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Migratory decisions in birds: extent of genetic versus environmental control

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Abstract Migration is one of the most spectacular of animal behaviors and is prevalent across a broad array of taxa. In birds, we know much about the physiological basis of how birds migrate, but less about the relative contribution of genetic versus environmental factors in controlling migratory tendency. To evaluate the extent to which migratory decisions are genetically determined, we examined whether individual western burrowing owls (*Athene cunicularia hypugaea*) change their migratory tendency from one year to the next at two sites in southern Arizona. We also evaluated the heritability of migratory decisions by using logistic regression to examine the association between the migratory tendency of burrowing owl parents and their offspring. The probability of migrating decreased with age in both sexes and adult males were less migratory than females. Individual owls sometimes changed their migratory tendency from one year to the next, but changes were one-directional: adults that were residents during winter 2004–2005 remained residents the following winter, but 47% of adults that were migrants in winter 2004–2005 became residents the following winter. We found no evidence for an association between the migratory tendency of hatch-year owls and their male or female parents. Migratory tendency of hatch-year owls did not differ between years, study sites or sexes or vary by hatching date. Experimental provision of supplemental food did not affect these relationships. All of our results suggest that heritability of migratory tendency in burrowing owls is low, and that intraspecific variation in migratory tendency is likely due to: (1) environmental factors, or (2) a combination of environmental factors and non-additive genetic variation. The fact that an individual's migratory tendency can change across years implies that widespread anthropogenic changes (i.e., climate change or changes in land use) could potentially cause widespread changes in the migratory tendency of birds.

Keywords Avian migration · Behavioral plasticity · Condition dependence · Heritability · Migratory tendency

Introduction

Migration is among the most remarkable behaviors observed in animals and occurs in virtually all major animal taxa. Migration has received more attention in birds than in other taxa because of the long distances traveled by some birds, and the reliability with which individual birds often return to specific breeding and wintering areas each year. Many hypotheses have been proposed to explain the evolution of migration in birds, but most of these hypotheses fail to explain why some species migrate while similar coexisting species do not (Boyle and Conway 2007). We often see a similar pattern within species, whereby some individuals migrate while others within the same breeding population remain sedentary (i.e., partial migration; Terrill and Able 1988). However, the selective pressures that favor partial migration and the proximate mechanisms which affect migratory tendency remain unresolved. Lack (1943, 1944, 1968) suggested that migration and residency in many species were genetically governed behaviors and that individuals possess different hereditarily based thresholds of migration, an idea more recently formalized in the threshold

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model of Berthold and colleagues (Berthold 1988; Pulido et al. 1996). However, Lundberg (1988) noted that genetically different individuals could express similar phenotypes, and that partial migration may instead represent a conditional strategy in which factors that affect social dominance and competition for resources determine whether an individual migrates in a given year.

The roles of genetic versus environmental factors in controlling individual migratory tendency remain equivocal, due in part to variation in the migratory behaviors examined. Evidence for genetic control comes primarily from laboratory studies which have focused not on migration per se but on the expression of migratory restlessness (*Zugunruhe*) in captive birds. Selective breeding experiments with blackcap warblers (*Sylvia atricapilla*) and European robins (*Erithacus rubecula*) have demonstrated relatively high heritability of *Zugunruhe* (Biebach 1983; Berthold et al. 1990; Berthold and Helbig 1992; Pulido et al. 1996; Berthold 2001), and the proportions of blackcaps and robins exhibiting *Zugunruhe* in captivity paralleled the overall proportions of migrants in the respective wild populations (Berthold and Querner 1981; Biebach 1983). However, the functional relationship between *Zugunruhe* as observed in captive birds and migratory tendency in the wild is probably indirect, because: (1) the proportions of captive female and male European robins exhibiting *Zugunruhe* (Biebach 1983) differed from the proportions of female and male robins that migrated in a field study (Adriaensen and Dhondt 1990), (2) non-migratory stonechats (*Saxicola torquata*) exhibited *Zugunruhe* when held under conditions of constant equatorial daylength (Helms 2006), and (3) long-distance migrant songbirds exhibited phenotypic plasticity in the expression of *Zugunruhe* when exposed to manipulated photoperiods (Coppack et al. 2003). In contrast, evidence for environmental control of migratory tendency comes primarily from field studies which suggest that the migratory tendency of individual birds may change over time and vary with environmental conditions. For example, the proportion of migrant individuals often differs among age classes (Gauthreaux 1982; Schwabl 1983; Smith and Nilsson 1987; Cristol et al. 1999). European blackbirds (*Turdus merula*) sometimes shift from migrant one year to resident the next year (but seldom the reverse; Schwabl 1983; Harper 1985). Finally, subordinate dark-eyed juncos (*Junco hyemenalis*) exhibited higher levels of *Zugunruhe* compared to dominant birds in response to experimental food restriction (Terrill 1987).

The extent of genetic versus environmental control of migratory tendency likely varies among species. Genetic control may be more common in birds that breed in strongly seasonal environments where resource fluctuations are predictable within and across years (e.g., obligate long-distance migrants). By contrast, environmental factors may play a greater role in birds that experience less predictable resource variation and migrate facultatively (Winkler 2005), as is the case with irruptive migrants (Newton 2006) in which the proportion of individuals migrating fluctuates greatly from year to year in response to the abundance of their preferred food (Hagen 1969; Bock and Lepthien 1976; Enemar et al. 1984; Korpimaki 1986; Sonerud et al. 1988; Korpimaki and Norrdahl 1991; Hochachka et al. 1999; Koenig and Knops 2001; Wiggins et al. 2006).

Migratory decisions in birds thus appear to be governed by both genetic and environmental controls, and the importance of each likely varies both within and across species. More information is needed to establish the relative contribution of genetic versus environmental factors in explaining variation in migratory tendency and the lack of congruence between the results of selective breeding experiments and field-based studies. We need more studies which assess the heritability of migratory tendency in wild populations, where migration per se (rather than behavioral surrogates such as *Zugunruhe*) can be observed. Resolving this issue is a matter of practical as well as theoretical concern. Some populations may have a relatively limited capacity to adapt behaviorally to an altered climate, whether through phenotypic plasticity or genetic variation (Sutherland 1998; Fiedler 2003). The need for such information is urgent given the apparently quickening pace of climatic changes (Intergovernmental Panel on Climate Change 2007) and the uncertainty surrounding their likely effects on bird populations (Winkler et al. 2002; Archaux 2003; Wormworth and Mallon 2006).

In this study, we examined whether migratory tendency of western burrowing owls (*Athene cunicularia hypugaea*) in southern Arizona was influenced primarily by genetic or environmental factors based on year-round nest monitoring and resighting of uniquely banded individuals. Burrowing owls are well suited for studying the control of migratory tendency. Unlike many other owl species, the burrowing owl is a generalist predator that does not exhibit irruptive movements (Jaksic et al. 1992; Haug et al. 1993; Poulin et al. 2001), and breeding populations throughout western North America vary in the proportion of individuals that migrate south during winter (Haug et al. 1993; Klute et al. 2003; Conway et al. 2006). Populations in southern Arizona appear to be partially migratory: some individuals disappear during winter while others are present year round (Conway et al. 2005; Conway and Ogonowski 2005; Ogonowski and Conway 2006). Annual nest site fidelity is high in burrowing owls (Haug et al. 1993; Klute et al. 2003; Conway et al. 2006) and they often perch at the entrance to their nest burrow during daylight hours, facilitating band resighting. These traits allowed us to examine the consistency of individual owls' migratory tendency in successive

years and to estimate the strength of association between the migratory tendency of parents and their offspring. We restricted our study to banded owls that bred on our study sites in 2 successive years so that we could differentiate winter migrants from birds that died and birds that permanently dispersed from our study area.

Materials and methods

Study area

We conducted the research at two study sites in southern Arizona: one within the city limits of Tucson (Pima County, elevation 728 m), and another surrounding the town of Coolidge (Pinal County, 435 m). Both study 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 (National Oceanic and Atmospheric Association 2007). Burrowing owls nested in abandoned round-tailed ground squirrel (*Spermophilus tereticaudus*) burrows, in erosional cavities or metal culverts along desert washes, and in the banks of earthen canals and concrete irrigation troughs abutting agricultural fields.

Methods

Trapping and banding owls

We used color marking and band resighting to determine whether each individual owl migrated or not. We began color marking owls at the Tucson study site in 2001 and at the Coolidge study site in 2003 as part of a larger demographic study (Conway and Ellis 2004). We captured adult and juvenile owls using two-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 United States Geological Survey band and one alphanumeric color-coded band (ACRAFT Sign and Nameplate, Edmonton, Alberta) on opposite legs of each owl. Owls were aged based on the year in which they were banded as juveniles. We placed unique color bands on a total of 1,916 owls (590 adults and 1,326 juveniles) as part of an ongoing demographic study from 2001 to 2006 at the two study sites (Conway and Ellis 2004; Conway and Ogonowski 2005), and virtually all owls (≥90% at each study site) were color banded at the outset

of this study. This intensive banding effort enabled us to obtain a sufficient sample of parent–offspring pairs with known migratory tendencies during 2004–2006 and of known-age owls (those banded as juveniles that recruited into the local populations).

Nest monitoring

We visited all known current and past nest burrows ($n = 260$) and several hundred potential nest burrows once per week from March 2004 up to and including June 2006 to identify which owls were present. We detected 151 burrows that were occupied by individual owls or pairs ("active nests"). During each weekly nest visit, we first observed burrows from a distance of >100 m with binoculars 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 occupancy (e.g., whitewash, feathers) and nesting activity (lining, decor, manure; Smith and Conway 2007), and used an infrared video probe (Sandpiper Technologies, Manteca, Calif.) to look for eggs within all burrows at which we observed owls or signs of occupancy. The infrared probe allowed us to locate owls not detected aboveground, determine whether elusive individuals were banded, and estimate reproductive parameters (clutch size, hatching date, hatching success, and number of fledglings). Repeated use of the infrared probe does not affect behavior or reproductive parameters in burrowing owls (Garcia and Conway 2009a). We estimated hatching date based on signs and behaviors observed during weekly nest visits using a standardized protocol (Garcia et al. 2007; Garcia and Conway 2009b). 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 signs of owls with a handheld GPS receiver (Garmin, Olathe, Kan.).

Determination of migratory status

Our classification of individual male and female adult and hatch-year owls as residents or migrants was based on their presence or absence from the study area during winter, defined as the interval from 15 November to 15 February of the subsequent year. We restricted our analysis to only include birds that were present and detected on our study sites during two consecutive breeding seasons (i.e., detected in both 2004 and 2005, or in both 2005 and 2006). Some of these return breeders were repeatedly detected during the intervening winter (residents) and some were never detected during weekly surveys during the intervening winter (migrants). Restricting our analyses to include only these return breeders ensured that our sample of migrants did not include birds that had permanently emigrated or had died.

Presence of owls on the study sites was based on band resight data collected during weekly nest visits and an intensive mid-winter survey conducted between 15 January and 6 February of two successive years (2004–2005 and 2005–2006) during which we attempted to determine the identity of all owls over-wintering at each site. During these winter surveys we visited each known burrow (occupied and unoccupied) at least twice and returned more frequently to burrows where we could not initially read an owl's band. We also placed traps at burrows when we had difficulty observing an owl's legs or to confirm the presence of individuals at burrows that we suspected were occupied, given that owls (especially females) often remained underground or retreated into the burrow when approached during winter months. We classified 65 adult and 42 hatch-year owls as winter residents (i.e., non-migrants) because they met three conditions: bred during summer of year t, were present during the subsequent winter (15 November–15 February), and bred during summer of year $t + 1$. We classified ten adult and 47 hatch-year owls as migrants because they: (1) bred during summer of year t, (2) were not observed during the subsequent winter (15 November–15 February), and (3) bred during summer of year $t + 1$. We also observed 11 additional adult owls and one hatch-year owl that: (1) bred during summer of year t, (2) were present during the subsequent winter, but (3) were not observed during summer of year $t + 1$. We analyzed our data with and without these 11 adult and one hatch-year owls (classified as winter residents) and obtained similar results, so we included them in our analysis.

Determining the sex of owls

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. Adult males are typically slightly larger (Martin 1973) and paler (Martin 1973; Haug et al. 1993) with less barring on the breast plumage than adult females. Also, adult males are usually found perching at or near the nest burrow during incubation and the early nestling period, while adult females usually remain underground during these periods (Coulombe 1971; Martin 1973; Haug et al. 1993). Incubating females exhibit a prominent and often vascularized brood patch (Coulombe 1971; Martin 1973) which we used to confirm our visual and behavioral determinations of sex whenever possible. We determined the sex of all returning hatch-year owls during their second year after they had attained their adult plumage.

Statistical analyses

We used logistic regression to evaluate the effect of age on migratory tendency (SPSS 2006), restricting our analysis to owls of known age (i.e., owls that had been banded as juveniles). We conducted the analysis in two steps. In step 1, we screened for the effects of four potential covariates (year, study site, sex, and food treatment) by entering these covariates, age, and two-way interaction terms (site $\times$ sex, age $\times$ sex, food treatment $\times$ sex, and food treatment $\times$ site) in a logistic regression model with migratory tendency as the response variable. We included food treatment (supplemented vs. unsupplemented) as a covariate because 75 of the 151 active nests we monitored received supplemental food as part of a related study (Ogonowski 2007). Sex was the only covariate that affected model performance or the sign, magnitude, and significance of other estimated coefficients, so we included sex as a covariate in step 2. In step 2, we re-ran the logistic regression including only age, sex, and the interaction between age and sex as explanatory variables.

We used a Mantel–Haenszel test of conditional independence to examine whether migratory tendency of individual adult owls was consistent in two successive years while controlling for the potentially confounding effect of food treatment (supplemented vs. unsupplemented), which we used as a blocking factor. We used a Mantel–Haenszel test rather than include prior-year migratory tendency in the logistic regression model described above because we only knew the exact age of 38 of 86 adult owls for which we had data on migratory tendency in two successive winters. We conducted a second Mantel–Haenszel test using prior-year migratory tendency as the blocking factor to determine if food treatment also affected migratory tendency.

We conducted a separate logistic regression analysis to examine the heritability of migratory tendency because we only knew the migratory tendency of both parents for 43 of 164 owls of known age. Logistic regression has been used previously to examine the heritability of migratory tendency in blackcap warblers (Pulido et al. 1996). We regressed the migratory tendency of first-year owls that returned to breed the following year (i.e., recruited into the local breeding population) on the respective migratory tendency of their male and female parents during the same year. We tested for the effect of five potential covariates in this analysis: year, study site, sex of first-year owl, hatching date, and food treatment. As with the analysis of the effect of age, we conducted the analysis in two steps. First, we screened for the effects of the five potential covariates by entering them in a logistic regression model along with paternal migratory tendency, maternal migratory tendency, and two-way interaction terms (food treatment $\times$ sex, food treatment $\times$ hatching date, food treatment $\times$ paternal migratory tendency, and food treatment $\times$ maternal migratory tendency) with offspring migratory tendency as the response variable. None of the covariates improved the performance of the model or affected the sign, magnitude, or

significance of other estimated coefficients so we did not include them in step 2. In step 2, we re-ran the logistic regression including only paternal migratory tendency and maternal migratory tendency as potential explanatory variables.
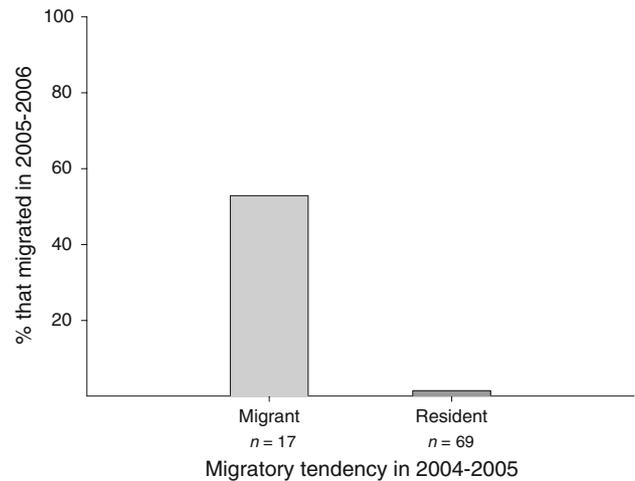
Results

Consistency of migratory tendency

To determine whether migratory tendency varied among age classes, we examined migratory tendency of 74 known-age adult owls (35 females, 39 males) and 90 hatch-year owls (40 females, 50 males) during 2004–2006. We found a significant interaction between age and sex on migratory tendency (partial $P = 0.008$ for age $\times$ sex interaction from logistic regression; Fig. 1). Age was negatively associated with the tendency to migrate for owls of both sexes (partial $P < 0.001$ for age) and adult males were less likely to migrate than females for all age classes (partial $P = 0.036$ for sex). Nearly all adult males (i.e., second year and older) were non-migratory, while females showed a steady monotonic decline in migratory tendency with age. We failed to detect a difference in migratory tendency between male and female hatch-year owls.

We obtained data on migratory tendency in two successive winters (2004–2006) for 86 adult owls (48 males, 38 females). Of the 17 adult owls (eight males, nine females) that left the study area during winter 2004–2005, 53% migrated again during winter 2005–2006. Of the 69 owls that overwintered on the study area in 2004–2005, 99% overwintered again in 2005–2006 (Fig. 2). This relationship was highly significant after controlling for the effect of food
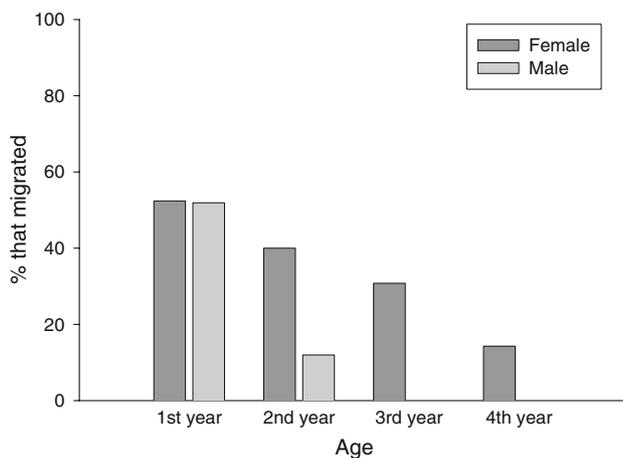
Fig. 2 Change in migratory tendency of individual adult burrowing owls across two winters in southern Arizona, USA, 2004–2006. *Bars* show the percent of previously migrant and resident adults that migrated during the 2005–2006 winter

treatment ($\chi^2 = 29.13$, $P < 0.001$), but food treatment had no effect after controlling for the effect of prior-year migratory tendency ($\chi^2 = 0.07$, $P = 0.795$). Males (63%) were more likely than females (33%) to switch from migrant to resident the subsequent year.

Heritability of migratory tendency

We used migratory tendency of 43 returning hatch-year owls for which we were also able to determine the migratory tendency of both parents. Neither of the two explanatory variables in our logistic regression model (paternal migratory tendency and maternal migratory tendency) were significant predictors ($P = 0.226$ and $P = 0.689$, respectively) of offspring migratory tendency. The offspring of both migrant ($n = 14$) and resident ($n = 29$) females were about equally likely to migrate (Fig. 3a). Fifty percent of the offspring of resident males ($n = 38$) migrated, and only one of the five offspring of migrant males ($n = 5$) migrated (Fig. 3b).

Discussion

Our results provide support for a condition-dependent control mechanism underlying burrowing owl migratory tendency. We found that hatch-year owls were more likely to migrate than adults, the probability of migrating decreased with age in owls of both sexes, and adult males were significantly less migratory than females at all ages. While the number of 3- and 4-year-old owls in our sample was relatively small, our results were nonetheless consistent with those of other studies of partial migrants (Lack 1943, 1944;

Fig. 1 Effect of age on migratory tendency of male and female burrowing owls in southern Arizona, USA, 2004–2006. Sample sizes for *bars* from left to right: 40, 50, 15, 25, 13, 13, 7, 1

Fig. 3 Percent of migrant hatch-year burrowing owls produced by migrant and resident **a** female and **b** male parents in southern Arizona, USA, 2004–2006
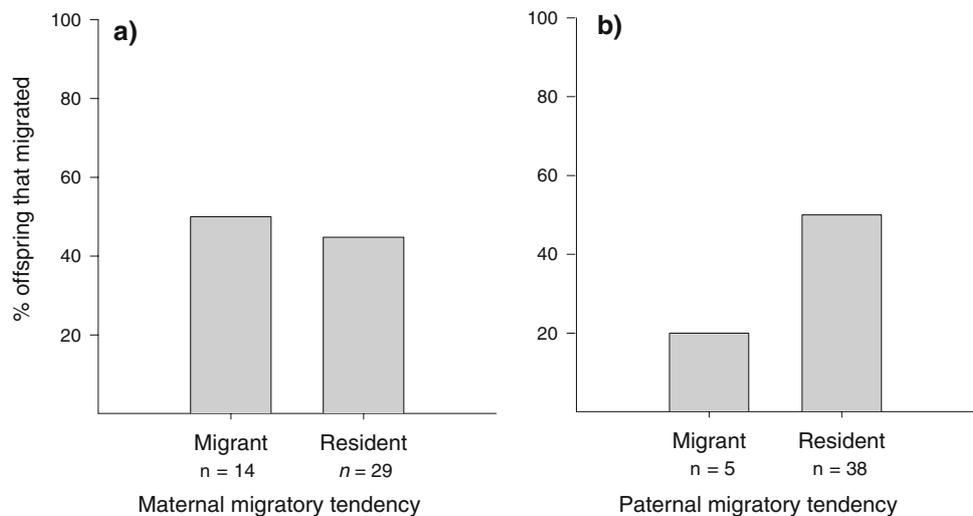
Ketterson and Nolan 1976; Gauthreaux 1982; Schwabl 1983; Smith and Nilsson 1987; Adriaensen and Dhondt 1990; Cristol et al. 1999). A greater tendency to migrate among hatch-year birds could reflect a heritable maturational process whereby migratoriness decreases with age (Berthold 1991), but that would not explain why only slightly more than half of the hatch-year birds in our study migrated. Alternatively, this pattern may reflect a behavioral dominance mechanism whereby subordinate owls are excluded from wintering sites by older owls (Cristol et al. 1999; Bell 2005). Experimental removals of wintering adults would provide a useful approach to test this behavioral dominance hypothesis.

We found that individual owls sometimes changed their migratory status. Nearly half (47%) of adult owls that migrated out of our study area during the winter of 2004–2005 changed strategies and overwintered during 2005–2006. In contrast, 68 of 69 owls that overwintered in 2004–2005 overwintered again in 2005–2006. A similar one-directional change in migratory tendency has been observed in European blackbirds (Schwabl 1983; Harper 1985). These findings provide further evidence that burrowing owl migratory tendency is a behaviorally plastic, condition-dependent trait. We recommend that future studies examine why resident owls rarely become migratory in a subsequent year, for example, by evaluating whether residency confers an advantage during the subsequent breeding season as it does in Tengmalm's owls *Aegolius funereus* (Korpimaki 1987); sparrowhawks *Accipiter nisus* (L.) (Newton and Marquiss 1983; Newton 1985), and great tits *Parus major* (Sandell and Smith 1991).

Interpretation of studies of migratory tendency based on band resighting must consider the possibility that some individuals not seen during winter may have been present but went undetected (Williams et al. 2002). By restricting our analysis to owls that were detected during two consecutive

breeding seasons, owls that had died or those that permanently emigrated were not included in our analysis. It is possible that we failed to detect some banded owls that were present on our study sites during winter (i.e., misclassified some residents as migrants because we failed to detect them during winter). However, several lines of evidence suggest that our detection probability during winter was very high, and that most if not all owls classified as migrants in our sample were in fact absent from our study sites. First, our survey effort was exhaustive and included weekly visits throughout the year to all known burrow locations, underground observation of burrows with an infrared probe, and extensive winter trapping. These methods allowed us to locate and identify banded owls at virtually all burrows that had any signs of occupancy. Second, only one banded owl in our sample (an adult female) was observed on only one occasion during winter, while all others were resighted on multiple occasions. Third, several patterns we observed corroborated other studies of partial migrants and hence lend confidence to our monitoring approach: migratory tendency decreased with age, and female owls were more migratory than males. Moreover, 68 of 69 owls that were resident in one year were resident the subsequent year, but only eight of 17 migrants were residents in the subsequent year. If detection probability during winter was a significant problem, we would have expected it to plague both groups equally (i.e., we would have failed to detect more of the 69 owls that were residents in winter 2004–2005 during the subsequent winter and mistakenly classified them as migrants).

Our results suggest low heritability of migratory tendency in burrowing owls. Returning first-year owls at both study sites were about equally likely to migrate during their first winter regardless of the migratory tendency of either parent. While the small number of migrant male parents in our sample is too small to permit strong inference, the low

percentage (20%) of migrant offspring they produced is the opposite of what we would expect if migratory tendency had high heritability. This suggests that the observed variation in burrowing owl migratory tendency is due either to environmental variation or to a combination of environmental and non-additive genetic variation (i.e., that portion of genetic variation that does not contribute to heritability; Frankham et al. 2002).

The results of our field study contrast with the findings of laboratory studies of other migratory birds reporting high heritability of behavioral and physiological components of migration, such as the intensity and duration of *Zugunruhe* (Berthold et al. 1990; Helbig 1991; Berthold and Pulido 1994; Pulido et al. 1996). Differences between laboratory and field studies regarding the heritability of migratory tendency may reflect: (1) differences in the actual behaviors measured (laboratory studies have focused on orientation and vigor of *Zugunruhe*, rather than on migratory tendency per se); (2) differences in the species and populations examined (e.g., completely migratory populations might exhibit less intraspecific variation in, and higher heritability of, migratory behaviors compared to partially migratory populations); or (3) that individuals inherit behavioral plasticity for migratory tendency that enables them to respond to variation in environmental and social conditions (Lundberg 1988; Adriaensen et al. 1990; Kaitala et al. 1993; Coppack and Both 2002; Coppack et al. 2003).

Our study is one of the first to assess the heritability of migratory tendency directly in a wild population of birds (but see Nice 1937; Dhondt 1983; Schwabl 1983; Berthold 1984). The sample size used in our parent–offspring logistic regression was limited given the relatively low proportion of migrant adults (especially males) in our study populations, but the concordance of our other results with those of prior studies makes us confident that migratory tendency has low heritability in burrowing owls. We encourage additional studies of migratory tendency in wild populations of birds to help shed more light on the extent to which migratory tendency (measured directly, as done here) is genetically controlled. Future research should focus on a variety of species with all types of migration strategies, but particularly on species whose migration strategies vary geographically. In burrowing owls, we recommend future studies examine the heritability of migratory tendency in populations with roughly equal proportions of migrants and residents, such as those in southern Washington and the northern Great Plains (Conway et al. 2006). Studies that include larger numbers of individuals and longer time frames would also help reveal the extent to which the proportion of migrants varies over time within individual populations.

Given our lack of support for genetic control of migratory tendency in burrowing owls, one might expect supplemental food to alter migratory tendency. However, supplemental food did not affect migratory tendency in any of our analyses. A larger sample of birds may be necessary to detect an effect of supplemental food on migratory tendency in burrowing owls. Regardless, any evidence that supplemental food affects migratory tendency in burrowing owls would only lend added support to the primary conclusion of this paper: that migratory tendency has low heritability and appears to be under conditional control in burrowing owls.

The evidence for individual behavioral plasticity in migratory behaviors provided by this and other studies (e.g., Coppack et al. 2003) provides some hope that birds will be able to respond flexibly and relatively quickly to environmental change. However, we cannot assume that these responses will necessarily improve the probability of persistence without a better understanding of reaction norms for specific traits within individual species (van Noordwijk et al. 2006). Furthermore, climate and land-use changes could adversely affect migratory birds through decoupling of the proximate cues and ultimate processes that affect migratory decisions (Coppack and Both 2002; Gienapp and Visser 2006). For example, altered climatic conditions may cause some birds to arrive earlier to breed, but earlier arrival times may not correspond to an advanced peak in food availability. Indeed, spring arrival and other aspects of avian breeding phenology no longer coincide with peak resource availability in some species and these changes have been shown to have fitness consequences (Both et al. 2006; Visser et al. 2006). We need to increase our understanding of the various ways in which migratory birds may respond behaviorally to environmental change, at both the individual (plasticity) and population (selection) levels, so that we can predict how future environmental changes will affect species' persistence.

References

Adriaensen F, Dhondt AA (1990) Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. J Anim Ecol 59:1077–1090

Adriaensen F, Dhondt AA, Matthysen E (1990) Bird migration. Nature 347:23

Archaux F (2003) Birds and climate change. Life Environ 53:33–41

Bell CP (2005) Inter- and intrapopulation migration patterns. Ideas, evidence, and research priorities. In: Greenberg R, Marra PP (eds) Birds of two worlds. The ecology and evolution of migration. Johns Hopkins University Press, Baltimore, pp 44–52

Berthold P (1984) The control of partial migration in birds: a review. Ring 10:253–265

Berthold P (1988) Evolutionary aspects of migratory behavior in European warblers. J Evol Biol 1:195–209

Berthold P (1991) Genetic control of migratory behaviour in birds. Trends Ecol Evol 6:254–257

Berthold P (2001) Bird migration: a general survey, 2nd edn. Oxford University Press, Oxford

Berthold P, Helbig AJ (1992) The genetics of bird migration—stimulus, timing, and direction. Ibis 134(Suppl 1):35–40

Berthold P, Pulido F (1994) Heritability of migratory activity in a natural bird population. Proc R Soc Lond B 257:311–315

Berthold P, Querner U (1981) Genetic basis of migratory behavior in European warblers. Science 212:77–79

Berthold P, Mohr G, Querner U (1990) Steuerung und potentielle Evolutionsgeschwindigkeit des obligaten Teilzieherverhaltens: ergebniesse eines Zweiweg-Selektionsexperiments mit der Monchsgrasmucke (*Sylvia atricapilla*). J Ornithol 131:33–45

Biebach H (1983) Genetic determination of partial migration in the European robin (*Erithacus rubecula*). Auk 100:601–606

Bock CE, Lepthien LW (1976) Synchronous eruptions of boreal seed-eating birds. Am Nat 110:559–571

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature 441:81–83

Boyle WA, Conway CJ (2007) Why migrate? A test of the evolutionary precursor hypothesis. Am Nat 169:344–359

Conway CJ, Ellis LA (2004) Demography of burrowing owls nesting in urban and agricultural lands in southern Arizona. Report to Arizona Game and Fish Department. Wildlife research report no. 03-2004, US Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, AZ

Conway CJ, Ogonowski MS (2005) Determining migratory status of burrowing owls in the Tucson Basin. Final Report to Arizona Bird Conservation Initiative. Wildlife research report no. 2005-06, US Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, AZ

Conway CJ, Ellis LA, Rogne M (2005) Ecological and migratory status of burrowing owls nesting at Casa Grande Ruins National Monument and surrounding agricultural areas. Wildlife research report no. 2005-08. US Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, AZ

Conway CJ, Garcia V, Smith MD, Ellis LA, Whitney J (2006) Comparative demography of burrowing owls within agricultural and urban landscapes in southeastern Washington. J Field Ornithol 77:280–290

Coppack T, Both C (2002) Predicting life-cycle adaptation of migratory birds to global climate change. In: Both C, Piersma T (eds) The avian calendar: exploring biological hurdles in the annual cycle. Proceedings of the 3rd Conference of the European Ornithologists Union, Groningen, August 2001. Ardea 90:369–378

Coppack T, Pulido F, Czisch M, Auer DP, Berthold P (2003) Photoperiodic response may facilitate adaptation to climatic change in long-distance migratory birds. Proc R Soc Lond B Suppl 270:S43–S46

Coulombe HN (1971) Behavior and population ecology of the burrowing owl, *Speotyto cunicularia*, in the Imperial Valley of California. Condor 73:162–176

Cristol DA, Baker MB, Carbone C (1999) Differential migration revisited. Latitudinal segregation by age and sex class. In: Nolan V, Ketterson ED, Thompson CF (eds) Current ornithology, vol 15. Kluwer, New York, pp 33–88

Dhondt AA (1983) Variations in the number of overwintering stonechats possibly caused by natural selection. Ring Migr 4:155–158

Enemar A, Nilsson L, Sjostrand B (1984) The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. Ann Zool Fenn 21:321–338

Fiedler W (2003) Recent changes in migratory behavior of birds: a compilation of field observations and ringing data. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin, pp 21–38

Frankham R, Ballou JD, Briscoe DA (2002) Introduction to conservation genetics. Cambridge University Press, Cambridge

Garcia V, Conway CJ (2009a) Use of video probe does not affect burrowing owl reproductive parameters or return rates. J Wildl Manage 731):154–157

Garcia V, Conway CJ (2009b) What constitutes a nesting attempt? Variation in criteria causes bias and hinders comparisons across studies. Auk 126(1):31–40

Garcia V, Conway CJ, Ellis LA (2007) Protocols for estimating burrowing owl reproductive parameters based on data recorded during repeated visits to occupied burrows. Wildlife research report no. 2007-06. USGS Arizona Cooperative Fish and Wildlife Research Unit, Tucson, AZ

Gauthreaux SA (1982) The ecology and evolution of avian migration systems. In: Farner DS, King JR, Parkes KC (eds) Avian Biology 6. Academic Press, New York, pp 93–168

Gienapp P, Visser ME (2006) Possible fitness consequences of experimentally advanced laying dates in great tits: differences between populations in different habitats. Funct Ecol 20:180–185

Hagen Y (1969) Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent population fluctuations. Fauna 22:73–126

Harper D (1985) Pairing strategies and mate choice in female robins (*Erithacus rubecula*). Anim Behav 33:862–875

Haug EA, Millsap BA, Martell MS (1993) Burrowing owl (*Speotyto cunicularia*). In: Poole A, Gill F (eds) The birds of North America, no. 61. The Academy of Natural Sciences, Philadelphia, pp 1–20

Helbig AJ (1991) Experimental and analytical techniques used in bird orientation research. In: Berthold P (ed) Orientation in birds. Birkhauser, Basel, pp 270–306

Helms B (2006) *Zugunruhe* of migratory and non-migratory birds in a circannual context. J Avian Biol 37:533–540

Hochachka WM, Wells JV, Rosenberg KV, Tessaglia-Hymes DL, Dhondt AA (1999) Irruptive migration of common redpolls. Condor 101:195–204

Intergovernmental Panel on Climate Change (ed) (2007) Climate change 2007: the physical science basis. Summary for policymakers. IPCC Secretariat, Geneva

Jaksic FM, Jimenez JE, Castro SA, Feinsinger P (1992) Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. Oecologia 89:90–101

Kaitala A, Kaitala V, Lundberg P (1993) A theory of partial migration. Am Nat 142:59–81

Ketterson ED, Nolan V Jr (1976) Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). Ecology 57:679–693

Klute DS, Ayers LW, Green MT, Howe WH, Jones SL, Shaffer JA, Sheffield SR, Zimmerman TS (2003) Status assessment and conservation plan for the western burrowing owl in the United States. Biological technical publication FWS/BTP-R6001-2003. US Department of Interior, Fish and Wildlife Service, Washington, DC

Koenig WD, Knops JMH (2001) Seed crop size and eruptions of North American boreal seed-eating birds. J Anim Ecol 70:609–620

Korpimaki E (1986) Gradients in population fluctuations of Tengmalm's owl *Aegolius funereus* in Europe. Oecologia 69:195–201

Korpimaki E (1987) Selection for nest-hole shift and tactics of breeding dispersal in Tengmalm's owl *Aegolius funereus*. J Anim Ecol 56:185–196

Korpimaki E, Norrdahl K (1991) Numerical and functional responses of kestrels, short-eared owls and long-eared owls to vole densities. Ecology 72:814–825

Lack D (1943) The problem of partial migration. Br Birds 37:122–130

Lack D (1944) The problem of partial migration (concluded). Br Birds 37:143–150

Lack D (1968) Bird migration and natural selection. Oikos 19:1–9

Lundberg P (1988) The evolution of partial migration in birds. Trends Ecol Evol 3:172–175

Martin DJ (1973) Selected aspects of burrowing owl ecology and behavior. Condor 75:446–456

National Oceanic and Atmospheric Association (2007) National Weather Service Internet Services Team. Monthly precipitation for Tucson, Arizona. <http://www.wrh.noaa.gov/twc/climate/reports.php>. Accessed 17 November 2007

Newton I (1985) Lifetime reproductive output of female sparrowhawks. J Anim Ecol 54:241–253

Newton I (2006) Advances in the study of irruptive migration. Ardea 94:433–460

Newton I, Marquiss M (1983) Dispersal of sparrowhawks between birthplace and breeding place. J Anim Ecol 52:463–477

Nice MM (1937) Studies in the life history of the Song sparrow, I. Trans Linn Soc NY 4:1–247

Ogonowski MS (2007) Factors influencing migratory decisions of western burrowing owls. M.S. thesis, School of Natural Resources, University of Arizona, Tucson, AZ

Ogonowski MS, Conway CJ (2006) Migratory status and factors influencing winter residency of burrowing owls in southern Arizona. Final report to Arizona Bird Conservation Initiative. US Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, AZ

Poulin RG, Wellicome TI, Todd LD (2001) Synchronous and delayed numerical responses of a predatory bird community to a vole outbreak on the Canadian prairies. J Raptor Res 35:288–295

Pulido F, Berthold P, van Noordwijk AJ (1996) Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. Proc Natl Acad Sci 93:14642–14647

Sandell M, Smith HG (1991) Dominance, prior occupancy, and winter residency in the great tit (*Parus major*). Behav Ecol Sociobiol 29:147–152

Schwabl H (1983) Auspragung und Bedeutung des Teilzugverhaltens iener sudwestdeutschen Population der Amsel *Turdus merula*. J Ornithol 124:101–116

Smith MD, Conway CJ (2007) Use of mammal manure by nesting burrowing owls: a test of four functional hypotheses. Anim Behav 73:65–73

Smith HG, Nilsson J-A (1987) Intraspecific variation in migratory pattern of a partial migrant, the blue tit (*Parus caeruleus*): an evaluation of different hypotheses. Auk 104:109–115

Sonerud GA, Solheim R, Prestrud K (1988) Dispersal of Tengmalm's owl *Aegolius funereus* in relation to prey availability and nesting success. Ornis Scand 19:175–181

SPSS (2006) Version 15.0 for Windows. SPSS, Chicago

Sutherland WJ (1998) Evidence for flexibility and constraint in migration systems. J Avian Biol 29:441–446

Terrill SB (1987) Social dominance and migratory restlessness in the dark-eyed junco (*Junco hyemalis*). Behav Ecol Socio 21:1–11

Terrill SB, Able KP (1988) Bird migration terminology. Auk 105:205–206

Turner RM, Brown DE (1994) Sonoran desertscrub. In: Brown DE (ed) Biotic communities. Southwestern United States and northwestern Mexico. University of Utah Press, Salt Lake City, pp 181–221

van Noordwijk AJ, Pulido F, Helm B, Coppack T, Delingat J, Dingle H, Hedenstrom A, van der Jeugd H, Marchetti C, Nilsson A, Perez-Tris J (2006) A framework for the study of genetic variation in migratory behavior. J Ornithol 147:221–233

Visser ME, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164–172

Wiggins DA, Holt DW, Leasure SM (2006) Short-eared Owl (*Asio flammeus*). In: Poole A (ed) The birds of North America online. Cornell Lab of Ornithology, Ithaca. <http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/062 doi:10.2173/bna.62> Accessed 5 November 2008

Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations. Modeling, estimation, and decision making. Academic Press, San Diego

Winkler DW (2005) How do migration and dispersal interact? In: Greenberg R, Marra PP (eds) Birds of two worlds. The ecology and evolution of migration. Johns Hopkins University Press, Baltimore, pp 401–413

Winkler DW, Dunn PO, McCulloch CE (2002) Predicting the effects of climate change on avian life history traits. Proc Natl Acad Sci 99:13595–13599

Wormworth J, Mallon K (2006) Bird species and climate change: the global status report. Report prepared for the World Wide Fund for Nature, Gland, Switzerland