual fecundity or nesting success as a proximate cue to assess habitat quality which could in turn affect an owl’s decision regarding whether to migrate. We also measured breeding density as a possible index of intraspecific competition because some authors have proposed that competition may affect migratory decisions or migratory distance in birds (Cox 1968, Terrill 1987, Lundberg 1988, Cristol et al. 1999). We examined whether burrow or mate loss increased the likelihood of migration. Mate loss has been shown to increase the probability of breeding dispersal and dispersal distance in burrowing owls (Catlin et al. 2005), and may serve as a proximate cue for site quality in this species. Finally, we controlled for the effect of 3 intrinsic variables known or believed to affect migratory behavior in other species (see review by Cristol et al. 1999): sex (Ketterson and Nolan 1976, Myers 1981, Mead 1983), age (Gauthreaux 1982, Schwable 1983), and body size (Lack 1954, Ketterson and Nolan 1976, Arnold 1991).

STUDY AREA

Our study area was composed of two sites in southern Arizona: an urban study site within the city limits of Tucson (Pima County, elevation 728 m, population 518,956), and a predominantly agricultural study site surrounding the small town of Coolidge (Pinal County, 435 m, population 8,154). Both sites are located in the basin and range province of southern Arizona and the Arizona Upland subdivision of the Sonoran Desert ecoregion (Turner and Brown 1994). Average rainfall in Tucson is 29.7 cm per year, with average temperatures ranging from lows of 3.9 C in winter to 37.8 C in the summer and highs often exceeding 43.3 C. Average rainfall in Coolidge is 29.0 cm per year, with average temperatures ranging from lows of 0.6 C in winter to 42.2 C in summer and highs exceeding 46.1 C (all weather data from National Oceanic and Atmospheric Association 2007). In Tucson, burrowing owls nested in four locations: in abandoned round-tailed ground squirrel (*Spermophilus tereticaudus*) burrows 1) on and adjacent to Davis-Monthan Air Force Base, 2) along the banks of the Santa Cruz River and smaller tributary washes, 3) on several isolated parcels of commercial land including the grounds of Tucson Electric Park, and 4) in erosional cavities and metal culverts along washes. In Coolidge, owls nested in four locations: in abandoned ground squirrel burrows 1) within creosote (*Larrea tridentata*) stands on Casa Grande Ruins National Monument, 2) along earthen canals and concrete irrigation troughs abutting agricultural fields, 3) in abandoned fields overgrown with grasses and scattered shrubs, and 4) in erosional cavities under concrete irrigation troughs.

METHODS

Banding and nest monitoring

Trapping and banding owls. We used color-marking and band resighting to determine whether individual owls migrated or not. Many adult owls were already banded as part of a larger demographic study (Conway and Ellis 2004). We captured owls using 2-way modified “havahart” traps placed in the burrow entrance, or spring-loaded bownet traps baited with live rodents placed next to the burrow entrance. We placed one aluminum U.S.G.S. band and one alphanumeric color-coded band (ACRAFT Sign and Nameplate Co., Edmonton, Alberta, CA) on opposite legs of each owl. We also trapped owls for which we could not determine band status observationally and to confirm the presence of individuals at burrows that we suspected were occupied, particularly during winter months when female owls often remained underground or retreated into the burrow when approached. We trapped and banded juvenile owls at all nests in 2005 to improve our estimates of annual fecundity and nesting success.

Nest-monitoring. We visited all known current and past nest burrows (n = 123 in Tucson, n = 137 in Coolidge) and potential nest burrows once per week from March 2005 through June 2006 to identify which owls were present and to estimate nesting success and annual fecundity at each nest burrow. During each weekly nest visit, we first observed burrows from a distance of >100m with binoculars to look for owl activity and used a spotting scope to read the alphanumeric ACRAFT codes of banded birds. We then approached burrows on foot to look for signs of use (e.g., whitewash, feathers) and nesting activity (lining, décor, manure), and used an infrared video probe (Sandpiper Technologies, Inc., Manteca, CA) to look for eggs within all burrows at which we observed owls or owl sign. The infrared probe allowed us to locate owls not detected aboveground, determine whether elusive individuals were banded, and estimate reproductive parameters (clutch size, hatching success, and number of fledglings). To increase the probability of detecting owls that had dispersed locally, we systematically searched areas surrounding all monitored burrows throughout the year. We mapped the location of all burrows at which we observed owls or owl sign with a handheld GPS receiver (Garmin, Olathe, KS).

Determination of migratory status. We conducted an intensive mid-winter survey between 15 January and 6 February 2006 to determine the identity of all owls over-wintering at each study area. We visited each known burrow (occupied and unoccupied) at least twice within a 10-14 day window, returning more frequently to burrows where we could not initially read a owl's band and trapping owls to read bands when necessary. We classified an owl as a winter resident (i.e., non-migrant) if the owl met all these conditions: 1) bred during summer 2005, 2) was observed between 15 November 2005 and 15 February 2006, and 3) bred during summer 2006. We classified an owl as a migrant if the owl: 1) bred during summer 2005, 2) was not observed between 15 November 2005 and 15 February 2006, and 3) bred during summer 2006. We classified owls that were observed between 15 November 2005 and 15 February 2006 (i.e. overwintered) but were not breeders during summer 2006 as winter residents, and analyzed our data with and without these individuals. We used the criteria above to determine the migratory status of all 2005 hatch-year owls in order to assess the correlation between the migratory tendency of parents and their offspring (see "Statistical Methods" below), and included data from a comparable winter survey and monitoring program conducted in Tucson from March 2004 through March 2005 in the context of a prior study to increase our sample size. Finally, we estimated the proportion of male and female owls breeding on our study sites in 2005 that returned to breed in 2006.

Supplemental food experiments

Experimental design. We used a blocked experimental design to assess the effect of food abundance on probability of over-wintering by adult owls at our two study sites. We controlled for the possible confounding effect of surrounding land use by dividing each study site into subsegments. We divided the urban study area into five subsegments: active airfield, aircraft storage area, desert wash, residential, and industrial/urban. We divided the agricultural study area into three subsegments: active agricultural field, abandoned agricultural field, and creosote flat. We were not able to secure permission to supplement food at nest burrows within the creosote flats on Casa Grande Ruins National Monument (CGRNM), so our experimental manipulation was limited to the first two subsegments at the agricultural study area. Owls nesting on CGRNM were thus excluded from all subsequent analyses.

We controlled for the possible effect of breeding phenology on the effectiveness of our treatment by alternating the assignment of nests to food-supplemented and control groups within each subsegment in order of increasing hatching date. For each subsegment, we flipped a coin to determine whether the earliest-hatching nest would be assigned to the food-supplemented or control treatment group, then alternated the assignment of treatments to nests with successive hatching dates. We were concerned that hatching date could affect migratory behavior of adult owls, e.g. if breeding later in the summer limited the time available for acquisition of necessary fat stores and thus reduced the probability of migrating. We used a standardized protocol to estimate hatch date based on signs and behaviors observed during weekly nest visits (Garcia et al. 2007). We used the infrared video probe on repeated nest visits which allowed us to estimate the onset of incubation at each nest, because burrowing owls typically lay 2 eggs every 3 days and initiate incubation at the midpoint of laying (Olenick 1990, C. Nadeau, pers. observ.). Repeated use of the infrared probe does not affect burrowing owl reproduction (Garcia and Conway, in review). Estimated hatch date was based on an incubation period of 26 days, and confirmed by noting the presence and age of hatchlings with the infrared video probe. We also used hatch date as a covariate in our analyses to control for any remaining effect of hatch date on the effects of our supplemental food experiment. Owls at 20 burrows either failed to lay eggs or we were unable to document egg laying. We randomly assigned these burrows to experimental and control groups and included laying status (documented vs. non-documented) as a covariate in our analyses.

Supplemental feeding. We obtained dead laboratory mice weighing 20-25 grams each from a commercial breeder (Perfect Pets, Inc., Belleville, MI) to supplement food at experimental nests. Small vertebrates, chiefly mammals such as mice and voles, typically account for 78-95% of the biomass in the diet of burrowing owls throughout the year (Green 1983, Thompson and Anderson 1988, Green and Anthony 1989) and have been used to supplement food in prior burrowing owl studies (Wellicome 1997, 2005; Garcia 2005). We estimated weekly energetic needs for owls present at each burrow based on Marti (1973) and placed enough biomass to equal 50% of total energetic needs in the burrow entrance during weekly nest visits. Mice were provided during weekly nest visits so that control and experimental nests were visited with equal frequency.

Our sample included a total of 75 experimental and 76 control nests. We attempted to begin food supplementation at experimental nests when the oldest juvenile was estimated to be approximately 14 days old (range 12 - 23 days) and continued weekly food supplementation through the end of December 2006. We located 20 nests after juveniles had already hatched and at which the oldest juvenile was greater than 14 days old; 8 of these nests were selected as experimental nests at which we began weekly food supplementation immediately. We controlled for potential effects of finding nests before or after hatching by including this variable as a covariate in our analyses. Although we expected that most migrant owls would leave our study sites by November, we provided supplemental food through the end of December to reduce the likelihood that adult owls would disperse locally and escape detection during the winter survey. We continued to provide supplemental food to adults and juveniles from experimental nests if owls moved to a new burrow during the experiment **(***n* **=** 13 nests) and to adults whose nests failed (*n* = 12 nests) or who lost a mate during the experiment **(***n* **=** 3 nests). Supplemental food was split among several satellite burrows when owl families appeared to be using more than one burrow.

Burrow characteristics

Burrow density. We measured burrow density in the vicinity of active nests in two ways: number of available burrows within 100 m and number of used burrows. A burrow was considered "available" if the opening was large enough for an owl (minimum inner diameter approximately 12 cm) and not visibly collapsed upon external inspection. We determined the number of used burrows by locating and monitoring all satellite burrows used by adult and juvenile owls at each nest burrow during weekly nest visits throughout the summer and early fall regardless of distance from the nest, noting when any of these burrows collapsed or became inactive (indicated by lack of pellets, whitewash, and feathers, or presence of cobwebs across entrance).

Burrow condition and disturbance. We used the infrared video probe to determine whether nest burrows were intact or had collapsed internally throughout the breeding season and in early fall. We also recorded all instances of temporary or permanent disturbance to active nests throughout the year, including flooding of burrows abutting agricultural fields, collapse due to overrun by vehicles, occupation by bees, deliberate filling by humans, and predation or other sources of mortality to adults and juveniles.

Reproductive parameters

Nesting success. We considered a nest successful if the nest produced at least one 44-day-old juvenile owl. Although considerable variation exists in the age at which juvenile burrowing owls depart from their natal area (Garcia 2005), young are considered fledged (i.e., capable of sustained flight) at 44 days after hatching (Landry 1979, Haug et al. 1993). We used both aboveground observations and the infrared video probe to determine the cause of failure and the nesting stage when failure occurred at all unsuccessful nests.

Annual fecundity. We used a standardized protocol to determine critical dates in the nesting cycle and daily survival of nestlings (Garcia et al. 2007), and then used this information to estimate the number of fledglings produced at each nest in 2005. We defined annual fecundity as the number of juvenile owls estimated to have survived to fledging age (44 days post-hatch) after excluding brood-mixing with young from other nearby nests.

Nesting density

We used georeferenced points taken with a handheld GPS unit and ArcGIS mapping software (ESRI, Redlands, CA) to determine the density of active nests within 300 meters (±5 m) of each nest in our sample. All nest locations at each study area were first downloaded into a file using MapSource software (Garmin, Olathe, KS) and this file was exported to ArcGIS. We then used the ArcGIS Point Distance function to determine the distance to all neighboring nests within a 300 m buffer of each georeferenced nest point.

Intrinsic factors

Sex. We used a combination of plumage characteristics, behavioral observations, and presence of a brood patch on captured females to determine the sex of all adult owls. Burrowing owl adults are slightly dimorphic. Males are typically larger and paler with less barring on the breast plumage than females. Males are usually found perching at or near the nest burrow during incubation and the early nestling phases, while females usually remain underground. Incubating females exhibit a prominent and often vascularized brood patch which we used to confirm our visual and behavioral determinations of sex whenever possible.

Age. Owls banded as juveniles in prior years were of known age. Owls banded as adults in prior years were assigned minimum ages (e.g., ASY for “After second year” if banded as an adult in 2004 and observed nesting in 2005).

Body size. Some authors have suggested that body size should be negatively correlated with migratory tendency and migratory distance in partially migrant populations, either because larger size is associated with: 1) higher quality and superior ability to compete for limited winter food resources (Lack 1954, Arnold 1991), or 2) physiological ability of an individual to endure periods of adverse weather and/or food shortage (Ketterson and Nolan 1976, Belthoff and Gauthreaux 1991). Support for the body size hypothesis is equivocal (Cristol et al. 1999, Bell 2005). We used tarsus length as an index of body size to evaluate the body size hypothesis. We measured the combined length of the tarsus and the middle metatarsus to the end of the first joint with Vernier calipers. We failed to measure tarsus length on 35 (13 females and 22 males) of our 152 owls so we used the sex-specific mean from all adult owls banded on our 2 study sites from 2003-2005 (n = 422) as the tarsus length of these 35 individuals.

Animal welfare protocol review

A description of all methods involving burrowing owls that were employed in this study and the number of individual birds affected by each were submitted for review to and approved by the University of Arizona’s Institutional Animal Care and Use Committee (IACUC) under the animal use protocol entitled “Burrowing owl demography in urban Tucson” (control number 02-041, January 2005 renewal).

Statistical methods

Association between migratory tendency of parents and their offspring. We examined the heritability of migratory tendency in burrowing owls using logistic regression (SPSS 15.0 for Windows 2006). We regressed the migratory tendency of all first-year owls that returned to breed the following year on the migratory tendency of their returning male and female parents during the same year. For this analysis we used data from Tucson from 2004-2006 (two annual cycles) and from Coolidge from 2005-06 (one annual cycle). We controlled for the effect of four covariates by including them in our analyses: year (for Tucson owls), study site, treatment group (food supplementation or control), and sex of first-year owl. We conducted the analysis in two steps. We first screened for the effects of covariates by entering all 7 variables (the 4 covariates, father's migratory tendency, mother's migratory tendency, and the interaction of the latter two factors) in the logistic regression model, then dropped all nonsignificant covariates and re-ran the logistic regression.

Factors affecting migratory tendency: variable reduction phase. Our efforts to determine which factors influenced migratory tendency in burrowing owls proceeded in two phases. In the first phase, we screened 15 main effect variables and 31 interaction terms in order reduce the number of parameters we used to construct explanatory models. We entered all main effects and interactions as explanatory variables in a logistic regression analysis with forward variable entry using migratory tendency (migrated vs. overwintered) as the response variable (SPSS 15.0 for Windows 2006). This initial analysis revealed that 6 main effects (number of available burrows, hatch date, nesting success, laying status, found after hatching, and minimum age) and 13 interactions did not improve model performance or significantly affect the sign, magnitude and significance of other estimated coefficients, so these were excluded from subsequent model development. As a result of this variable reduction phase we retained 8 main effects: 4 numerical and 4 categorical variables (Table 1). We used these remaining variables and interactions to develop explanatory models in the second model-selection phase of data analysis.

Model selection phase. We used binary logistic regression to analyze our data and both information-theoretic (Burnham and Anderson 2002) and traditional frequentist approaches to select models. Our purpose was twofold: 1) to determine which variables best explain the migratory tendency of burrowing owls in our sample, with special emphasis on the effect of our experimental food supplementation, and 2) to compare the results from several common approaches for model selection, given the recent debate surrounding the benefits and drawbacks of each approach (Steidl 2006, Stephens et al. 2006).

Although few field studies have used an experimental approach for examining the environmental factors that affect migratory tendency, our study was hypothesis-driven as it was based on prior knowledge of burrowing owl habitat requirements and published hypotheses regarding the factors that influence avian migratory behavior in general. This allowed us to develop a set of 67 candidate models (Appendix D) including main effects and what we deemed to be biologically-relevant 2-way interactions. At the same time, our study was exploratory in that it is one of the first to experimentally manipulate food abundance and to explore the combined effects of extrinsic and intrinsic factors on the plasticity of avian migratory behavior in a controlled field study. Because we could not be certain we had included all potentially relevant combinations of factors and interactions in our list of candidate models, we used stepwise logistic regression to re-analyze our dataset. We included all main effects and interactions that appeared at least once in our set of candidate models from our information-theoretic approach. We also compared the results of both forward and backward stepwise regression procedures to further explore any differences that might result from these alternative methods of model selection.

Information-theoretic approach. We compared the ability of our 67 candidate models (Appendix D) to predict the probability of migrating with logistic regression with migratory tendency (migrated vs. overwintered) as the response variable (GLM platform, SPSS 15.0 for Windows 2006). We ranked models according to Akaike's Information Criterion (AIC; Burnham and Anderson 2002), and used finite sample-corrected AIC values (AIC_c) to account for potential problems associated with small sample size relative to the number of parameters. We ranked models in order of ascending AIC_c values, calculated ΔAIC_c values and AIC_c weights as measures of relative support for each model, and examined the extent to which the same variables appeared among our top-ranked models. We also compared the proportion of individuals that were correctly classified as migrants or residents by each model.

Frequentist approach. We conducted stepwise logistic regression to assess which factors and interactions influenced migratory tendency of burrowing owls (Multinomial Logistic platform, SPSS 15.0 for Windows 2006). We included all 8 main effects and the

18 interactions that appeared at least once in the set of 67 candidate models we had developed for the information-theoretic approach. Migratory tendency was the response variable and we created two models by employing both forward and backward stepwise variable selection procedures (probability to enter = 0.2, probability to leave = 0.1 for both procedures). Using both forward and backward stepwise procedures allowed us to further explore the effect of model selection procedures on our results.

Return rates. We used contingency table analysis (Fisher's one-sided exact test) to determine whether the proportion of male and female owls that returned to breed (residents and migrants combined) in 2006 differed by treatment group.

RESULTS

Heritability of migratory tendency

We used migratory tendency of 43 returning first-year breeders for which we were also able to determine the migratory tendency of both parents. We used these 43 individuals to examine the heritability of migratory tendency in burrowing owls. None of the covariates were significant so we pooled data across categories of year, study site, treatment group, and sex of first-year bird. Our logistic regression model included migratory tendency of first-year breeder as the response variable and 3 explanatory variables: paternal migratory tendency (MTend), maternal migratory tendency (FTend), and their interaction (MTend*FTend). We were not able to obtain a stable estimate of the interaction term due to the small number of migrant males in our sample (only 5 of the 43 adult males were migratory) which resulted in much smaller numbers of observations in 2 of 4 levels of the interaction, so we removed the interaction from our model. Neither FTend (*P*=0.689) nor MTend (*P*=0.226) were significant predictors of offspring migratory tendency. The offspring of both migrant (*n*=14) and resident (*n*=29) females were about equally likely to migrate (Figure 1a). Fifty percent (*n*=38) of the offspring of resident males migrated, but only 1 of the 5 offspring of migrant males migrated (Figure 1b). This pattern is opposite of what we would expect if migratory tendency had high heritability. Hatch-year owls with two resident parents were slightly less likely to migrate (46% migrants, *n*=26) than hatch-year owls with a resident male and a migratory female parent (58%, *n*=12), but these differences were not significant.

We also examined whether migratory tendency of individual owls was consistent from year to year. We could only obtain data on migratory tendency in the previous year for 86 of the 152 owls in our sample (48 males, 38 females), so we excluded prior-year status from our logistic regression analyses and analyzed its effect separately. Of the 17 owls classified as migrants in the year prior to our study, 53% were migrants the subsequent year. Of the 69 owls classified as residents in the year prior to our study, 99% were residents the subsequent year (Figure 2; $P < 0.001$, Fisher's 2-sided exact test). This pattern was consistent across sexes and treatments.

We also examined whether the effect of prior-year migratory tendency varied with age. We obtained data on migratory tendency for 44 owls of known age (i.e., owls banded as juveniles in a previous year). Of these, we also knew the migratory tendency in the previous year for 38 owls (17 females, 21 males). Of the 28 known-age owls that were residents in the year prior to our study, all 28 were also resident during the following year (Figure 3). Of the 10 known-age owls that were migrants in the year prior to our study, 50% were migratory the following year. There was a nonsignificant trend of age being inversely related to the probability of migrating among these 10 owls (Figure 3, data pooled by sex and treatment group, $\chi^2=0.5$, $P=0.766$). This pattern was consistent across sexes but differed between food-supplemented and unsupplemented owls (no known-age food-supplemented individuals were migratory).

Model selection: AIC vs. forward and backward stepwise variable selection

We used observations of 152 color-marked individuals (82 males and 70 females) to examine the effect of food and other factors on migratory tendency in burrowing owls. Our sample included 14 owls (4 males, 10 females) that were present throughout the fall and winter months but that we did not observe during the 2006 breeding season. We analyzed our data with and without these 14 individuals and our results did not change, so we retained these “winter only” owls as residents in our sample. We excluded 7 owls (3 males, 4 females) that were observed at least once within the 15 November and 15 February cutoff dates but that were not observed during the mid-winter survey, given that we could not be certain of their migratory tendency.

Only 7% of owls nesting in Coolidge and 17% of owls nesting in Tucson migrated. Hence, the distribution of our response variable was unbalanced (18 migrants and 134 residents in our sample). Several variables appeared to influence migratory tendency regardless of the model-selection approach employed. Study site (S) was included in 7, sex (X) in 5, and tarsus (T) in 4 of the 7 competing models (i.e. those with $\Delta AIC_c \leq 2.0$) selected via information criteria (Table 2). The direction of each effect was similar across the 7 competing models, and all 3 of these variables were included in many of the 20 highest-ranked models. Study site and tarsus were included in both of the stepwise models, and sex was included in the backward (but not the forward) stepwise model. Owls nesting in Coolidge were less likely to migrate than owls nesting in Tucson. This effect was due primarily to a higher proportion of migratory females in Tucson (28%, *n*=18) compared to Coolidge (0%, *n*=20, control group birds only). Indeed, the sex*site interaction was in 3 of 7 competing models and 6 of the 20 highest-ranked models selected by AIC_c values, and was also retained by backward stepwise regression (β = -6.4, P = 0.006 from stepwise model). Tarsus length was negatively related to migratory tendency (β = -1.4, P = 0.002 from backward stepwise model; Figure 4). This pattern was more obvious among owls that did not receive supplemental food, but the tarsus*treatment interaction was not in the final models for any of our three model-selection approaches, and owls with the largest tarsi ($\geq$72mm, n=25) were non-migratory regardless of treatment group or sex.

Aside from these similarities, the 3 model-selection approaches suggest ambiguity in which variables explain migratory tendency (Table 2). Neither forward nor backward stepwise variable selection produced a model that was among the 7 competing models or the 20 highest-ranking models chosen on the basis of AIC_c values. Indeed, neither of the models resulting from the two stepwise approaches had been among the 67 candidate models we examined via AIC. Models differed markedly in their complexity. Five of the 7 competing models (ΔAIC_c values $\leq$2.0) and the model selected by forward stepwise variable selection included only 1-3 explanatory variables (primarily sex, site, tarsus, and interactions between these). The forward stepwise model included mate_or_burrow loss, which was positively related to the probability of migrating, but this variable appeared in only 2 of the 7 competing models (ΔAIC_c values $\leq$2). Two of 7 competing models from the information-theoretic approach were much more complex, composed of 11 and 10 variables each, and the model selected by backward stepwise regression was composed of 18 variables. Model complexity was directly related to how well models performed at classifying owls as residents or migrants (Table 2). All the selected models correctly classified $\geq$ 97% of resident owls. However, all of the competing models ($\Delta\mathrm{AIC}_c$ values $\leq$2.0) composed of 1-3 explanatory variables, and the forward stepwise model, incorrectly classified all 18 migrant owls. The 2 more-parameterized competing models performed better, correctly classifying 22% and 11% of migrants, respectively. The backward stepwise model performed best, correctly classifying 39% of migrant owls.

Effect of food and other environmental factors on overwintering

Inclusion of food effects in models. The information-theoretic approach provided some support for an effect of food on migratory tendency. Food appeared in 1 of the 7 competing models and in 4 of the 20 highest-ranked models as both a main effect and in interaction terms with sex, study site, and number of juveniles fledged (Table 2). Backward stepwise logistic regression also provided support for an effect of food on migratory tendency; the model included food as a main effect and interactions between food and sex, study site, and number of juveniles fledged. The backward stepwise approach also included the interaction between food treatment and nesting density, indicating that owls nesting in areas with more nearby nests were more likely to migrate but only if not provided supplemental food. In contrast, we found that forward stepwise regression provided no support for an effect of food on migration as this model included only study site, mate loss, and body size.

Strength and direction of food effects. Experimental food supplementation affected migratory tendency of burrowing owls, but the effects were conditional on other explanatory variables (four 2-way interactions with food were included among the 7 competing models selected via AIC_c values and backward stepwise regression). Males provided with supplemental food were slightly less likely to migrate than unsupplemented males, as we predicted, though this difference was not significant. However, females provided with supplemental food were significantly more likely to migrate ($\beta = -3.6$, $P = 0.042$ for treatment*sex interaction from backward stepwise regression model; Figure 5). The pattern was the same at both study sites. The food treatment by study site interaction appeared in 2 of the 20 highest-ranked models in the information-theoretic approach and in the model selected by backward stepwise regression.

Interaction of food and number of juveniles fledged. The number of juveniles fledged (and $\geq$1 of the 2-way interactions including this variable) appeared in 2 of 7 competing models and 5 of the 20 highest-ranked models in our information-theoretic approach and in the model selected by backward stepwise regression. The number of juveniles fledged also entered but then was removed on the last step in the forward stepwise regression model ($P = 0.163$). Among unsupplemented owls, those fledging 0 offspring were least likely to migrate (Figure 6), contrary to our predictions. However, migratory tendency was negatively related to the number of juveniles fledged (as we had predicted) for unsupplemented owls that successfully fledged $\geq$1 offspring. Supplemental food affected migratory tendency differently depending on the number of juveniles fledged ($\beta = 1.8$, $P = 0.005$ for interaction between food and number fledged in backward stepwise regression model). Supplemental food decreased the probability of migrating for owls that fledged 1-4 juveniles, but increased the probability of migrating for owls that fledged either 0 juveniles or $\geq$ 5 juveniles. These patterns were driven primarily by variation among female owls due to the small number (n = 7) of migrant males in our sample**.** We also found limited evidence of an interaction between the number of juveniles fledged and study site (included in 1 of the 7 competing models with $\Delta\text{AIC}_c \leq 2$ and included in the backward stepwise model; $\beta = 1.3$, $P = 0.030$, Table 2).

Effect of satellite burrows on migratory tendency. Three of the 20 highest-ranking models from the information-theoretic approach (but 0 of 7 competing models with $\Delta\text{AIC}_c \leq 2$) and the model selected by backward stepwise regression included the number of satellites used and $\geq$ 1 2-way interaction involving this variable. The relationship between satellite burrows and migratory tendency was not straightforward. The number of satellites used appears to have affected burrowing owl migratory tendency differently at our 2 study sites ($\beta = 1.2$, $P = 0.028$ for interaction between number of satellites used and study site in backward stepwise model). The number of satellites was positively associated with migratory tendency of burrowing owls in Coolidge, where owls had access to fewer satellite burrows, but negatively associated with migratory tendency in Tucson, where owls had access to more satellite burrows (Figure 7).

Effect of nesting density on migratory tendency. We found limited evidence for an effect of breeding density on burrowing owl migratory tendency. The number of nests within 300 m was included in 1 of 7 competing models ($\Delta\text{AIC}_c \leq 2$) and 2 of the 20 highest-ranking models in the information-theoretic approach and in the backward stepwise model. The interaction between number of nests and study site was included in 1 of the 20 highest-ranking models (0 of 7 competing models). Two-way interactions between number of nests and food treatment ($\beta = 0.7$, $P = 0.062$) and number of nests and number of juveniles fledged ($\beta = -0.3$, $P = 0.048$) were included in the backward stepwise model. Unsupplemented owls were more migratory if they nested in areas with 0 or moderate-to-high (3-9 nests within a 300 m radius) breeding density (Figure 8), and this pattern was similar at both study sites. We found no systematic relationship between breeding density and migratory tendency among food-supplemented owls (Figure 8).

DISCUSSION

Our results suggest low heritability of migratory tendency in burrowing owls. Decisions regarding whether or not to spend the winter in the vicinity of the nest burrow (i.e., to migrate or overwinter) appear to be condition-dependent in burrowing owls. Returning first-year owls at both study sites were equally likely to be migrant or resident during their first winter regardless of the migratory tendency of either parent. This suggests that the observed variation in migratory tendency is due either to environmental variation or to a combination of environmental and non-additive genetic variation (that portion of genetic variation that does not contribute to heritability). Moreover, owls that were migrants in one year had a 47% chance of being residents in the subsequent year, providing further evidence that migratory tendency in burrowing owls was condition-dependent and not due to a genetic dimorphism.

Our results contradict a number of laboratory studies that report high heritability for several behavioral and physiological components of migration (Berthold et al. 1990, Helbig 1991, Berthold and Pulido 1994, Pulido et al. 1996). These laboratory studies did not examine actual migratory movements but relied instead on indices such as the intensity and duration of *zugunruhe* in classifying individuals as migrants or residents. In contrast, a field study examining individual behavioral plasticity of the migratory tendency of European blackbirds (Schwable 1983) corroborates our results: the migratory tendency of individual blackbirds often changes from one year to the next, with the switch from migrant to resident happening much more frequently than the switch from resident to migrant. Differences between laboratory and field studies regarding the heritability of migratory behaviors may reflect: 1) differences in the behaviors measured (laboratory studies have focused on orientation and vigor of *zugunruhe*), 2) differences in species examined (completely migratory populations might exhibit less intraspecific variation and higher heritability in migratory behaviors compared to partially migratory species or populations), or 3) that individuals inherit behavioral plasticity for migratory tendency that enables them to respond to varying degrees to variation in environmental conditions (Lundberg 1988, Adriaensen et al. 1990, Kaitala et al. 1993, Coppack and Both 2002, Coppack et al. 2003). Our results suggest that burrowing owls breeding in southern Arizona exhibit behavioral plasticity for migratory tendency.

Both intrinsic and environmental factors affected migratory tendency of burrowing owls. These results corroborate some other theoretical and empirical accounts of partially migrant birds (Smith and Nilsson 1987, Terrill 1987, Lundberg 1988). For example, subordinates exhibited higher levels of *zugunruhe* at the end of the fall migratory period among captive pairs of food-restricted dark-eyed juncos (*Junco hyemenalis;* Terrill 1987). These results suggest that subordinates might be more likely to migrate when food becomes scarce. We also found evidence that age (or prior experience) influences migratory decisions. However, we lacked sufficient data on past-year's migratory tendency to include age in our modeling effort. A fruitful area of future research would be to further examine factors influencing the migratory decisions of first-year owls, given that this age class was much more likely to migrate in southern Arizona (50% of first-year birds were migrants) than were adults of either sex, and that we found no evidence of a food treatment effect in our parent-offspring regression.

Our results suggest that many related environmental factors influence burrowing owl migratory decisions, as evidenced by the presence of several 2-way interactions included among the models selected by the information-theoretic and backward stepwise frequentist approaches. For example, burrowing owls of both sexes nesting in Coolidge were chiefly non-migratory (0% of unsupplemented female owls and 11% of unsupplemented male owls migrated), whereas 28% of unsupplemented female owls (and 13% of unsupplemented male owls) nesting in Tucson migrated. Brief winter surveys from past years at the Coolidge study site indicated that a high proportion of banded owls were not present during winter (Conway and Ellis 2004, Conway et al. 2005). We believe this discrepancy was due to higher detection probability in the present study due to increased monitoring during the winter compared to past years. Extensive use of winter trapping and weekly year-round nest visits allowed us to locate and identify many owls that would not have been detected during 1 or 2 brief winter visits, because burrowing owls (especially females) are more cryptic during the winter months (Butts 1973, Martin 1973, Haug et al 1993, M. Ogonowski, pers. obs.). The lower probability of migration in the agricultural landscape of Coolidge (despite its being further north than our urban Tucson study site) is consistent with the hypothesis that formerly migratory owls are becoming year-round residents in irrigated agricultural areas in desert regions of North America. Agricultural fields on our study area are cultivated year-round, and presumably provide a reliable supply of invertebrate and vertebrate prey throughout the winter.

Results of our supplemental feeding experiment lend partial support to the altered migration hypothesis but also raise new questions. Food influenced migratory tendency, but the effect was not straightforward. Two-way interactions between food and sex, number of juveniles fledged, and breeding density were included in our models. Supplemental food caused a non-significant decrease in the probability of migration for male owls (i.e. in the predicted direction) but significantly increased the probability of migration for females at both study sites. A possible explanation for this paradox is that there are different tradeoffs associated with migration for each sex. Male birds are typically the more philopatric sex (Gill 2007), and in burrowing owls and many other species males arrive earlier in spring to secure territories and attract mates (Haug et al. 1993). Males that migrate could potentially lose their territory the following year to a competitor. Released of this pressure, females in particularly good condition could find it advantageous to leave their breeding territory during winter, either to overwinter at a more favorable location or to "prospect" for a quality mate and/or quality territory locally.

Interestingly, slightly fewer food-supplemented females returned to breed in 2006 (60%, n = 57) than unsupplemented females (65%, n=72) while more food-supplemented males returned to breed (82%, n=54) than unsupplemented males (73%, n=63), though these trends were not significant (females: P = 0.378, males: P = 0.194, Fisher's one-sided exact test). We do not know whether disappearances represent breeding dispersal or mortality, but they suggest that the effect of food supplementation on female migratory activity may have been somewhat greater than we measured. At a minimum, the trend toward a lower return rate for food-supplemented females suggests that the food by sex interaction we observed is real. This finding is at odds with the hypothesis proposed above that the lower percentage of migrant females observed at Coolidge was due to differences in winter food abundance, which we posited might be higher in the agricultural landscape of Coolidge. However, it is possible that the lower percentage of migrant females in Coolidge resulted from interactions of food with other factors we failed to test, or from interactions we included in our models but whose effects we could not detect due to the small number of migrant owls in our sample.

We found some support for the hypothesis that burrowing owls use annual fecundity as a proximate cue in deciding whether to migrate, but again the patterns we obtained were not straightforward. Unsupplemented owls were less likely to migrate if they had higher annual fecundity, provided they successfully fledged at least 1 offspring. This is consistent with our hypothesis that burrowing owls may use annual fecundity as an index of site quality, and with our prediction that owls fledging more young would be less likely to migrate to prevent the loss of a quality breeding site to a resident competitor. However, unsupplemented owls whose nesting attempt failed were less migratory than owls fledging at least 1 owlet. These results could reflect an energetic tradeoff between reproduction and the maintenance of adult condition. Given the large size of most burrowing owl broods (range 4-10 nestlings), adult owls whose nests fail may be in better condition at the end of the breeding season. Alternatively, owls whose nesting attempt failed may have initiated second or third nesting attempts relatively late in the breeding season, leaving them less time for developing fat stores necessary for successful migration. A third possibility is that this pattern results from differences in individual quality, with individuals of lower-quality (presumably most of those fledging 0 young) overwintering due to being in poor condition, and individuals of higher-quality (those fledging more offspring) overwintering in order to retain a high-quality territory.

Other environmental factors also appeared to affect burrowing owl migratory tendency but require further study to determine whether the patterns we observed are robust. The number of satellite burrows used per nest was negatively associated with migratory tendency in Tucson, as we predicted, but was positively associated with migratory tendency in Coolidge. The difference between sites may simply be an artifact of the small sample of migrants at Coolidge (n = 5) compared to Tucson (n = 13) and the small number of owls using 4 or more satellites at Coolidge (n = 6). Alternatively, it may indicate a difference in the factors that influence migratory decisions of burrowing owls at these two locations.

We also found limited support for an effect of breeding density on migratory tendency: unsupplemented owls were more migratory in areas of low density or high density than in areas of intermediate density. We have no adequate explanation for this unexpected pattern or for the interaction we observed between breeding density and food supplementation. Other researchers have suggested that intraspecific competition influences migratory decisions of partially migrant birds (Smith and Nilsson 1987, Terrill 1987, Lundberg 1988). We recommend additional studies to examine the influence of breeding density on migratory tendency at numerous spatial scales, given our lack of knowledge regarding the scale at which burrowing owls, which can range up to 2 km from the nest while forgaging (Haug et al. 1993), may assess the intensity of intraspecific competition.

Our conclusions regarding the role of environmental variables on migratory tendency are tempered by the unexpectedly small number of migrants in our sample and the different results from each model-selection approach we employed. Hence, we believe that the patterns we found in our data merit further study. Our study is one of the first to directly assess the causal mechanisms underlying individual behavior in partially migrant populations by experimentally manipulating food availability in a field setting (see Olsson et al. 2006 for a field study with brown trout), or to assess the heritability of migratory tendency directly in a wild population of birds. Future studies examining the factors that influence migratory decisions in free-ranging birds should include a large number of individuals (i.e., > 200) in each of several populations that have relatively equal proportions of migrant and resident individuals. Large sample sizes are necessary given the number of intrinsic and extrinsic factors (and interactions among factors) that appeared to influence migratory tendency of burrowing owls in our study.

Because migratory tendency appears to be plastic and is affected by local conditions, the proportion of migrants will likely vary across years in concert with changes in abiotic and biotic factors that affect migratory decisions. This implies that field-based manipulative studies should be conducted across multiple annual cycles to more clearly elucidate relationships. The 2004-2005 winter which preceded the first year of this study was the 25th wettest on record in southern Arizona with 8.5 cm of rainfall recorded in Tucson (National Oceanic and Atmospheric Association 2007), and owls provisioning for young during the ensuing breeding season may have had access to atypically high food resources. If so, this may have dampened the effect of our experimental food supplementation. In addition to the need to conduct future studies of migratory tendency across multiple annual cycles, studies that supplement food abundance should also assess ambient levels of food; supplemental food may not have the intended effect during years of high food abundance.

One limitation of our study was that we did not know the winter location of owls we classified as migrants. We defined migration as the absence of an individual from our study area based on band resighting. Restricting our analyses to return breeders eliminated the possibility that owls not seen during winter had died or permanently emigrated. However, we can not be certain that some or all of our “migrants” were present but not detected, or had moved locally to sites adjacent to our study areas and then moved back the next breeding season, rather than having engaged in longer-distance seasonal movements. Although we likely failed to detect one or more overwintering owls and misclassified these as migrants, we believe that our methodology led to high detection probability and that most birds classified as migrants were not present on our study sites. We continuously monitored a large survey area throughout the year at both study sites, encompassing all areas of potential habitat within 400 m of regularly-traveled roads and within 400 m all known burrow locations, and including over 20 km of washes and man-made drainage channels. We visited all known burrow locations including burrows that had been unoccupied in previous years and that had recently collapsed. We regularly expanded our search area outward to find new burrows (e.g., by driving roads bordering agricultural fields in Coolidge and searching new washes in Tucson) and both study areas had high levels of vehicle access. In Tucson, we also had the advantage that owls nested in close proximity to humans and that areas of potential habitat are fairly easy to identify. We exchanged information regularly with biologists studying burrowing owls at the Arizona Game & Fish Department, who shared with us any burrowing owl sightings they received from the public. Moreover, the airfield at Davis-Monthan AFB is closely and continuously monitored due to staff concerns about air-strike hazards to planes.

Other aspects of our methodology make it unlikely that we failed to detect wintering owls. We inspected the interior of all occupied burrows with an infrared video probe, and set traps extensively during the winter months at all burrows known to be occupied but where we could not identify bands using spotting scopes, or where we suspected a second adult might be present. We detected movements of several kilometers made by several banded owls between known burrows within each study site. This further increases our confidence that we had included most if not all active burrows within our survey area. If poor detection probability alone accounted for the owls we did not resight during winter, then owls nesting in Coolidge would have been incorrectly assumed to be more migratory than owls nesting in Tucson (as they had during past years when winter surveys were brief), because burrowing owls in Coolidge were much more cryptic in all seasons than owls nesting and roosting in Tucson (M. Ogonowski, pers. obs.). Finally, we detected an increase in the number of unbanded adults in Tucson each spring. Given the extent to which we have colormarked both adults and juveniles each breeding season, we are certain that a portion of this influx of unmarked individuals represents immigration from other sites. We cannot at this time determine the origins of these immigrants, but their presence reinforces the idea that burrowing owls, at least in Tucson, are partially migratory.

Our findings have implications for the conservation of and future prospects for burrowing owls in North America. The western subspecies of the burrowing owl is a priority species in the Arizona Partners-in-Flight Bird Conservation Plan and a species of national conservation concern (U. S. Fish and Wildlife Service 2002). Although owls appear to have declined in many portions of their range, high densities are sometimes found in agricultural landscapes such as the Imperial Valley in California (Klute et al. 2003, DeSante et al. 2004). We found some evidence to support the altered migration hypothesis for burrowing owl population trends: owls of both sexes were chiefly non-migratory in Coolidge, and experimental food supplementation was associated with a lower probability of migration for male (though not female) owls at both study sites. We of course do not know if some of these individuals formerly migrated during winter to more northern areas to breed. From a conservation perspective, although some agricultural and urban landscapes support high densities of burrowing owls, the long-term stability of these populations remains in doubt given the potential for future changes in land-use in human-dominated landscapes across the rapidly-developing southwest. Agricultural lands in southern Arizona and other areas of the southwest are being rapidly converted to urban and suburban residential development. Furthermore, the stability of arid croplands is subject to the viccisitudes of globalized agriculture, and global climate change is expected to lead to more arid conditions across much of the western United States which may in turn lead to increased conflict over the distribution of water between farmers and expanding western cities. Thus significant amounts of burrowing owl habitat could be lost in coming decades in human-dominated landscapes. If many of the owls nesting in these areas represent former migrants from the northern and northeastern parts of their breeding range, it is possible that these individuals could regain the migratory habit and recolonize areas to the north. However, re-establishment of these northern breeding populations will depend on the preservation of habitat in the northern areas of their range. If burrowing owls continue to disappear from southern Canada and the northern United States, there is considerable risk that areas of habitat in which they formerly bred will be lost to human uses, making them unavailable for re-establishment of these northern populations. Finally, there is some suggestion that burrowing owl population trends may be negative even in some agricultural areas where nesting density is high, indicating that such areas may represent ecological traps for this species (C. Conway, pers. com.). It is imperative that we better understand the extent to which human modification of the western landscape has altered burrowing owl migratory behavior and act to protect remaining areas of historic native habitat throughout the owl's breeding range, given the uncertain prospects for the species in human-dominated landscapes.

The differential effect of supplemental food on males and females points to a complex interplay of ecological and intrinsic influences in determining whether individual birds migrate. The fact that we were able to alter the proportions of migrants using relatively straightforward methods of augmenting food abundance shows that migratory behavior is plastic, and that changes in resource levels in the future may be expected to have marked effects on migratory birds and the communities of which they belong. Although individual behavioral plasticity for migratory behaviors provides some hope that birds will be able to respond flexibly and relatively quickly to environmental change, we cannot assume that these responses will necessarily improve their probability of persistence. We need more manipulative studies aimed at elucidating the nature and extent of the effects that anthropogenic alteration of habitat and climate may be having on organisms and the mechanisms through which these effects are manifested (Coppack and Both 2002, van Noordwijk et al. 2006).

We used three alternative model-selection approaches for examining the factors that affect migratory tendency of burrowing owls and each approach led to different conclusions. There is a lack of consensus among ecologists on when different model-selection approaches are most appropriate (Anderson et al. 2000, Hobbs and Hillborn 2006, Steidl 2006, Stephens et al. 2006). Even within the information-theoretic paradigm, methods for selecting from among the myriad of potential candidate models vary. Although all investigators strive to develop candidate models *a priori* on the basis of variables believed to be important in a given context, studies vary widely in the methods used to select explanatory variables for model development and to define lists of candidate models. In some studies, a full list of candidate models is developed at the outset based on variables known to be important from prior studies, with covariates subsequently found to have no effect in initial model runs dropped from all models in some cases (e.g. Lantz et al. 2007). In other studies, investigators first attempt to reduce the number of possible covariates and their combinations by running a set of initial models that exclude either the variables of interest (e.g. Wilson et al. 2007) or variables that can be analyzed separately from other effects on conceptual grounds (e.g. Colwell et al. 2007), using an AIC or frequentist approach. The remaining variables of interest are then added to the top model or selected variables from the prior step. Other investigators have used sequential rounds of stepwise regression to winnow down their list of candidate variables and arrive at a final model (Morrissey et al. 2003).

We chose to specify a set of candidate models in advance after initial screening of a large suite of potential variables to eliminate insignificant interaction terms and redundant parameters, and compared the results of model selection using information criteria to a frequentist approach including both forward and backward stepwise variable selection. One drawback of the use of information criteria for model selection is the potential failure to specify all potentially relevant models for comparison (Burnham and Anderson 2002, Johnson and Omland 2004, Steidl 2006, Stephens et al. 2006). We examined this possibility directly after completing our analyses by determining AIC_c values of the models produced by forward and backward stepwise variable selection and comparing the results to the models with the lowest AIC_c from the information-theoretic approach. The models produced by both forward and backward stepwise regression had lower AIC_c values than all the candidate models we developed. Failure to include these as candidate models in our information-theoretic approach appears to have been only moderately consequential, as most of the 7 competing models would have still had a $\Delta AIC_c \leq 2.0$.

Forward stepwise logistic regression offered no support for an effect of our food supplementation treatment on burrowing owl migratory tendency, whereas a number of 2-way interactions involving the supplemental food treatment were retained by the more permissive backward stepwise approach. The information-theoretic approach provided some support for an effect of supplemental food. The most appropriate model-selection approach was not obvious to us at the outset, so we chose to compare 3 common approaches. Although we tested a focused hypothesis (food alters migratory tendency) in a controlled experiment and several others through correlative methods, our study was to some extent exploratory. We do not believe that the dilemma we faced in choosing a model-selection approach is unique. The problem of how to choose an appropriate model is likely to be particularly acute for questions that have not been well-studied, in which investigators may have limited *a priori* knowledge regarding which variables are most important and, precisely because of this, the exclusion of variables and models of potential interest must proceed more cautiously. Investigators need to be cognizant of the fact that alternative approaches to model selection can lead to disparate conclusions, and exercise caution in their choice of approach including careful consideration of the nature and limitations of their dataset.

APPENDICES

Appendix A: Figures

Figure 1. Percent of migrant hatch-year burrowing owls produced by migrant and resident (a) female and (b) male parents in southern Arizona, USA, 2004-2006 (treatment groups and study sites pooled).

a) b)

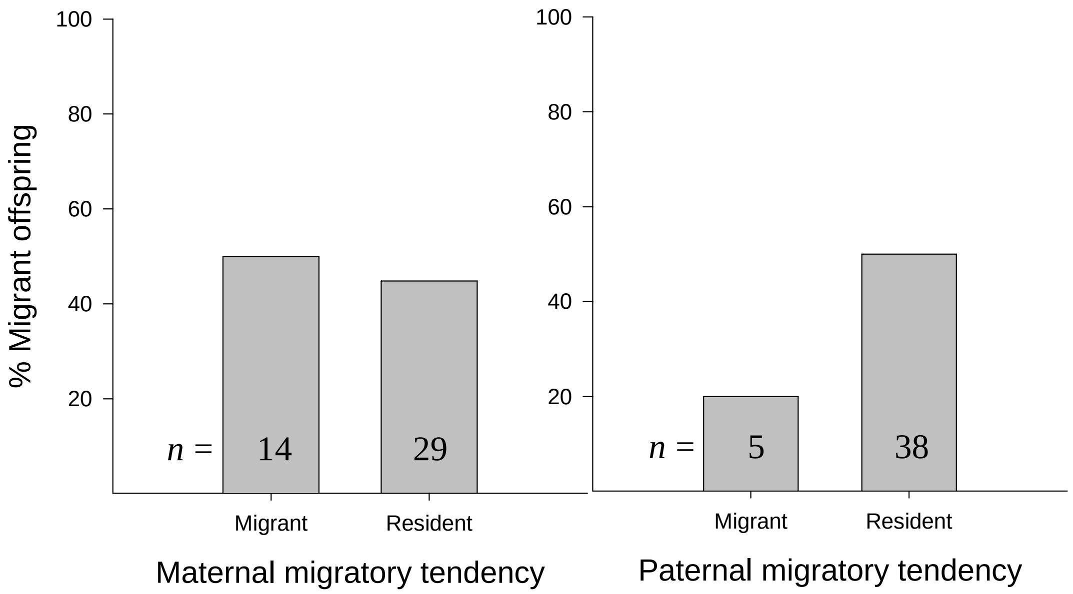


Figure 2. Consistency of migratory tendency of burrowing owls in southern Arizona, USA, 2004-2006. Bars show the percent of previously migrant and resident owls that migrated during the 2005-2006 winter (sexes, treatment groups, and study sites pooled).

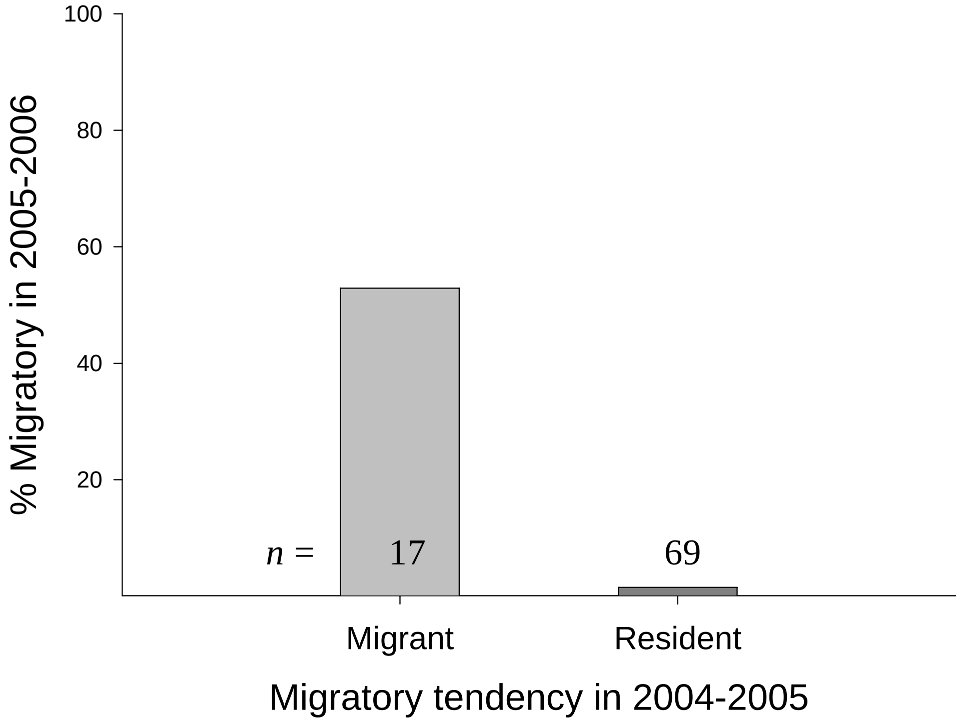


Figure 3. Effect of age on the relationship between prior- and current-year migratory tendency of burrowing owls in southern Arizona, USA, 2004-2006. Bars show the percent of previously migrant and resident owls of different ages that migrated during the 2005-2006 winter (sexes, treatment groups, and study sites pooled).

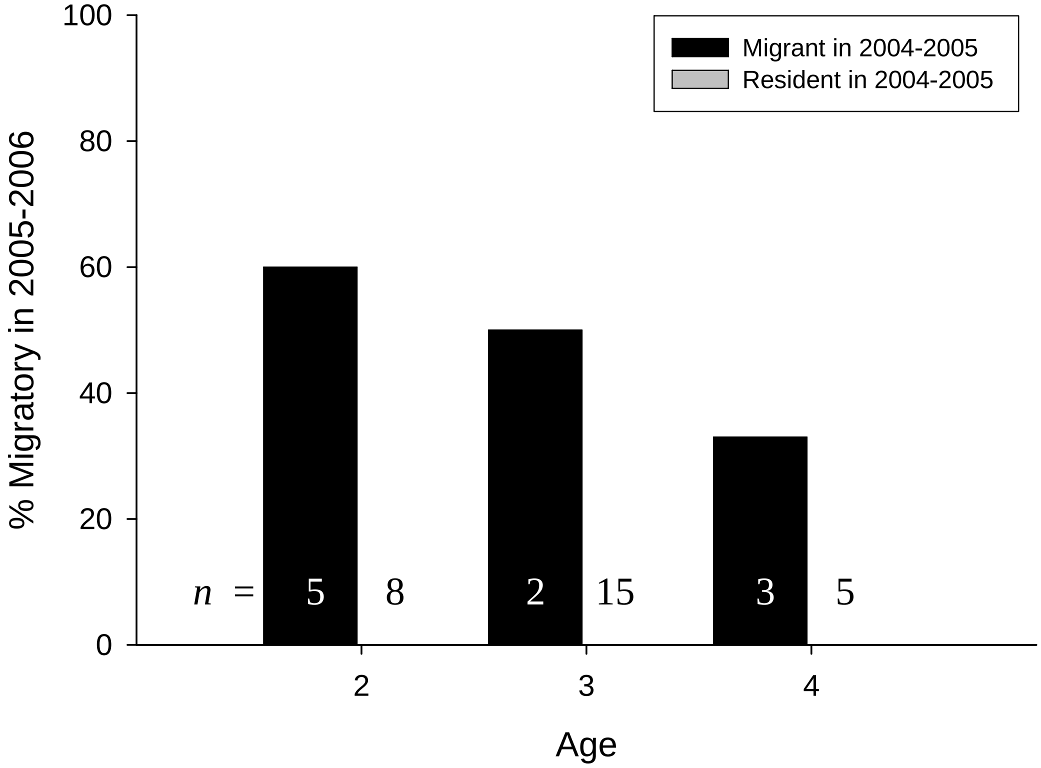


Figure 4. Effect of tarsus length on migratory tendency of burrowing owls in southern Arizona, USA, 2005-2006. Bar heights represent the percent of owls that migrated in each group (sexes, treatment groups, and study sites pooled).

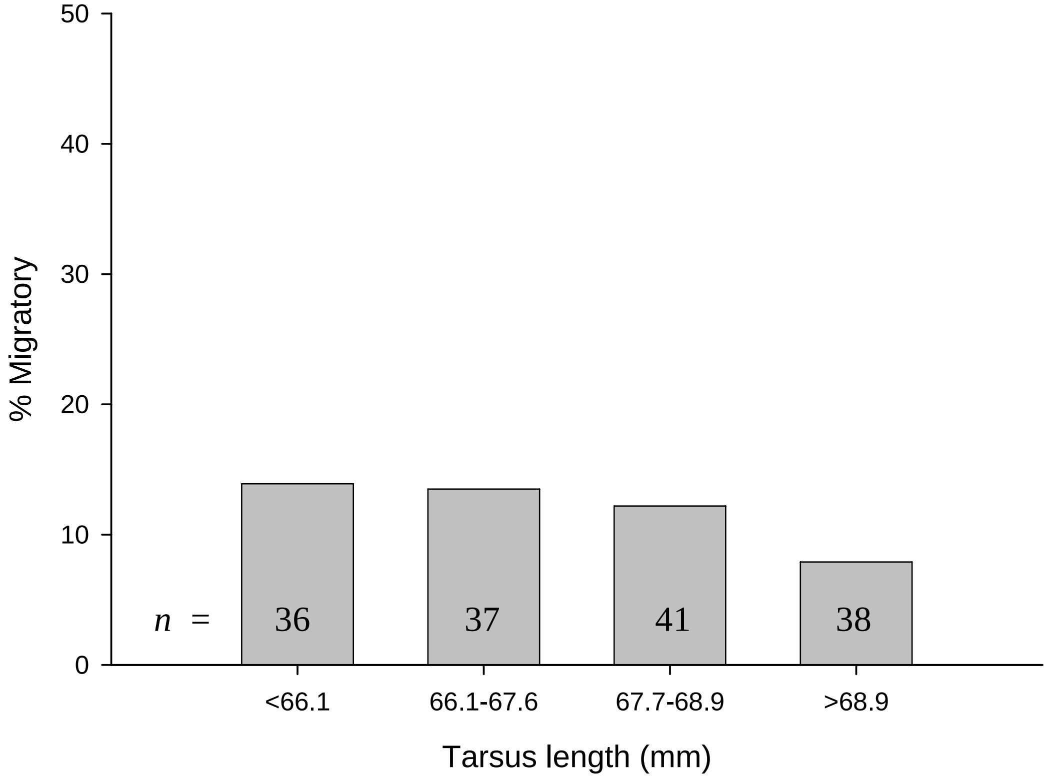


Figure 5. Effect of supplemental food on migratory tendency of male and female burrowing owls in southern Arizona, USA, 2005-2006. Bars represent the percent of food-supplemented (gray) and control (black) owls that migrated (estimated marginal means from backward stepwise logistic regression with study sites pooled). Error bars represent standard errors.

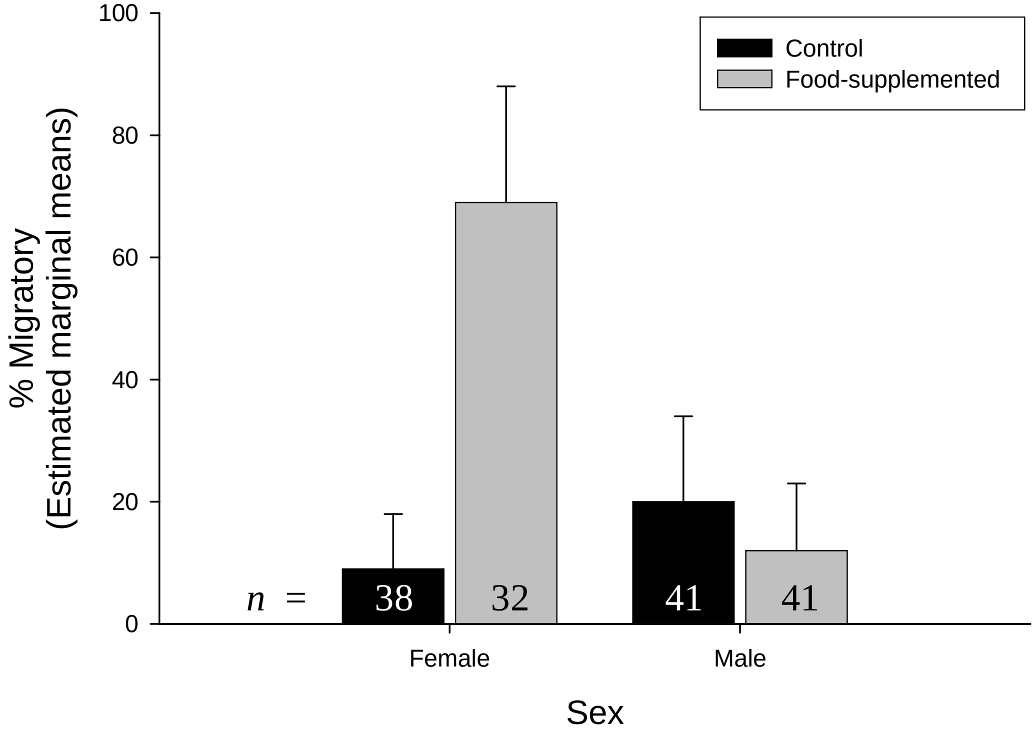


Figure 6. Interaction between supplemental food and number of juveniles fledged on migratory tendency of burrowing owls in southern Arizona, USA, 2005-2006. Bars represent the percent of owls that migrated grouped into 4 categories based on annual fecundity (sexes and study sites pooled).

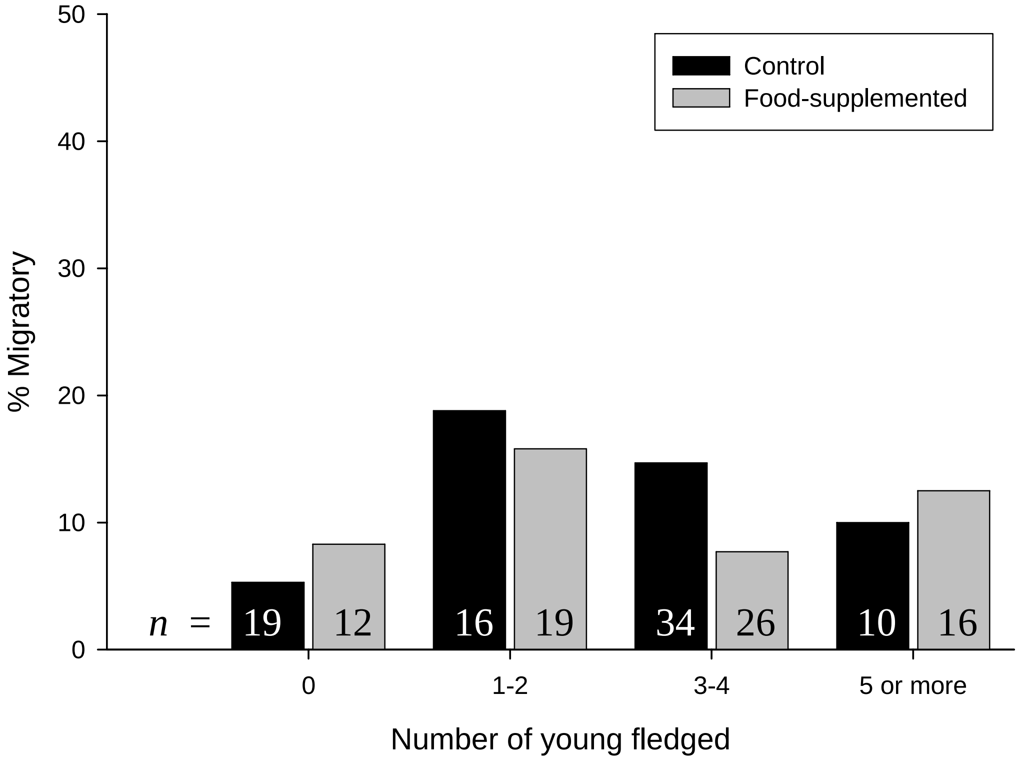


Figure 7. The relationship between number of satellites used and migratory tendency of burrowing owls differed between our 2 study sites in southern Arizona, USA, 2005-2006. Bars represent the percent of owls that migrated grouped into 3 categories based on number of satellite burrows used (sexes and treatment groups pooled).

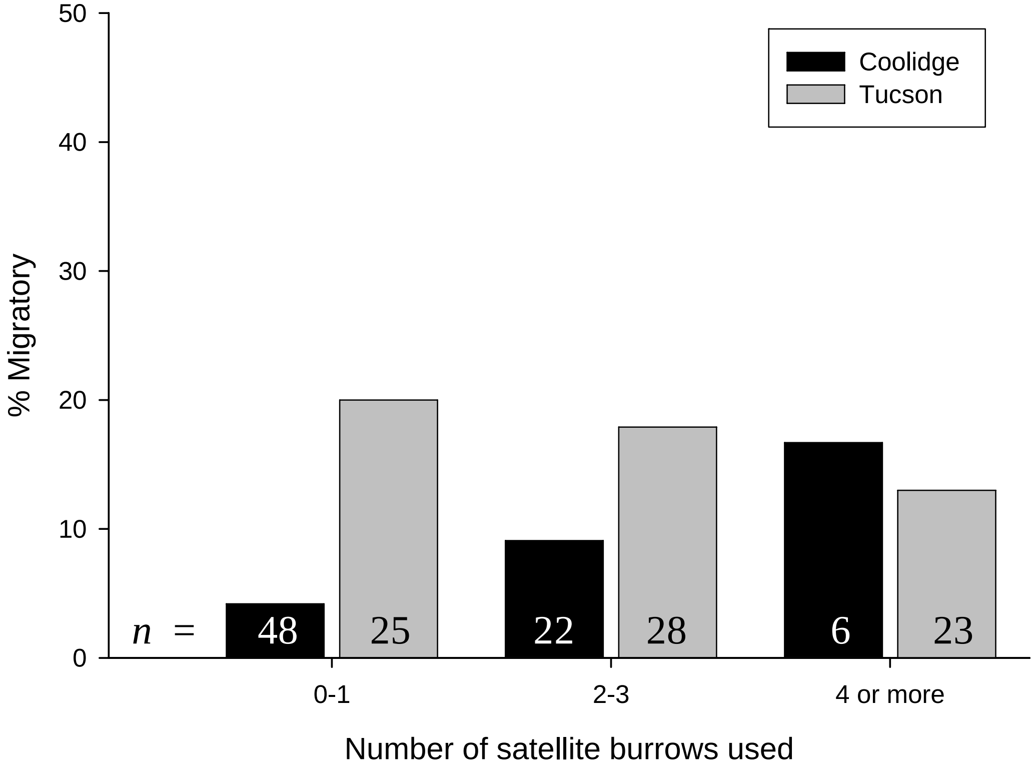
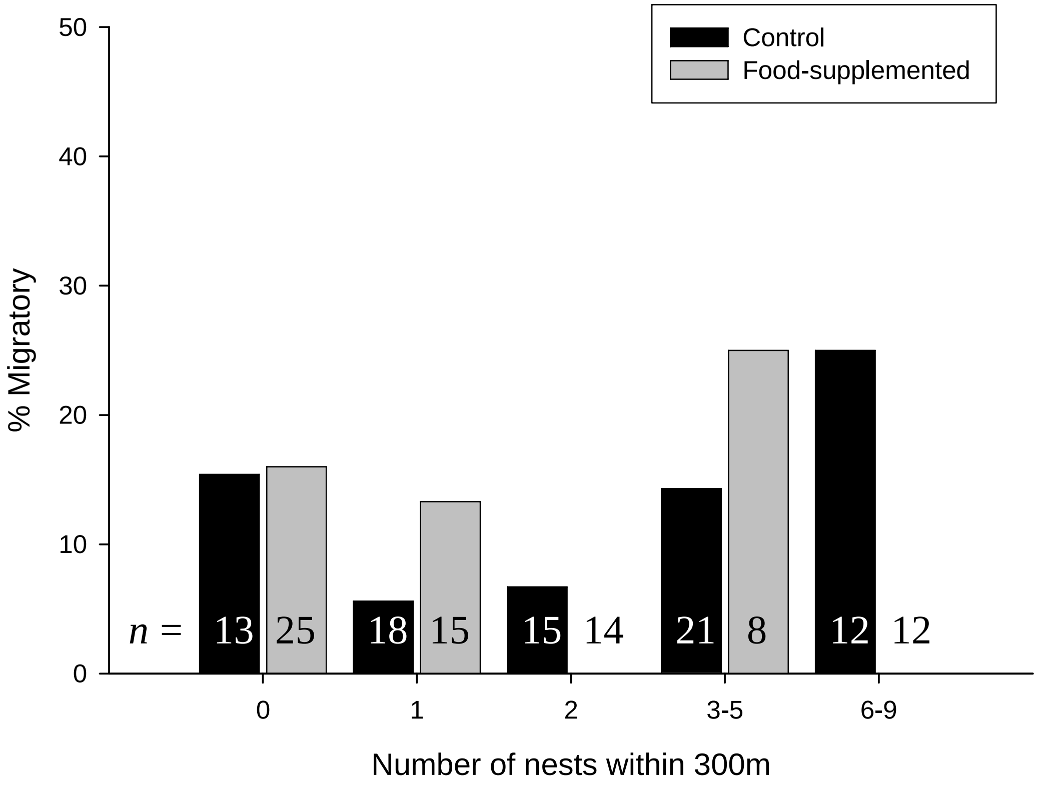


Figure 8. The effect of supplemental food on migratory tendency of burrowing owls differed depending on breeding density in southern Arizona, USA, 2005-2006. Bars represent the percent of owls that migrated (sexes and study sites pooled).



Appendix B: Tables

Table 1. Potential explanatory variables used to develop models to distinguish migratory from non-migratory burrowing owls in southern Arizona, USA, 2005-2006.

Variable	**Abbrev.**	**Mean**	**95% CI**	**Min**	**Max**	**Levels (n)**	
Satellites used (No.)	U	1.9	1.6-2.2	0	9		
Juveniles fledged (No.)	J	2.6	2.3-2.9	0	10		
Nests within 300m (No.)	N	2.3	1.9-2.7	0	9		
Left tarsus length (mm) [a]	T	67.7	67.3-68.1	61.2	74.6		
Food treatment	F					Fed (73)	Unfed (79)
Sex	X					Male (82)	Female (70)
Site	S					Tucson (76)	Coolidge (76)
Mate_or_Burrow loss	MB					Yes (11)	No (141)

[a] Tarsus data on some older owls were collected between the years 2002-2004.

Table 2. Summary of three model selection approaches examining the factors that affected migratory tendency of burrowing owls in southern Arizona, USA, 2005-2006. *k* is the number of model parameters. AIC_c is Akaike's information criterion corrected for small samples, and $\Delta\mathrm{AIC}_c$ is the scaled AIC_c relative to the top model. % correct is the percentage of all cases that were correctly classified by each model, and the number in parentheses is the percentage of migrants (n=18) that were correctly classified. ω_i is the Akaike model weight of evidence. R^2 is Nagelkerke's psuedo R^2 indicating the proportion of variance explained by each stepwise model. P is from the likelihood ratio χ^2 test comparing each stepwise model to the intercept-only model.

Model	***k***	**AIC_c**	**$\Delta\mathrm{AIC}_c$**	**% correct**	**ω_i**	**R^2**	***P***
Forward stepwise							
S MB T	4			87.5 (0)		0.134	0.012
Backward stepwise							
F U J X S MB N T F*X F*S U*S J*F J*S J*N J*T X*S F*N T*X	19			90.8 (39)		0.508	0.000
Information-theoretic							
S T	3	108.8	0.0	88.2 (0)	0.14		
X S X*S	4	109.0	0.2	88.2 (0)	0.13		
Natural break AIC							
F J X S MB N T F*X J*F X*S T*X	12	109.5	0.7	90.8 (22)	0.10		
X S	3	109.8	1.0	88.2 (0)	0.09		
X S T	4	110.0	1.2	88.2 (0)	0.08		
J X S MB T J*X J*S J*T X*S T*X	11	110.1	1.3	89.5 (11)	0.08		
S	2	110.4	1.6	88.2 (0)	0.06		
X S T T*X	5	110.9	2.1	88.2 (0)	0.05		
J T J*T	4	111.3	2.5	88.2 (0)	0.04		
X S MB N T X*S N*S T*X	9	111.6	2.8	88.8 (6)	0.04		
F X S F*X F*S X*S	7	111.6	2.8	88.2 (0)	0.04		
Natural break AIC							
J X S T J*T T*X	7	112.3	3.5	88.2 (0)	0.02		
F S	3	112.4	3.6	88.2 (0)	0.02		
X	2	112.7	3.9	88.2 (0)	0.02		
J X S	4	113.0	4.2	88.2 (0)	0.02		
U X S	4	113.2	4.4	88.2 (0)	0.02		
U S T U*T U*S	6	113.3	4.5	88.2 (0)	0.02		
X T T*X	4	113.3	4.5	88.2 (0)	0.02		
Natural break AIC							
F S F*S	4	113.8	5.0	88.2 (0)	0.01		
U X S MB T U*X U*S X*S U*T T*X	11	113.9	5.1	89.5 (11)	0.01		

Appendix C: Candidate models tested in information-theoretic analysis

1. Sex
2. Site
3. Sex + Site
4. Sex + Site + Sex*Site
5. Sex + Site + Mate_Or_Burrow_Loss + Sex*Site
6. Sex + Site + Nests_in_300m + Sex*Site + Nests_in_300m*Site
7. Sex + Tarsus + Tarsus*Sex
8. Site + Tarsus
9. Sex + Site + Tarsus
10. Sex + Site + Tarsus + Tarsus*Sex
11. Sex + Site + Mate_Or_Burrow_Loss + Nests_in_300m + Tarsus + Sex*Site + Nests_in_300m*Site + Tarsus*Sex
12. TRT
13. TRT + Sex
14. TRT + Sex + TRT*Sex
15. TRT + Site
16. TRT + Site + TRT*Site
17. TRT + Sex + Site
18. TRT + Sex + Site + TRT*Sex + TRT*Site + Sex*Site
19. TRT + Nests_in_300m + Nests_in_300m*TRT
20. TRT + Tarsus + Tarsus*TRT
21. TRT + Sex + Site + Mate_Or_Burrow_Loss
22. TRT + Sex + Site + Mate_Or_Burrow_Loss + TRT*Sex + TRT*Site + Sex*Site
23. TRT + Sex + Site + Tarsus + Tarsus*TRT + Tarsus*Sex
24. TRT + Sex + Site + Tarsus + TRT*Sex + TRT*Site + Sex*Site + Tarsus*TRT + Tarsus*Sex
25. TRT + Sex + Site + Mate_Or_Burrow_Loss + Tarsus + TRT*Sex + TRT*Site + Sex*Site + Tarsus*TRT + Tarsus*Sex
26. #Used
27. #Used + Sex
28. #Used + Site
29. #Used + Sex + Site
30. #Used + Sex + Site + #Used*Sex + #Used*Site + Sex*Site
31. TRT + #Used + #Used*TRT
32. #Used + Nests_in_300m + #Used*Nests_in_300m
33. #Used + Tarsus + #Used*Tarsus
34. #Used + Sex + Tarsus + #Used*Tarsus + Tarsus*Sex
35. #Used + Site + Tarsus + #Used*Tarsus + #Used*Site
36. #Used + Sex + Site + Mate_Or_Burrow_Loss + #Used*Sex + #Used*Site + Sex*Site
37. #Used + Sex + Site + Tarsus + #Used*Tarsus + Tarsus*Sex
38. #Used + Sex + Site + Tarsus + #Used*Sex + #Used*Site + Sex*Site + #Used*Tarsus + Tarsus*Sex

39. #Used + Sex + Site + Mate_Or_Burrow_Loss + Tarsus + #Used*Sex + #Used*Site + Sex*Site + #Used*Tarsus + Tarsus*Sex
40. TRT + #Used + Sex + Site + #Used*TRT + #Used*Sex + #Used*Site + Sex*Site
41. TRT + #Used + Sex + Site + TRT*Sex + TRT*Site + #Used*TRT + #Used*Sex + #Used*Site + Sex*Site
42. TRT + #Used + Sex + Site + Mate_Or_Burrow_Loss + TRT*Sex + TRT*Site + #Used*TRT + #Used*Sex + #Used*Site + Sex*Site
43. TRT + #Used + Sex + Site + Mate_Or_Burrow_Loss + Tarsus + TRT*Sex + TRT*Site + #Used*TRT + #Used*Sex + #Used*Site + Sex*Site + #Used*Tarsus + Tarsus*TRT + Tarsus*Sex
44. Juv44
45. Juv44 + Sex
46. Juv44 + Site
47. Juv44 + Sex + Site
48. Juv44 + Sex + Site + Juv44*Sex + Juv44*Site + Sex*Site
49. TRT + Juv44 + Juv44*TRT
50. Juv44 + Nests_in_300m + Juv44*Nests_in_300m
51. Juv44 + Tarsus + Juv44*Tarsus
52. Juv44 + Sex + Site + Mate_Or_Burrow_Loss + Juv44*Sex + Juv44*Site + Sex*Site
53. Juv44 + Sex + Site + Tarsus + Juv44*Tarsus + Tarsus*Sex
54. Juv44 + Sex + Site + Tarsus + Juv44*Sex + Juv44*Site + Juv44*Tarsus + Sex*Site + Tarsus*Sex
55. Juv44 + Sex + Site + Mate_Or_Burrow_Loss + Tarsus + Juv44*Sex + Juv44*Site + Juv44*Tarsus + Sex*Site + Tarsus*Sex
56. TRT + Juv44 + Sex + Site + Juv44*TRT + Juv44*Sex + Juv44*Site + Sex*Site
57. TRT + Juv44 + Sex + Site + TRT*Sex + TRT*Site + Juv44*TRT + Juv44*Sex + Juv44*Site + Sex*Site
58. TRT + Juv44 + Sex + Site + Mate_Or_Burrow_Loss + TRT*Sex + TRT*Site + Juv44*TRT + Juv44*Sex + Juv44*Site + Sex*Site
59. TRT + Juv44 + Sex + Site + Mate_Or_Burrow_Loss + NestsA_300m + Tarsus + Juv44*TRT + TRT*Sex + Sex*Site + Tarsus*Sex
60. TRT + Juv44 + Sex + Site + Mate_Or_Burrow_Loss + Tarsus + TRT*Sex + TRT*Site + Juv44*TRT + Juv44*Sex + Juv44*Site + Juv44*Tarsus + Tarsus*TRT + Tarsus*Sex + Sex*Site
61. TRT + #Used + Juv44
62. TRT + #Used + Juv44 + #Used*TRT + #Used*Juv44 + Juv44*TRT
63. TRT + #Used + Juv44 + Mate_Or_Burrow_Loss + Nests_in_300m + Tarsus + #Used*TRT + #Used*Juv44 + Juv44*TRT + Nests_in_300m*TRT
64. TRT + #Used + Juv44 + Sex + Site + Sex*Site
65. TRT + #Used + Juv44 + Sex + Site + TRT*Sex + TRT*Site + #Used*Sex + #Used*Site + Juv44*Sex + Juv44*Site + Sex*Site
66. TRT + #Used + Juv44 + Sex + Site + Mate_Or_Burrow_Loss + Nests_in_300m + Tarsus + TRT*Sex + TRT*Site + #Used*Sex + #Used*Site + Juv44*Sex + Juv44*Site + Sex*Site + Tarsus*Sex

67. TRT + #Used + Juv44 + Sex + Site + Mate_Or_Burrow_Loss + Nests_in_300m + Tarsus + TRT*Sex + TRT*Site + #Used*TRT + #Used*Juv44 + #Used*Sex + #Used*Site + #Used*Nests_in_300m + #Used*Tarsus + Juv44*TRT + Juv44*Sex + Juv44*Site + Juv44* Nests_in_300m + Juv44*Tarsus + Sex*Site + Nests_in_300m*TRT + Nests_in_300m*Site + Tarsus*TRT + Tarsus*Sex

Appendix D: Locations of burrowing owl nests and satellites monitored in Coolidge, AZ, USA, 2005-2006 (NAD27CONUS datum)

Name	UTM coordinates
AIR02A	12 S 454757 3644039
AIR02B	12 S 454758 3644058
AIR03	12 S 454753 3643978
ATTA03A	12 S 456300 3645651
BART03	12 S 446032 3645177
BART05A	12 S 446420 3645021
BART05B	12 S 446415 3645018
BART05C	12 S 446270 3645024
BART05D	12 S 446359 3645042
BART08	12 S 446899 3644713
BART10A	12 S 445919 3645695
BART11	12 S 445639 3645432
BART12	12 S 445844 3645432
BART13	12 S 445999 3645434
BART15A	12 S 446417 3644706
BART15B	12 S 446308 3644711
BART15C	12 S 446471 3644709
BART16	12 S 446666 3644311
BART17	12 S 447492 3645338
BART18	12 S 447488 3645909
BART19	12 S 447747 3646051
BARTE05	12 S 454343 3644712
BARTE07	12 S 455550 3644783
BARTE08A	12 S 454537 3644261
BARTE08C	12 S 454530 3644234
BARTE08D	12 S 454532 3644267
BARTE09B	12 S 454322 3643947
BARTE12	12 S 454918 3644843
BARTE13	12 S 454535 3644105
BARTE14	12 S 454326 3644614
BARTE15	12 S 454338 3644462
BARTE15B	12 S 454326 3644507
BARTE16	12 S 455549 3645014
BARTE17	12 S 454330 3643325
BARTE18	12 S 454538 3644317
BARTE19	12 S 454323 3644083
BARTE20	12 S 454329 3644831
CANAL01	12 S 439141 3634041
CANAL05A	12 S 440853 3635177
CANAL08	12 S 440670 3635215
CANAL12	12 S 439272 3634109
CANAL13	12 S 440607 3635207

CANAL14	12 S 440649 3635211
CANAL15	12 S 440579 3635202
CGMO	12 S 450446 3650899
CGMO01A	12 S 450018 3650955
CGMO01B	12 S 450142 3651022
CGMO01C	12 S 450024 3650961
CGMO01D	12 S 450207 3650922
CGMO01E	12 S 450030 3650952
CGMO02	12 S 450698 3651148
CGMO03	12 S 450662 3651203
CGMO04A	12 S 450798 3650900
CGMO04B	12 S 450811 3650869
CGMO04C	12 S 450733 3650815
CGMO04D	12 S 450792 3650863
CGMO05	12 S 450115 3650729
CGMO06	12 S 450398 3651351
CGMO08A	12 S 449990 3651040
CGMO08B	12 S 449980 3651044
CGMO10A	12 S 450206 3651284
CGMO10B	12 S 450132 3651172
CGMO11	12 S 449983 3651148
CGMO12	12 S 449818 3650952
CGMO13	12 S 449729 3651021
CGMO14A	12 S 450764 3651086
CGMO14B	12 S 450833 3651079
CGMO14C	12 S 450844 3651106
CGMO16A	12 S 450331 3650486
CGMO16B	12 S 450383 3650447
CGMO16C	12 S 450410 3650487
CGMO17B	12 S 450711 3650381
CGMO18	12 S 450619 3650415
CGMO20	12 S 449657 3651178
CGMO21	12 S 450716 3650955
CGMO22	12 S 450900 3650655
CGMO23A	12 S 449761 3651338
CGMO23B	12 S 449813 3651325
CGMO24	12 S 449658 3651117
CGMO25A	12 S 450349 3650595
CGMO25B	12 S 450323 3650559
CGMO26A	12 S 450612 3650918
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CGMO26C	12 S 450622 3650952
CGMO27A	12 S 450235 3651202
CGMO27B	12 S 450298 3651227
CGMO29	12 S 450454 3650504
CGMO30	12 S 449814 3651225
CGMO31A	12 S 449769 3651101
CGMO31B	12 S 449785 3651070

CGMO32	12 S 450486 3650596
CGMO33	12 S 450477 3651091
CGMO34	12 S 450511 3651123
CGMO35	12 S 450757 3650974
CGMO36	12 S 450191 3650997
CGMO37A	12 S 449826 3650999
CGMO37B	12 S 449822 3650985
CGMO38	12 S 449825 3650996
CGMO39	12 S 450441 3651217
CGMO40	12 S 450564 3650914
CGMO41	12 S 450633 3651058
CGMO42	12 S 449786 3651144
CGMO43	12 S 449611 3650971
CGMO44	12 S 450565 3651150
CGMOSAT	12 S 450504 3651079
COOL01C	12 S 453540 3648684
EARL01	12 S 441416 3636317
EARL02	12 S 440497 3636670
EARL03A	12 S 440542 3637099
EARL03B	12 S 440544 3637105
EARL04	12 S 440703 3637097
EARL05	12 S 441276 3637093
EARL06A	12 S 440488 3636608
EARL06B	12 S 440402 3636578
EARL07A	12 S 441151 3637102
EARL07B	12 S 441149 3637092
EARL08A	12 S 440993 3637104
EARL08B	12 S 440992 3637094
EARL08C	12 S 441001 3637094
EARL09A	12 S 440846 3637103
EARL09B	12 S 440846 3637094
EARL10A	12 S 440693 3637105
EARL10B	12 S 440692 3637096
EARL11A	12 S 440505 3637440
EARL11B	12 S 440504 3637367
GROG01B	12 S 439295 3633904
GROG02	12 S 439291 3633989
GROG03A	12 S 439969 3633892
GROG03C	12 S 439870 3633892
GROG04	12 S 439834 3633890
GROG05	12 S 439295 3633963
GROG06	12 S 439794 3633888
GROG07	12 S 439904 3633887
GROG08A	12 S 440005 3633896
GROG08B	12 S 440009 3633897
HELI01	12 S 439174 3633803
HELI02	12 S 439219 3633711
HELI03A	12 S 439118 3633492

HELI03B	12 S 439139 3633488
HELI04A	12 S 438942 3633583
HELI04B	12 S 438907 3633586
HELI04C	12 S 438876 3633571
HELI05A	12 S 438960 3633619
HELI05C	12 S 438964 3633637
HELI06A	12 S 438972 3633568
HELI06B	12 S 439025 3633490
HELI07	12 S 438940 3633603
HELI08	12 S 439229 3633806
HELI09A	12 S 439110 3633412
HELI09B	12 S 439056 3633409
HELI10	12 S 439056 3633468
HELI11	12 S 439341 3633555
HELI12	12 S 439359 3633644
HWY287-1B	12 S 440523 3638040
HWY287-1C	12 S 440521 3638123
HWY287-2A	12 S 440937 3638451
HWY287-2B	12 S 440939 3638532
HWY287-4A	12 S 440938 3638612
HWY287-4B	12 S 440936 3638583
HWY287-6	12 S 440312 3639099
HWY287-7A	12 S 440165 3639350
HWY287-8A	12 S 440937 3638078
HWY287-8B	12 S 440937 3638069
HWY287-8C	12 S 440522 3638102
KENW03A	12 S 449410 3645055
KENW03B	12 S 449337 3645049
KENW05	12 S 449311 3645051
KENW06A	12 S 450636 3645066
KENW06B	12 S 450631 3645067
LAUR01A	12 S 453553 3649496
LAUR01C	12 S 453920 3649221
LAUR01D	12 S 453833 3649107
LAUR01E	12 S 453637 3649097
LAUR02	12 S 453922 3649390
LAUR03	12 S 453921 3649344
LAUR04	12 S 453711 3649104
LAUR05A	12 S 454077 3649101
LAUR05B	12 S 454034 3649102
LAUR06	12 S 453922 3649385
LAUR07	12 S 453921 3649439
MACR02A	12 S 446512 3649144
MACR02B	12 S 446523 3649238
MACR03A	12 S 446545 3649146
MACR03B	12 S 446517 3649133
MACR04	12 S 446542 3649125
MART01A	12 S 453900 3646362

MART01B	12 S 453898 3646395
MART03B	12 S 455461 3645911
MART03C	12 S 455462 3645920
MART03D	12 S 455461 3645917
MART05A	12 S 448558 3646377
MART05B	12 S 448396 3646375
MART06A	12 S 453922 3646464
MART07	12 S 454997 3645875
MART09	12 S 454730 3646165
MART10	12 S 454729 3645964
MART11	12 S 455415 3645862
NAF04	12 S 454368 3646266
NAF05A	12 S 454293 3647413
NAF05B	12 S 454293 3647440
NAF05C	12 S 454132 3647480
NAF05D	12 S 454091 3647479
NAF05E	12 S 454158 3647475
OVER01	12 S 438780 3624293
OVER03	12 S 438840 3624051
OVER04	12 S 438857 3635691
RAND03A	12 S 445945 3642488
RAND03B	12 S 445965 3642416
RAND04	12 S 445862 3642437
RAND05A	12 S 445857 3642332
RAND05B	12 S 445856 3642314
RAND06	12 S 445413 3641240
RAND07	12 S 446062 3642417
SKOUS04A	12 S 448327 3651975
STOR01A	12 S 451543 3639721
STOR01B	12 S 451548 3639719
STOR02A	12 S 451547 3639656
STOR02B	12 S 451544 3639648
STOR02C	12 S 451552 3639649
STOR03	12 S 451035 3639869
STOR04A	12 S 451024 3639846
STOR04B	12 S 450979 3639820
STOR04C	12 S 451021 3639853
STOR05A	12 S 451068 3639612
STOR05B	12 S 451073 3639617
STOR06A	12 S 451029 3639744
STOR06C	12 S 451031 3639727
STOR06D	12 S 451037 3639724
STOR06E	12 S 450953 3639740
STOR07A	12 S 450969 3639863
STOR07B	12 S 450901 3639834
STOR07C	12 S 450967 3639846
STOR07D	12 S 450922 3639845
STOR07E	12 S 450920 3639840

STOR07F	12 S 450977 3639864
STOR08A	12 S 451549 3639709
STOR08B	12 S 451556 3639717
STOR09	12 S 450959 3639751
SUN01A	12 S 448761 3644240
SUN01B	12 S 448758 3644241
SUN01C	12 S 448874 3644220
SUN02A	12 S 448871 3643944
SUN02B	12 S 448881 3643930
SUN03	12 S 449382 3644048
SUN04B	12 S 449318 3644032
SUN05A	12 S 449304 3643992
SUN05B	12 S 449351 3643994
SUN06A	12 S 449240 3643935
SUN06C	12 S 449229 3643975
SUN07B	12 S 449012 3644017
SUN08A	12 S 448984 3643957
SUN08B	12 S 448980 3643958
SUN09	12 S 449338 3643916
SUN10	12 S 449201 3643927
SUN11	12 S 449211 3644208
SUN12	12 S 449345 3644014
SUN13A	12 S 449383 3643964
SUN13B	12 S 449397 3643981
SUN13C	12 S 449418 3643936
SUN14	12 S 449386 3643920
SUN15A	12 S 449304 3643933
SUN15B	12 S 449324 3643948
SUN15C	12 S 449307 3643931
SUN16A	12 S 448914 3644010
SUN16B	12 S 448927 3644160
SUN17A	12 S 449135 3644195
SUN17B	12 S 449112 3644235
SUN18	12 S 448881 3644081
SUN19A	12 S 448866 3644070
SUN19B	12 S 448863 3644072
SUN20A	12 S 449224 3644145
SUN20B	12 S 449231 3644142
SUN21A	12 S 449212 3644021
SUN21B	12 S 449162 3644023
SUN21C	12 S 449212 3644066
SUN21D	12 S 449108 3644006
SUN21E	12 S 449109 3644000
SUN21F	12 S 449085 3643977
SUN22	12 S 448787 3644223
VAH04C	12 S 448282 3648954
VALV02B	12 S 445717 3647603
VALV02D	12 S 445743 3647602

VALV02E	12 S 445702 3647607
VALV02F	12 S 445938 3647602
VALV02G	12 S 445936 3647600
VALV02H	12 S 445942 3647602
VALV02I	12 S 445924 3647599
VALV02J	12 S 445928 3647597
VALV03	12 S 445425 3647605

Appendix E: Locations of burrowing owl nests and satellites monitored in Tucson, AZ, USA, 2005-2006 (NAD27CONUS datum)

Name	UTM coordinates
AMARC 01	12 S 514966 3558536
AMARC 02	12 S 514896 3558590
AMARC 03	12 S 514951 3558752
AMARC 05	12 S 514893 3559187
AMARC 06	12 S 514705 3559190
AMARC 07B	12 S 514809 3559340
AMARC 07C	12 S 514783 3559328
AMARC 07E	12 S 514810 3559339
AMARC 09	12 S 514812 3559569
AMARC 10	12 S 514715 3559744
AMARC 12	12 S 514285 3559686
AMARC 14B	12 S 514217 3559488
AMARC 14C	12 S 514217 3559490
AMARC 15A	12 S 514125 3559153
AMARC 15B	12 S 514021 3559153
AMARC 16A	12 S 514111 3559095
AMARC 17B	12 S 514027 3559009
AMARC 17D	12 S 514102 3559021
AMARC 20	12 S 513163 3558181
AMARC 21A	12 S 512609 3558639
AMARC 21B	12 S 512635 3558716
AMARC 21C	12 S 512635 3558716
AMARC 24B	12 S 512071 3559236
AMARC 25A	12 S 512369 3559010
AMARC 25D	12 S 512402 3559076
AMARC 25E	12 S 512460 3558984
AMARC 26B	12 S 512872 3558960
AMARC 26C	12 S 512732 3558984
AMARC 26D	12 S 512915 3558819
AMARC 26E	12 S 512872 3558962
AMARC 27B	12 S 513665 3559166
AMARC 27C	12 S 513559 3559050
AMARC 27D	12 S 513708 3559127
AMARC 27E	12 S 513671 3559029
AMARC 28C	12 S 512564 3558848
AMARC 29A	12 S 513978 3559494
AMARC 30	12 S 513912 3559607
AMARC 31	12 S 512810 3558214
AMARC 32A	12 S 512968 3558662
AMARC 33B	12 S 513050 3558910
AMARC 33D	12 S 513070 3558805

AMARC 34	12 S 513662 3558097
AMARC 36A	12 S 515144 3557034
AMARC 36B	12 S 515161 3557155
AMARC 37	12 S 513027 3558270
AMARC 38A	12 S 512818 3558764
AMARC 38B	12 S 512822 3558810
AMARC 39A	12 S 513449 3558674
AMARC 39B	12 S 513466 3558753
AMARC 39C	12 S 513467 3558737
AMARC 40A	12 S 515398 3556396
BANK 01	12 S 507074 3561094
CRAY 01A	12 S 511713 3561273
CRAY 01B	12 S 511722 3561272
CURT 01	12 S 498473 3573832
DREX 01B	12 S 499256 3556931
DREX 01C	12 S 499298 3556895
DREX 01D	12 S 499267 3556850
DREX 01F	12 S 499356 3556973
DREX 01H	12 S 499333 3556950
DREX 01I	12 S 499213 3556860
DREX 01K	12 S 499306 3556991
DREX 01L	12 S 499363 3557001
DREX 01M	12 S 499281 3556880
DREX 01N	12 S 499351 3556975
DREX 01O	12 S 499363 3556995
DREX 01P	12 S 499305 3556896
DREX 01Q	12 S 499275 3556838
DREX 01R	12 S 499255 3556829
DREX 02B	12 S 499500 3557538
DREX 02C	12 S 499499 3557530
DREX 03D	12 S 499377 3557177
DREX 03F	12 S 499405 3557098
DREX 04A	12 S 499444 3557197
DREX 04B	12 S 499458 3557235
DREX 04C	12 S 499444 3557199
DREX 05A	12 S 499545 3557647
DREX 05B	12 S 499659 3557807
DREX 05C	12 S 499594 3557795
DREX 05D	12 S 499547 3557649
DREX 05E	12 S 499571 3557729
DREX 07	12 S 499400 3557078
DREX 08A	12 S 499515 3557578
DREX 08B	12 S 499523 3557605
DREX 09	12 S 499591 3557780
DREX 11A	12 S 499667 3557842
DREX 11B	12 S 499663 3557843
DREX 13A	12 S 499237 3556900
DREX 13B	12 S 499284 3556883

DREX 14	12 S 499666 3557803
DREX 15A	12 S 499218 3556764
DREX 15B	12 S 499178 3556774
DREX 16	12 S 499294 3556974
DREX 17	12 S 499600 3557819
ENGH 10D	12 S 510330 3560954
ENGI 01	12 S 510404 3560862
ENGI 02A	12 S 510406 3560813
ENGI 02D	12 S 510405 3560792
ENGI 02E	12 S 510344 3560803
ENGI 06B	12 S 510235 3560772
ENGI 06C	12 S 510259 3560798
ENGI 06D	12 S 510264 3560755
ENGI 06E	12 S 510270 3560726
ENGI 07A	12 S 510306 3560887
ENGI 07C	12 S 510282 3560940
ENGI 08B	12 S 510312 3561064
ENGI 09A	12 S 510250 3561215
ENGI 09D	12 S 510227 3561196
ENGI 10A	12 S 510352 3560973
ENGI 10B	12 S 510368 3560930
ENGI 11A	12 S 510417 3561025
ENGI 11B	12 S 510430 3561052
ENGI 11C	12 S 510425 3561090
FORT 01	12 S 512983 3557089
FUEL 05	12 S 510459 3560426
FUEL 06	12 S 510513 3560412
FUEL 08	12 S 510330 3560537
FUEL 09A	12 S 510490 3560130
HELIC 01	12 S 511193 3561240
HELIC 02B	12 S 510355 3561203
HELIC 02C	12 S 510378 3561170
HELIC 03	12 S 510474 3561318
LINKS 02B	12 S 512967 3561513
LINKS 02E	12 S 512952 3561513
LINKS 02F	12 S 512991 3561537
LINKS 02G	12 S 513028 3561528
LINKS 03A	12 S 513233 3561511
LINKS 03B	12 S 513201 3561509
LINKS 04A	12 S 513276 3561508
LINKS 05A	12 S 513307 3561505
LINKS 05C	12 S 513308 3561511
LINKS 05D	12 S 513344 3561505
LINKS 06A	12 S 512887 3561513
LINKS 06B	12 S 512857 3561511
LINKS 06C	12 S 512767 3561512
LINKS 06D	12 S 512895 3561512
LINKS 07A	12 S 512517 3561513

LINKS 07B	12 S 512507 3561510
LINKS 07D	12 S 512660 3561513
LINKS 07F	12 S 512306 3561712
LINKS 08A	12 S 512273 3561514
LINKS 08B	12 S 512244 3561513
LINKS 13A	12 S 513108 3561513
LINKS 13C	12 S 513163 3561515
LINKS 13D	12 S 513147 3561527
LIVE 02	12 S 510168 3560831
LIVE 03A	12 S 510054 3561147
LIVE 03B	12 S 510030 3561063
LIVE 04C	12 S 509873 3561209
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LIVE 07A	12 S 509717 3560966
LIVE 07B	12 S 509668 3560963
LIVE 07C	12 S 509630 3560993
LIVE 07D	12 S 509387 3561164
LIVE 07E	12 S 509383 3561110
LIVE 07F	12 S 509422 3561146
LIVE 08B	12 S 509723 3560621
LIVE 09B	12 S 509899 3561091
LIVE 09C	12 S 509946 3561114
LIVE 10	12 S 509515 3561079
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MISS 01C	12 S 499798 3559344
MISS 01D	12 S 499793 3559370
MISS 01E	12 S 499804 3559361
MISS 01F	12 S 499814 3559295
OPS 02A	12 S 512336 3557901
OPS 02C	12 S 512360 3557976
OPS 02D	12 S 512360 3557976
OPS 05A	12 S 512084 3558255
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OPS 06A	12 S 512103 3558162
OPS 06B	12 S 512225 3558159
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PALO 01B	12 S 508201 3561602
PALO 02	12 S 508149 3561706
PALO 03A	12 S 508095 3561852
PERIM 01A	12 S 509253 3560445

PERIM 01B	12 S 509248 3560337
PERIM 02A	12 S 509455 3560295
PERIM 02B	12 S 509481 3560312
PERIM 04	12 S 509094 3560907
PERIM 05A	12 S 509102 3560888
PERIM 05B	12 S 509133 3560874
PERIM 05C	12 S 509455 3561036
PERIM 05E	12 S 509436 3560790
PERIM 05F	12 S 509463 3560981
PERIM 05G	12 S 509436 3561060
PERIM 05H	12 S 509408 3560804
PERIM 05I	12 S 509477 3560975
PERIM 05J	12 S 509476 3561012
PERIM 05K	12 S 509476 3560707
PERIM 06A	12 S 509453 3560553
PERIM 06B	12 S 509449 3560569
PERIM 08A	12 S 509352 3560975
PERIM 08B	12 S 509288 3561022
PERIM 09A	12 S 509396 3560659
PERIM 09B	12 S 509473 3560741
PERIM 10	12 S 509248 3560575
PERIM 11	12 S 509510 3560851
PERIM 12A	12 S 509546 3560724
PERIM 12B	12 S 509551 3560720
PIMA 01A	12 S 500930 3556398
PIMA 01B	12 S 500951 3556388
PIMA 02	12 S 500544 3555923
QUIJ 01B	12 S 511949 3561068
QUIJ 01G	12 S 511888 3561258
QUIJ 01I	12 S 511799 3561251
QUIJ 02A	12 S 512233 3561161
QUIJ 02B	12 S 512165 3561127
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QUIJ 06A	12 S 512323 3561030
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QUIJ 07A	12 S 512487 3560978
QUIJ 07B	12 S 512514 3560990
QUIJ 07C	12 S 512477 3561016
QUIJ 07D	12 S 512478 3560984
QUIJ 08A	12 S 511873 3561311

QUIJ 08B	12 S 511881 3561346
QUINCY 01A	12 S 504844 3561678
QUINCY 01B	12 S 504862 3561690
RANDO 03	12 S 507386 3560056
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RANDO 04B	12 S 507380 3560074
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RANDO 05B	12 S 507396 3560114
SANTA 10A	12 S 499800 3557964
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SANTA 13B	12 S 499471 3557822
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SANTA 15C	12 S 500673 3558644
SANTA 15D	12 S 500659 3558637
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SANTA 19	12 S 500632 3557806
SANTA 20	12 S 499537 3557940
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SILVER 02B	12 S 498935 3569308
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SILVER 03C	12 S 498906 3569058
SILVER 04A	12 S 498895 3568892
SILVER 04B	12 S 498881 3568836
SILVER 04C	12 S 498889 3568824
SILVER 05	12 S 498910 3568742
SLAK 01A	12 S 501259 3561638
SLAK 02A	12 S 501257 3561464
SLAK 02B	12 S 501265 3561492
SLAK 03A	12 S 501228 3560481
STAXI 01B	12 S 512923 3556941
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STAXI 04B	12 S 512461 3557042
STAXI 06A	12 S 512468 3557115
STAXI 07A	12 S 512679 3556753
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STAXI 08	12 S 512305 3557126
STAXI 09A	12 S 512975 3556474
STAXI 09B	12 S 513010 3556437
SUNG 01	12 S 511024 3561386
SUNG 03A	12 S 510844 3561589

SUNG 03B	12 S 510836 3561623
SUNG 04A	12 S 510803 3561609
SUNG 04B	12 S 510775 3561634
SUNG 05A	12 S 510755 3561674
SUNG 05C	12 S 510805 3561685
SUNG 05D	12 S 510778 3561680
SUNG 05E	12 S 510820 3561686
SUNG 06A	12 S 510730 3561754
SUNG 06F	12 S 510749 3561717
SUNG 06H	12 S 510740 3561813
SUNG 07A	12 S 510651 3561770
SUNG 07B	12 S 510647 3561768
SUNG 10A	12 S 510334 3561706
SUNG 10B	12 S 510287 3561793
SUNG 12A	12 S 511277 3561490
SUNG 12B	12 S 511276 3561492
SUNG 13	12 S 510512 3561745
TAXI 01A	12 S 512837 3557080
TAXI 01B	12 S 512831 3557080
TAXI 01C	12 S 512858 3557113
TAXI 02B	12 S 512519 3557328
TAXI 02C	12 S 512444 3557387
TAXI 02E	12 S 512774 3557281
TAXI 08A	12 S 510670 3559405
TAXI 08B	12 S 510552 3559421
TAXI 08C	12 S 510555 3559388
TAXI 10	12 S 512166 3557927
TAXI 11A	12 S 512344 3557540
TAXI 13A	12 S 511296 3558724
TAXI 13B	12 S 511310 3558678
TAXI 14A	12 S 511368 3558593
TAXI 14B	12 S 511509 3558586
TAXI 16B	12 S 512422 3557480
TAXI 16D	12 S 512466 3557475
TAXI 17	12 S 511854 3558146
TAXI 20	12 S 511414 3558569
TAXI 21	12 S 511316 3558541
TAXI 22A	12 S 510550 3559576
TEP 01	12 S 506219 3559540
TEP 02A	12 S 506061 3559668
TEP 02B	12 S 506126 3559665
TEP 03A	12 S 505931 3559864
TEP 03B	12 S 505958 3559844
TEP 03C	12 S 505931 3559901
TEP 04	12 S 506304 3559433
TEP 05A	12 S 506019 3559895
TEP 06A	12 S 506215 3559643
TOWER 01	12 S 511420 3558096

TOWER 02A	12 S 510357 3559318
TOWER 03A	12 S 510701 3558877
TOWER 04A	12 S 510711 3558867
TOWER 05A	12 S 510728 3558845
TOWER 06A	12 S 510405 3559256
TOWER 07A	12 S 510535 3559089
TUC 01A	12 S 519219 3551917
TUC 01B	12 S 519224 3551924
TUC 04A	12 S 520196 3552435
TUC 04B	12 S 520110 3552554
TUC 04C	12 S 520190 3552429
TUC 05A	12 S 520365 3552184
TUC 06A	12 S 520277 3552302
WFUEL 01B	12 S 510200 3560471
WFUEL 01G	12 S 510254 3560425
WFUEL 02	12 S 510294 3560293
WFUEL 03C	12 S 510320 3560243
WFUEL 03F	12 S 510257 3560246
WFUEL 03H	12 S 510332 3560254
WFUEL 04A	12 S 510275 3559709
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WFUEL 05B	12 S 510354 3559710
WFUEL 06B	12 S 510178 3560060
WFUEL 06C	12 S 510254 3560136
WFUEL 07B	12 S 510161 3560306
WFUEL 08	12 S 510329 3559640
WFUEL 09	12 S 510384 3559859
WFUEL 11	12 S 510138 3560238
WFUEL 12A	12 S 510185 3560252
WFUEL 13A	12 S 510080 3560471
WFUEL 14A	12 S 510116 3560514
WILM 01	12 S 513410 3560790
WILM 02A	12 S 513412 3560770
WILM 02C	12 S 513411 3560789
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WILM 03C	12 S 513466 3560130
YUMA 02C	12 S 513323 3557736
YUMA 02D	12 S 513259 3557780
YUMA 02E	12 S 513326 3557739
YUMA 02H	12 S 513386 3557778
YUMA 02I	12 S 513281 3557775
YUMA 03A	12 S 513382 3557675
YUMA 03B	12 S 513369 3557678
YUMA 04A	12 S 513559 3557194
YUMA 04B	12 S 513541 3557236
YUMA 04C	12 S 513739 3557170

YUMA 05	12 S 512028 3559250
YUMA 07A	12 S 512191 3559341
YUMA 07C	12 S 512189 3559338

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