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Authors: Riding, Corey S., and Belthoff, James R.

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BREEDING DISPERSAL BY BURROWING OWLS (*ATHENE CUNICULARIA*) IN IDAHO

COREY S. RIDING¹ AND JAMES R. BELTHOFF

Department of Biological Sciences and Raptor Research Center, Boise State University, Boise, ID 83725 USA

ABSTRACT.—Breeding dispersal, the movement between successive breeding sites, is important to many aspects of life history and population dynamics but poorly understood for many raptor populations. We used longitudinal data collected from Burrowing Owls (*Athene cunicularia*) nesting in southwestern Idaho from 1994–2007 to examine characteristics of breeding dispersal behavior. First, we measured frequency and distance of breeding dispersal and compared those to published results from other owl populations. The dispersal frequency (78%, $n = 86$) was greater than previously reported for any Burrowing Owl population and for most owl species. The mean distance dispersed (835 ± 98 m [SE]) was slightly greater than reported distances for most other Burrowing Owl populations. Second, we examined factors associated with two decisions owls faced between breeding seasons: whether to move to a new nest site (dispersal likelihood), and how far to move if dispersing to a new site (dispersal distance). We assessed the potential effects of sex, productivity, age, and site quality on breeding dispersal likelihood and distance. Owls were more likely to disperse if they were female and if they had fledged fewer young in the previous breeding season. Nesting failure was a perfect predictor of breeding dispersal, but high productivity did not always result in philopatry. Owls dispersed farther if they were relatively younger, female, had lower productivity in the previous breeding season, and had previously nested in lower quality sites. Our comparisons to other studies indicate that the factors that most influence breeding dispersal behavior in Burrowing Owls appear to vary among populations and may relate to migration tendency and geographic heterogeneity.

KEY WORDS: *Burrowing Owl*, *Athene cunicularia*; *breeding dispersal*; *dispersal distance*; *dispersal likelihood*; *Idaho*.

DISPERSIÓN REPRODUCTIVA DE *ATHENE CUNICULARIA* EN IDAHO

RESUMEN.—La dispersión reproductiva (los movimientos entre sitios de cría sucesivos) es importante en muchos aspectos de la historia de vida y la dinámica poblacional, pero es poco comprendida en muchas especies de aves rapaces. Utilizamos datos longitudinales de individuos de *Athene cunicularia* que nidifican en el suroeste de Idaho obtenidos entre los años 1994 y 2007 para examinar las características del comportamiento de la dispersión reproductiva. Primero, medimos la frecuencia y la distancia de la dispersión reproductiva y comparamos estos datos con resultados publicados para otras poblaciones de *A. cunicularia*. La frecuencia de dispersión (78%, $n = 86$) fue mayor que la publicada anteriormente para cualquier población de *A. cunicularia* y para la mayoría de las especies de búhos. La distancia de dispersión promedio (835 ± 98 m [SE]) fue ligeramente mayor que las distancias publicadas para la mayoría de las otras poblaciones de *A. cunicularia*. Segundo, examinamos los factores asociados con dos decisiones a las que se enfrenta la especie entre las estaciones reproductivas: si moverse o no a un nuevo sitio de nidificación (probabilidad de dispersión), y a qué distancia moverse al dispersarse a un nuevo sitio (distancia de dispersión). Evaluamos los efectos potenciales del sexo, la productividad, la edad y la calidad del sitio sobre la probabilidad y la distancia de dispersión reproductiva. Los búhos fueron más propensos a dispersarse si eran hembras y si produjeron un menor número de polluelos en la estación reproductiva previa. El fracaso del nido fue un predictor perfecto de la dispersión reproductiva, pero una elevada productividad no siempre tuvo como resultado la filopatría. Los búhos se dispersaron a mayores distancias si eran relativamente más jóvenes, de sexo femenino, tuvieron una baja productividad en la época reproductiva anterior y nidificaron previamente en sitios de menor calidad. Nuestras comparaciones con otros estudios indican que los factores que mayor influencia tuvieron en el comportamiento de dispersión reproductiva en *A. cunicularia* parecen

¹ Present address: Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078 USA; email address: corey.riding@okstate.edu

variar entre poblaciones y pueden estar relacionados con la tendencia a la migración y la heterogeneidad geográfica.

[Traducción del equipo editorial]

The mobility of birds allows them to vacate their natal areas and to relocate between breeding events. These movements, generally called dispersal, can affect individual fitness, genetic structure of populations, population dynamics, geographic distribution, and social behavior (see Morrison and Wood 2009). Thus, characterizing patterns of dispersal and the selective forces that shape them is important for understanding the biology of raptors and for species conservation and management. However, dispersal behavior often exhibits spatiotemporal variation (Clarke et al. 1997), and dispersal research is challenging because it requires longitudinal study of marked individuals (Nathan 2001).

Greenwood (1980) described breeding dispersal as the movement between successive breeding sites. Such movements offer an individual the opportunity to avoid inbreeding (Johnson and Gaines 1990) or to improve fitness by moving to a better breeding site (Blakesley et al. 2006) or by breeding with a better mate (Daniels and Walters 2000). However, individuals that disperse are not guaranteed to acquire better territories or mates (Forero et al. 1999), and they could experience decreased reproductive success after dispersing (Vergara et al. 2006, Arlt and Pärt 2008a) or fail to breed entirely (Danchin and Cam 2002). In addition, dispersing may increase predation risk (Ims and Andreassen 2000, Yoder et al. 2004) or otherwise lead to increased mortality (Brown et al. 2008; but see Beaudette and Keppie 1992, Van Vuren and Armitage 1994). Conversely, philopatry, or fidelity to a breeding territory, bestows familiarity, which may increase reproductive success (Johnson and Walters 2008). Familiarity with a territory's resources such as food, shelter, and breeding sites likely make it more valuable than an unknown site (Pärt 1994, 1995, Brown et al. 2008). Familiarity with a mate also increases reproductive success (Schieck and Hannon 1989, Bradley et al. 1990), and familiar pairings may be more likely under philopatry. Given the potentially higher costs of dispersal relative to philopatry, an individual should be expected to disperse when reasonably certain of experiencing suboptimal fitness if it nests again at the same location. But, deciding whether to disperse and deciding how far to disperse are likely separate processes because selection pressures sur-

rounding these decisions may differ (Forero et al. 1999, Doerr and Doerr 2005).

Among birds, females tend to disperse more often and/or farther than males (Clarke et al. 1997). Greenwood (1980) speculated that sex-biased dispersal evolved as a consequence of mating system type. In a resource defense system, the sex that selects and defends a territory (males in most birds) is less likely to disperse because of benefits accrued via resource familiarity (Pärt 1995, Piper et al. 2008) and increased ability to retain a territory previously held (Lanyon and Thompson 1986, Shutler and Weatherhead 1992). Females, however, could use dispersal for inspecting and choosing among males or their resources. Although males may choose from any available territory, females may be limited to territories where males are present (Arlt and Pärt 2008b), and females may have no option aside from dispersal if their previous territory is not occupied by a male because of his death or dispersal. Avian species exhibiting no sex bias or, rarely, male-biased dispersal typically deviate from the resource defense mating system (e.g., Schamel and Tracy 1991).

Dispersal likelihood and distance usually both decrease with increasing age, which may be related to competitive ability or familiarity with a location (Andreu and Barba 2006, Kim et al. 2007). But age appears to have no effect or affects only one sex in other cases (Montalvo and Potti 1992, Pyle et al. 2001, Payne and Payne 1993, Arlt and Pärt 2008b). Breeding dispersal also usually varies inversely with reproductive success, such that individuals experiencing breeding failure are more likely to disperse and/or disperse farther (Haas 1998, Porneluzi 2003). Reusing a location when the previous nesting attempt produced young, but moving if the attempt failed has been termed the "Win-Stay, Lose-Switch" strategy (Switzer 1993, Hoover 2003). There also can be a negative relationship between site or habitat quality and dispersal (Przybylo et al. 2001, Sergio and Newton 2003, Sergio et al. 2009), as individuals tend to disperse away from inferior sites. Mate fidelity may also influence breeding dispersal, such that birds that retain a mate are less likely to disperse or disperse shorter distances (Andreu and Barba 2006, Blakesley et al. 2006, Middleton et al. 2006, Kim et al. 2007). Therefore, a mated pair may not act

Table 1. Predictions related to factors with potential to affect breeding dispersal likelihood or breeding dispersal distance of Burrowing Owls in southwestern Idaho.

FACTOR	DISPERSAL LIKELIHOOD ^a	DISPERSAL DISTANCE ^b
Sex	Female	Female
Age	Younger	Younger
Productivity ^c	None	None
Site Quality		
Proportional occupation	Low	Low
Burrow productivity	Low	Low
Distance to nearest neighbor	Large	Large
Distance to agriculture	Large	Large

^a Level of factor with greatest expected likelihood of dispersal.

^b Level of factor with largest expected dispersal distance.

^c Number of young fledged per nesting attempt.

independently, which could confound the relationship of breeding dispersal of an individual with other correlates (Cézilly et al. 2000).

In the face of population reductions and range contractions, Burrowing Owls (*Athene cunicularia*) have been listed as an endangered species in Canada, threatened in Mexico, and as a species of conservation concern in at least nine western US states (Klute et al. 2003). Understanding crucial elements of their natural history, such as breeding dispersal, and how it varies among populations is important for species conservation. Thus, we used data collected from 1994–2007 for Burrowing Owls nesting in southwestern Idaho to conduct an observational study of breeding dispersal. Our first objective was to describe breeding dispersal patterns and compare them to published reports of dispersal in other populations of Burrowing Owls and other owl species. Our second objective was to assess relationships of breeding dispersal likelihood and distance with sex, age, reproductive success, and site quality, which are important correlates of breeding dispersal in other species. Based on the tendencies noted above, we made predictions for each factor (Table 1) and contrasted observed patterns with these predictions using a model selection framework. As breeding dispersal has high potential costs (e.g., loss of breeding opportunity), we predicted that owls may favor philopatry. Because philopatry may enhance reproductive efforts, we also predicted that owls not dispersing between nesting attempts would increase productivity over their previous attempt and fledge more young in the next attempt than owls that had dispersed. However, the costs of

dispersal (and the benefits of philopatry) are not always realized, and they may be offset if dispersing increases fitness (e.g., moving to an area with greater food resources). Therefore, we also evaluated the prediction that dispersing individuals would fledge more young post-dispersal than they fledged pre-dispersal.

METHODS

Study Site. We studied Burrowing Owls nesting in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho in 1994–2007. The NCA was established in 1993 by Congress (Public Law 103-64) for the conservation, protection, and enhancement of raptor populations and habitats, and covers >2400 km² (about 1960 km² of public land) in Ada, Elmore, and Owyhee Counties. The area was historically shrub-steppe habitat dominated by big sagebrush (*Artemisia tridentata*) and other native shrub species, but fire and anthropogenic disturbances have converted portions to grasslands dominated by exotic annual grasses and forbs. The Snake River Canyon is the major geologic feature, but the area also contains irrigated agricultural fields, dairy farms, roads and rights-of-way, Bureau of Land Management-owned open rangelands, military training facilities, and structures such as homes, barns, and silos.

Study Species. Western Burrowing Owls (*A. c. hypugaea*) occur in grasslands, steppes, deserts, prairies, and some agricultural lands of western North America (Poulin et al. 2011). Northern populations tend to be migratory, whereas those in the southern US and Mexico may be year-round residents (Poulin et al. 2011). In southwestern Idaho, Burrowing Owls are typically present from March to October, but occasionally individuals occupy the study area during winter. A few band encounters indicate that at least some of the owls nesting in the NCA winter in California (King and Belthoff 2001). Although the longevity record for a Burrowing Owl in the wild is >8 yr (Poulin et al. 2011), only five individuals from our study population were known to breed after their fourth calendar year during 1994–2007 (J. Belthoff unpubl. data).

Western Burrowing Owls nest primarily in abandoned mammal burrows and exhibit a resource defense mating system whereby nest burrows and the area around them are defended from conspecifics (Moulton et al. 2004). Natural burrows are available throughout our study site for nesting and shelter,

and badgers (*Taxidea taxus*) are the primary excavators of burrows suitable for Burrowing Owl nests (Belthoff and King 1997). There are also many artificial burrow systems (ABSs), which the owls commonly use (Belthoff and Smith 2003), consisting of two or three buried plastic chambers with tunnels of flexible plastic pipe that open to the ground surface (Smith and Belthoff 2001).

Nest Monitoring. Our data on breeding dispersal came from a longitudinal study of owls nesting in both natural and artificial burrows within the NCA. In 1994–1996, most monitored Burrowing Owl pairs nested in natural burrows in the northwestern part of the NCA (near Kuna, Ada County). Artificial burrows were added to the study area in 1997–2000 in the northwestern and south-central (near Grand View and Mountain Home, Elmore County) regions of the NCA. By 2001–2007, a large number of artificial burrows had been added across larger portions of the NCA, and nearly all monitored pairs nested in ABSs in these years. In all years, non-standardized foot and vehicle surveys for Burrowing Owls nesting in natural and artificial burrows began in March and continued throughout the breeding season. In earlier years (1994–1996), the smaller study area was more intensively surveyed to discover nests among natural burrows. From 1997–2007, detection efforts focused primarily on artificial burrows and historical nest sites in natural burrows.

At all located nests, we monitored reproductive activities and attempted to capture adults and young for marking. Monitoring included nonstandardized observation bouts at natural burrows and excavations of nest chambers at ABSs. Adults were captured using one-way traps or noose carpets placed at the mouth of nest burrows, and juveniles were captured with noose carpets or other traps at natural burrows and usually by hand when researchers excavated nests in ABSs. Adult males typically spend less time inside nest burrows and therefore were captured less frequently than adult females. This gave a female bias to the sample and hindered our ability to statistically assess mate change via death or divorce. We fitted captured owls with a combination of colored leg bands and a USGS aluminum band, which allowed for later identification.

Reproductive Definitions. We considered that an individual attempted nesting if it attended a burrow (natural or artificial) where at least one egg was laid. We defined philopatry as an owl using the same ABS or natural burrow in consecutive nesting attempts, and breeding dispersal as an owl nesting in a

different ABS or natural burrow in its subsequent attempt. We used a geographic information system (GIS) to measure dispersal distance as the Euclidean distance between an individual's consecutive nest burrows. Although >1 nesting attempt by an individual in one year occurred infrequently, most observations were between-year events in which an owl had known nesting locations in year_i and year_{t+1}. We did not perform statistical analyses of within-year dispersals. Statistical analyses included only observations for which we knew nesting locations in consecutive years, and we used the percent frequency (hereafter simply frequency) to describe the quantity of dispersing owls.

We defined productivity as the number of young fledged per single nesting attempt. We considered any young alive at approximately 4 wk post-hatching as fledged and estimated the number of fledglings as the maximum number of young observed or captured at the burrow near that time. As there are no definitive methods for distinguishing among adult age classes in Burrowing Owls (Pyle 2008), we used minimum possible calendar years for assigning age to adults. For example, an individual first captured as a nesting adult was aged as after-hatch-year (AHY); in subsequent years, its age classification increased to after-second-year, after-third-year, and so on. Because of the owls' short life span, we believe that most individuals captured and banded for the first time as adults (AHY) were probably in their second or third calendar year. We had only a few individuals in the data set that were originally banded as nestlings and subsequently followed through life, so we placed all owls in one of two age classes as an index for assessing potential effect of age on patterns of breeding dispersal: (1) younger, if they were known or suspected to be 2–3 yr old, and (2) older, if they were known to be ≥4 yr old.

Habitat Quality Indices. It is important to use multiple metrics when indirectly measuring habitat quality (Johnson 2007), so we used four proxies for the site quality of each nest burrow. First, we used proportional occupation, which was the number of years a burrow was occupied by nesting owls divided by the number of years it was available during a 7-yr span (year_{t-3} to year_{t+3}). Second, burrow productivity was the total number of young fledged at a burrow divided by the number of years it was available during year_{t-3} to year_{t+3}. We used a 7-yr moving window for both indices because sites were generally the same from one year to the next but sometimes

exhibited great change over longer periods. We expected that better sites should be occupied more often (Linkhart and Reynolds 1997, Sergio and Newton 2003) and more young should be produced at better sites, so higher values indicate higher quality for both indices. Some evidence suggests that Burrowing Owls derive benefits from nesting close to irrigated agriculture (Moulton et al. 2005, Conway et al. 2006, Restani et al. 2008) and to other Burrowing Owls (Welly 2010), indicating that shorter distances to either may indicate a higher quality site. Thus, our third and fourth indices of site quality were distance (measured in a GIS) from the nest burrow to (1) the nearest irrigated agriculture, and (2) the closest neighboring Burrowing Owl nest.

Statistical Analyses. We performed analyses using SAS 9.4 (SAS Institute Inc., Cary, NC USA) with individual owls as the unit for analyses, and we report means \pm SE unless otherwise noted. We assessed the repeatability of breeding dispersal distance per Lessells and Boag (1987) for individuals with multiple observations, using a dispersal distance of 0 m for cases of philopatry. We used PROC GENMOD with Poisson distribution, log link function, and individual as a repeated factor to assess owl productivity relative to the effects of dispersal status (dispersed or philopatric), year (t or $t+1$), and the interaction term status \times year. Based on this model, we made pairwise comparisons of relevant means with the LSMEANS statement and considered the difference between least squares (LS) means important if the 95% confidence interval (CI) for the estimated difference did not contain zero.

We used a model selection framework to examine the potential influence of sex, age, year, number of young fledged, and four indices to site quality (distance to nearest neighbor, distance to agriculture, burrow productivity, and proportional occupation) on breeding dispersal likelihood in a generalized linear mixed model (GLMM) using PROC GLIMMIX (binomial distribution, logit link function, and individual as a random effect). We created 18 ecologically plausible models in addition to global and null models and used Akaike's Information Criterion corrected for small samples (ΔAIC_c) and Akaike weights (w_i) to rank them. We investigated potential effects of these same variables on dispersal distance but restricted analysis to owls that dispersed. We conducted GLMM using PROC GLIMMIX with lognormal distribution, identity link function, and individual as a random effect to examine relationships with breeding dispersal dis-

tance. We assessed the same models as in the likelihood analysis and ranked them using ΔAIC_c and w_i . For analyses of both breeding dispersal likelihood and breeding dispersal distance, we considered models with more support ($\Delta\text{AIC}_c < 6$ and $w_i > 0.15$) important, unless they were more complex versions of higher-ranking models (Richards 2008, Arnold 2010), and model-averaged when multiple candidate models met criteria for importance.

RESULTS

Dispersal Patterns. Of 488 adult and 2354 nestling Burrowing Owls banded during 1994–2007, marked owls returned to nest within the study site 172 times, among which 86 individual owls had known nesting locations in consecutive years. Of these, 22 owls had multiple cases, resulting in 113 total observations (76% dispersed) of owls nesting in consecutive years within the NCA. The geometric mean dispersal distance including philopatric individuals and all repeat observations was 546 m (range: 0–3454 m; $n = 113$). For individuals with multiple observations, within-individual repeatability was moderately high ($r = 0.648$; see Harper [1994] for interpretation), as 68% always dispersed or were always philopatric. Thus, multiple observations from an individual may not be independent, so we used only one randomly selected observation per individual to calculate the following dispersal metrics. Burrowing Owls displayed high breeding dispersal frequency (78%; 67 of 86), and dispersing owls moved $835 \text{ m} \pm 98$ (range: 55–3396 m; $n = 67$) between nest sites.

Productivity Comparisons. The number of young fledged in year $t+1$ did not differ between philopatric and dispersing owls (LS mean difference = 0.038, lower 95% CI = -0.201 , upper 95% CI = 0.278), nor did number fledged differ between year t and year $t+1$ for philopatric (LS mean difference = 0.089, lower 95% CI = -0.236 , upper 95% CI = 0.415) or dispersing (LS mean difference = -0.155 , lower 95% CI = -0.334 , upper 95% CI = 0.025) owls (Fig. 1).

Within-year Dispersal and Mate Fidelity. Within-year breeding dispersal, i.e., an owl sequentially nesting in two separate locations in one breeding season, was recorded eight times ($n = 2$ males, 6 females), dispersal distance for these observations was $119 \text{ m} \pm 30$ (range: 50–312 m), and all recorded within-year dispersals occurred after an unsuccessful nesting attempt. We never recorded a second nesting attempt (at the same burrow or elsewhere)

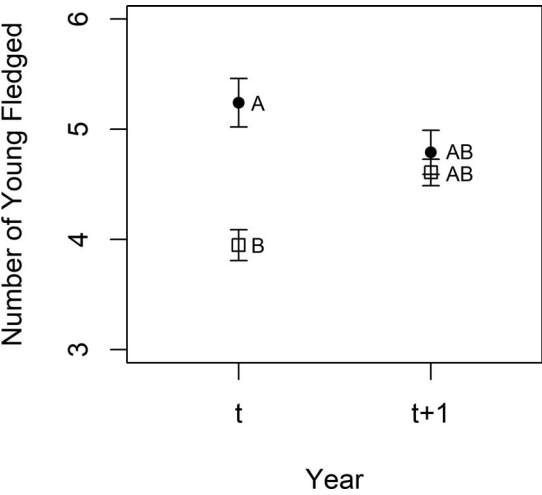


Figure 1. Least squares mean (\pm SE) number of young fledged per nesting attempt by philopatric (filled circles) and dispersing owls (open squares) in years t and $t+1$. Letters indicate means with overlapping 95% confidence intervals, and $n = 26$ and 87 for philopatric and dispersing owls, respectively.

within a breeding season by any owls that successfully reared a brood, which indicates that owls in this population are single-brooded. Although we lacked sufficient sample size to statistically assess mate fidelity as a correlate of breeding dispersal, we observed little mate fidelity in this population of Burrowing Owls: of 15 pairs where nesting locations of both owls were known in consecutive years, only one pair (6.7%) reunited in the subsequent year. Thus, very few of our observations might be affected by this potential lack of independence.

Breeding Dispersal Likelihood. Two candidate models of breeding dispersal likelihood were strongly supported, but only one met criteria for importance (Table 2). The important model included the factors sex and productivity (number of young fledged per nesting attempt). Owls were more likely to undertake breeding dispersal if they were female or had fledged fewer young in year_t (Table 3, Fig. 2), such that odds of breeding dispersal were almost six times higher in females and decreased by 17% with each additional fledgling. Without exception, owls that failed to produce fledglings (i.e., had nesting success = 0; $n = 9$ females and 2 males) underwent breeding dispersal in the subsequent year (Fig. 2). High productivity was not a perfect predictor of philopatry, however, as owls with the highest productivity ($n = 10$ or 11 fledglings) also always

Table 2. Model selection results for GLMM of breeding dispersal likelihood of Burrowing Owls in southwestern Idaho. Models are sorted by Akaike's Information Criterion corrected for small sample size.

PARAMETERS ^a	K	ΔAIC_c	LIKELIHOOD	ω_i
Sex, Fledge	4	0.000	1.000	0.678
Sex, Fledge, Age	5	1.690	0.430	0.291
Sex	3	7.640	0.022	0.015
Sex, Age	4	8.870	0.012	0.008
Sex, Age, PO, MP	6	10.920	0.004	0.003
Fledge	3	12.630	0.002	0.001
Dnn	3	12.650	0.002	0.001
PO, MP, Dag, Dnn	6	13.150	0.001	0.001
Global	20	13.200	0.001	0.001
MP	3	15.720	0.000	0.000
Sex, Fledge, Year	15	16.810	0.000	0.000
Dag	3	17.420	0.000	0.000
Null	2	17.710	0.000	0.000
PO, MP	4	17.840	0.000	0.000
PO	3	18.810	0.000	0.000
Age	3	19.210	0.000	0.000
PO, MP, Dnn, Year	16	25.450	0.000	0.000
Sex, Age, Year	15	27.380	0.000	0.000
Year	13	34.790	0.000	0.000
PO, MP, Year	15	36.640	0.000	0.000

^a Possible parameters, which are described in methods, include Sex, Fledge (number of young fledged in year_t), Age (categorical age: younger or older), PO (proportional occupation), MP (mean productivity), Dag (distance to agriculture), Dnn (distance to nearest neighbor), and Year (categorical: 1995 – 2006).

dispersed, although the number of such owls was very low (Fig. 2).

Breeding Dispersal Distance. Three candidate models of breeding dispersal distance were considered important (Table 4). The factor year appeared in all, the factor sex was in two, and productivity, age, proportional occupation, and mean productivity appeared in one model each. The averaged model indicated that for those owls that dispersed, they went farther if they were female (females: 895 ± 113 m, $n = 55$; males: 558 ± 169 m, $n = 12$), were younger (younger: 837 ± 106 m, $n = 60$; older: 491 ± 174 m, $n = 4$), fledged fewer young in year_t, nested in burrows in year_t that were less frequently occupied, and nested in burrows in year_t with lower mean productivity (Table 5, Fig. 3).

DISCUSSION

Productivity Comparisons. We predicted that (1) philopatric owls would fledge more young in year_{t+1} than in year_t, (2) dispersing owls would fledge more young in year_{t+1} than they did in year_t, and (3)

Table 3. Parameter estimates (with standard errors and 95% confidence intervals) from the top-ranked GLMM of breeding dispersal likelihood for Burrowing Owls in Idaho predicting odds of dispersing relative to not dispersing (philopatry).

PARAMETER ^a	ESTIMATE	SE	95% CI	
			LOWER	UPPER
Intercept	0.7305	0.5503	-0.3643	1.8253
Sex:				
Female	1.7843	0.5019	0.7526	2.8160
Male ^b	0			
Fledge	-0.1586	0.0851	-0.3336	0.0163

^a Parameters, which are described in methods, include Sex and Fledge (number of young fledged in year_i).

^b Served as reference category for categorical variable.

philopatric owls would fledge more young than dispersing owls in year_{t+1}. None of these predictions surrounding productivity were supported. Combined with the high frequency of dispersal we observed, this indicates that philopatry did not confer realized fitness benefits over dispersal in this population. However, we did not monitor survival of young beyond fledging to independence, which may

be a better measure of reproductive success (Streby et al. 2014). Variation in fledgling survival could have led to differential fitness between the pairs we compared, but such variation may be minimal, as juveniles in this population have exhibited frequent and distant movements post-fledging to satellite burrows in the same general areas (King and Belthoff 2001).

Dispersal Frequency and Likelihood Modeling. The frequency of breeding dispersal that we observed was much higher than previously reported for Burrowing Owls in lower latitudes, but it was only slightly higher than in northern populations (Table 6). The combined frequency of breeding dispersal for both sexes also appears to be among the highest for any owl species previously studied (Table 6). The high dispersal frequency was unexpected, in part, because in mark-recapture studies such as ours, individuals dispersing beyond study area boundaries will go undetected, which reduces estimates of dispersal frequency (Barrowclough 1978, Koenig et al. 1996).

There are several factors that may have contributed to the relatively high breeding dispersal frequency we observed in Burrowing Owls nesting in the

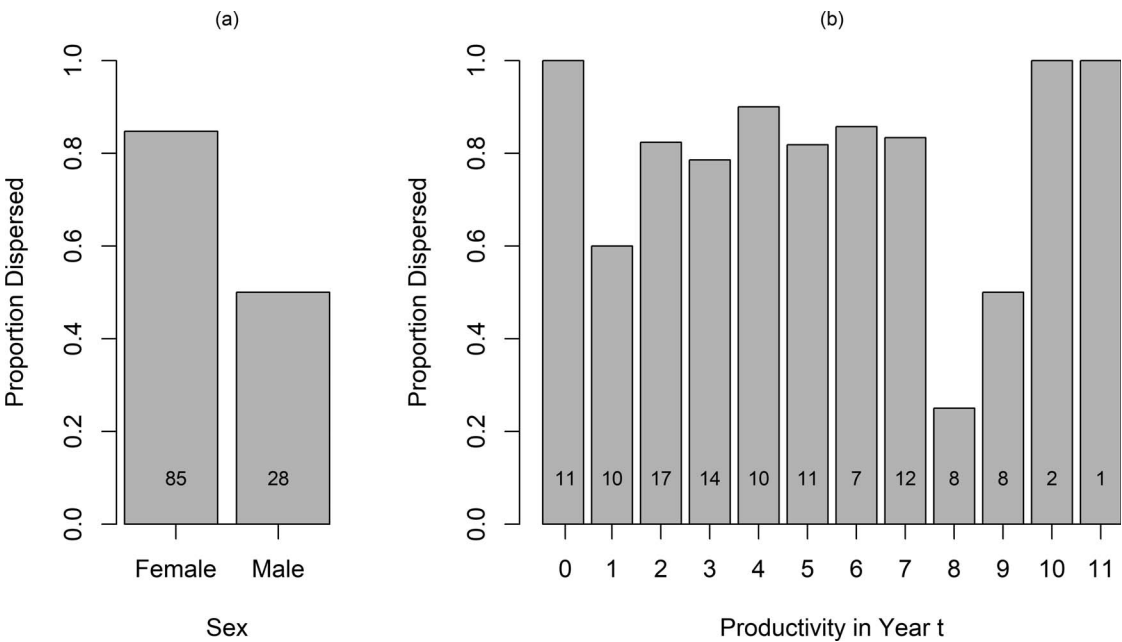


Figure 2. Proportion of Burrowing Owls nesting in southwestern Idaho that underwent breeding dispersal as a function of (a) their sex and (b) number of young fledged per nesting attempt (productivity) in year_t. For (a): $n = 85$ and 28 for Female and Male, respectively. For (b): the number in each bar indicates sample size.

Table 4. Model selection results for GLMM of breeding dispersal distance of Burrowing Owls in southwestern Idaho. Models are sorted by Akaike’s Information Criterion corrected for small sample size.

PARAMETERS ^a	K	ΔAIC _c	LIKELIHOOD	w _i
Sex, Fledge, Year	15	0.000	1.000	0.495
Sex, Age, Year	15	1.100	0.577	0.285
PO, MP, Year	15	2.290	0.318	0.157
Year	13	4.300	0.116	0.058
PO, MP, Dnn, Year	16	9.140	0.010	0.005
PO	3	22.350	0.000	0.000
Sex, Fledge	4	23.270	0.000	0.000
Sex, Age, PO, MP	6	23.430	0.000	0.000
Sex, Age, Fledge	5	24.110	0.000	0.001
PO, MP	4	24.360	0.000	0.000
Sex	3	25.120	0.000	0.000
Sex, Age	4	25.920	0.000	0.000
Fledge	3	26.610	0.000	0.000
MP	3	27.340	0.000	0.000
Null	2	27.840	0.000	0.000
Age	3	28.580	0.000	0.000
Dnn	3	33.780	0.000	0.000
Global	20	39.660	0.000	0.000
PO, MP, Dag, Dnn	6	41.250	0.000	0.000
Dag	3	42.210	0.000	0.000

^a Possible parameters, which are described in methods, include Sex, Fledge (number of young fledged in year_i), Age (categorical age: younger or older), PO (proportional occupation), MP (mean productivity), Dag (distance to agriculture), Dnn (distance to nearest neighbor), and Year (categorical: 1995 – 2006).

NCA. First, Burrowing Owls have low annual adult survival rates (Poulin et al. 2011, Newton et al. 2016) and philopatry does not appear to provide fitness benefits in this population. Because they do not live long, perhaps this favors owls moving to different sites when they become vacant and helps explains the high dispersal frequency we observed in the migratory population of Burrowing Owls inhabiting the NCA. Second, the sample was biased toward females, and females dispersed more frequently than males (87% and 52%, respectively). Thus, the larger number of females contributing to our analysis increased the measured frequency for the population as a whole. However, the frequency of dispersal for females was lower in other studies (De Smet 1997, Millsap and Bear 1997, Lutz and Plumpton 1999, Catlin et al. 2005, Conway et al. 2006), so even with a comparably female-biased sample those studies would still have recorded lower dispersal frequencies. Third, different methods may have contributed to differences in recorded frequencies. For example, Catlin et al. (2005) focused

Table 5. Model-averaged parameter estimates (with standard errors and 95% confidence intervals) from the top-ranked GLMM models of breeding dispersal distance for Burrowing Owls in Idaho.

PARAMETER ^a	ESTIMATE	SE	95% CI	
			LOWER	UPPER
Intercept	6.538	0.558	5.423	7.653
Year:				
1995	−1.353	0.830	−3.396	0.691
1996	−1.156	0.621	−2.690	0.378
1997	−0.551	0.536	−1.875	0.773
1998	−0.342	0.514	−1.610	0.926
1999	0.089	0.559	−1.291	1.469
2000	−0.050	0.541	−1.384	1.285
2001	−0.578	0.433	−1.639	0.484
2002	0.710	1.026	−1.821	3.24
2003	−0.667	0.605	−2.159	0.826
2004	0.488	0.562	−0.897	1.874
2005	0.484	0.634	−1.082	1.049
2006 ^b	0			
Sex:				
Female	0.431	0.250	−0.182	1.043
Male ^b	0			
Fledge	−0.042	0.023	−0.098	0.015
Age:				
Older	−0.093	0.079	−0.296	0.089
Younger ^b	0			
MP	−0.018	0.017	−0.063	0.026
PO	−0.127	0.116	−0.426	0.172

^a Parameters, which are described in methods, include Sex, Fledge (number of young fledged in year_i), Age (categorical age: younger or older), PO (proportional occupation), MP (mean productivity), and Year (categorical: 1995 – 2006).

^b Served as reference category for categorical variable.

on the movement away from a territory, so they defined dispersal as movement >100 m from the previous nest. We focused on movement away from a nest site, so we measured dispersal when owls used a different nest burrow. Five of 67 dispersing owls in our study moved <100 m from their previous nest burrow, but all moved >50 m. Applying Catlin et al.’s (2005) definition would decrease dispersal frequency in our study to 72%, which still exceeds other reported breeding dispersal frequencies. Finally, migratory birds tend to disperse longer distances than nonmigrants (Paradis et al. 1998), and they may also disperse with greater frequency. Resident Burrowing Owl populations in Florida (Millsap and Bear 1997) and California (Catlin et al. 2005), for instance, have relatively low dispersal frequencies, and published frequencies from migratory populations (De Smet 1997, Lutz and Plumpton

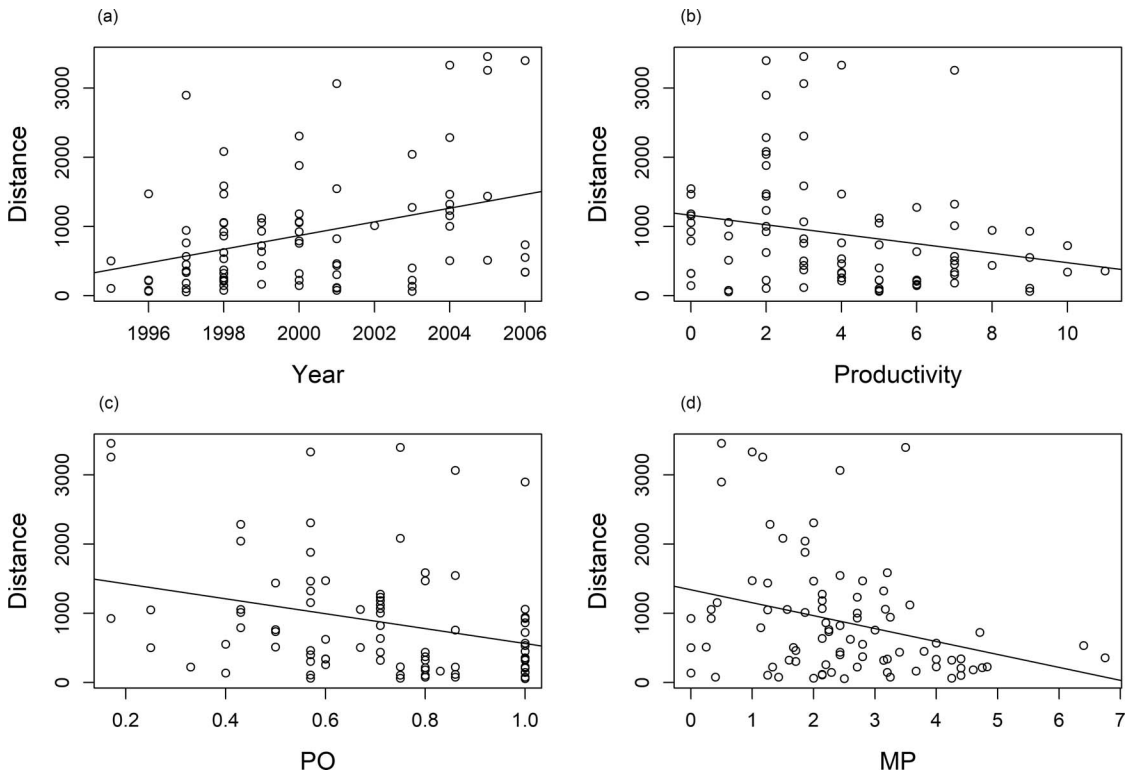


Figure 3. Breeding dispersal distance (m) by (a) year_{t+1}, (b) productivity in year_t, (c) proportional occupation (PO), and (d) mean productivity (MP) for Burrowing Owls nesting in southwestern Idaho that undertook dispersal. PO and MP are indices of site quality. Simple linear regression lines are shown.

1999, Conway et al. 2006) are generally higher. Thus, some variation in Burrowing Owl breeding dispersal frequency appears to be related to migratory habit among populations, with dispersal frequency higher in migratory populations such as the one we studied.

None of the proxies for site quality appeared in important models of breeding dispersal likelihood, i.e., whether an owl dispersed or was philopatric. This is somewhat surprising because the literature includes examples of strong relationships for avian breeding dispersal with site occupancy (Newton and Marquiss 1982, Montalvo and Potti 1992, Arlt and Pärt 2008a), site productivity (Forero et al. 1999, Blondel et al. 2000, Blakesley et al. 2006, Pasinelli et al. 2007), and other measures of site quality, although these examples are from species other than Burrowing Owls. The lack of a relationship between these indices and dispersal likelihood in our study population of Burrowing Owls may have two interpretations. First, these indices may not have tracked site quality as closely as we expected. Second,

other factors may have induced some owls to regularly select suboptimal sites, which undermines the value of these indices. This does not mean that site quality had no effect on Burrowing Owl breeding dispersal; in fact, it was related to distance dispersed, but it appears the chosen site quality indices were less important than other factors for owls in deciding whether to disperse.

When examining relationships to dispersal likelihood, we found that the factors age and year did not appear in any important candidate models. Although it is possible that young and old owls did not differ in their propensity to disperse, our inability to precisely age adults into more than just two estimated categories and the relatively small number of owls in the “older” category probably obscured the relationship between individual age and dispersal likelihood, if indeed one existed. That year was not an important factor suggests that annually variable environmental factors had relative-

Table 6. Percent frequency and mean distance of breeding dispersal for several owl species based on literature estimates. Actual frequency and distance values are likely greater than those given because they were obtained from returning owls only, and non-returning owls may have dispersed beyond study area boundaries.

SPECIES	LOCATION	% FREQUENCY			DISTANCE (m)			SOURCE
		MALES	FEMALES	COMBINED	MALES	FEMALES	COMBINED	
<i>Aegolius acadicus</i>	Oregon	–	–	94	770	3400	2490	Marks et al. 2015
<i>A. acadicus</i>	British Columbia	–	–	86	–	–	–	Cannings 1987
<i>A. acadicus</i>	Idaho	–	–	98	–	–	–	Marks and Doremus 2000
<i>A. funereus</i>	Finland	–	–	–	~1200 ^a	~5000 ^a	~3100 ^b	Korpimäki 1987
<i>A. funereus</i>	Finland	0 ^c	91 ^c	≤ 36 ^c	–	–	–	Korpimäki 1988
<i>A. funereus</i>	Finland	–	–	–	1300 ^a	5500 ^a	3400 ^b	Korpimäki 1993
<i>A. funereus</i>	Finland	25 ^d	–	–	0 ^{a,d}	–	–	Hakkarainen et al. 2001
<i>Athene noctua</i>	Denmark	–	–	≤ 15 ^c	–	–	–	Sunde et al. 2009
<i>A. cucularia</i>	Manitoba	49	67	55	200 ^f	10900	3900 ^g	De Smet 1997
<i>A. cucularia</i>	Florida	17	26	22 ^b	96 ^a	230 ^a	163 ^b	Millsap and Bear 1997
<i>A. cucularia</i>	Colorado	25	37	31 ^b	–	–	–	Lutz and Plumpton 1999
<i>A. cucularia</i>	California	32	37	34	431	526	472	Catlin et al. 2005
<i>A. cucularia</i>	Washington	60	71	64	–	–	–	Conway et al. 2006
<i>A. cucularia</i>	Idaho	52	87	78	558	895	835	This study
<i>Otus elegans</i>	Lanyu Island	–	–	–	1700	1800	1750 ^b	Severinghaus 2002
<i>O. elegans</i>	Lanyu Island	48	60	53 ^h	–	–	–	Bai and Severinghaus 2012
<i>Psiloscops flammeolus</i>	New Mexico	20	46	33	179	289	263	Arsenault et al. 2005
<i>P. flammeolus</i>	Colorado	8	44	25 ⁱ	–	–	–	Linkhart and Reynolds 2007
<i>Strix occidentalis</i>	Oregon, Washington	–	–	–	–	–	6100	Forsman et al. 2002
<i>S. occidentalis</i>	California	–	–	7	–	–	7000 ^a	Blakesley et al. 2006
<i>S. occidentalis</i>	California	–	–	9	–	–	–	Seamans and Gutierrez 2007
<i>S. occidentalis</i>	California	4 ^j	6 ^j	5 ^j	–	–	–	Gutierrez et al. 2011
<i>S. occidentalis</i>	New Mexico	–	–	5	3600	5100	4511 ^k	Ganey et al. 2014
<i>Tyto alba</i>	Utah	–	–	4 ^l	2200	2300	2300	Marti 1999

^a Denotes a median distance. Mean distance is probably greater.

^b Not given by authors. We assumed an equal number of males and females to derive.

^c Not given by author. “Only two females stayed on the same territory...there are no observations of territory shifts by males within the study area and no recoveries of males outside the study area” (p. 103). Sample size for females appears to be 22 (from Table 5, p. 101); hence, female frequency is 90.9% (20 of 22). Based on Table 8 (p. 102), there were ≥33 males, so combined frequency is ≤ 36.4% (20 of ≥55).

^d Values are for a control group, and median distance includes those not dispersing. An experimental group exposed to predation risk had a frequency of 80% and a median distance of 1.5 km.

^e Not given by authors. “Of 27 owls, 23 stayed in the territory...” (p. 543); hence 4 of 27 (14.8%) dispersed or died.

^f Excludes one exceptional movement of 99 km that would increase mean to 3 km.

^g Calculated from sample sizes given in abstract and means given in text.

^h Not given by authors. Based on sample sizes given in Fig. 1a (p. 254) of 231 males and 190 females.

ⁱ Not given by authors. Derived from sample sizes provided by Linkhart and McCallum (2013).

^j Not given by authors. Derived from yearly values in Table 1 (p. 595).

^k Not given by authors. Derived from mean distances and sample sizes for each sex (p. 520).

^l Includes some within-year observations.

ly little effect on decisions by owls to disperse or remain philopatric.

Only sex of an owl and productivity in the previous breeding season were important factors in explaining dispersal likelihood, and their relationships matched our predictions. Females were more likely than males to disperse, and philopatry increased with number of young fledged in year_t. One perfect predictor of breeding dispersal appeared to be nesting failure (i.e., zero production in year_t), but owls with the highest productivity similarly always dispersed. Notably, all three instances of breeding dispersal following high productivity (number fledged in year_t ≥ 10) were of female owls, which is the sex class that undergoes dispersal most frequently.

The results of the breeding dispersal likelihood modeling agree in part with previous studies of Burrowing Owls (Millsap and Bear 1997, Lutz and Plumpton 1999, Catlin et al. 2005). Consistent with our results, two previous studies found that nesting failure in year_t increased the likelihood of dispersal (both sexes: Catlin et al. 2005; females only: Lutz and Plumpton 1999). Catlin et al. (2005) did not test directly for effects of sex but appeared to assume that they would differ. Other studies found no difference in dispersal likelihood between males and females (Millsap and Bear 1997, Lutz and Plumpton 1999). Only Millsap and Bear (1997) studied the effects of age and found that younger owls were more likely to undertake breeding dispersal than older owls. Catlin et al. (2005) were able to investigate the effects of mate fidelity, which we could not, and found that owls not re-mating with the same individual dispersed more often than owls that retained mates. Unlike ours, previous studies did not examine the effects of site quality on breeding dispersal in Burrowing Owls, but we found that site quality did not strongly relate to whether owls dispersed or remained philopatric. Two indices of site quality did, however, influence how far owls dispersed when they were not philopatric, as we describe below.

Dispersal Distance and Distance Modeling. The method of data collection we used to assess Burrowing Owl breeding dispersal in southwestern Idaho should have biased distance estimates by shortening them (Barrowclough 1978, Porter and Dooley 1993, Thompson and Goodman 1997, Brommer and Fred 2007). However, mean breeding dispersal distance in the NCA was greater than distances for Burrowing Owls in most other locations (Table 6). Birds in migratory populations tend to disperse farther than those in sedentary populations (Paradis et al. 1998, Belliure et al. 2000; but see Middleton et al. 2006).

Migratory populations of Burrowing Owl populations also appear to move farther when undertaking breeding dispersal, but owls in the NCA were closer in mean breeding dispersal distance to nonmigratory populations (see Table 6 for sedentary populations in Florida and California and migratory populations in Canada and Idaho). Other than Flammulated Owls (*Psiloscops flammeolus*), owl species for which breeding dispersal data are published had much longer mean dispersal distances. Bowman (2003) found that natal dispersal distances covary with territory size in some birds. If habitats or life history attributes necessitate large territories or low nesting densities, then dispersal distances are longer, as individuals have to travel farther to move beyond occupied territories. Therefore, longer breeding dispersal distances by other owl species could simply be a function of these owls having larger territories than Burrowing Owls. Indeed, some of the other species in Table 6 defend all-purpose territories, whereas Burrowing Owls appear to defend only the space around their nest and forage outside of this area (Moulton et al. 2004). Finally, it is also possible that differences in mean dispersal distance among Burrowing Owl studies (De Smet 1997, Millsap and Bear 1997, Catlin et al. 2005) indicate nesting density variation among locations or different spatial distributions of available nest burrows, such that large distances between nesting sites may require longer dispersal movements to move between sites.

We believe the association of year with dispersal distance in all top models was at least partially related to the increase in study area size over time, which allowed us to observe increasingly longer dispersal movements. Interannual variation in environmental conditions, prey populations, and predators also may have influenced annual differences in dispersal distances, although we did not measure these factors. Among the variables we measured, only distance to agriculture and distance to nearest neighbor did not appear in any of the important models of breeding dispersal distance. All of the remaining factors that appeared in top models were associated with dispersal distance in the predicted direction. Younger owls, females, less productive owls, and owls nesting in lower quality sites (based on proportional occupation and mean productivity) undertook longer breeding dispersal movements. This is consistent with the dispersal movements of Burrowing Owl populations in Florida (Millsap and Bear 1997), where females dispersed farther than males, and in California (Catlin et al. 2005), where

owls whose nests failed dispersed farther than owls that successfully bred.

Separate modeling of breeding dispersal likelihood and breeding dispersal distance was validated because important models varied between the two processes. Although sex of the owl and productivity in the previous year affect both dispersal likelihood and distance, year, age, and site quality were variables that associated only with how far owls dispersed. However, because owls did not produce more fledglings following dispersal, the fitness consequences of philopatry and dispersal for this population are unclear. For instance, one of the strongest predictors of dispersal was nesting failure, but the highest levels of productivity were not equally reliable predictors of philopatry. Additionally, the factors influential for breeding dispersal in southwestern Idaho did not completely coincide with results from other studies of Burrowing Owls. Even within a species, dispersal trends often vary spatiotemporally, and other studies differed in geographic location, local habitat, migratory tendency of the population, and time frame. Any of these aspects could have contributed to the differences in dispersal trends among the various Burrowing Owl populations.

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