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Comparative demography of Burrowing Owls in agricultural and urban landscapes in southeastern Washington

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ABSTRACT. Anecdotal evidence suggests that Burrowing Owls have declined in the state of Washington. We examined the status of these owls in agricultural and urban habitats to better understand the underlying causes of these declines. Nest density was higher in the area dominated by agriculture (0.67 nests/km^2) than in the urban area (0.28 nests/km^2), and re-use of nest burrows was more common in the agricultural area. We found no difference in mean clutch size between the two areas, but nesting success was higher in the agricultural area. The mean number of fledglings per nesting attempt was higher in the agricultural area (2.02 vs. 1.47), but we found no difference between the two areas in the mean number of fledglings per successful nest (3.2 vs. 3.1). Both natal recruitment (4% vs. 8%) and annual return rate of adults (30% vs. 39%) were lower in the agricultural area than in the urban area, suggesting that the owl population in the agricultural area may not be stable and may be a "sink" population. Due to high burrow fidelity from year to year, and the tendency of some owls in Washington to overwinter, we recommend that legal protection of nest burrows be extended to the nonbreeding season.

SINOPSIS. **Demografía comparativa de *Athene cunicularia* entre áreas agrícolas y urbanas en el sudeste de Washington**

Evidencia aneedótica ha sugerido que el buho *Athene cunicularia* se ha reducido en números en el estado de Washington. Examinamos el estatus de dichos buhos en áreas agrícolas y en urbanas para tratar de determinar las causas de la merma poblacional. Se encontró una densidad mayor de nidos en áreas agrícolas (0.67 nidos/km cuadrado) que en áreas urbanas (0.28 nidos/km cuadrado). No encontramos diferencias en la camada promedio entre ambos tipos de áreas, pero el éxito de anidamiento fue mayor en áreas agrícolas. El número promedio de volantones por intento de anidamiento fue más alto en áreas agrícolas (2.02 vs. 1.47) pero no encontramos diferencias en el número promedio de volantones por nido exitoso (3.2 vs. 3.1). El reclutamiento poblacional (4% vs. 8%) y el retorno anual de adultos fue menor en áreas agrícolas, lo que sugiere que la población de buhos en áreas agrícolas no es estable, o se está reduciendo. Dada la alta fidelidad de año a año por madrigueras y la tendencia de muchos buhos en Washington de pasar el invierno en las mismas, recomendamos que la protección legal de estas aves incluyendo el periodo en el cual no se están reproduciendo.

Key words: agriculture, *Athene cunicularia*, fecundity, land use, natal recruitment, nesting success, reproductive success, shrub-steppe.

Burrowing Owl (*Athene cunicularia*) populations are thought to be declining in eastern Washington (Smith et al. 1997, Klute et al. 2003, Conway et al. 2005a), and in other portions of their breeding range in North America (Dechant et al. 1999, Wellicome and Holroyd 2001, but see DeSante et al. 2004). Burrowing Owls are listed as a "Species of National Conservation Concern" on the federal level and in every U.S. Fish and Wildlife Service Region where they occur (U.S. Fish and Wildlife Service 2002). They are listed as endangered, threatened, or a species of concern in nine U.S. states (Klute et al. 2003). Due to contraction of the historical breeding range (Wellicome and Holroyd 2001) and perceived population declines in Washington, the

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Washington Department of Fish and Wildlife is currently evaluating the status of Burrowing Owls for consideration as a state threatened or endangered species. Causes of localized population declines are not the same throughout their western range. Eradication of prairie dogs (*Cynomys* spp.) has caused declines in the Great Plains (Desmond and Savidge 1996, Desmond et al. 2000), habitat destruction due to urban growth has caused declines in coastal California (Trulio 1995, 1997b, Klute et al. 2003), and reduction in numbers of colonial ground squirrels (*Spermophilus* spp.), yellow-bellied marmots (*Marmota flaviventris*), and American badgers (*Taxidea taxus*) has likely caused declines in Washington (Conway et al. 2005a).

Burrowing Owls breed in areas with a variety of different land uses in eastern Washington, but nesting densities appear to be higher in agricultural and urban areas than in areas of native shrub-steppe habitat. To determine the status of Burrowing Owls in these areas and to better understand underlying causes of population declines in the state, we conducted field studies of Burrowing Owls in the southeastern quarter of Washington from 2000 to 2004. We compared demographic parameters between two study areas: a predominantly agricultural landscape in east-central Washington and an urban landscape in southeastern Washington.

METHODS

Study area. We conducted field work at two study areas in the southeastern quarter of the state of Washington. The centers of the two study areas were 97 km apart and the edges of the study areas were 47 km apart. The more northern study area (hereafter referred to as the agricultural area) was approximately 3600 km^2 and located in Adams and Grant counties. The primary land use is irrigated cropland, but also includes pasture, urban, suburban, and undisturbed shrub-steppe. Most nest burrows were adjacent to agricultural fields, with $>50\%$ of the area within 100 m of the nest consisting of agricultural fields at 60% of the nest burrows. The study area encompassed the towns of Moses Lake, Warden, and Othello. Elevation varies from 316 to 398 m above sea level. Annual precipitation is usually <25 cm, primarily rain from October to May (Blackwood et al. 1997). The more southern study area (hereafter referred to as the urban area) was approximately 1500 km^2 and located in Benton, Franklin, and Walla Walla counties. Nest burrows were concentrated in and around the towns of Pasco, Kennewick, Richland, and West Richland. The primary land uses include urban, suburban, industrial, abandoned fields, and undisturbed shrub-steppe (57% of nests had some form of urban or industrial development within 100 m of the nest burrow and 64% had some native shrub-steppe within 100 m). Elevation varies from 109 to 150 m above sea level. Annual precipitation averages 18 cm, primarily rain from November to February (Hoitink and Burk 1995, Benton Clean Air Authority 2004).

Breeding density and timing of breeding. We established roadside survey points in southeastern Washington and used a standardized survey protocol to locate newly established owl nests each year (Conway and Simon 2003). Each year, we added additional survey points and, by 2004, conducted surveys at 1165 points (627 in the agricultural area and 535 in the urban area). We used data from 2004 surveys to estimate breeding density. We conducted all surveys from 15 April to 15 June 2004, and adjacent survey points were separated by approximately 0.4 km. Surveys were conducted either in the morning (05:15–08:45) or the evening (18:00–20:45) to coincide with times when owls are most often present at burrow entrances. We used these survey data to estimate density of Burrowing Owls in the two study areas. We only used owls detected within 200 m of each survey point (57% of the owls detected on our roadside surveys were within 200 m of the survey point) and assumed that our detection probability within this radius was 64.3% (Conway and Simon 2003). Hence, we effectively surveyed 146 km^2 of southeastern Washington during 2004 (1165 survey points $\times 3.14 \times [0.2\ km^2]$). Assuming 64.3% detection probability, we estimated the density of Burrowing Owl nests in each study area using this equation: density of nests = ([number of nests detected within 200 m of survey points/0.643]/146 km^2). Estimates of nesting densities may not be indicative of eastern Washington as a whole. We chose these study areas because, based on anecdotal information available when we began the study, they were thought to have the two largest concentrations of Burrowing Owls in eastern Washington.

Furthermore, we initiated survey routes in the areas where nesting densities were highest and subsequently expanded the survey area beyond those two core areas. As a result, we believe that our estimates represent the highest nesting densities of Burrowing Owls in the state of Washington.

In addition to nest burrows located during standardized roadside surveys, we located additional nest burrows incidentally during daily field activities and by asking landowners where they had seen owls. We monitored 1006 nesting attempts from 2000 to 2004 (512 in the agricultural area and 494 in the urban area). We visited all burrows once a week from February to September to document occupancy, determine dates of nest initiation, and estimate nesting success and annual fecundity. We visited nests at all times of day, but 75% of nest visits were from 09:00 to 15:00. We first observed burrows from >100 m away using binoculars to check for owl activity and then slowly approached on foot to look for signs of use (e.g., owl that retreats or flushes from burrow, pellets, feathers, nest lining, whitewash, and footprints) or vacancy (presence of cobwebs at burrow entrance). This initial period of observation typically lasted about 10 min. Gorman et al. (2003) reported that the maximum number of juvenile owls was typically observed during the first 10 min of a nest visit. We periodically removed pellets, feathers, whitewash, and footprints from around burrow entrances so that new sign present on future visits would reliably indicate recent use by owls. We saw no indication that removing this material affected the owls' behavior. During weekly visits, we also recorded the presumed stage of the nesting cycle and the number of adult and juvenile owls observed. We also used an infrared video probe (Peeper Video Probe, Sandpiper Technologies, Manteca, CA) to examine the contents of occupied burrows. Repeated use of the peeper did not affect nest abandonment or nesting success (V. Garcia and C. Conway, unpubl. data). Use of the peeper helped us determine nesting stage and the number of eggs or juveniles present even when no owls were visible at the burrow entrance. The peeper was ineffective on 30% of the attempts due to the depth of the burrow, structural features of the tunnel, or excessive lining in the tunnel.

Clutch size, nesting success, and annual fecundity. Estimating parameters associated with reproduction for Burrowing Owls is challenging because nest chambers are typically >2 m underground. Hence, we developed a standardized protocol for determining nest fate and estimating reproductive parameters based on weekly nest visits (V. Garcia and C. Conway, unpubl. data). We considered a burrow to be a "nest" if one or more adult Burrowing Owls were present on ≥2 visits between the dates the first egg was laid and the last egg hatched (based on estimates for these dates from all nesting attempts in the population that year for which laying and hatching was confirmed). Hence, even a burrow defended by an unpaired male that failed to attract a mate (or we failed to detect a mate) was considered a "nest" under this definition. Any nest definition has to clarify how to classify burrows (as nests or not as nests) based on observations at the entrance to the burrow because even studies where infrared probes are used (like ours) can only access a subset of the nest chambers with those probes. Some nest attempts that fail before juveniles emerge (or prior to being probed) have likely been disregarded as "not nests" in previous studies and the frequency with which this occurs depends on how "nests" are defined. We believe that our definition reduces bias and subjectivity and allows comparison of reproductive parameters among studies. We considered a nesting attempt successful if at least one juvenile reached 44 d of age. To estimate annual fecundity, we used the minimum number of juveniles that must have been alive at 44 d of age (i.e., the maximum number of juveniles observed on weekly visits between the date when the first-hatched juvenile reached 44 d of age and the date when juveniles dispersed, discounting suspected brood-mixing events). The maximum number of juveniles observed during repeated short-duration nest visits provides a useful index of brood size in Burrowing Owls (Gorman et al. 2003). To estimate clutch size, we only used nesting attempts where we observed the nest chamber with the infrared peeper and the number of eggs in the clutch was the same on ≥2 occasions (to eliminate incomplete clutches observed once that failed prior to completion).

Annual return rates. We trapped juvenile Burrowing Owls at nest burrows and placed a U.S. Geological Survey band on one leg and a uniquely-numbered aluminum color-band (Acraft Bird Bands, Edmonton, Alberta, Canada) on the other leg of each owl. We banded 1132 juvenile Burrowing Owls in the agricultural area and 863 in the urban area from 2000 to 2004. For each study area, we calculated the proportion of juvenile owls recruited into the local population using the following equation: (number of owls originally banded as juveniles subsequently detected as breeders in 2001–2004)/(number of juvenile owls banded in 2000–2003). We calculated this proportion for both males and females, assuming that the sex ratio of banded juveniles was 50:50 (Burrowing Owls are not sexually dimorphic until their first breeding plumage).

We trapped adult Burrowing Owls at nest burrows and placed a U.S. Geological Survey band on one leg and an aluminum color band (Acraft Bird Bands, Edmonton, Alberta, Canada) on the other leg. We used the following criteria to identify males and females: presence of a brood patch, plumage (males are often lighter than females), body size (males are often larger than females), and behavior prior to trapping. From 2000 to 2004, we banded 170 adult males and 246 adult females in the agricultural area, and 130 adult males and 141 adult females in the urban area. From 2001 to 2004, we made a systematic effort to read band combinations of banded owls at each study area. We made efforts to resight bands during each weekly nest visit from March to September each year. Standardized roadside surveys allowed us to locate new nests each year and find banded owls that returned to the study area, but used new nest burrows. We also had 13 banded owls reported to the National Bird Banding Laboratory or other entities as recoveries or resightings outside the study area where originally banded. We calculated adult return rates for both males and females in each study area as the proportion of banded adults resighted in a subsequent year.

Annual nest burrow fidelity and migratory tendency. The location of each nest burrow and all satellite burrows around each nest were recorded using a GPS receiver. We also noted the location of each burrow relative to nearby burrows and other landmarks on maps of the study areas so we could determine whether owls reused burrows in subsequent years. For adult owls that returned to breed the following year, we calculated the proportion that nested in the same burrow and the proportion that nested in the same nesting area (in the same nest burrow or another burrow within 200 m of the previously used nest burrow).

We conducted band resight surveys during the winters of 2001–2002, 2002–2003, and 2003–2004 to estimate the proportion of breeding owls that overwintered. We visited all burrows used by owls during the previous breeding season at least twice during a 2-week period in either December or January during each winter survey. For each owl detected, we attempted to determine if it was banded and to identify the unique band combination. If signs of activity were observed at a burrow (e.g., feathers, pellets, or whitewash) on the first visit (but no owl), we removed the sign and noted any new sign on the next visit. If we observed sign but no owls, the burrow was visited until the resident bird was observed. We also used the infrared video probe to determine band status of owls down in the burrow. We developed the following equation to estimate the proportion of breeding owls that overwintered in each study area:

$$\begin{aligned}&\textit{proportion of breeding males}\\&\textit{(or females) that overwinter} =\\&\quad((((((A_w/(A_w + J_w)) * O_u)\\&\quad * (A_w/(A_w + ((A_w * O_{nb})/(A_w + J_w)))))\\&\quad * (M_w/A_w)) + M_w)/M_b),\end{aligned}$$

where A_w is the number of banded adults detected during winter, J_w is the number of banded juveniles detected during winter, O_u is the number of owls with band status unknown detected during winter, O_{nb} is the number of unbanded owls detected during winter, M_w is the number of banded males (or females) detected during winter, and M_b is the number of banded males (or females) present during the previous breeding season. Estimates based on this equation accounted for owls detected during winter surveys whose legs were not observed (band status unknown).

Statistical analyses. We used χ^2 tests to compare nesting success (proportion of nesting attempts that produced at least one 44-d-old juvenile; Landry 1979), juvenile and adult return rates, annual burrow fidelity, and probability of overwintering between study areas. We also used χ^2 tests to compare juvenile and adult return rates, annual burrow fidelity, and probability of overwintering between males and females. We used *t*-tests to compare the number of fledglings per nesting attempt and the number of fledglings per successful nest between study areas. We used SPSS (2002) for all analyses. Values are presented as mean ± 1 SE.

RESULTS

Breeding density and timing of breeding. We detected 58 owls (44 in the agricultural area and 14 in the urban area) associated with 46 nests (34 in the agricultural area and 12 in the urban area) during 1165 roadside point-count surveys in 2004. The density of Burrowing Owl nests was 0.67 nests/km^2 in the agricultural area and 0.28 nests/km^2 in the urban area.

Mean date of arrival was 27 March for migratory males and 29 March for females, but some owls arrived as early as 20 February (and some overwintered; see below). The mean date that the first egg was laid was 10 March in the urban area and 18 March in the agricultural area. Nest initiation (first egg laid) dates ranged from 27 February to 9 June in the urban area ($N = 324$), and 16 March to 4 July in the agricultural area ($N = 382$). Most (90%) eggs hatched between 1 May and 26 June. The nesting cycle (from first egg until juveniles fledge at 44 d) lasts 2.5 mo, but, because of variation in nest initiation dates, the breeding season for Burrowing Owls in southeastern Washington extended from 27 February to 5 September (dates when $\geq$1 nest had eggs or nestlings). Because many juvenile owls remained at nest burrows even when capable of sustained flight (i.e., up to 150 d of age; Garcia 2005), 20% of successful nests were still occupied (usually by fledged juveniles) on 1 September.

Clutch size, nesting success, and annual fecundity. Mean clutch size was 8.6 ± 0.1 eggs in the agricultural area (range = 4–13, $N = 123$) and 8.4 ± 0.2 eggs in the urban area (range = 4–11, $N = 66$). Nesting success was higher ($\chi^2 = 10.9$, $P = 0.001$) in the agricultural area, with 51% of 535 nesting attempts successful ($\geq$1 juvenile survived $\geq$44 d) in the agricultural area and 41% of 553 successful in the urban area. Of 139 banded females whose initial nesting attempt failed after the first egg was laid, 10 laid a new clutch in the same burrow, 14 remained at the original burrow but did not lay a new clutch (that we detected), nine moved to a different burrow and laid a new clutch, seven moved to a different burrow but did not lay a new clutch (that we detected), and 99 were not observed the rest of the year. No double brooding was observed.

From 2000 to 2004, the mean number of fledglings per nesting attempt was 2.02 ± 0.14 in the agricultural area and 1.47 ± 0.09 in the urban area. The mean number of fledglings per successful nest was 3.20 ± 0.15 in the agricultural area and 3.10 ± 0.12 in the urban area. The number of fledglings per nesting attempt was higher ($t_{706} = 3.3$, $P = 0.001$) in the agricultural area, but the number of fledglings per successful nest did not differ ($t_{369} = 0.5$, $P = 0.63$) between the two areas.

Annual return rates. From 2000 to 2003, a greater proportion of banded juveniles were resighted in the urban area than in the agricultural area ($\chi^2 = 6.7$, $P = 0.009$). We resighted 34 of 758 juvenile owls (4%; 25 males and nine females) in the agricultural area, and 54 of 699 (8%; 31 males and 23 females) in the urban area (Table 1). Assuming a 50:50 sex ratio of juveniles, more juvenile males returned to natal areas than juvenile females in both study areas (Table 1), but the difference was significant only in the agricultural area ($\chi^2 = 7.9$, $P = 0.005$). Four juvenile females banded in the urban area were subsequently resighted in a subsequent year breeding in the agricultural area. However, no juveniles from the agricultural area were found breeding in the urban area.

From 2000 to 2003, we resighted 101 of 332 adult owls (30%) banded in a previous year in the agricultural area, and 94 of 243 adult owls (39%) in the urban area (Table 1). A greater proportion of adult females was resighted in the urban area than in the agricultural area ($\chi^2 = 4.9$, $P = 0.026$), but there was no difference between areas in the proportion of adult males resighted ($\chi^2 = 0.1$, $P = 0.7$; Table 1). More banded males were resighted in subsequent years than females ($\chi^2 = 17.7$, $P < 0.001$). Only 4% of banded adults in the agricultural area and 10% in the urban area were resighted 3 yr later.

One adult female fledged young in the urban area in 2002 and was resighted repeatedly 375 km southwest of its nest site in Linn County, Oregon, from October to February in 2002–2003, 2003–2004, and 2004–2005. Although not detected during the 2003 breeding season,

Table 1. Number of Burrowing Owls banded from 2000 to 2004 and subsequently resighted at two study areas in southeastern Washington.

	Agricultural area AHY			Urban area AHY		
Year	Male	Female	HY	Male	Female	HY
2000	11	14	63	7	12	57
2001	47	52	172	36	44	218
2002	60	78	308	48[1]	36	198
2003	23	47	215	32	28	226
2004	29	55	374	7	21	164
2000–2004	170	246	1132	130	141	863
Returned in subsequent year	59	42[2]	34	54	40	54
% AHY returned[3]	42%	22%		44%	33%	
% HY males recruited[3,4]			6.6%			8.9%
% HY females recruited[3,4]			2.4%			6.6%

[1] Includes two males banded during winter.

[2] Includes two owls banded in the agricultural study area that were subsequently resighted in the urban study area.

[3] Percentage of owls banded 2000–2003 that were resighted as a breeder in at least one subsequent year.

[4] Assumes a 50:50 sex ratio of juveniles at time of banding.

this female returned to the urban area in 2004 and fledged at least seven young. Two adult owls (both females) banded in the agricultural area were resighted in a subsequent year breeding in the urban area. However, no adults were known to disperse from the urban area to the agricultural area.

Annual nest burrow fidelity and migratory tendency. Of 335 adult owls that returned to breed on the same study area the following year, 36% used the same nest burrow and 62% returned to the same nesting area. Fidelity to burrows was higher ($\chi^2 = 4.2$, $P = 0.042$) for males (40%) than females (29%), and fidelity to nesting areas was also higher ($\chi^2 = 10.6$, $P = 0.001$) for males (69%) than females (51%). Difference in fidelity to the same nesting area between the agricultural (67%) and urban (57%) areas approached significance ($\chi^2 = 3.6$, $P = 0.06$). The proportion of breeding owls that overwintered was higher ($\chi^2 = 11.0$, $P < 0.001$) in the urban area (17.4% of males, 2.6% of females, and 0.8% of juveniles) than the agricultural area (8.4% of males, 0.5% of females, and 0.3% of juveniles), and males were more likely to overwinter than females ($\chi^2 = 37.5$, $P < 0.001$).

DISCUSSION

Breeding density and timing of breeding. The density of Burrowing Owl nests was more than twice as high in the agricultural area than the urban area, possibly due to higher prey densities (i.e., small mammals) in agricultural areas (V. Garcia and C. Conway, unpubl. data). Breeding densities at both of our study areas (0.67 nests/km^2 in the agricultural area and 0.28 nests/km^2 in the urban area) were higher than the 0.11 nest sites/km^2 in eastern Wyoming (Conway and Simon 2003), but lower than the 2.1 pairs/km^2 (DeSante et al. 2004) and the 8.3 pairs/km^2 (Rosenberg and Haley 2004) estimates for agricultural areas of southeastern California.

Burrowing Owls began breeding 1–2 weeks later in our agricultural study area, probably because this area was over 200 m higher in elevation than the urban area. Hence, snow often covered burrow entrances in this area into March and owls were less likely to overwinter in the area.

Clutch size, nesting success, and annual fecundity. Mean clutch sizes were similar at the two study areas despite differences in land use. Clutch sizes of Burrowing Owls at our study areas in Washington were higher than in Florida ($\bar{x} = 4$; Millsap 1993), California ($\bar{x} = 7.0$, Landry 1979; $\bar{x} = 6.7$ Rosenberg and Haley 2004), Wyoming ($\bar{x} = 7.4$; C. Conway, unpubl. data), and Arizona ($\bar{x} = 7.4$; C. Conway, unpubl. data), but lower than in Idaho ($\bar{x} = 9.9$; Olenick 1990). Clutch size is positively correlated with latitude and migratory tendency in Burrowing

Owls (C. Conway, unpubl. data), and burrow availability and elevation may explain additional variation in mean clutch size among studies. Variation in food availability may also explain some variation among populations, but experimental food supplementation did not cause females to increase clutch size in Saskatchewan (Wellicome 2005).

Nesting success was higher in our agricultural study area possibly because badgers (and perhaps other mammalian predators) are considered pests by farmers and their numbers are actively controlled. In addition, many nests in the agricultural area were in holes below concrete irrigation drains and these were probably less likely to collapse than nests in burrows dug by fossorial mammals. Nesting success of Burrowing Owls in our study was similar to estimates from Oregon (53% and 57%; Green and Anthony 1989, Holmes et al. 2003), but lower than estimates for other migratory populations in Saskatchewan (59–69%; Haug 1985, James et al. 1997, Wellicome et al. 1997), Idaho (67–68%; Olenick 1990, Lehman et al. 1998), South Dakota (76%; Griebel 2000), and Colorado (82%; Lutz and Plumpton 1999). Nesting success may be higher in areas where Burrowing Owls nest primarily in black-tailed prairie dog colonies because owls may benefit from predator swamping or from the vigilance of and alarm calls given by prairie dogs in response to approaching predators (Desmond et al. 2000). However, making inferences based on comparisons of nesting success across studies is complicated by the fact that investigators differ in how they define what constitutes a Burrowing Owl "nest." Because Burrowing Owls nest underground and nest contents are seldom observed, deciding which burrows to include in calculations of nesting success varies among studies and this variation undoubtedly influences estimates of reproductive parameters. Hence, there is a need for standardized methods for estimating Burrowing Owl reproductive parameters (e.g., Gorman et al. 2003), and we encourage all researchers to use those standardized methods, define all terms, and provide more details concerning how each parameter was estimated.

The number of fledglings per nesting attempt was higher in our agricultural study area because nesting success was higher, but we found no difference between our two study areas in the number of fledglings per successful nest. The number of fledglings per nesting attempt in our study was lower than reported for most other populations (Conway et al. 2005a), but several other investigators have reported ≤ 2 fledglings per nesting attempt (Botelho and Arrowood 1998, Desmond et al. 2000, Warnock and Skeel 2002, Klute et al. 2003). The mean number of fledglings per successful nest in our study (3.2 in the agricultural area and 3.1 in the urban area) was also lower than for most other populations that have been studied (Conway et al. 2005a), but several investigators have also reported ≤ 3 fledglings per successful nest (Johnson et al. 1997, Trulio 1997a, Restani et al. 2001, Warnock and Skeel 2002, Klute et al. 2003). As with nesting success, comparing measures of Burrowing Owl fecundity among studies is hampered by differences among investigators in the burrows that are included in calculations of fecundity and variation in the number and duration of nest visits (Gorman et al. 2003).

Annual return rates. Although the higher natal recruitment in the urban study area could have been due to greater food (Todd et al. 2003) or burrow availability, we have no data to support this conclusion. Natal recruitment is negatively correlated with migratory tendency across populations of Burrowing Owls (C. Conway, unpubl. data), so differences between our two study areas could reflect differences in migratory tendency. Natal recruitment in our agricultural area (4%) was similar to the estimates of 2–5% for other migratory populations of Burrowing Owls (Haug 1985, Belthoff and King 1997, DeSmet 1997, Lutz and Plumpton 1999, Todd et al. 2003, Conway et al. 2005b). Our estimate of natal recruitment in the urban study area (8%) was the highest for any northern migratory population of Burrowing Owls in North America. All estimates of natal recruitment are biased low to some extent because observers undoubtedly fail to detect some banded juveniles that return to breed. The extent of the bias is negatively correlated with size of the study area and the proportion of nest burrows located. Our estimate may be higher (and more precise) than others because we worked in a large study area and monitored hundreds of nest burrows each year. However, our agricultural study area was also large and so this does not explain the difference in natal recruitment between our two study areas. Future studies are needed to examine the effects of land use on natal recruitment using a comparative approach across populations after controlling for latitude and migratory tendency.

Juvenile males in our study were more likely to return to natal sites to breed than were females, and the difference was more pronounced in our agricultural study area. Higher natal recruitment by male Burrowing Owls has also been reported elsewhere in their breeding range (Millsap and Bear 1992). This pattern is consistent with the fact that females typically disperse further than males in most avian taxa (Greenwood 1980). Differences between sexes in probability of natal recruitment may be more pronounced in more migratory populations or in areas where burrows are less limiting (i.e., less likely to be destroyed).

Two banded juveniles (one from our agricultural area and one from the urban area) were resighted alive during the winter in coastal southern California and another juvenile (from our urban area) was found dead in San Francisco during November. These observations suggest that juvenile owls from eastern Washington may migrate south along the west coast and at least some appear to winter in central and southern California. However, another juvenile owl banded in our urban study area was recovered dead during the fall in Havre, Montana.

Return rates of adult Burrowing Owls in our study were also higher in the urban area than the agricultural area. Higher return rates of juveniles and adults in the urban area were likely related to the higher probability of overwintering in that area. Year-round residency is correlated with high juvenile recruitment and high adult return rates throughout the range of Burrowing Owls (C. Conway, unpubl. data). Hence, it is not clear whether differences in return rates between study areas are related to differences in land use, habitat quality, or climate and elevation. To address this question, a comparative analysis across studies is needed. Annual return rates of adults in Washington (30% in the agricultural area and 39% in the urban area) were lower than some estimates, but higher than others from northern migratory populations of Burrowing Owls (16% in Colorado, Lutz and Plumpton 1999; 13% and 44% in Saskatchewan, Haug 1985, James et al. 1997; 16% and 52% in Alberta, Hjertaas et al. 1995, Clayton and Schmutz 1999; 33% in Manitoba, DeSmet 1997). Some variation among studies is due to differences in the size of study areas, proportion of nests detected, number of breeding owls banded and resighted each year, and the number of years studied. All of these factors relate to sampling intensity and influence estimates of annual return rates, so these parameters should be taken into account when making inferences based on comparisons across studies. Adult males were more likely to return to the study area to breed in a subsequent year in both of our study areas, a pattern also reported in other Burrowing Owl populations (DeSmet 1997, but see Lutz and Plumpton 1999) that probably reflects the fact that females typically disperse further than males in most avian taxa (Greenwood 1980).

Annual nest burrow fidelity and migratory tendency. Because Burrowing Owls often use the same burrow in subsequent years, destruction of nest burrows during the nonbreeding season can have a negative impact on abundance and population trends. Any activity that destroys a nest burrow, even if it is destroyed outside of the breeding season and does not result in the direct take of owls, will potentially have a negative impact on population stability. For this reason, burrows used by Burrowing Owls should receive legal protection even during the nonbreeding season. Efforts to protect nest burrows outside (as well as inside) of the breeding season are essential for the maintenance of Burrowing Owls in eastern Washington.

Annual nest burrow fidelity was 10% higher in the agricultural area than in the urban area. Factors affecting variation among sites or years in burrow fidelity include differences in soil texture and composition, natural erosion processes, burrow availability, and frequency of trampling by livestock (Green and Anthony 1989, Desmond et al. 2000, Holmes et al. 2003). Our estimates of annual burrow fidelity were lower than those reported from Manitoba (51% for males and 33% for females; DeSmet 1997), Colorado (75% for males and 63% for females; Lutz and Plumpton 1999), and California (68% for males and 63% for females; Catlin et al. 2005). As in other populations, male Burrowing Owls had higher burrow fidelity than females in Washington.

Our estimate for the proportion of breeders that overwinter underestimates the true proportion because an unknown number of adults banded during the previous breeding season undoubtedly died prior to the winter survey (and hence should be excluded from the denominator of our equation). However, our estimates do provide a metric for comparing migratory tendency among populations and across years. A greater proportion of owls overwintered in our urban study area than in the agricultural area further north, probably due to a warmer winter climate or more stable winter food source. We found that adults were more likely to overwinter than juveniles and males more likely to overwinter than females, both patterns that are common in many other birds exhibiting partial or differential migration (Gauthreaux 1982, Cristol et al. 1999). Persistence of viable Burrowing Owl populations in Washington depends on identification and proper management of wintering areas, in addition to protection of breeding areas. To accommodate these year-round needs, migratory movement patterns and wintering areas of Burrowing Owls that breed in Washington should be identified.

CONCLUSIONS

Fewer juveniles and fewer females returned to breed in our agricultural study area than our urban study area. In addition, two adult females from the agricultural area were resighted in a subsequent year breeding in the urban area, but we never observed breeding dispersal in the opposite direction. Four juvenile owls from the urban study area were resighted in a subsequent year breeding in the agricultural study area, but we never observed natal dispersal in the opposite direction. One interpretation of such observations is that the population in the agricultural area (on the northern periphery of the species' current breeding range; Wellicome and Holroyd 2001) is more dependent on successful reproduction and natal dispersal from owl populations further south. Moreover, many differences between study areas are potentially correlated with differences in migratory tendency rather than differences in land use. The proportion of resighted birds is not equivalent to survival because it does not account for emigration or detection probability. However, fewer juveniles returned to become local breeders and fewer females returned to breed each year, suggesting that owls in the agricultural area may be a population "sink." Despite the higher nesting densities in the agricultural area, persistence of the Burrowing Owl population appears to depend on immigration. Persistence also depends on cooperation between natural resource managers and local ranchers and farmers because most owls are nesting on private property.

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