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FACTORS INFLUENCING BURROWING OWL REPRODUCTIVE PERFORMANCE IN CONTIGUOUS SHORTGRASS PRAIRIE

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Abstract.—We analyzed Burrowing Owl (*Athene cunicularia*) reproductive performance (i.e., clutch size, brood size, and number of young fledged) in relation to nest and colony factors in Buffalo Gap National Grassland, South Dakota. We monitored 129 pairs of Burrowing Owls in 43 prairie dog (*Cynomys ludovicianus*) colonies in 1999 and 143 pairs in 45 colonies in 2000. Mean clutch size was 7.2 and ranged from 3–10 eggs. Pairs averaged 2.6 fledglings per nesting attempt and 76% of the nesting pairs were successful in fledging at least one young. Abandonment appeared to be the primary cause of nest failures. Variables measured at the colony level explained more (34–70%) of the variability in reproductive performance than did variables measured at the nest level (7–33%). In general, Burrowing Owls that arrived early, initiated clutches sooner, and either nested at greater distances from nearest neighbors or had fewer owl nests within 250 m of the nest burrow, had larger clutches, larger broods, and more fledglings. Seventy percent of prairie dog colonies were occupied by owls; most (85%) unoccupied colonies were <10 ha in size. Larger prairie dog colonies supported greater numbers of owl nests and consequently produced more total fledglings than did smaller colonies ($P < 0.001$).

Key Words: *Burrowing Owl*; Athene cunicularia; *prairie dog*; Cynomys ludovicianus; *Buffalo Gap*; *Peeper video probe*; *reproductive performance.*

FACTORES QUE INFLUYEN SOBRE EL DESEMPEÑO REPRODUCTIVO DE *ATHENE CUNICULARIA* EN PRADERAS CONTIGUAS DE PASTOS CORTOS

Resumen.—Analizamos el desempeño reproductivo (i.e., tamaño de la nidada, tamaño de la parvada, número de volantones) de *Athene cunicularia* en relación con factores que caracterizan los nidos y las colonias en Buffalo Gap National Grassland, Dakota del Sur. Monitoreamos 129 parejas de *A. cunicularia* en 43 colonias de perritos de las praderas (*Cynomys ludovicianus*) en 1999, y 143 parejas en 45 colonias en 2000. El tamaño promedio de la nidada fue 7.2, y varió entre tres y diez huevos. En promedio, las parejas criaron 2.6 volantones por intento de nidificación, y el 76% de las parejas nidificantes tuvieron éxito en criar al menos un volantón. El abandono pareció ser la causa principal de fracaso de los nidos. Las variables medidas a nivel de las colonias explicaron una mayor parte (34–70%) de la variación en el desempeño reproductivo que las variables medidas a nivel de los nidos (7–33%). En general, los individuos que arribaron temprano, iniciaron sus nidadas más temprano y nidificaron a mayores distancias de los vecinos más cercanos o presentaron menos nidos a menos de 250 m de su madriguera, presentaron nidadas y parvadas más grandes, y un mayor número de volantones. El 70% de las colonias de *C. ludovicianus* estuvieron ocupadas por *A. cunicularia*; la mayoría de las colonias no ocupadas fueron de menos de 10 ha de tamaño. Las colonias de *C. ludovicianus* más grandes sostuvieron una mayor cantidad de nidos de *A. cunicularia*, por lo que produjeron un número total de volantones mayor que las colonias más pequeñas ($P < 0.001$).

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In the Great Plains region, Burrowing Owls (*Athene cunicularia*) are most commonly associated with black-tailed prairie dog (*Cynomys ludovicianus*) colonies for nesting, shelter and raising young. Historically, black-tailed prairie dog colonies were common in prairies from Canada to Mexico and from the eastern edge of the Rocky Mountains to the western edge of the tallgrass prairie (Hoogland 2006). However, prairie dogs have been subjected to major population control efforts by humans and as a result, have been extirpated from much of their historic range. Biggens et al. (2006) estimates prairie dog population declines of about 98%, which has led to severe fragmentation of remaining prairie dog colonies and in some cases, corresponding declines in Burrowing Owls (Desmond et al. 2000). Habitat fragmentation of breeding grounds is a major factor in the decline of Burrowing Owls in Saskatchewan (Warnock and James 1997).

Buffalo Gap National Grassland (hereafter ''Buffalo Gap'') in South Dakota contains large expanses of continuous shortgrass prairie associated with numerous prairie dog colonies, some of which are very large (i.e., >700 ha) and protected from shooting and poisoning (at the time of our research). A large portion of Buffalo Gap's landscape is not fragmented and probably resembles historical conditions 100 yr ago. If in fact prairie dog eradication threatens the future of Burrowing Owls in the Great Plains, Buffalo Gap may provide baseline data needed to assess Burrowing Owl reproduction at other sites.

Burrowing Owl reproductive performance may be influenced by a number of factors, including date of arrival on the breeding grounds and subsequent clutch initiation date, intraspecies competition for scarce resources, and both the quantity and quality of nesting and foraging habitat. Early arriving females produced larger clutches in Canada (Wellicome 2000), possibly a result of having better body condition and greater nutrient reserves for egg production. In Oregon, abandonment was the major cause of nest failures for owls nesting in badger (*Taxidea taxus*) burrows; at least one nest always failed if owls nested within 110 m of each other (Green and Anthony 1989). However, Rosenberg and Haley (2004) found no evidence that nearest neighbor distance affected the number of young produced per female for Burrowing Owls in California's Imperial Valley, a heavily farmed area. Burrowing Owls tend to nest near the edges of prairie dog colonies (Toombs 1997, Orth and Kennedy 2001, Teaschner 2005); Ekstein (1999) found nesting success was positively related to nest distance from the colony edge in Nebraska. Owls nesting close to the colony edge may benefit from higher prey diversity and possibly greater prey abundance, but they may be more vulnerable to predators. Burrowing Owls in Thunder Basin National Grassland, Wyoming, preferentially selected nest burrows with longer tunnels (Lantz 2005). Although Lantz (2005) found no correlation between tunnel length and nesting success, predators, such as badgers, may eventually abandon their effort if the nest is located deep in the burrow (R. Griebel pers. observ.). Additionally, a nest located farther in the burrow and lined with cow dung should have a better chance of withstanding flooding during a heavy rain event.

At a colony scale, the density of burrows may influence fledging success of Burrowing Owls. Badger predation on owl nests in Nebraska was lower when densities of active prairie dog burrows were high (Desmond et al. 2000). Larger prairie dog colonies may provide more prey and also allow owls to space themselves more widely, possibly reducing competition. However, in fragmented grassland in northeastern Colorado, Orth and Kennedy (2001) found no difference in colony size between prairie dog colonies occupied by Burrowing Owls and those not occupied.

In our study, we analyzed Burrowing Owl reproductive performance (i.e., clutch size, brood size, and number of young fledged) in relation to variables of the nest (i.e., the burrow the nest is located in) and the prairie dog colony in which the nest is located. We predicted that owl clutch size would be negatively related to pair arrival date and clutch initiation date, and that owl reproductive performance would be negatively related to the number of owl nests in the vicinity of a nest and positively related to nearest neighbor distance, distance from the colony edge, nest location in the burrow, burrow density, and colony size.

We compare our results with past research on Burrowing Owls nesting in fragmented prairie dog colonies within the Great Plains ecosystem. These colonies were generally subjected to one or more of the following influences: shooting, poisoning, plague, and/or conversion of native grasslands to agriculture.

STUDY AREA

Buffalo Gap is located in southwestern South Dakota (43°44′N, 102°20′W) and has approximately 220 prairie dog colonies that range in size from 0.5 to >700 ha, covering around 4000 ha. The study area was primarily in the Conata and Scenic Basins, which contain numerous, large prairie dog colonies. In late summer of 1998, prairie dog shooting was prohibited as a recreational activity in the Conata Basin and Heck Table area of the Scenic Basin, both of which are black-footed ferret (*Mustela nigripes*) reintroduction sites; shooting is still allowed on areas outside of this zone. All prairie dog colonies were subject to rotational grazing by domestic cattle, which has taken place on the Buffalo Gap National Grassland since 1900 (MacCracken et al. 1985a, 1985b). The entire area, including adjacent sites without colonies, is characterized as shortgrass prairie dominated by red three-awn (*Aristida longiseta*), blue grama (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), cheat grass (*Bromus tectorum*), plains prickly pear (*Opuntia polyacantha*), wooly Indian wheat (*Plantago spinulosa*) and scarlet globe mallow (*Sphaeralcea coccinea*).

The climate is semiarid continental and characterized by cold winters and hot summers. The 100-yr mean temperature (1900–2000) over the four-mo period of 1 April–1 August (time period of our research) was 15.6°C, and the mean precipitation was 6.1 cm (National Climate Data Center 2000). The average temperature in 1999 over this same 4-mo period was cooler, with a mean of 14.9°C and wetter with a mean precipitation of 8.9 cm. In 2000, the means were closer to normal, with an average temperature of 15.9°C and mean precipitation of 7.1 cm (National Climate Data Center 2000).

METHODS

Our study spanned April–August, 1999 and 2000. It was not possible to survey all prairie dog colonies because of the large number scattered throughout the project area and inaccessibility of some colonies. We divided the study area into five sections using a geographic information system (GIS). Within each section, a driving route was identified on the GIS and all accessible colonies along the route were chosen for study. We attempted to survey colonies at least two times per wk. Strict inference from results is limited to the study area because colonies were not selected randomly. In 1999, we surveyed owls in 63 prairie dog colonies ranging in size from 1.4–452 ha; 30 were 1–10 ha, 25 were 10–50 ha, 3 were 50–100 ha and 5 were >100 ha. We surveyed the same subset of colonies in 2000. However, due to shooting restrictions and a relatively dry winter, several of these prairie dog colonies expanded. Thus, the range in colony size changed to 1.4–700.0 ha in the second yr of our study; the number of colonies sampled within the various size classes was similar except two colonies expanded from 1–10 ha to 10–50 ha.

We intensively searched each prairie dog colony for Burrowing Owl nests at least twice a wk. We searched small to medium colonies (i.e., 1–50 ha) using a combination of walking the entire area and scanning colonies from a distance using a window-mounted spotting scope within a vehicle. We searched large colonies (i.e., >50 ha) by walking and driving with an all-terrain vehicle (ATV) along transects spaced at 300-m intervals. We stopped every 300 m along transects and surveyed for owls with binoculars. We conducted surveys from 2 April–16 June 1999 and from 11 April–17 June 2000. After 17 June, we shifted our efforts from nest searches to monitoring. It was possible that we failed to find some nests, particularly in the largest colonies, but because of the intensive search effort we believe few nests were overlooked.

We included four nests in our analyses that were established between 1–17 June. We did not band adults, and it is possible that some nests located late in the field season were renests by pairs that had already failed. However, because of our frequent monitoring, we believe the number of renests were relatively low.

We identified occupied owl burrows by the presence of shredded cow dung at the burrow entrance, one or more owls in the area, and/or nearby perch burrows covered in whitewash. We obtained grid coordinates for each nest with a global positioning system (GPS, ±5 m). The U.S. Forest Service produced digital maps of the prairie dog colonies by walking and/or driving an ATV around the outer perimeter and recording grid coordinates with a GPS unit. We entered all nest locations into the GIS using ArcView® 3.0 (ESRI 1996).

We used an underground video probe (Peeper Video Probe™, Sandpiper Technologies, Manteca, California, U.S.A.) to confirm Burrowing Owl nests. We repeated probing efforts on a weekly basis; on rare occasions ($N < 5$), owls nested in burrows lacking any evidence of owl occupancy (e.g., shredded cow dung, pellets and whitewash), and on two occasions in 2000, nests were lined heavily with cow dung, but no clutch was initiated.

Reproductive Performance. We considered that egg-laying had begun once the female was no longer seen consistently above ground with the male and large amounts of nesting material (shredded cow dung) were deposited around the burrow entrance, and we defined a nesting attempt as a nest in which we either confirmed or had a strong suspicion that eggs had been laid. We used the video probe to get an initial egg count. If the female was sitting on the eggs, she was gently nudged with the camera head. If she refused to move or aggressively attacked the probe, we made another probe attempt a few d later. If the female repeatedly attacked the probe on subsequent attempts or would not move off the eggs, we did not probe the nest until the female left the burrow. We attempted to get two clutch counts per nest to ensure that the clutch was complete. Burrowing Owls lay one egg every 1.5 d (Olenick 1990), and we considered a clutch size of 12 the maximum that most females could lay (Wellicome 2000, 2005). We adjusted the time interval between probe attempts accordingly.

We usually counted young from sunrise to approximately 1000 H and from 1800 H to sunset and at distances ≥100 m using a window-mounted spotting scope within a vehicle. We spent 15–45 min to count nestlings, remaining longer at a nest site if there were fewer nestlings observed than on the previous visit. Since our study, Gorman et al. (2003) have recommended standardized visitation times, and we recommend future researchers follow these guidelines to allow better comparisons among studies. As recommended by Gorman et al. (2003), we made repeated visits to colonies at least twice per wk but usually three or four times per wk during the nestling phase. We defined brood size as the maximum number of young seen at a nest site at any time prior to fledging. We monitored each nesting attempt until it was either terminated or had successfully fledged young. We defined a successful nest as one in which ≥1 nestling survived to fledging age (approximately 42 d of age; Haug 1985).

Nest and Pair Factors. When we initially found a pair of Burrowing Owls, their arrival date was recorded as the midway point between the date they were first observed and the date of the previous visit (Wellicome 2000). The Julian Day was used in place of the calendar day for data analysis. Thus, 1 April was identified as day 91 while 2 May would be day 122 and so forth. Arrival dates for 1999 were not included in the analysis because of the extremely wet weather that year which limited our ability to reach certain prairie dog colonies.

We measured burrow length while conducting egg counts with the Peeper video probe. After we counted eggs, we placed the camera head within 1 cm of the nearest egg, and marked the probe at the top of the burrow entrance. After pulling the probe back out of the burrow, we took a measurement. We analyzed burrow length data in two ways. First, any nest located beyond the length of the probe (3 m) was arbitrarily assigned a length of 3.5 m for data analyses. We also excluded nests located beyond the length of the probe from the analyses to prevent a ''ceiling'' effect in the data. Nests located in burrows too difficult to probe were left out of clutch size and burrow length analyses.

We determined both nearest neighbor distance and the number of nests within 250 m of a particular nest using GIS. Desmond et al. (2000) suggested that 250 m was the maximum distance at which owls were able to communicate vocally or behaviorally. We defined nearest neighbor distance as the next closest nest site, even if that nest was located in a different prairie dog colony. If an unsampled prairie dog colony was located next to a sampled colony that had only one nest in it, we excluded the nest from the nearest neighbor analysis because of the possibility that owls were nesting in the unsampled colony. Additionally, nests were excluded if nearest neighbor distances within the colony were larger than distances to the nearest unsampled colony. We measured the distance from a nest location to the edge of the prairie dog colony (i.e., area where clipped vegetation ceased) to the nearest meter using a Rolotape measuring wheel.

Colony Factors. We determined prairie dog colony size using GIS. We estimated mean owl clutch size, brood size and number of young fledged per nesting attempt for each colony. Also, we calculated mean nest and pair variables (pair arrival date, clutch initiation date, burrow length, distance to edge, number of nests within 250 m of a nest and nearest neighbor distance) for each colony. We determined owl density (breeding pairs/ha/prairie dog colony) and number of nests per prairie dog colony. We defined colony productivity as the total number of owl nestlings fledged from a prairie dog colony, based on counts described earlier.

Following protocol developed by Biggens et al. (1993), we measured factors related to prairie dogs (i.e., active burrows/ha, inactive burrows/ha, total burrows/ha and prairie dog density/ha) for 26 of the 63 prairie dog colonies. A prairie dog burrow was considered active if fresh prairie dog scat (i.e., not dried hard and bleached white) was located <0.5 m from the opening. Any burrow without fresh scat <0.5 m from the opening was considered inactive (Biggens et al. 1993). To obtain this subset, we stratified the 63 colonies into small, medium, and large size classes and randomly selected colonies from among each size class in each of the five sections; colonies ranged in size from 4.8–281.3 ha. We sampled prairie dog colonies from 7–29 June 1999 and from 27 May to 19 June 2000.

We used stepwise multiple regression (PROC REG, SAS Institute Inc. 1999) to analyze the relation between reproductive performance (i.e., clutch size, brood size, and number of young fledged per nesting attempt) and the independent variables at the nest and colony scales. The multiple regression analyses at the colony scale included only those prairie dog colonies that had at least one nesting attempt and were measured for prairie dog factors. The colony scale variables were also regressed against prairie dog colony size using simple linear regression. We tested the hypothesis that prairie dog colonies occupied by owls were larger than unoccupied colonies on our study site using a one-tailed t-test assuming equal variances after transformation.

All variables were tested for normality (PROC UNIVARIATE, SAS Institute Inc. 1999) and transformed to LOG(y) or LOG(y + 1) as necessary. We then examined variables for collinearity (PROC CORR, SAS Institute Inc. 1999); we considered two variables correlated if the Pearson's Correlation Coefficient (r) was ≥0.7. Arrival date and clutch initiation date were correlated in 2000. Nearest neighbor distance and the number of nests within 250 m of a nest were negatively correlated for both years. Active burrows/ha were correlated with inactive burrows (2000), total burrows/ha (1999 and 2000) and prairie dog density (1999 and 2000). Inactive burrows/ha were correlated with total burrows/ha (2000) and prairie dog density (2000). Lastly, brood size and number fledged per nesting attempt were highly correlated for both years ($r = 0.90$, $P < 0.001$ [1999]; and $r = 0.95$, $P < 0.001$ [2000]). For the stepwise multiple regression analysis, correlated variables were run separately, and we selected the one producing the largest R^2 value for the final model. We used an entry P-value of 0.15 for selecting significant variables to be retained in models. We analyzed data separately for each year because of the differences in weather and prairie dog activity. Means are presented ±SE. Significance was established at $P \leq 0.05$.

RESULTS

We located and monitored reproductive performance of 129 Burrowing Owl pairs in 43 colonies in 1999 and 143 pairs in 45 colonies in 2000. The 129 breeding pairs had 131 nesting attempts in 1999; 94 (73%) of these were successful. In 2000, 113 out of 143 pairs (79%) were successful. Reproductive performance was determined for all nesting attempts and for successful nests (Table 1). For all nesting attempts with years combined, owls averaged 7.2, 3.1 and 2.6 for clutch size, brood size, and number fledged per nesting attempt, respectively, and 7.3, 4.0 and 3.5 for clutch size, brood size, and number fledged per successful nest, respectively. In 2000, owls that selected nest burrows used the previous year ($N = 17$) fledged more young (3.8 ± 0.43)

Table 1. Mean reproductive performance and statistical difference between years for Burrowing Owls nesting in Buffalo Gap National Grassland, South Dakota, 1999 and 2000.

	1999			2000			
	N	MEAN	RANGE	*N*	MEAN	RANGE	*P*
All nesting attempts:							
Clutch size	77	7.2	3–10	105	7.1	4–10	0.565
Brood size	131	2.8	0–7	143	3.3	0–8	0.053
Number fledged	131	2.3	0–6	143	2.9	0–7	0.015
Successful nests only:							
Clutch size	59	7.4	3–10	83	7.2	4–10	0.571
Brood size	94	3.9	1–7	113	4.1	1–8	0.023
Number fledged	94	3.3	1–6	113	3.7	1–7	0.004

than those using new burrows ($N = 126$, 2.8 ± 0.18, $t_{141} = -1.96$, $P = 0.05$). Owls using the 17 nests were all successful in fledging young in 1999. Owls in 16 of the 17 nests successfully fledged at least one nestling, a 94% success rate, in 2000. We found no significant differences in nest level variables between owls using new burrows and those in reused burrows.

Identifying the cause of nest failure was difficult since prairie dogs typically reoccupied the burrow immediately following owl pair dispersal and destroyed evidence. Nonetheless, the main reason for nesting failures appeared to be abandonment. In abandoned nests, eggs typically were within 0.5 m of the original nest location within the burrow; sometimes eggs were in a line, possibly a result of manipulation by prairie dogs. Abandoned nests lacked any evidence of depredation, and adults usually were still in the general vicinity. In 1999, flooding following a long period of heavy rain may have precipitated nest abandonment. Based on evidence left after badger predation (Green and Anthony 1989, Desmond 1991) and black-footed ferret predation (Griebel 2000), only one nest in 1999 and three nests in 2000 were lost to badgers and four nests in 1999 and one nest in 2000 were likely depredated by black-footed ferrets.

Nest and Pair Factors. The mean pair arrival date in 2000 was 29 April (range: 11 April–10 June); however, pair arrival sharply decreased after 7 May. Mean clutch initiation date was 15 May (range: 28 April–16 June) in 1999, and 9 May in 2000 (range: 1 May–17 June). In 2000, successful pairs had earlier clutch initiation dates (8 May ± 0.01 d) than unsuccessful pairs (11 May ± 0.03 d, $t_{111} = 2.63$, $P = 0.02$).

The mean nearest neighbor distance was 296.3 m (range: 25.0–1773.0 m) and 266.7 m (range: 21.0–997.0 m) in 1999 and 2000, respectively. The mean number of nests within 250 m of a nest was 1.2 (range: 0–5.0) in 1999 and 0.9 (range: 0–3.0) in 2000. Successful pairs had greater average nearest neighbor distances (251.1 ± 0.1 m) compared to unsuccessful pairs (135.0 ± 0.1 m, $t_{139} = -2.5$, $P = 0.01$) and averaged fewer nests within 250 m of their nest (0.8 ± 0.1) than unsuccessful pairs (1.3 ± 0.2, $t_{141} = 2.19$, $P = 0.03$) in 2000.

The mean distances to edge were 74.4 m (range: 5.0–347.0 m) in 1999 and 82.2 m (range: 1.0–500.0 m) in 2000. Distance to the nest in the burrow ranged from 1.1 to >3.5 m in 1999 and from 0.8 to >3.5 m in 2000. There were eight nests in 1999 and one nest in 2000 that were located >3.5 m down burrows. Neither of these variables was correlated to nest success.

Those pairs that initiated nests earlier had larger clutches and broods in 1999 (Table 2). No variables were retained in the multiple regression model for number fledged in that year. In 2000, those pairs that initiated nests earlier and had either greater nearest neighbor distances or fewer nests within 250 m had larger clutches, broods, and fledged more young (Table 2).

Colony Factors. In 1999, 43 of the 63 prairie dog colonies (range: 2.6–452.0 ha) were selected as nesting areas by Burrowing Owls (68%); in 2000, 45 colonies (range: 1.5–700.0 ha) were chosen as nesting sites (71%). Prairie dog colonies occupied by nesting Burrowing Owls were significantly larger (47.0 ± 7.3 ha) than unoccupied colonies (4.8 ± 2.8 ha; $t_{61} = -7.44$, $P < 0.001$) in 1999 and in 2000 (occupied: 52.8 ± 17.0 ha; unoccupied: 5.9 ±

Table 2. Results of stepwise multiple regression showing which variables were the best predictors of Burrowing Owl reproductive performance per nesting attempt at the nest scale in Buffalo Gap National Grassland, South Dakota, 1999 and 2000.

YEAR	REPRODUCTIVE OUTPUT VARIABLE	R^2	df	F	P	VARIABLES RETAINED IN MODELS (REGRESSION COEFFICIENTS)
1999	Clutch size	0.18	49	10.81	0.002	Clutch init. date (−0.40**)
	Brood size	0.07	63	4.35	0.04	Clutch init. date (−0.26*)
	Young fledged					None retained
2000	Clutch size	0.33	97	23.70	<0.001	Clutch init. date (−0.55***) Nests within 250 m (−0.17*)
	Brood size	0.12	110	7.51	0.001	Clutch init. date (−0.25**) Near. neigh. dist. (0.24*)
	Young fledged	0.16	110	9.96	<0.001	Clutch init. date (−0.28**) Near. neigh. dist. (0.27**)

* $P \leq 0.05$, ** $P < 0.01$, *** $P < 0.001$.

1.1 ha; $t_{61} = -4.83$, $P < 0.001$). Of the 43 colonies chosen as nest sites in 1999, 86% were selected again in 2000.

Burrowing Owls nested in 19 (1999) and 18 (2000) of the prairie dog colonies that were measured for prairie dog activity. Owl density (breeding pairs/ha/prairie dog colony) was similar with a mean of 0.2 owls in each year. The prairie dog colonies averaged 130 ± 5.75 (range = 66.7–208.3) active burrows/ha (94%) and 8.5 ± 1.33 (range = 0.0–34.4) inactive burrows/ha (6%) for both years combined.

Colony-scale variables explained a greater amount of the variation in owl reproductive performance than did nest and pair variables (Table 3). Average clutch size was larger in prairie dog colonies with lower densities of owls in 1999. In 2000, mean clutch initiation date, which was negatively related, and mean nearest neighbor distance, which was positively related, explained 70% of the variation in mean clutch size. No variables were retained in the multiple regression model for brood size in 1999. In 2000, average brood size was negatively related to the mean number of nests within 250 m of a nest. On average, fledging success (mean number of young fledged per nesting attempt per colony) was greater in larger colonies in 1999. In 2000, mean nearest neighbor distance (positive coefficient) and mean clutch initiation date (negative coefficient) explained 55% of the variation in mean number of young fledged per nesting attempt.

Several variables were related to prairie dog colony size. In 1999, the number of nests/colony and mean distance of nests to edge ($r^2 = 0.44$, $P < 0.001$) were both positively related to prairie dog colony size. In 2000, the number of nests/colony ($r^2 = 0.58$, $P < 0.001$) and mean distance of nests to edge ($r^2 = 0.35$, $P < 0.001$) were positively related to colony size. Owl density/colony was negatively related to colony size in both years (1999: $r^2 = 0.49$, $P < 0.001$; 2000: $r^2 = 0.58$, $P < 0.001$).

Table 3. Results of stepwise multiple regression showing which variables were the best predictors of Burrowing Owl reproductive performance per mean nesting attempt at the prairie dog colony scale in Buffalo Gap National Grassland, South Dakota, 1999 and 2000.

YEAR	REPRODUCTIVE OUTPUT VARIABLE	R^2	df	F	P	VARIABLES RETAINED IN MODELS (REGRESSION COEFFICIENTS)
1999	Clutch size	0.37	12	6.51	0.03	Pair density (−0.61*)
	Brood size					None retained
	Young fledged	0.34	13	6.25	0.03	Colony size (0.59*)
2000	Clutch size	0.70	15	15.24	<0.001	Clutch init. date (−0.63**) Near. neigh. dist. (0.38*)
	Brood size	0.41	16	10.10	0.006	Nests within 250 m (−0.63**)
	Young fledged	0.55	16	8.64	0.004	Near. neigh. dist. (0.55*) Clutch init. date (−0.32*)

* $P \leq 0.05$, ** $P < 0.01$, *** $P < 0.001$.

DISCUSSION

Burrowing owls that initiated their clutches earlier in the season had better reproductive performance. Birds in our study were not banded, and it is possible that at least some of the later nests could have been renesters that had moved to another burrow. Thus, the observed decrease in clutch size could be in part a function of subsequent clutches for some pairs. However, in a study of banded Burrowing Owls in the grassland ecoregion of Saskatchewan, Canada, Wellicome (2000) reported findings similar to ours for female arrival date, clutch initiation date, and clutch size during initial nesting attempts. Females wintering in good habitat are most likely in better physical condition and have more nutrient reserves, allowing them to migrate earlier and produce more eggs. Studies of arctic-nesting geese and temperate-nesting ducks have suggested that storage of nutrients is essential for egg-laying and subsequent incubation (Ankney and MacInnes 1978, Raveling 1979, Wypkema and Ankney 1979, Drobney 1980, Krapu 1981, Ankney and Afton 1988).

In general, Burrowing Owls having greater distances between nests or fewer nests located within 250 m of a nest demonstrated better reproductive performance. (Nest spacing was not a significant factor in 1999 nest-scale models, possibly due to the number of flooded nests in that year.) It is unclear why decreased nest spacing negatively influenced clutch sizes in our study. Wellicome (2000) found that clutch size was not affected by supplemental feeding in Burrowing Owls in Canada, indicating that food likely was not limiting during the egg-laying period there. However, he did conclude that food intake was limited during brood-rearing and that reproductive output for Burrowing Owls varied with the amount of food resources (Wellicome 1997).

Burrow length and nest distance to colony edge were not significantly related to any of the reproductive performance variables (i.e., clutch size, brood size, and number fledged per nesting attempt) in our study. In Nebraska, Burrowing Owl nests were more successful when located further from the edge of prairie dog colonies (Eckstein 1999). Prairie dog colonies in that study were adjacent to agriculture fields, roads, and wooded habitat, which may have concentrated certain predators along edges. Unlike many previous studies, our research was conducted in continuous habitat where all adjacent habitat was also shortgrass prairie, minimizing potential edge effects on nesting success.

Contrary to findings in Nebraska (Desmond et al. 2000), none of the prairie-dog-related factors were retained in the multiple regression models for reproductive performance, possibly because of the relative uniformity of ecological factors of prairie dog colonies in Buffalo Gap. Prairie dog densities and burrow activity were relatively high in most of the colonies because of management practices on the Buffalo Gap National Grassland; Buffalo Gap prairie dogs experienced neither a plague epidemic nor poisoning during the time of our research, both of which can severely reduce populations or cause the extinction of the affected colony.

In 1999, size of prairie dog colonies was positively related to mean number of owlets fledged per nesting attempt. Contrary to Orth and Kennedy's (2001) findings of no size difference between occupied and unoccupied prairie dog colonies, colonies used by Burrowing Owls in Buffalo Gap were significantly larger than unoccupied prairie dog colonies. Most (80% in 1999 and 89% in 2000) of the unoccupied prairie dog colonies in our study were <10 ha. Although the average density of owl pairs was lower in larger prairie dog colonies than in smaller ones, total numbers of owls there were greater in both years. Neither the mean nearest neighbor distance nor the mean number of nests within 250 m of a nest was related to prairie dog colony size. Thus, it appears that owls chose to nest in certain desirable portions within a large prairie dog colony, rather than randomly place their nests throughout the prairie dog colony. This was consistent with clumping of nests seen in Nebraska (Desmond et al. 1995).

Nesting success (76%) and number of young fledged per nest attempt (2.6) at our study site were generally equal to or greater than that found at prairie dog colonies in more fragmented habitat in the Great Plains. Burrowing Owls in the Nebraska panhandle had a mean success rate of 48% during 1989–93 (M. Desmond pers. comm.) and 58% during 1996–97 (Ekstein 1999); Burrowing Owl fledglings per nesting attempt averaged 1.9 (Desmond et al. 2000) and 2.6 (Ekstein 1999). In Wyoming, the success rate was 80% in 2003 and 76% in 2004 (Lantz 2005), while in North Dakota it was 75% and 87% for the same two years, respectively (Davies 2005). A success rate of 92% in southeast Montana was reported by Restani et al. (2001) with pairs fledging 2.6 nestlings per nesting attempt. Nearest neighbor distances recorded on Buffalo Gap were within the range reported in other Great Plains prairie dog colonies (e.g., Plumpton 1992, Desmond and Savidge 1996, Restani et al. 2001, Restani 2002, Davies 2005, Teaschner 2005).

Burrow reuse on our study site (13%) was slightly lower than that recorded in prairie dog colonies in northeastern Colorado (20%; Plumpton 1992), and much lower than for owls nesting in badger burrows in Oregon (57–87%; Holmes et al. 2003). The latter difference is most likely a function of burrow limitation. As in Colorado (Lutz and Plumpton 1999), Burrowing Owls at Buffalo Gap that selected a burrow used in the previous year produced more young than those using new burrows, and owls nesting in these burrows were very successful in both years of our study. It is unknown if any of the same owls were reusing nest burrows. Plumpton (1992) reported burrow reuse typically occurring by a different pair of owls, whereas Martin (1973) found returning male owls selecting the same burrow used the previous year.

Only four Burrowing Owl nests were lost to badgers during our study. Badger predation was responsible for up to 48% of nest failures in low density prairie dog colonies but was relatively unimportant in high density colonies in western Nebraska (Desmond et al. 2000). High densities of prairie dogs, like those at Buffalo Gap, should decrease the chances of a badger selecting a Burrowing Owl nest as opposed to a prairie dog burrow.

Several aspects of Burrowing Owl reproduction in Buffalo Gap were similar to that reported for owls nesting in more fragmented landscapes (e.g., nesting success, number of young fledged per nest attempt, a decrease in reproductive performance with decreased nearest neighbor distance). One obvious difference was the percentage of colonies occupied by nesting Burrowing Owls (i.e., 70% for both years combined), which is higher than that reported in a number of other studies of owls in prairie dog colonies: 16% in southeastern Montana (Restani et al. 2001), 21–29% in North Dakota's Little Missouri National Grassland (Davies 2005, Restani 2002), 59% in western Nebraska (Ekstein 1999), and 21–26% in northeastern Colorado (Pezzolesi 1994). However, further south, owls in prairie dog colonies in the Comanche National Grassland, in southeastern Colorado, had owl occupancy rates similar to our study area (76%; Toombs 1997). All of the above sites were more fragmented and did not contain colonies approaching the size of the largest ones on Buffalo Gap.

Burrowing Owls prefer to nest in active prairie dog colonies (Toombs 1997, Desmond et al. 2000, Lantz 2005), and events such as plague or poisoning remove available habitat. Management decisions undertaken by the U.S. Forest Service for black-footed ferret recovery, including shooting and poisoning restrictions, appear to have beneficial effects on Burrowing Owls at Buffalo Gap. The Burrowing Owl population is large, and an extensive banding effort may elucidate whether Buffalo Gap is serving as a source for other nearby populations.

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