$$N_0(t) = bs_0s_1 \sum_{x=T}^{w-1} s^{x-2}\lambda^{-x}N_0(t)$$

or

$$1 = [(bs_0s_1)/s^2] \sum_{x=T}^{w-1} (s/\lambda)^x$$
$$= [(bs_0s_1)/s^2] \sum_{x=0}^{w-1-T} (s/\lambda)^{x+T}$$
$$= [(bs_0s_1)/s^2](s/\lambda)^T \sum_{x=0}^{w-1-T} (s/\lambda)^x. \quad (11)$$

Recall, in general

$$\sum_{k=0}^{n} x^k = (1 - x^{n+1})/(1 - x).$$

Incorporating this relationship into (11),

$$1 = [(bs_0s_1)/s^2](s/\lambda)^T \div [1 - (s/\lambda)^{(w-1-T)+1}] \div [1 - (s/\lambda)]. \quad (12)$$

Expressing (12) in terms of λ and setting it equal to 0,

$$\lambda^T - s\lambda^{T-1} - bs_0s_1s^{T-2}[1 - (s/\lambda)^{w-T}] = 0. \quad (13)$$

Equation (13) is equivalent to equation (8). Letting w be undefined and setting $T = 2$ gives equation (7). Letting $w = \infty$ and $T = 2$ in equation (13) gives equation (3).

MOVEMENTS, ACTIVITY PATTERNS, AND HABITAT USE OF BURROWING OWLS IN SASKATCHEWAN

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Abstract: We studied the breeding ecology of burrowing owls (*Athene cunicularia*) in central Saskatchewan during 1982–83. We determined home range, activity patterns, and habitat used for foraging for 6 radio-tagged adult male owls. Owls used grass-forb areas for foraging and avoided croplands and grazed pasture. Mean home-range size was 2.41 km² (range = 0.14–4.81 km²). Peak foraging activity occurred between 2030 and 0630 hours. Ninety-five percent of all movements were within 600 m of the nest burrows. The nesting habitat requirements of short grass, open sites, and burrow availability can be met by managing and protecting existing historic sites.

J. WILDL. MANAGE. 54(1):27–35

The burrowing owl is classified as a threatened species in Canada because of an apparent decline of the small breeding population (Wedgwood 1978). In Saskatchewan, the primary breeding range of the burrowing owl in Canada, much of the native habitat originally occupied by burrowing owls has been converted to cropland. Loss of nesting habitat has also been implicated as a leading cause of the population decline in the United States, but the causes appear to be more complex on the Canadian prairies (Wedgwood 1978).

As nesting habitat of the burrowing owl declines, it becomes increasingly important to understand the habitat requirements of the species for management and conservation. Many investigators (Coulombe 1971, Thomsen 1971, Martin 1973, Ross 1974, Wedgwood 1976) have documented various aspects of the diurnal activities of burrowing owls during the breeding season. We studied nocturnal movements, activity patterns, and habitat use of burrowing owls in Saskatchewan with radio telemetry.

We thank the World Wildlife Fund, Canada, and the Saskatchewan Department of Parks and Renewable Resources for financial support. J. A. King, W. J. Maher, M. R. Duwors, R. J. Smith, D. W. Leach, S. Jana, University of Saskatchewan; J. B. Gollop, Canadian Wildlife Service;

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and M. K. Mukerji, Agriculture Canada contributed time and effort to the project. J. B. Gollop and J. A. Wedgwood provided the historical locations of burrowing owl nest sites across Saskatchewan. A special thanks goes to the Deschamps, the Thompsons, and the many farmers who allowed access to their land and provided encouragement during the field work. We also acknowledge A. B. Didiuk, who worked long hours in the field and edited many manuscripts.

STUDY AREAS

Two nesting areas, approximately 15 km apart, were selected for telemetry studies. Both were located in southcentral Saskatchewan, approximately 100 km south of Saskatoon. This area is part of the Saskatchewan Rivers Plain Physiographic Region and is comprised of undulating lacustrine, fluvial, aeolian, and till (moraine) lands (Hart and Hunt 1981) with elevations ranging from 490 to 640 m. Intensive agriculture in the form of cereal crops was grown throughout the area. Native vegetation included mixed prairie grassland associations (Coupland and Rowe 1969) that were restricted to uncultivated areas primarily associated with stoney soils, excessive slopes, and/or poor soil moisture.

Both study areas were heavily grazed livestock pastures with ≥3 breeding pairs of owls. Study area A was centered on a 32-ha pasture near Ardath, Saskatchewan. Study area B was centered on a 65-ha pasture near Bounty, Saskatchewan. The land surrounding both study areas was a mixture of fallow, cereal crops, and pasture. All nesting burrows were excavated by badgers (*Taxidea taxus*), and burrow availability did not appear to limit production. A survey conducted in 1981 assessed the availability and use of satellite burrows around 27 nest burrows and found a mean of 6 available burrows within a 30-m radius of the existing nest burrows (Haug 1985).

METHODS AND DEFINITIONS

Field work was conducted from May to September 1982 and 1983. Each nesting area was systematically searched on foot to count the number of breeding pairs and to locate their nest burrows.

During late May and early June of both years we attempted to capture all adult owls at the 2 telemetry study areas for radiotagging and/or colormarking for individual recognition. Adults were captured using padded steel leg-hold traps (no. zero) buried at burrow entrances. Owls were weighed, measured, sexed by presence or absence of a brood patch, banded with a U.S. Fish and Wildlife Service aluminum leg band and colormarked with plastic leg jesses (F. Hamerstrom, Univ. of Wisconsin, pers. commun.). Nine male owls were radiotagged over the 2-year study period. Transmitter packages weighed 8–9 g and were modified (Haug 1985) from a poncho design used with sharp-tailed grouse (*Tympanuchus phasianellus*) (Amstrup 1980). Transmitters operated from 10 to 74 days. All were collars sewn with cotton thread and were designed to "break away." Should attempts to retrap an owl and remove its collar be unsuccessful, the cotton thread would rot and the collar would fall off within a few months.

A receiver and 1 5-element Yagi or 2 5-element Yagi antennas mounted in null-peak configuration on a cartop carrier were used to monitor radio-tagged owls. Vehicle access in and around the study area allowed for 95% of the bearings to be determined from a distance of ≤0.8 km. This system was tested for accuracy at varying distances with stationary transmitters and telemetry checks of stationary owls during daylight. At a distance of 0.8 km, accuracy of bearings was within 2°. Radio signal strength and direction were compared between stationary and flying owls to verify signal changes created by movements and flight.

Radio-telemetry studies were conducted from 13 June to 27 August 1982 and from 6 June to 8 July 1983. Adult male burrowing owls were visually monitored from their first appearance in early May until their departure from nesting sites in August or September. To minimize the possibility of nest desertion, attachment of the transmitters was delayed until female owls were in late stages of incubation, estimated as mid-June in this area.

During daylight, transmitter signals were used to visually locate owls. Once located, all owls on a study area were observed with binoculars or a 20× spotting scope. At night, radio-tagged owls were located by triangulating from 2 signals and plotted on 1:20,000 photo maps. One observer recorded both locations with the mobile telemetry unit from stations 0.4 km apart within 3 minutes. A moving owl could be de-

tected by changes in signal strength and direction, and we ensured it was stationary before determining its position. Owl locations were determined every 15–120 minutes depending upon the owl's activity and the weather conditions. We attempted to obtain a minimum of 3 nocturnal and 3 diurnal monitoring periods each week of ≥2 hours for all radio-tagged owls. Up to 3 owls could be monitored during a nocturnal telemetry period, although normally only 2 owls were monitored at 1 time. Attempts to achieve the same number of observations for all owls were confounded by weather conditions and occasional equipment failures.

Regurgitated pellets, small mammal populations (Haug 1985), and grasshopper numbers (M. K. Mukerji, Agric. Canada, pers. commun.) were monitored on the study areas to assess food habits and availability in relation to owl movements and activity periods.

We defined the home range of an adult male owl as the area used for foraging, roosting, nesting, and raising young, from the first appearance of male owls at their nest burrows until dispersal. Size of home ranges was determined using the minimum convex polygon technique (Jennrich and Turner 1969) after first plotting all visual and telemetry locations for each male owl. Activity patterns were evaluated using visual observations and telemetry data. Because daytime observations demonstrated that the area within a 50-m radius of nest burrows was used primarily for roosting and loafing, all telemetry locations and areas of habitat within 50 m of nest burrows were excluded from analyses of foraging habitat use. This avoided a bias toward the nesting habitat type. Accurate determination of the distance between owls and their burrows was possible because all nest burrows were <100 m from roads.

Cover types on the study areas were mapped based on current and past agricultural activity and vegetation composition. Habitat use was determined by comparing observed versus expected numbers of locations in each habitat type through Chi-square analysis and the Bonferroni normal statistic (Neu et al. 1974). We assumed that all owl locations were random.

Tame pasture was defined as a grazed area that had been tilled and planted to domesticated grasses and forbs such as crested wheatgrass (*Agropyron cristatum*), brome grass (*Bromus* spp.), and alfalfa (*Medicago sativa*). Native pasture was a grazed area dominated by mixed grass prairie (Coupland and Rowe 1969) in which the major grass species were spear grasses (*Stipa* spp.), June grass (*Koeleria cristata*), wheatgrasses (*Agropyron* spp.), and blue grama grass (*Bouteloua gracilis*). Grass-forb areas included road and railway rights-of-way, hayland, ungrazed pasture, and uncultivated areas. These areas were lumped together because of similar vegetation height (≥30 cm) and density. Plant species common to these areas were the domestic grasses previously described, thistles (*Sonchus* spp., *Cirsium* spp.), clovers (*Melilotus* spp.), and a variety of species from the mustard (Cruciferae) family.

A nesting attempt was defined as any pair of owls that selected a burrow and appeared to initiate egg laying. A nest was considered successful when ≥1 young was raised to fledging. No information was gathered regarding clutch size or hatching success. Productivity estimates were based upon the maximum number of young observed at nest burrows.

RESULTS

Study Area A

In 1982, 4 pairs of burrowing owls nested in Area A. During the second week of June, 2 pairs deserted due to predation of adults or eggs. Both males of the 2 remaining pairs (owls 73 and 75) were radiotagged, but the home range of owl 73 was not determined because its transmitter failed within 10 days of attachment. These 2 pairs nested 170 m apart.

In 1983, 3 pairs of owls attempted to nest in Area A. All 3 pairs deserted in May due to predation and disturbance from badgers. No telemetry information was obtained from this study area in 1983.

Study Area B

In 1982, 6 breeding pairs of burrowing owls nested in Area B. Four of the 6 breeding males were radiotagged (owls 76, 77, 78, 79). The transmitter of owl 78 failed within 2 weeks of attachment, and the home range was not calculated. The mean nearest-neighbor distance between nest burrows of all 6 breeding pairs was 214 m (range = 165–351 m). Although telemetry observations ceased between 14–15 Au-

Table 1. Movement parameters of radio-tagged burrowing owls in Saskatchewan, 1982–83.

Year	Owl no.	Dates of monitoring	No. young fledged	No. hr monitored	No. locations		Home-range size (km^2)	Major axis (km)	Max. distance from burrow (km)
					Day	Night			
1982	76	13 Jun–15 Aug	4	98	99	114	3.43	3.41	2.70
	77	13 Jun–15 Aug	0	90	75	95	1.04	1.70	1.02
	79	18 Jun–14 Aug	1	63	61	59	0.14	0.67	0.47
	75	15 Jun–27 Aug	3	106	92	160	2.04	2.60	1.46
1983	78	6 Jun–8 Jul	6	60	43	147	4.81	2.81	2.43
	82	9 Jun–23 Jun	0	23	20	51	3.02	3.37	2.32
Totals				440	390	626	$\bar{x}$ 2.41	2.43	1.73
							SE 0.69	0.43	0.36

gust, 2 of the 3 radiotagged males and families were still present on the study area on 23 September when visual observations were terminated.

In 1983, 3 pairs nested and all 3 males were radiotagged (owls 78, 80, 82). The transmitter of owl 80 failed 10 days after attachment, and the home range was not calculated. This pair deserted a week later due to badger predation. The 2 remaining pairs nested 214 m apart. Owl 78 was monitored until transmitter failure on 8 July with visual observations continuing until 13 September. Owl 82 disappeared after 23 June, and remains of young owls were found outside his nest burrow on 25 June, suggesting mammalian predation.

In total, 9 adult males were radiotagged, but 3 were dropped from the study because of pre-

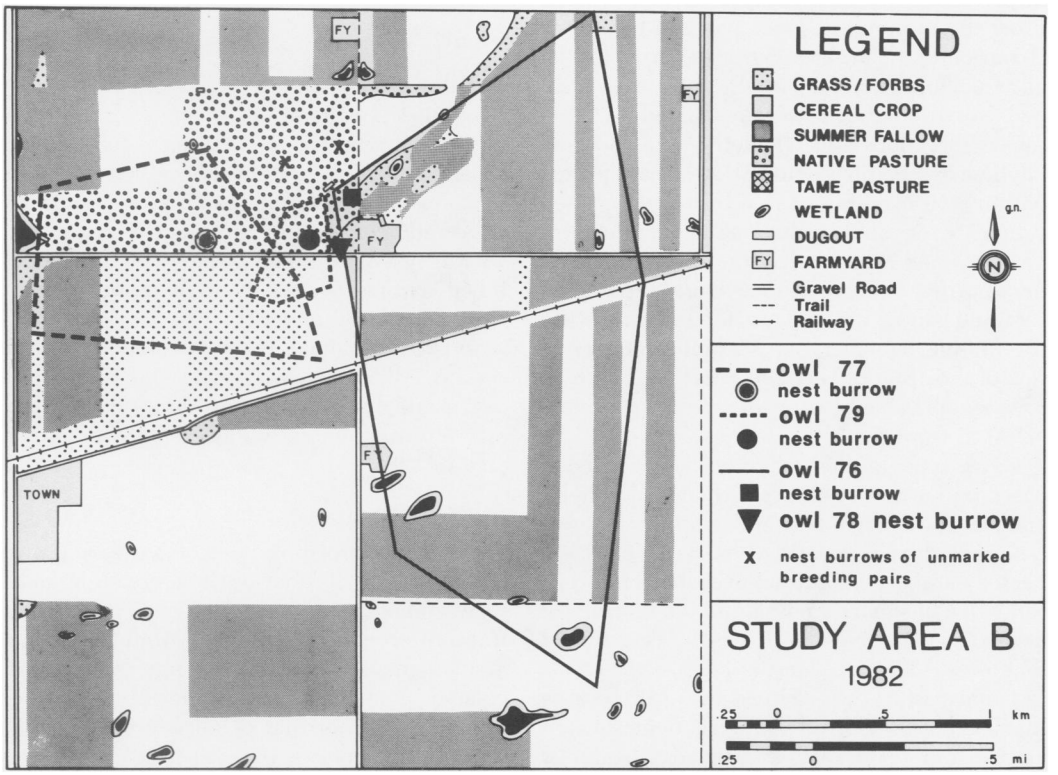

Fig. 1. Home ranges of radio-tagged burrowing owls 77, 79, and 76 on Area B, Saskatchewan, 1982.

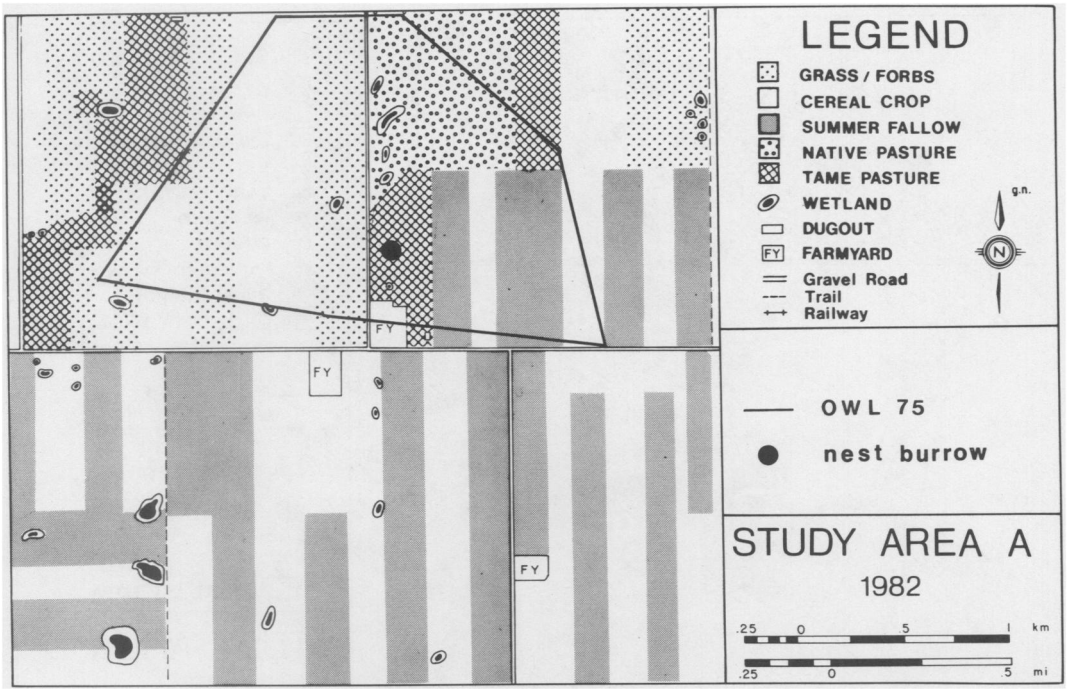

Fig. 2. Home range of radio-tagged burrowing owl 75 on Area A, Saskatchewan, 1982.

mature transmitter failure. We obtained 1,016 telemetry and visual locations for 6 radio-tagged owls ($\bar{x}$ = 169/owl, range = 71–252) (Table 1).

Home-Range Characteristics

As owls were not tracked continuously, the home ranges of the 6 radio-tagged owls are considered minimum breeding home ranges (Figs. 1–3). From the 1982 telemetry data, the largest biweekly home ranges were evident during the last 2 weeks in June or the first 2 weeks in July and decreased thereafter. Maximum home-range size (Table 1) was reached by 31 July for all 4 owls monitored in 1982. Because of transmitter failures early in the season, biweekly home ranges were not calculated for owls monitored in 1983. During both years, home-range overlap for neighboring radio-tagged male owls ranged from 4.8 to 58.9% ($\bar{x}$ = 34.1%).

Activity Patterns

Diurnal observation periods demonstrated that male owls foraged at all hours of the day but spent most of the daylight hours roosting or loafing within 50 m of the nest burrow and/or satellite burrows. They were occasionally seen foraging for insects farther than about 50 m, but they were never seen to travel farther than 250 m from the nest burrow during the day (Fig. 4). Adult owls were never observed foraging for or carrying small mammals during the day.

Peak activity hours, as determined by flights >50 m from nest burrows, occurred between 2030 and 0630 hours. Males became more active, frequently engaging in long-distance flights and hovering, suggestive of foraging for small mammals. Most of this activity began within 1 hour of sunset and ended at sunrise (Fig. 4). In 1982, 95% of all owl locations were within 600 m of nest burrows (range = 0–2,700 m).

Foraging Habitat Use

When all locations ≤50 m from nest burrows were eliminated from analysis, 5 of the 6 radio-tagged owls exhibited significant preference or avoidance of particular habitats during foraging as determined by Chi-square analysis and the Bonferroni normal statistic. With 1 exception, all owls selected grass-forb areas for foraging (Table 2). When this category was divided into its components, rights-of-way and uncultivated

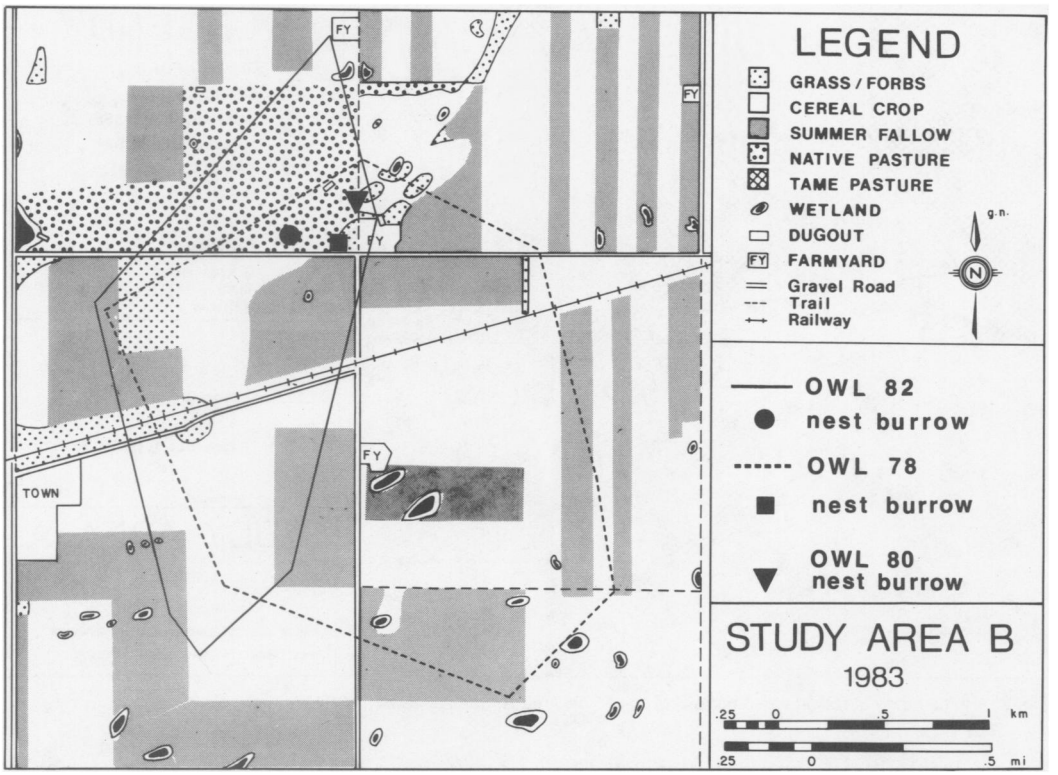

Fig. 3. Home ranges of radio-tagged burrowing owls 82 and 78 on Area B, Saskatchewan, 1983.

areas were used more than expected by chance alone. Crop and native pasture were generally avoided in comparison to their occurrence within home ranges. Selection for wetlands and summerfallow was generally in proportion to availability (Table 2).

DISCUSSION

Home-Range Characteristics

Little comparative information is available regarding home-range characteristics of burrowing owls. Previous authors have reported diurnal observations only. Butts (1973) reported the radii of burrowing owl home ranges in Oklahoma to be <2.4 km. Grant (1965) stated that 2 pairs of burrowing owls in Minnesota confined their activities, including hunting, to areas of 6.5 and 4.9 ha, respectively.

In 1982, different nesting outcomes might have been partially responsible for the large variation in home-range size. The 2 owls (75 and 76) with the largest home-range sizes (2.04 and 3.43 km², respectively) fledged the greatest number of young. Owls 77 and 79 lost all or most of their young to predators and had smaller home ranges (1.04 and 0.14 km², respectively).

The observed reduction in biweekly home-range size in mid-July corresponded with a rapid increase in consumption of grasshoppers as determined by pellet analysis (Haug 1985). The adult owls might have been able to obtain adequate food for themselves and their young in a smaller area with abundant grasshoppers. Cumulative maximum home ranges were reached by 31 July by all owls in 1982. Young produced by the radio-tagged adults were 4–6 weeks old at this time and were taking a greater proportion of their own food.

The variation in home-range size between 1982 and 1983 might, in part, be due to differences in prey availability. Small mammal snap-trapping results indicated no significant difference in mouse populations between 1982 and 1983 (Haug 1985). However, grasshopper survey results (M. K. Mukerji, Agric. Canada, pers.

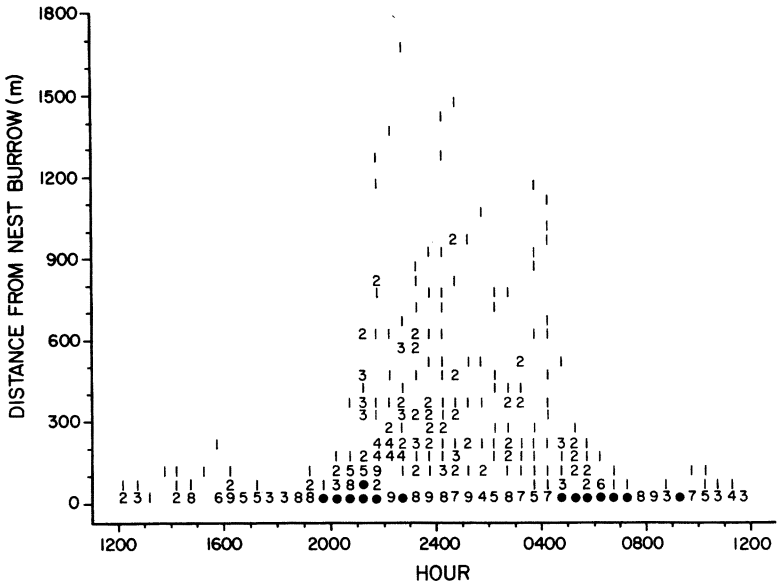

Fig. 4. Distance traveled by 4 radio-tagged burrowing owls from their nest burrows versus time of day, Saskatchewan, 1982. One additional telemetry location (not shown) was recorded at 2,700 m at 2210 hours. ● = no. of locations ≥10.

commun.) showed a significant difference between years (t = 3.57, 86 df, $P < 0.001$) with a mean of 5.28 grasshoppers per m² in 1982 versus 3.06 grasshoppers per m² in 1983 (Haug 1985). Mean home-range size appeared inversely proportional to grasshopper availability. Schoener (1968) also found home ranges of raptors to be significantly correlated with an index of the numerical density of their prey.

Although not significant, home ranges were smaller in 1982 than in 1983, even though the owls were monitored 4–5 weeks longer in 1982. Even greater differences in home-range sizes may have been evident if owls had been tracked for equal periods of time.

Activity Patterns

Many researchers have reported the burrowing owl to be strictly diurnal because of its high visibility and diurnal activity during the breeding season (Scott 1940, Grant 1965, Eckert 1974). Marti (1969) stated they were apparently poorly adapted for nocturnal foraging as Dice (1945) found they could not locate dead mice in light intensity of 26 foot-candles.

Nocturnal activity has been reported in a number of studies in the western United States (Coulombe 1971, Thomsen 1971, Ross 1974). Gleason (1978) found burrowing owls in Idaho restrict most daytime foraging to within 100 m

Table 2. Foraging habitats of radio-tagged burrowing owls in Saskatchewan, 1982–83, expressed as observed versus expected number of locations >50 m from nest burrow for each habitat within home range.

Cover type	Radio-tagged owls					
	75	76	77	79	78	82
Crop	13/31.9***	8/31.1***	1/3.8*	8/8.7	27/65.7***	8/14.4
Summer fallow	18/15.8	28/28.2	6/9.7	NA[a]	41/52.7	16/9.6
Native pasture	3/17.4***	3/0.3	19/32.1**	8/16.8***	2/5.4	9/10.3
Tame pasture	18/8.9	NA	NA	NA	NA	NA
Wetland	1/1.2	0/0.9	0/0.5	0/0.4	5/0.9	0/0.3
Grass-forbs	45/22.4***	23/1.8***	61/40.8***	38/28.0**	59/7.9***	5/3.1
Total observed	98	62	87	54	134	38

[a] NA = Habitat not available in owl's home range.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

of the nest burrow, and leave the nest area between 2200 and 2300 hours for long-distance foraging. In Wyoming, Thompson and Anderson (1988) found males made diurnal hunting flights >250 m from the nest burrows. They also observed that long-distance flights occur at night.

The results of our study indicate male owls were predominantly nocturnal and flew long distances to find food during darkness. From the time the young hatched until their independence, the adults were also observed foraging for insects within 250 m of the nest burrows during daylight hours.

Activity patterns of the owls also reflected activity patterns of their prey. During May and June, a preponderance of small mammals was taken as determined by pellet analyses (Haug 1985). Although the owls were not radiotagged at this time, visual observations showed roosting and loafing during daylight hours with long distance flights (>250 m) beginning at sunset. As the number of grasshoppers increased during July and August, diurnal foraging was observed near nest burrows with a corresponding decrease in nocturnal flights. However, the owls continued some nocturnal foraging for small mammals throughout the breeding season.

As the young developed hunting skills, the diurnal and nocturnal activity of the adults was reduced. They were increasingly observed roosting and loafing near the nest burrows.

Foraging Habitat Use

Limited information exists regarding foraging habitat of burrowing owls. Butts (1973) found owls in Oklahoma foraged extensively in wheat fields that supported substantial rodent populations. He believed owls ate rodents during early spring before insects became numerous. Gleason (1978) also found that nesting owls in Idaho used agricultural areas supporting montane voles (*Microtus montanus*).

We found that crop areas were avoided by radio-tagged owls. Snap-trapping results suggested crop areas did have the greatest densities of deer mice (*Peromyscus maniculatus*) and voles (*Microtus* spp.), the major mammalian prey items as determined by pellet analyses (Haug 1985). The avoidance of crop areas by adult owls may have reflected prey availability rather than absolute density. Bechard (1982) found the vegetative concealment of prey more important than total prey biomass in the selection of foraging sites by Swainson's hawks (*Buteo swainsoni*). Avoidance of cropland may also have reflected the owls' tendency to prey heavily upon grasshoppers that were predominantly found in rights-of-way and uncultivated areas, the areas most extensively used by radio-tagged owls.

The use of agriculture areas during May and June may have been underestimated because of the delayed radiotagging of the adult males. Rich (1986) reported a positive correlation between the number of voles in burrowing owl pellets and the amount of farmland within 1 km of occupied nest burrows.

Scott (1940) estimated land use within a 0.4-km radius of 3 nest burrows in Iowa and concluded the habitat most often used was the pasture with the nest burrow. Konrad and Gilmer (1984) concluded that the observed preference for closely cropped pasture for nesting appeared to be related to increased visibility for hunting. During our study, grazed pastures were avoided for foraging in relation to their abundance. Because of overgrazing by livestock, all pasture areas probably lacked cover for small mammals and food for grasshoppers. The prey items most often observed in these areas were dung and carrion beetles (Coleoptera).

MANAGEMENT IMPLICATIONS

Our study indicated burrowing owls will breed on small parcels of pasture with an adequate supply of nest burrows, but prefer to forage in areas of denser vegetation where greater densities of prey species occur. The preferred nesting habitat requirements of short grass, open sites, and burrow availability (Zarn 1974) can be met by managing and protecting existing historic nesting sites. We recommend

1. Preserve historic nesting sites by encouraging landowners to maintain small farmyard pastures in their present condition. Install artificial burrows in areas where burrows are lacking (Collins and Landry 1977).
2. Maintain a 600-m radius around nest burrows (95% of all recorded movements) free of pesticide application (James and Fox 1987), gopher control, herbicide application, and other human activities or disturbances that might jeopardize survival of young and adult owls. All areas considered for installation of

artificial burrows and/or release programs should be located at least 600 m from primary and secondary roads (Haug 1985).

3. Maintain rights-of-way, haylands, and uncultivated areas of dense vegetation within a 600-m radius of nest burrows to supply habitat for prey used by burrowing owls.

These recommendations apply to burrowing owls during the breeding season. Assessment and mitigation of limiting factors during fall and winter are currently not possible because migration routes and wintering areas are unknown.

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Received 22 March 1988.
Accepted 7 May 1989.
Associate Editor: Witter.