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SEX AND NEST STAGE DIFFERENCES IN THE CIRCADIAN FORAGING BEHAVIORS OF NESTING BURROWING OWLS

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Abstract. We used infrared cameras to accurately record the circadian provisioning behaviors of nesting Burrowing Owls (*Athene cunicularia*) in southern Saskatchewan, Canada. We monitored 19 nests over three years and recorded 4675 prey deliveries. We found a sex-based difference in foraging behavior: males hunted vertebrates during crepuscular periods, and females hunted insects during diurnal periods. Males delivered between 82% and 96% of all vertebrate prey depending on the stage of the nest. Males delivered at least 90% of all insects during early nest stages, after which females delivered an average of 76% of the insects. The rate of vertebrate deliveries increased from 1.3 to 7.7 per 24 hr as the summer progressed, and the number of insect deliveries increased from less than 1 to 18.6 per 24 hr. Vertebrates comprised 98%–99% of prey biomass delivered until females began delivering insects, but even then vertebrates still comprised 94% of prey biomass. Insects were consistently delivered at the highest rate during the day and vertebrates were consistently delivered at the highest rates during the dusk and dawn periods.

Key words: Athene cunicularia, *Burrowing Owl, diet, foraging behavior, provisioning.*

Diferencias Sexuales y en la Etapa del Nido en los Comportamientos de Forrajeo Circadianos de Individuos Nidificantes de *Athene cunicularia*

Resumen. Usamos cámaras infrarrojas para registrar con precisión los comportamientos de aprovisionamiento circadianos de *Athene cunicularia* en el sur de Saskatchewan, Canadá. Seguimos 19 nidos durante tres años y registramos 4675 entregas de presas. Encontramos diferencias entre sexos en el comportamiento de forrajeo: los machos cazaron vertebrados durante los periodos crepusculares y las hembras cazaron insectos durante los periodos diurnos. Los machos entregaron entre 82% y 96% de todas las presas de vertebrados, dependiendo de la etapa del nido. Los machos entregaron al menos el 90% de todos los insectos durante los estadios iniciales del nido, después de lo cual las hembras entregaron en promedio el 76% de los insectos. La tasa de entrega de vertebrados incrementó entre 1.3 y 7.7 por 24 h a medida que avanzó el verano, y el número de entregas de insectos aumentó desde menos de 1 a 18.6 por 24 h. Los vertebrados representaron entre el 98% y el 99% de la biomasa de presas entregada hasta que las hembras comenzaron a entregar insectos, pero incluso en este momento los vertebrados todavía representaron el 94% de la biomasa de las presas. De modo consistente, los insectos fueron entregados a la mayor tasa durante el día y los vertebrados a las mayores tasas durante el anochecer y el amanecer.

INTRODUCTION

Accurately identifying life-history characteristics is essential to the understanding of relationships among species and factors that are relevant to their persistence in an environment. Identifying even the most fundamental behaviors can be challenging in rare, secretive, cryptic, or nocturnally active species. However, the ability to study behaviors of these somewhat difficult species has been significantly improved with the advent of miniature infrared video systems. Video systems allow behaviors to be recorded and reviewed in very fine detail, with minimal disturbance to the study subjects and minimal biases in data collection (Delaney and Grubb 1999).

Burrowing Owls (*Athene cunicularia*) are listed as Endangered in Canada, Threatened in Mexico, and as a National and Regional Bird of Conservation Concern in the U.S. (Holroyd et al. 2001). Despite the attention this species has received, many of its fundamental behaviors remain poorly documented. Without video cameras, accurate behavioral observations of this small owl are difficult because it nests

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underground within open grasslands, areas where human observers have difficulty remaining camouflaged during observations.

There have been a multitude of papers and dissertations reporting Burrowing Owl diet based on the contents of regurgitated pellets (Haug et al. 1993). These studies have included Burrowing Owls in Argentina (Bellocq 1997), Chile (Silva et al. 1995), Mexico (Rodriguez-Estrella 1997), the United States (Marti 1974, Green and Anthony 1989, Green et al. 1993, Restani et al. 2001), and Canada (Schmutz 1991, Poulin 2003, Sissons 2003). These studies suggest that Burrowing Owls are generalists that feed on a wide variety of prey items. Quantitatively, arthropods (e.g., grasshoppers, beetles, crickets, earwigs, scorpions, and moths) dominate (~80%–90%) the diet, while small mammals (e.g., *Microtus* spp., *Peromyscus* spp., and heteromyids) tend to dominate biomass consumed. Several studies (MacCracken et al. 1985, Green and Anthony 1989, York et al. 2002, Sissons 2003) also suggest the composition of the owl's diet changes toward a greater arthropod dominance as the summer progresses, but none have examined foraging behaviors or diet in direction relation to nesting stage.

Some authors (Green et al. 1993, Yosef and Deyrup 1994) have drawn conclusions about the hunting behaviors of Burrowing Owls based on the diurnal or nocturnal nature of the prey items found in their pellets. One of the most common prey taxa in Burrowing Owl diets is grasshoppers, a taxon that is primarily active during the day, suggesting that owls are hunting during the day. This notion is given credence by the easily observable fly-catching behaviors of Burrowing Owls during daylight (Coulombe 1971, Marti 1974, Thompson and Anderson 1988). However, their diet also includes many arthropods (e.g., scorpions, crickets, moths, and earwigs) and small mammals that are primarily active during crepuscular or nocturnal periods, suggesting Burrowing Owls are also hunting after sunset. This notion is supported by reports of increases in foraging activity during crepuscular or nocturnal periods (Thomsen 1971, Haug and Oliphant 1990, Pezzolesi and Lutz 1994).

Attempts to directly observe and record Burrowing Owl foraging patterns have been biased because daytime observations have been limited by the use of binoculars or spotting scopes, and nocturnal observations have been limited by the use of spotting scopes with the aid of flashlights (Grant 1965), night-vision spotting scopes (Thompson and Anderson 1988, Pezzolesi and Lutz 1994), observations associated with radio-tracking (Haug and Oliphant 1990, Sissons 2003), and the indistinguishable behaviors recorded from an event recorder at the burrow entrance (Marti 1974). These methods are limiting because they do not provide equal information from an entire 24-hour period. The purpose of this study was to accurately record the circadian pattern of Burrowing Owl hunting activities during the nesting period and to determine the importance of particular prey taxa to the overall diet of Burrowing Owls during this period.

METHODS

STUDY AREA

We studied the foraging activities of Burrowing Owls during the spring and summer months of 2002–2004 in the Regina Plain (Harris et al. 1983), part of the moist mixed grassland ecoregion of southern Saskatchewan, Canada. Specifically, the owls we observed were nesting in grassland pastures near the towns of Lang (49°54′N, 104°21′W), Milestone (49°59′N, 104°30′W), and Rouleau (50°11′N, 104°53′W). Native grass communities in this area are primarily composed of Junegrass (*Koeleria macrantha*), blue gramma grass (*Bouteloua gracilis*), needlegrass (*Stipa* spp.), and wheatgrass (*Agropyron dasystachyum*). However, the landscape is presently dominated by agriculture, and only a small fraction of native prairie remains (Gauthier et al. 2002). Remaining areas of native prairie tend to be small, highly fragmented parcels of land used for the production of cattle. Burrowing Owls in this area tend to nest in the remnant grasslands (Poulin et al. 2005).

Only nests in nest boxes (Poulin 2003) were included in this study. The use of nest boxes allowed us to accurately determine when eggs were laid and when chicks hatched. These boxes were installed several years prior to this study, in burrows that owls had previously chosen as nesting sites. We have no reason to believe that nest boxes had any influence on the foraging behaviors of the owls presented in this study.

DATA COLLECTION

We used small, infrared-sensitive video camera systems (MicroVideo™ model MVC2000, MicroVideo Products, Bobcaygeon, Ontario, Canada) to record behaviors and prey deliveries at Burrowing Owl nests. Cameras were barrel shaped, 35 mm in diameter and 47 mm in length, and emitted infrared light from six light-emitting diodes located around the circumference of the lens area. We housed cameras in short (105 mm) pieces of polyvinylchloride (PVC) tubing to protect them from cattle trampling, to minimize sun glare, and to protect the recorded images from being blurred by raindrops and dust. Tubes were painted in a camouflage pattern and were concealed with pieces of dried cow manure or rocks. Cameras were set on the ground, 10–30 cm behind the nest-burrow entrance, and positioned so that the burrow entrance and entire mound were in focus.

Cameras were connected to professional grade 24-hour real time videocassette recorders (VCR; Sanyo® model SRT-612DC) with 4 mm black coaxial cable. To minimize disturbance to the owls, VCRs were placed at least 30 m from the nest, housed in weatherproof, cow-proof, hard-sided cases, and camouflaged in burlap. Each camera and VCR unit was powered by a rechargeable 12 V battery, housed in a weatherproof container. A charged battery allowed us to run a system continuously for 24 hr, the limit of each videocassette tape. Each day, usually before noon, the videotape and battery were changed and the system reset to record for the next 24-hr period. These actions only took a few minutes and, based on our observations from the videos, our visits had no impact on the behaviors of the owls once we left the area. Each video was date- and time-stamped in the frame, allowing us to record exactly (accurate to 1 sec) when each prey delivery was made to the nest.

DATA ORGANIZATION

We noted the time of day the camera started recording, the times the camera was blacked out (because of direct sunlight or other incidents), and the time recording ended. Recordings ended when the battery failed, the videotape ended, or when a person approached to change the battery and videotape. We also recorded the time of day each prey item was delivered to the nest area, regardless of whether it was fed to the young, eaten by an adult, or stored in the nest burrow. We recorded the identity of the owl delivering each prey item (male or female), and the identity of the prey item itself (insect or vertebrate). It was rarely possible to identify the taxon of insects being delivered (e.g., beetle versus grasshopper), but we could regularly identify vertebrate species.

We divided the day into periods in two ways: 1) 24 1-hr periods corresponding to each hour of the day, and 2) by sun position: "day," "dusk," "dawn," and "night." Day was defined as the period when the upper edge of the sun was above the horizon; night was defined as the period when the center of the sun was lower than 12° below the horizon; dusk and dawn were defined as the times when the center of the sun was less than 12° below the horizon (nautical twilight) in the evening and morning, respectively. All sun position times were determined from the U.S. Naval Observatory Astronomical Applications Department website (<http://aa.usno.navy.mil/>).

We calculated an hourly delivery rate by dividing the number of prey deliveries in each hour by the proportion of that hour that was videotaped. This allowed us to correct for those hours of the day in which videotaping did not cover the entire hour. For analysis, we only included hours with at least 30 min of recording. This method was also used to calculate a delivery rate for each daily time period (i.e., day, dusk, night, and dawn). We assigned our observations to four nest stages: "pre-egg laying," "incubation," "brooding" (1–10 days posthatching), and "nestling" (11–29 days posthatching).

STATISTICAL ANALYSIS

We used paired *t*-tests to determine differences in the proportion of vertebrates and insects delivered to nests by paired males and females from the same nest. We used ANOVA to determine between-year differences in delivery rates and we used ANOVA and Tukey *post-hoc* tests to compare differences in the number of prey delivered among nesting stages. We included only those nests for which we had at least three complete days of video observations.

Estimates of biomass were based on the premise that the average insect delivered to the nest had a mass of 0.5 g and each vertebrate

TABLE 1. Differences in prey delivery rates between male and female Burrowing Owls over the course of four nesting stages. We included only those nests with at least three days of video recording. Numbers in parentheses are the number of prey items we observed being delivered for each nesting stage. Males provided the vast majority of vertebrate prey in all nest stages. Males also provided the majority of insect prey while females were incubating and brooding; in the nestling stage, females delivered the majority of insect prey.

	Males	Females	t_{df}	P
Vertebrates				
Pre-egg laying (63)	86%	14%	$t_{13} = 18.3$	< 0.001
Incubation (284)	93%	7%		
Brooding (726)	96%	4%	$t_{10} = 42.2$	< 0.001
Nestling (862)	82%	18%	$t_{10} = 8.9$	< 0.001
Insects				
Pre-egg laying (44)	91%	9%	$t_7 = 8.3$	< 0.001
Incubation (168)	90%	10%		
Brooding (428)	68%	32%	$t_{10} = 2.8$	< 0.05
Nestling (1814)	24%	76%	$t_9 = -3.6$	< 0.01

delivered to the nest had a mass of 20.0 g. Average insect mass was based on Marti (1974), who estimated that Carabidae, Scarabaeidae, and Silphidae beetles were an average of 0.3 g and grasshoppers were an average of 0.6 g. Since we were unable to determine the relative proportions of grasshoppers and beetles being delivered to nests in this study, we settled on the somewhat arbitrary but reasonable estimate of 0.5 g per insect. Our estimate of average vertebrate mass was based on the proportion of small mammals and birds in Burrowing Owl pellets from this study area and the average fresh mass of each prey species determined by Poulin (2003).

All statistical tests were performed using Systat 9.0 for Windows (SPSS 1998) and differences were considered significant at $P < 0.05$. Means are presented ± SE.

RESULTS

SEX DIFFERENCES IN PREY DELIVERED

We videotaped 19 Burrowing Owl nests (three nests in 2002, eight in 2003, and eight in 2004) between 18 April and 13 July each year. We recorded and analyzed 7180 hours of video from 333 days. In all, we recorded 4675 prey deliveries, 2221 vertebrate prey items and 2454 insect prey items.

Males delivered significantly more vertebrates than females during all nesting stages (Table 1). Males delivered at least 82% of the vertebrates in each nesting stage and effectively all of the vertebrates while females were incubating eggs or brooding chicks. We believe these proportions represent a minimum estimate of male deliveries because we are confident that females occasionally received prey items from the male out of view of the camera (i.e., from our vantage point the female returned with the prey item, when in fact she simply received it from the male). In the majority of vertebrate deliveries, males returned to the nest with a prey item and immediately delivered it to the female, who in turn gave it to a chick or cached the item in the nest burrow. During nonhunting periods, cached vertebrates were often brought up from the nest burrow and either eaten at the nest or carried away, presumably to be consumed elsewhere or cached in another burrow.

Males delivered significantly more insects than females prior to the "nestling" stage, at which time females delivered significantly more insects (Table 1). In general, males delivered almost all insects prior to the eggs hatching, but females became the primary insect providers once they were freed from their incubation duties. When a male owl returned with an insect, he either ate it immediately or gave it to the female. After receiving the insect, the female would either eat it immediately or give it to a chick. Male owls very rarely fed a chick directly. Even if besieged by the brood, the male would rarely give up the insect, but instead wait for the female to take the insect from him to feed to a chick. We rarely observed insects being cached.

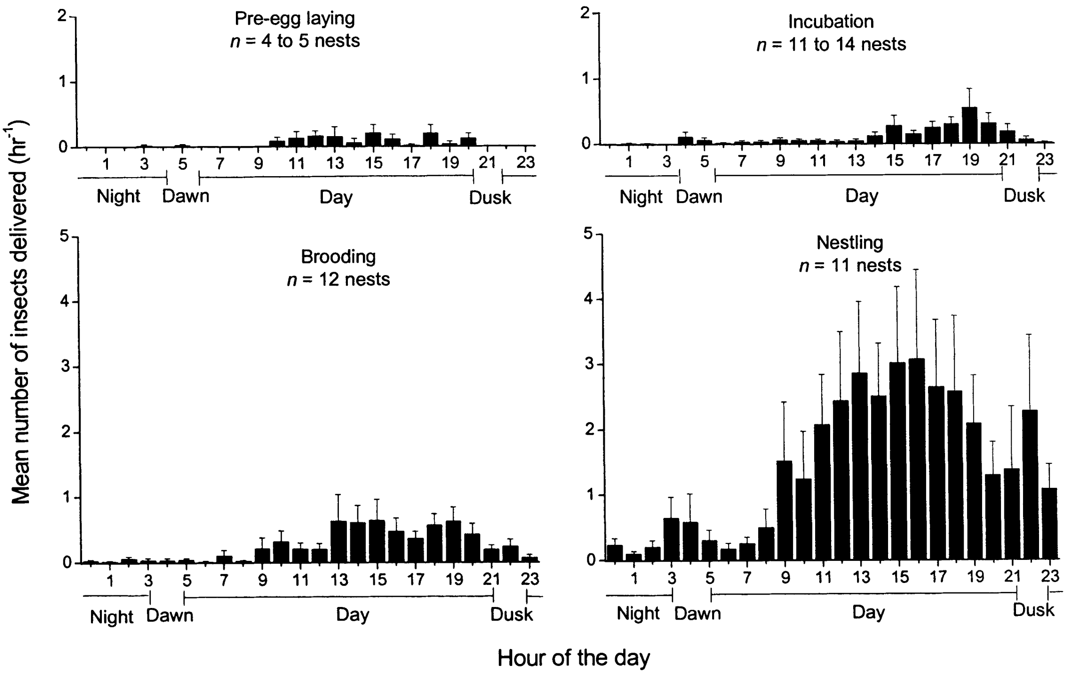

FIGURE 1. Circadian foraging patterns of Burrowing Owls based on insect delivery rates (mean insects hr^{-1} ± SE) for each hour of the day. Burrowing Owls delivered insect prey to their nests at higher rates during daylight hours and in the "nestling" stage (11–29 days posthatching). Data were collected in southern Saskatchewan in 2002–2004 using 24-hr video cameras, and are divided among nesting stages and daily periods (n = number of nests used to calculate mean for each hour).

DIET COMPOSITION

There was no significant difference (year: $F_{2,22} = 1.2$, $P = 0.33$; nest stage: $F_{1,22} = 26.8$, $P < 0.001$; year*nest stage: $F_{2,22} = 0.5$, $P = 0.63$) among years in the rate vertebrates were delivered to nests within pre- and posthatching periods (prehatching, 2002: $\bar{x} = 1.4 \pm 0.4$, 2003: $\bar{x} = 2.2 \pm 0.3$, 2004: $\bar{x} = 3.7 \pm 0.6$; posthatching, 2002: $\bar{x} = 6.1 \pm 0.5$, 2003: $\bar{x} = 7.0 \pm 1.7$, 2004: $\bar{x} = 6.9 \pm 1.0$). However, there was a significant difference (year: $F_{2,22} = 5.4$, $P = 0.01$; nest stage: $F_{1,22} = 28.1$, $P < 0.001$; year*nest stage: $F_{2,22} = 5.0$, $P = 0.02$) in the rate of insect deliveries (prehatching, 2002: $\bar{x} = 1.4 \pm 0.2$, 2003: $\bar{x} = 1.3 \pm 0.5$, 2004: $\bar{x} = 0.9 \pm 0.6$; posthatching, 2002: $\bar{x} = 20.0 \pm 3.7$, 2003: $\bar{x} = 6.3 \pm 0.9$, 2004: $\bar{x} = 6.6 \pm 2.5$). This difference was due to a significantly higher delivery rate during the posthatching period in 2002 compared to 2003 or 2004. In general, prior to the "nestling" stage, Burrowing Owls delivered about twice as many vertebrates as insects to the nest (Fig. 1, 2). During the "nestling" stage, the majority of prey deliveries were insects; however, in terms of biomass, vertebrates were always the primary source of food (pre-egg laying = 0.4 ± 0.2 g insects vs. 25.2 ± 7.8 g vertebrates; incubation = 0.7 ± 0.2 g insects vs. 50.4 ± 7.8 g vertebrates; brooding = 1.5 ± 0.4 g insects vs. 120.3 ± 11.6 g vertebrates; nestling = 9.3 ± 2.5 g insects vs. 149.4 ± 17.5 g vertebrates). The number of deliveries of both insects and vertebrates increased as the season progressed. During the "nestling" stage, Burrowing Owls delivered an average of 18.6 insects per 24-hr period, the biomass equivalent of approximately 0.5 vertebrates. The maximum number of insects we observed delivered to any one nest in a single 24-hr period was 205, the biomass equivalent of about five vertebrates. The maximum number of vertebrates we observed delivered to any one nest in a 24-hr period was 29.

CIRCADIAN PATTERNS

Over the course of our study, dawn and dusk ranged from 77 to 111 min each, night ranged

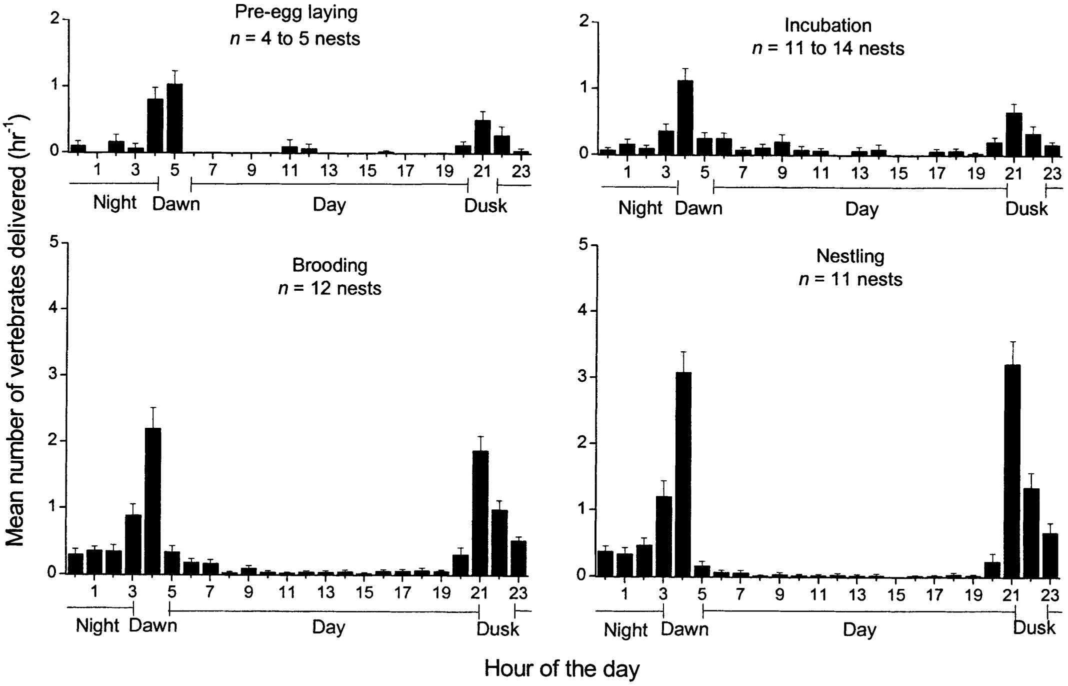

FIGURE 2. Circadian foraging patterns of Burrowing Owls based on vertebrate delivery rates (mean vertebrates hr^{-1} ± SE) for each hour of the day. Burrowing Owls delivered vertebrate prey to their nests at higher rates during crepuscular periods and increased delivery rates throughout the nesting period. Data were collected in southern Saskatchewan in 2002–2004 using 24-hr video cameras, and are divided among nesting stages and daily periods (n = number of nests used to calculate mean for each hour).

from 3 hr 57 min to 7 hr 26 min, and day lengths ranged from 14 hr to 16 hr 22 min. This variation necessitated the calculation of delivery rates per time unit as opposed to delivery rates per daily period.

Insects were delivered in all hours of the day (Fig. 1), but delivery rates were significantly higher during daytime in all nesting stages (nesting stage: $F_{3,190} = 13.0$, $P < 0.001$; period of the day: $F_{4,190} = 10.8$, $P < 0.001$); nesting stage*period of the day: $F_{12,190} = 5.7$, $P < 0.001$); Tukey *post-hoc* tests showed that insect delivery rates during the "day" were significantly ($P < 0.001$) different than during other periods. In general, it appears that insects were only delivered during the warm period of the day; insect deliveries were effectively nonexistent during the night and early morning hours (Fig. 1). Although we could not identify many insects being delivered to nests, our few observations combined with pellet contents (unpubl. data) suggest that insects captured early in the spring were primarily beetles, whereas more grasshoppers were caught by owls as the summer progressed.

Vertebrate deliveries were centered on crepuscular periods (Fig. 2, Table 2) and were effectively nonexistent during daylight hours (nesting stage: $F_{3,190} = 22.4$, $P < 0.001$; period of the day: $F_{4,190} = 30.3$, $P < 0.001$; nesting stage*period of the day: $F_{12,190} = 3.4$, $P < 0.001$); Tukey *post-hoc* tests showed that vertebrate delivery rates were significantly higher during dusk and dawn and lowest during the day and after midnight.

DISCUSSION

We found significant sex-based differences in the circadian foraging behavior of Burrowing Owls. Essentially, male Burrowing Owls foraged crepuscularly for vertebrates while females foraged diurnally for insects. These results both confirm and help explain the generalized conclusions from previous studies, that Burrowing Owls actively forage 24 hours per day and their diet is a combination of insects and small mammals.

Although using the camera system provided us with a large amount of detailed data, we do acknowledge one significant limitation: the cameras were only capable of recording activities that took place at the nest burrow. Therefore, our conclusions are based on these activities. However, we are confident our data accurately reflect the foraging behaviors of the owls since the adults were almost always within sight of the camera, and when they were away, we could usually account for their activities. During the "pre-egg laying," "incubation," and "brooding" periods, the male and female were almost always at the nest. Females rarely left the burrow, and males generally only left during crepuscular foraging periods. During the "nestling" period, the male was rarely in sight of the camera, but was obviously perched nearby, as evidenced by his immediate return to warn of approaching predators. It is possible that when the male was out of the camera's view he was foraging and subsequently eating insects (therefore they were not delivered to the nest).

Vertebrates comprised more than 90% of the dietary biomass delivered to the nest during all periods of our study and are therefore the most important component of the Burrowing Owl's diet during all prefledging nest stages. The vast majority of these prey items were small mammals such as mice and voles, but also included a variety of other vertebrates such as frogs, snakes, salamanders, birds, and even 10 Burrowing Owl chicks (all captured from neighboring nests by one pair). To our knowledge, this is the first recorded instance of conspecific predation for this species. Although vertebrate prey items contributed the greatest proportion of biomass to the Burrowing Owl's diet, the contribution of insects is likely still significant. Burrowing Owls lay large clutches of up to 14 eggs (Todd and Skilnick 2002), and the number of fledglings that survive is related to the amount of food provided by the parents (Wellicome 2005). Therefore, the additional nutrition provided by insect prey likely results in more fledglings than would otherwise survive from a nest. This may be of most importance when insect populations are at high levels, as appears to have been the case during the posthatching period of 2002, when high grasshopper densities were widespread across our study area (S. Hartley, Saskatchewan Agriculture and Food, pers. comm). The timing of insect deliveries may also play a significant role—without the provisioning of diurnal insects, nestling Burrowing Owls would have to endure more than 16 hours between crepuscular feedings.

Although the delivery rate of both vertebrates and insects increased as the nesting

TABLE 2. Summary of prey items delivered to Burrowing Owl nests. Insects were mainly delivered by females during daylight periods. Vertebrates were mainly delivered by males during crepuscular periods. Most birds were delivered during dawn or early morning periods and most herptiles were delivered during daylight periods. Insects were primarily beetles, grasshoppers, and moths. Small mammals were primarily deer mice (*Peromyscus maniculatus*), but also included voles (*Microtus pennsylvanicus* and *Lagurus curtatus*), shrews (*Sorex* spp.), and other mice. All grounds squirrels were young Richardson's ground squirrels (*Spermophilus richardsonii*), all snakes were plains garter snakes (*Thamnophis radix*), all frogs were boreal chorus frogs (*Pseudacris maculata*), and all salamanders were tiger salamanders (*Ambystoma tigrinum*). Birds were mainly comprised of grassland songbirds such as Lapland Longspurs (*Calcarius lapponicus*), Chestnut-collared Longspurs (*C. ornatus*), and Horned Larks (*Eremophila alpestris*).

	Males				Females			
	Dawn	Day	Dusk	Night	Dawn	Day	Dusk	Night
Insects	21	644	31	54	71	1258	241	134
Salamanders	0	1	0	2	0	0	0	1
Frogs	0	1	1	0	0	0	1	0
Snakes	1	2	0	0	0	0	0	0
Ground squirrels	0	4	0	0	0	0	0	0
Other small mammals	660	306	572	411	73	18	84	40
Young Burrowing Owls	0	2	0	0	3	0	4	1
Other birds	10	8[†]	3	7	2	0	0	3

[†] Five of the eight birds captured during the day were captured in the early morning, between 04:59 and 08:37.

season progressed, it is possible that insects play an increasingly important role in the diet of Burrowing Owls even later in the summer, after we stopped collecting data. Shyry (2005) suggested that juvenile Burrowing Owls are almost completely insectivorous between fledging and migration. Our video recording concluded when chicks were less than 30 days of age, because as the chicks grew older they became more and more vigorous in their begging and we could not accurately record prey deliveries. We therefore hesitate to extrapolate our results beyond the prefledging period, when the behavior of owls and availability of particular prey may change. In particular, we suspect that grasshopper availability could increase as summer progresses, making this taxon increasingly important to Burrowing Owls.

We also advise caution in extrapolating our results to Burrowing Owls nesting in other areas of the continent, where latitude, time of year, and prey base may interact to alter Burrowing Owl foraging behavior. For example, at the summer solstice, a Burrowing Owl nesting in Phoenix, Arizona has 93 min less crepuscular time than a Burrowing Owl nesting in Regina, Saskatchewan. These sorts of differences create an opportunity for future study, to address how pervasive sex-based foraging differences truly are in Burrowing Owls.

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