SELECTED ASPECTS OF BURROWING OWL ECOLOGY AND BEHAVIOR

DENNIS J. MARTIN[1]

Department of Biology
University of New Mexico
Albuquerque, New Mexico 87106

INTRODUCTION

Publications dealing with the biology of the Burrowing Owl (*Speotyto cunicularia*) appeared as early as 1874 (Coues 1874). Most of the many brief accounts since published deal with the description of food habits or are casual observations of behavior. Much of the interest in Burrowing Owls is due largely to their diurnal activity and some of their odd behaviorisms.

Recently, Thomsen (1971) and Coulombe (1971) provided the first major studies of this species. Thomsen's (1971) study again considered food habits of Burrowing Owls, but she also investigated behavior and population dynamics. Coulombe (1970, 1971) investigated some physiological aspects of Burrowing Owls, their food habits, behavior, and seasonal movements.

The purpose of this study is to compare the habitat requirements, behavior, and population dynamics of Burrowing Owls in Central New Mexico with those in California.

MATERIALS AND METHODS

I studied a population of 15 breeding pairs of Burrowing Owls and their offspring from 5 May 1970 to 20 May 1971 near Albuquerque, New Mexico. Observation time totaled over 400 hr. Most observations were made from a car or on foot and 7 × 50 binoculars and a 20 × spotting scope were used. A portable blind was employed for close observations and for recording vocalizations. Lights disturbed the owls and thus were not used.

Vocalizations were recorded with a Uher 4000 Report-L Tape Recorder and Uher M-514 microphone at 7½ ips. A 24-inch parabolic reflector sometimes was used. A more complete analysis and discussion of vocalizations of Burrowing Owls can be found in Martin (1973).

Of breeding pairs, nine females and nine males were color-banded for individual recognition. At least one adult of each pair was banded at all but two burrows. One unmated adult and 48 young also were banded. Each owl received a U.S. Fish and Wildlife band and a two-color combination of red, white, green, or yellow color bands. Owls were captured by placing Havahart traps within the burrow mouth as described by Martin (1971a). All adult owls were sexed by presence or absence of a brood patch and by feather coloration. This later was confirmed by their behavior in the field. All owls were weighed, inspected for ectoparasites, examined for molt, and had their remiges and retrices measured before release.

Two young owls were captured during their first observed emergence from their nest burrow and maintained in captivity for behavioral studies.

ECOLOGY

Habitat description. The study area contained two concentrations of nesting holes 3 miles S of Albuquerque at an elevation of 5300 ft. One was a 1.8 mile-long section of Tijeras Arroyo; the second, a 0.5 mile-long section where a railway cut through a hillside. The two sites were 0.5 mile apart and the intervening area served as mutual foraging ground. The study area is characteristic desert grassland showing effects of overgrazing (fig. 1). Plant forms present are assorted annual grasses, snakeweed (*Gutierrezia* sp.), fourwing saltbrush (*Atriplex canescens*), rabbitbrush (*Chrysothamnus nauseosus*), and Russian thistle (*Salsola kali*). Within the arroyo area there were about 68 burrows that appeared suitable for Burrowing Owls; the railroad track area contained 10.

Burrow description. All burrows inhabited during the 1970 and 1971 breeding seasons had been used by owls in previous years. Therefore, little burrow excavation was recorded. However, "nesting" material was added each year.

Rock squirrel (*Spermophilus variegatus*) burrows are used exclusively by the owls. No prairie dogs presently live on the area. Burrows may be found at any position in the arroyo or railway cut. Burrow sites are designated as lip, wall, or bottom (fig. 2). Seven of the 15 breeding burrows were in the bottom, four were in the wall, and four were in the lip. The apparent preference for bottom burrows may result from frequent disturbance of lip burrows by hikers and horseback riders; also, wall burrows have few perch sites at the burrow entrance. Entrance sizes varied greatly (from 17 × 20 cm to 14 × 76 cm, $\bar{X}$ = 32 × 24 cm). This appeared to be a result of the relative age of the burrow (number of seasons used). Inner tunnel size, which conformed closely to the physical dimensions of the adult

[1] Present Address: Department of Zoology, Utah State University, Logan, Utah 84322.

FIGURE 1. Habitat of study area in central New Mexico. A = wall burrow of Burrowing Owls. B = breeding burrow of Barn Owls. The distance between A and B is about 3 m. Railroad cut-through is near poles in background.

FIGURE 2. Nesting sites of Burrowing Owls. A = lip; B = wall; C = bottom.

birds, was more uniform than the entrance size (10 × 13 cm to 50 × 12 cm, $\bar{X} = 11 \times 20$ cm). Regardless of burrow position, there was a slight angular drop from the entrance, both inside and outside. Wall burrows possessed the greatest drop to the outside, bottom burrows, the least. There appeared to be no preference for direction of burrow opening: three faced west; five, south; and seven, north. Vacant burrows were common. The average distance from an inhabited burrow to a vacant one was 25 m. The distance to the closest breeding neighbor averaged 166 m. This is considerably greater than that reported by Thomsen (1971). I feel, though, it is an accurate indication of territory size, due to the presence of apparently suitable unused burrows between nest sites. Territory parameters appear to be different in this population from those of a typical Burrowing Owl colony and will be discussed more fully later. Three burrows were considerably nearer, but this deviation probably resulted from the very close occurrence of 10 suitable breeding burrows present in a 140-m section of arroyo.

Reproductive success. Burrows were not excavated to determine clutch size. Bent (1938) reports normal clutch size as 7–9 eggs; thus, 15 breeding pairs, averaging 7 eggs per clutch, would produce 105 eggs. One clutch was laid per year in this population. The total maximum number of young observed on my study area during the summer of 1970 was 78. There probably was nestling mortality before the young began to perch at the burrow entrance (at about 2 weeks of age). Of the original 78 young observed, 74 or 94.9% fledged. Mean reproductive success was 4.9 young per pair. No correlation between burrow position and number of young fledged was apparent. The mean young fledged per lip burrow was 4.7; wall burrow, 5.5; and bottom burrow, 4.7. The lowest possible mean clutch size for my population was 5.2 eggs, based upon the 78 young seen. Thomsen (1971) states that productivity in her population of Burrowing Owls in California was 2.7 young per pair in 1965 and 1.9 young per pair in 1966. Thus, reproductive success, measured as young fledged, was considerably less in her population.

Sexual dimorphism. Males are larger in most species of birds. This pattern is reversed in most of the Strigiformes and Falconiformes; the only strigiform exception in North America is the Burrowing Owl (Earhart and Johnson 1970). My data confirm this dimorphism in size. Several weights were taken 2–4 weeks after the eggs hatched, at a time when the female's weight should not have been affected by egg laying. Males outweighed females by a mean of 7.9 g ($N = 7$ and 6, respectively), with the F test significant at the 0.05 level (Sokal and Rohlf 1969:208).

Feather coloration also varies with sex. Males appear lighter than females throughout the summer. After postnuptial molt, the sexes are alike dorsally. Females generally appear darker on their breast at this time due to more extensive barring. Barring varies individually, as some females are very white on the breast and some males quite dark; thus, this cannot be used as a reliable means of sexing individuals. By the first of June most males appear lighter than most females on the head, back, wings, and tail. This apparently is a result of fading, as the males remain outside the burrow during the day, and of wear, as they do most of the foraging throughout the summer.

Behavioral differences are numerous and will be discussed later. The only morphological character with behavioral implications is the female brood patch.

Wandering and migration. The young began to wander even before they could fly. Frequently, a family was divided between the breeding burrow and one or more accessory

TABLE 1. Seasonal fluctuations in a Burrowing Owl population in central New Mexico.

Burrow		Months												
		May	J	J	A	S	O	N	D	J	F	M	A	May
0	M	x	x	x	x	x						x	x	x
	F	x	x	x		x	x					n	n	n
1	M	x	x	x	x							u	u	u
	F	x	x	x								x	x	x
2	M	x	x	x	x		J					x	x	x
	F	x	x	x		?						x#9	x	x
3	M	x	x	x		?		?				u	u	u
	F	x	x	x								u	u	u
4	M	x	x	x	x	?								
	F	x	x	x	x									
5	M	x	x	x	x	x						x	x	x
	F	x	x	x								u	u	u
7	M	x	x	x	x							x	x	x
	F	x	x	x	x	?							u	u
8	M	x	x	x	x							n	n	n
	F	x	x	x	?							u	u	u
9	M	x	x	x	x							x	x	x
	F	x	x	x	x							n	n	n
10	M	x	x	x	x			?	?	J	?	u	u	u
	F	x	x	x	x							u	u	u
11	M	x	x	x	x	?	?					u	u	u
	F	x	x	x								n	n	n
12	M	x	x	x										
	F	x	x	x	x									
13	M	x	x	x						x	x	x	x	x
	F	x	x	x	x							n	n	n
16	M	x	x	x	x								u	u
	F	x	x	x	x								n	n
18	M	x	x	x	x		?					J#18	x	x
	F	x	x	x	x		J	J	?			n	n	n

M = male, F = female, underlined indicates bird was banded. Plain x = same bird present as indicated by burrow number on left margin. ? = sex and age unknown. u = unidentifiable adult. n = new bird at burrow. J = banded juvenile. Numbered symbol on right designates burrow used the previous year. Birds indicated for a specific month were not necessarily all seen on the same day.

burrows. Parents continued to feed young even when they moved as far as 100 m from the breeding burrow. My frequent disturbance of certain burrows undoubtedly was responsible for some wandering. Thomsen (1971) also describes this behavior, although she was careful not to disturb the burrows with traps.

Once the young could fly, they might be found at any vacant burrow within 300 m of the breeding burrow. As they became increasingly independent, they became more solitary. Few cases of family structure remaining intact throughout September were observed. In these cases, the young were completely independent. A few banded owls were observed during the winter (table 1). They usually were seen for a few days, disappear for a few weeks, and then reappear for a few days. This occurred with five individuals. Thus, some owls appear to wander sporadically in winter.

The migratory status of the Burrowing Owl in the West and Southwest is unclear. Brenckle (1936), working with data from 481 banded Burrowing Owls, demonstrated a definite migration from South Dakota to Texas. He further indicates that Burrowing Owls in California are nonmigratory. This view is shared by Thomsen (1971) for Burrowing Owls in the Oakland vicinity of California, and by Best (1969) and J. S. Ligon (1961) for Burrowing Owls in New Mexico. They suggest the owls may remain inside their burrows during the day, becoming strictly nocturnal during the winter months. Coulombe (1971) assumes that part of the California population is migratory, with immigration into Southern California occurring from the north.

Owls began leaving my study area as early as 2 August 1970 (table 1). In one case an entire family of eight disappeared simultaneously and was not seen again. Usually, juveniles began to disperse during the first

TABLE 2. Dates of arrival for part of a population of Burrowing Owls in central New Mexico, Spring 1971.

Arrival dates	Males of burrows	Females of burrows
~ 19 March	0, 1, and 11	1 and 11
19 March–20 March	5 and 9	5 and 9
21 March–26 March	7	
27 March–1 April	2 and 20	0, 2, and 20
2 April–3 April	15 and 21	21

half of August. Many adult females also left at this time. Approximately 10 banded owls remained on the area by the end of August. The population remained this size until mid-October. Only four owls could be located at any time throughout November; one, in December; three, in January; and two, in February (table 1).

All owls recorded during the period from November to February usually were seen sunning near a burrow entrance. The banded birds observed, as previously stated, were not always the same, indicating that they wandered over a larger area than my study plot or remained within the burrows during the day.

Between 15–21 March 1971, population size increased from its February level of 2 to 17. Males sang almost immediately after their arrival. This led to the collection of precise data for the arrival of 18 owls (table 2). If a male was paired, the female was nearby while he sang. Males and females appeared on the study area apparently paired or males arrived alone.

I conclude that migration occurred in my study population as evidenced by the striking reduction in population size in late October, when food was abundant, and the sharp and sudden increase in population size in mid-March. Where these owls winter is unknown.

BREEDING BEHAVIOR

Pair formation and burrow selection. Owls appear to arrive on the breeding area both paired and singly (table 2) during March and April. Of the nine breeding males and nine females banded in 1970, six males and two females returned (table 1). All returning males in 1971 selected the same burrow they had inhabited in 1970 (table 1), unless the burrow had been destroyed, in which case they assumed the same relative position they held in 1970 with respect to the other owls and burrows.

No pairs in which both male and female were banded in 1970 were paired in 1971. In one case, a pair banded in 1970 both reappeared on the area in 1971. The male had a new mate and the female mated with another banded male (table 1). This suggests that Burrowing Owls do not pair for life. Whether the low return rate for females is attributable to a higher mortality than males or to a weaker bond to a previous area is not known.

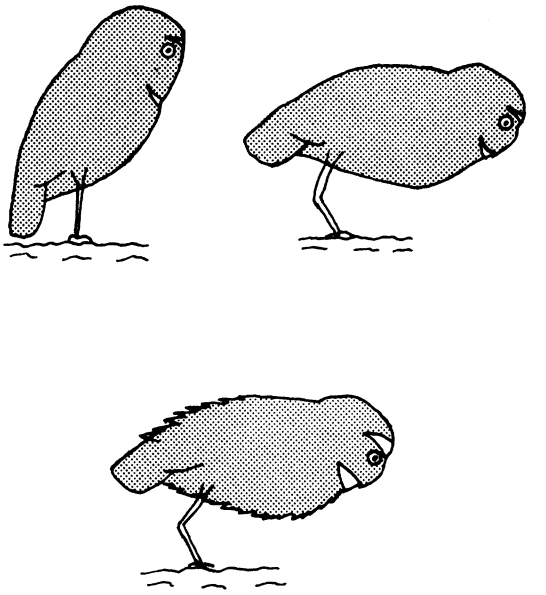

FIGURE 3. Bowing display of Burrowing Owls (above) and display used while giving primary song (below).

Upon arrival on the area, unpaired males immediately began to prepare their chosen burrow for habitation and to display for pair formation. At sunset they began singing and this continued throughout the night. Description of song and all other vocalizations discussed here can be found in Martin (1973). The behavior occurred while the owl stood at the mouth of his burrow or on the arroyo rim facing the arroyo. He bends forward so that his body nearly parallels the ground, with primaries and secondaries held underside together over his back and the white patches of the throat and brow are displayed to their fullest (fig. 3). This posture and behavior appeared to be stereotyped.

Nest preparation. Nest burrows inhabited during 1970 and 1971 had been occupied in previous years. Thus, little excavating was apparent. The only excavation observed was when male owls scratched dirt out of the burrow entrance. The owls faced into the burrows and scratched backwards with their feet. Best (1969) reports that the owls also walk through the burrow tunnel with outstretched wings, dislodging dirt from the walls. Thomsen (1971) indicates Burrowing Owls in

FIGURE 4. Breeding burrow of Burrowing Owls with dry feces shredded at entrance.

California may dig with their bills. I did not observe either of these behaviors in my study population but I acknowledge that bill-digging occurs in other New Mexican Burrowing Owls (Martin 1971b).

Soon after excavation ceased, lining material was brought to the burrow entrance. This material consisted of dry horse, cow, and dog feces. Once an adequate pile had been accumulated, the owls shredded the material and carried it into the burrow. The nest chamber floor was lined approximately 2.5 cm deep with the shredded feces. Through this process the tunnel and entrance also are lined (fig. 4).

The Burrowing Owl is one of the few North American owls which copiously line their nests. It is also the only small owl whose nest is readily accessible to ground-dwelling predators. The lining possibly provides insulation, but may also serve to camouflage the owls' scent, and possibly that of its prey, from predators such as badgers (*Taxidea taxus*), coyotes (*Canis latrans*), snakes, domestic dogs, cats, etc. This view is also shared by J. D. Ligon (pers. comm.). If one removes feces from the entrance and the first meter of the tunnel, they are replaced within one day.

Courtship behavior. Courtship behavior apparently had begun by 17 March when some mated Burrowing Owls arrived on the study area. It continued until mid-April. The behavior usually began shortly before dusk and continued for 1–2 hr. Courtship behavior involves assorted displays, vocalizations, and postures by both males and females: presentation of food, preening, leg- and wing-stretching, head-scratching, and bill-nipping. It always occurred within 15 m of the nesting burrow.

Precopulatory behavior. At the onset of precopulatory behavior, both male and female are near the burrow. The male and female preen and leg- and wing-stretch for a few minutes. The male engages in more of this activity than the female. The male may then display with primary song and its associated posture (fig. 3). While the male sings, the female sits near him or in the burrow entrance and displays with Rasp or Eep calls. This activity may stimulate the male to forage and, upon his return, to present the female with food. Following the exchange, males and females may nip each other's bills for a short time. If the female continues to Rasp and Eep, the cycle is repeated; if she ceases, copulatory behavior usually follows.

Copulatory behavior. This behavior, terminating in copulation, occurred frequently just after pair formation. The highest incidence was during the first hour after sunset. It was observed until mid-April at which time it became rare. By the end of April, the behavior as such was absent. The highest rate of copulation by a pair that I recorded was eight times in 35 min, although most pairs copulated only one to three times per evening. The highest frequency of copulation was in March, the lowest, in April.

The general sequence of a copulatory bout was: male singing; female moves toward or away from male 1 or 2 m; male ceases singing; stands up and looks down at the female with white patches exposed and feathers raised; female stands erect and exposes her white patches but does not raise body feathers; male flies to female and mounts. Once mounted, male gives Song During Copulation with or without a Male Warble, and they may terminate with a Tweeter call. During the bout, the female may give the Smack call and Copulation Warble. While mounted, the male usually flaps his wings but this appears to be more for balance than as a display. When the male is mounted, he may scratch the female's head and both individuals may bill nip. After termination, the male will usually stand for a moment looking down on the female, exposing

his white patches but without his body feathers raised, then fly back to where he was previously singing. The female may or may not stand erect with white patches exposed.

Copulatory behavior was fairly uniform throughout the entire population, although variations on this sequence occurred.

Egg laying, incubation, and brooding. Egg laying began about the third week of March if Burrowing Owls lay an egg on alternate days as reported by J. D. Ligon (1968) for the Elf Owl (*Micrathene whitneyi*) and Welty (1962) for certain other owls. This would apply only to the earlier arrivals, as some birds were unpaired until early April.

Female Burrowing Owls appear to incubate exclusively. Females alone develop a brood patch. Bent (1938) reports that both sexes incubate, but more recent works do not support his statement (Coulombe 1971; Thomsen 1971).

The female remains within the burrow throughout most of the day. In early morning and evening she appears at the burrow entrance and waits for the male to bring food. At this time she often gives the Rasp call. The male infrequently carries food into the burrow to the female during midday. Throughout most of the day the male remains perched quietly near the burrow. This pattern continues until the food demands of the young become great, at which time the female also gathers food.

Territory and territoriality. A territory consisted of the Burrowing Owl's burrow at the center and a portion of the arroyo extending in both directions. The foraging ground was not included within the boundaries of the territory. Males and females exhibited intrasexual territoriality, which generally was evident only during pair formation, although one encounter was observed as late as 10 May. The primary response of a male to an intruder more than 10 m from his burrow was to assume a bent-over posture, hold his wings over his back and flat together, exhibit white patches of the throat and brow, and give primary song (fig. 3). If this behavior failed to repel the intruder, the defending owl approached to within 1 m of the intruder and stood erect, without white patches exposed. If these behaviors were unsuccessful and/or the intruder was within 10 m of the defender's burrow, physical contact might ensue. Although physical contact is rarely employed, as with most species of birds, I observed the following sequence on 10 May. I drove a male to within 8 m of another's burrow. The owner flew slowly directly over the intruder. Giving no indication of a coming attack, he dropped on the intruder with outstretched talons, pinning him to the ground. The intruder gave a scream and the defender released him and flew back to his burrow. The intruder, slouching, then walked away into the grass.

Female territoriality was observed on one occasion as I played recordings of primary song to a mated male, causing him to sing for an extended period. His singing attracted an unbanded owl that was presumed to be female. She landed at the burrow and entered. The resident female ran into the burrow and momentarily both reappeared at the entrance. They stood erect within 5 cm of each other, exposing their white facial and throat patches. At this time the male ran into the burrow. The resident female began to give the Defense Warble and both females pecked at each other's bills. The resident female then sprang up and grasped the intruder with her talons. Both birds fell off the arroyo rim. Halfway to the ground, the resident female released her grip and flew to her burrow. The intruder dropped to the ground and then fled.

Territory defense continued until egg laying commenced, at which time the females remained in the burrows throughout the day and the males ceased singing. This was probably due to recognition by males of territorial boundaries and hormonal-psychological changes, although the events of 10 May demonstrated the potential was still present.

FEEDING BEHAVIOR

Periods of most intensive foraging behavior were just after sunset and before sunrise. Foraging behavior was greater from sunset to 24:00, than from 24:00 to dawn.

Foraging consisted of perching in a bush or flying low over a field until a prey item was observed. Adults did little flycatching or hovering while the food demands of the young were great. Hovering was performed at 10–30 m above the ground. During flycatching, prey were grasped in the talons rather than the bill.

Small prey, e.g. insects, were hopped upon and crushed with the bill. They were immediately eaten or carried in the bill to the burrow, although prey infrequently were transferred from the feet to the bill in flight. Large items, e.g. rodents, were attacked in a typical raptor manner. These were usually carried to the burrow.

Typical storage behavior was not observed. On occasion prey was killed in midday and laid at the burrow entrance until evening

before being eaten, but no "stock-piles" were formed.

Males fed females extensively during pair formation, incubation, and brooding. Males were never observed eating food gathered by females. Females gave Rasp calls during the evening and early morning, which appeared to stimulate the males to forage. As the male approached with food, the intensity of the call increased. Upon passage of food to the female, the male often gave a Rasp call. The female, if hungry, continued Rasping as she ate.

The male appeared to collect all food until the young were 3 or 4 weeks old. During this period, the male began foraging at sunset and completed two to three food trips per minute. This rate began to decrease around 21:00 to 22:00. The male carried food into the burrow or passed it to the female at the entrance and she carried it in. Upon receipt of the food, the female often gave a Rasp call. It could not be determined whether the young gave any vocalizations during this period.

Females began foraging for their own food and for the young after the young were 3–4 weeks old. By this time the young walked well. They stood at the burrow entrance giving Rasp calls, which appeared to stimulate both parents to forage. As the adult approached with food, the intensity of the Rasp increased and the young ran out to meet the adult. As a rule, the first chick to meet the adult received the food item. Other young owls not receiving food usually did not try to take food away from the recipient. The other young continued Rasping and the adults would leave immediately. During these food transfers, the adults often gave Rasp calls. Although the females gathered food, it appeared that they made only about a third as many trips as the males.

By the first of July most young were hopping and flying about the burrow collecting insects. Toward mid-July some juveniles accompanied parents on foraging flights and caught some of their own prey. During this period, food-gathering demands upon the parents decreased; by mid-August all birds appeared to be gathering food independently.

BEHAVIOR OF THE YOUNG

Young Burrowing Owls stand about the burrow entrance each day to sun themselves once they are able to move around well. During feeding periods they also stand about the burrow entrance. Upon receipt of food they may dash into the burrow to eat and then emerge again within seconds.

Nestlings 3–4 weeks old begin to display wing- and leg-stretching, preening and hopping about while flapping their wings. They appear to make an effort during such activity to jump onto some specific object, as if improving their coordination. At this stage of development they are capable of flight.

I am sure that on two occasions I witnessed the first flights of young Burrowing Owls. At first they were something less than graceful. The owls jumped up, flapped their wings wildly, then descended upon some precise point, e.g., rock or stick, and usually fell off or missed it. After only four or five such short flights, they attempted the width of the arroyo. They took off into the wind, then changed direction, and glided with it to the opposite rim. Upon landing, they usually crashed. Flapping flight improved rapidly and within two evenings the young owls began to accompany their parents on short foraging flights. Within a week they were accomplished fliers.

After the young can hop and flap their wings with a degree of coordination, they begin practicing prey killing. Two or three young will alternately jump on and crush a dead insect. The young later display the same behavior in flight as they hover over the prey and drop on it. During their first foraging flights with the adults, they are little more than spectators, but soon begin to capture their own prey. By August it was common to observe an entire family leave the burrow site together and forage in a given area. The young characteristically hovered at this time, whereas the parents hunted from a perch or by flying low.

By mid-August feeding Rasps given by self-supporting juveniles were ignored.

On the evening of 5 August 1970, I observed what could be described as play behavior. Young Burrowing Owls from the same burrow hovered about 10 m above the ground and 10 m apart and stooped at each other. By their continued hovering, stooping, and soaring, one could conclude that this activity was stimulating. They continued this behavior for 15–20 min before following their parents out to forage.

RESPONSE TO PREDATORS

Burrowing Owls of Central New Mexico have numerous potential predators. The more common predatory species the owls display against are: Prairie Falcons (*Falco mexicanus*), Red-tailed Hawks (*Buteo jamaicensis*), Swainson's Hawks (*B. swainsoni*), Ferruginous Hawks (*B. regalis*), Marsh Hawks (*Circus cyaneus*), Golden Eagles (*Aquila chrysaetos*), Great Horned Owls (*Bubo virginianus*), domestic

dogs and cats, and people. Other possible predators are: snakes, Barn Owls (*Tyto alba*), badgers, coyotes, and bobcats (*Lynx rufus*). The following general comments relate to the owls observed on my study area in New Mexico.

Predator displays by Burrowing Owls vary throughout the year, apparently correlating with their breeding cycle. In the field, between October and February, Burrowing Owls usually crouch low to the ground, run into a burrow, or fly away quietly when approached by a predator. In the spring (March–May) the owls usually give a warning call, then run into a burrow. When the call is given by either the male or the female, both usually run into a burrow, or the male may remain outside. From June until the young are independent, if the warning call is given by either parent, all young run into the burrow, with the female usually following the young. Males usually remain out unless a direct attack is in progress. If the attack is by another raptor, the male usually retreats into a burrow; if by terrestrial predator, the male will usually mob the predator.

When adult Burrowing Owls with young observe a terrestrial predator approaching their burrow, they give the Chuck warning call, which may be accompanied by a bow (fig. 3). The young run into the burrow upon hearing this call. The female, if not already in the burrow, may enter or may fly some distance away. If the predator approaches closer, the female may give Chuck and Chatter calls with bows. The male remains near the burrow and gives Chatter calls of three to seven notes and bows. If the predator continues to advance, the male begins to fly between areas about 100 m away from the burrow. When perched, he gives Chuck and Chatter calls with bows, but only Chatter calls while flying. This display usually causes the predator to follow the owl, thereby protecting the burrow and the young. Both parents return once the predator is a sufficient distance from the burrow.

The owls attack if their displays are not successful and the predator approaches the burrow. Males usually attack, although females also may do so. The owls fly in a circle about 100 m in diameter and 10 to 20 m high and give Chatter and Scream calls. Chatter calls are lengthened to 7 to 15 notes. The owls always dive at the predator from behind and give a startling Scream when within a meter of the intruder. The owls are very bold when performing this display and will strike the predator. I have seen male Burrowing Owls strike dogs, cats, and Great Horned Owls. I also was struck in the head by a Burrowing Owl.

When a predator is flying, the male Burrowing Owl watches it quietly until it is close enough to begin an attack and then gives a Chuck or Chatter call. The male then remains very still and the female and young run into the burrow. If the female gives the call, she and the young usually run into the burrow, while the male freezes, but remains outside.

A Scream is given by a Burrowing Owl when startled by a predator, such as a low flying Prairie Falcon. On hearing this call from the male, the young run into the burrow, but the female freezes if she is more than about 2 m from the burrow. If a female gives the call, the male freezes, and if she is near enough (about 2 m), she runs into the burrow.

Predator defense behavior employing attack displays does not appear in juvenile Burrowing Owls until they are almost completely self-supporting and are excellent fliers. This behavior develops through August. By the end of August most juveniles display in a manner identical to the adults. If the young are cornered before they can fly, they will bend over, rotate their wings, as is common in most owls, and give the Rasp call. This display is also performed by captive adults, but was never observed in the field.

Mobbing. Burrowing Owls display a predator defense approximating mobbing behavior. As defined by Hartley (1950), mobbing is a demonstration of one bird against a potential enemy of another and more powerful species; mobbing is initiated by the weaker species, and is not a reaction to an attack upon the person, mate, nest, eggs, or young of the mobbing bird.

Burrowing Owls usually do not harass a potential predator not within their territory, unless it is a Great Horned Owl. I initially tried to capture Burrowing Owls by placing mist nets and a Great Horned Owl at the burrow entrances. I found that not only the resident pair of Burrowing Owls mobbed the owl, but that adults from other burrows as far as 300 m away also joined in. During these bouts no aggressive territorial displays between male Burrowing Owls were observed. The display used against the Great Horned Owl was the same as described previously for a terrestrial predator near a burrow.

Burrowing Owls would continue harassment of the Great Horned Owl for more than an hour, for three to five bouts per week, before conspicuous habituation occurred. Burrowing Owl response to the Great Horned Owl fol-

lowed the same pattern described previously for other predators.

Two captive juvenile Burrowing Owls were shown a Great Horned Owl. One juvenile was exposed at about 6 weeks of age for 3 min and at 8 weeks for 5 min; no reaction occurred. The other juvenile was exposed at 16 weeks of age for 5 min; no reaction occurred.

It was also noted that Barn Owls nested within 5.2 m of a Burrowing Owl burrow (fig. 1). The Barn Owls were observed flying within 10 m of a breeding Burrowing Owl, but no warning call or displays were observed. The lack of displays in this case may have been due to habituation.

Bowing. Burrowing Owls are well known for the behaviors of bowing (fig. 3) and standing with their back to an intruder. Bowing occurs during predator defense and usually is associated with a Chuck or Chatter call. Turning the back to a predator also occurs as the predator approaches to a position from which it may begin a strike.

Bowing occurs before the owl leaves an area, and after it lands. The distance between the owl and predator is usually greater than that evoking back-turning. Bowing is never associated with a definite agonistic or hiding behavior. It appears to arise from an internal antagonism between drives to hide and to flee. When these two drives are balanced, the owl bows. This was demonstrated by one of the young captive owls. When frightened, the owl would hide by crouching behind a rock in its cage; if frightened further, it would try to flee by leaping onto the cage wall. A typical bowing sequence when I neared the caged owl would proceed like this: the owl first crouched behind the rock, then stood up looking at the wall farthest from me, then it bowed, crouched behind the rock again, then bowed again; but upon coming up this time, it jumped onto the wall.

Back-turning behavior appears to be an intention movement preceding flight. When a predator approaches too closely, the owl turns its back to the predator, but usually continues to watch it. If the predator moves closer, the owl flees. This behavior points the owl in a direction opposite to that of a possible attack by the predator. If an attack ensues, the owl is positioned for rapid escape.

DISCUSSION

Habitat requirements and general breeding behavior were similar in Coulombe's (1971), Thomsen's (1971), and my study populations. All breeding sites were in relatively open areas and had nearby accessory burrows. All the populations inhabited disturbed areas and have adapted to nesting in ground squirrel tunnels in the absence of prairie dog burrows. Because of their apparent behavioral plasticity, Burrowing Owls may be one of the least affected raptors by man-made environmental changes. Also, Thomsen (1971) feels, as I do, that although the owls prefer predug burrows, they are capable of excavating their own.

Burrowing Owls in the California population formed pair bonds earlier and retained them longer (Thomsen 1971) than those in the New Mexico population. This is probably a result of earlier growing seasons and a generally milder climate along the California coast. Regardless of the timing of the breeding effort, all populations were similar in parental and foraging behavior and development of the young. Estimated territory size varied considerably between my study population and Thomsen's (1971). This apparent territory size differential is probably more a result of habitat differences than of fundamental behavioral differences.

Some significant points of dissimilarity are apparent in these studies. Individuals of my study population acted more aggressively during predator and alarm displays than those in Thomsen's (1971) or Coulombe's (1971) populations. Coulombe (1971) did not report the two-noted primary song and its use in pair formation (Martin 1973; Thomsen 1971). Rather he described a five-noted song, with the last four notes slurred. I believe a spectrographic analysis of this call would reveal that it is two-noted, with the second note being considerably longer than the first (Martin 1973; Thomsen 1971).

Two other interpopulation behavioral differences are of interest. Thomsen (1971) reported one copulation per pair per evening as normal, with three coitions as a maximum. Pairs in my study population copulated more frequently. A maximum of eight coitions in 35 min was recorded. This may be a result of the shorter mating period of the New Mexico population which results in a more intense peak of sexual excitation. The selection of nesting material varied greatly between the study populations. Thomsen (1971) reported divots from a nearby golf course and grass were used to line nesting chambers. My study population used animal feces to line their nests. Whether this difference is related to habitat or fundamental behavioral difference could not be determined with the available data.

Reproductive effort and success of my study population was considerably higher than that reported by Thomsen (1971). During two

summers' observations I recorded only one unpaired and/or nonbreeding Burrowing Owl. Thomsen's (1971) study population contained 40% nonbreeders during one summer. The mean reproductive success of the New Mexico population was 4.9 young per pair, whereas the California population's mean reproductive success for 2 years was 2.7 and 1.9 young per pair. One cannot hope to show cause for this variation without a long-term study of both populations, but the migratory behavior of the New Mexico population may be significant. This behavior may result in a higher death or dispersal rate, resulting in lower year-round population densities in the vicinity, especially during the breeding season. Thus, limiting resources may be more abundant to the New Mexico population, allowing them to maximize natality in their reproductive strategy.

SUMMARY

1. A breeding population of Burrowing Owls (*Speotyto cunicularia*) in Central New Mexico was studied during 1970 and 1971. The colony nested within an arroyo and railroad cut-through.
2. Breeding success of this population was high. Fifteen breeding pairs fledged 74 young in 1970.
3. Young Burrowing Owls, although independent, remained on the breeding ground until mid-August.
4. Burrowing Owls exhibit sexual dimorphism. Female owls are smaller and usually darker than males.
5. It appears some Burrowing Owls in Central New Mexico wander extensively during the winter while others migrate. Time of departure is from August through September. Time of earliest arrival is mid-March. Winter residence of this population is unknown.
6. Returning males occupy the same burrows they occupied the previous season. Females did not exhibit a strong bond to any particular burrow.
7. Pair formation in some Burrowing Owls appears to occur before arrival on the breeding grounds. Pair formation on the area may take place within a single night.
8. Burrowing Owls do not appear to pair for life.
9. Males appear to do all the burrow modification, although females may help with the chamber lining.
10. No Burrowing Owls dug their own burrows. They used Rock Squirrel (*Spermophilus variegatus*) tunnels exclusively.
11. Nest chambers, tunnels, and burrow entrances were lined with dry feces. This probably aids in camouflaging the owl's scent.
12. Courtship behavior occurs from the time of pair formation or return to the nest site until mid-April.
13. Burrowing Owls exhibit intrasexual territoriality, which is most apparent during pair formation.
14. Territory size appeared larger than that of more typical populations due to the unusual spatial relationships of the owls to one another.
15. Females apparently incubate and brood exclusively.
16. Females are fed by their mates from the time of pair formation until some time after brooding of the young ceases.
17. Burrowing Owls exhibit predator mobbing, although it appeared to vary with the hormonal-psychological state of the owl.

ACKNOWLEDGMENTS

This investigation is based upon a thesis submitted in partial fulfillment of the requirements for the M.S. degree at the University of New Mexico. J. David Ligon provided helpful suggestions throughout the course of this study. He also was an invaluable aid in the preparation of this manuscript; for his guidance and boundless patience I am grateful. I also wish to thank Marvin L. Riedesel, James S. Findley, James R. Gosz, and Keith L. Dixon for reading an earlier version of the manuscript. Advice on statistical matters was offered by James R. Gosz. Live trapping and banding was aided by Barbara McKnight.

The help of my wife, Lana, in typing the many drafts of the paper and toleration of my summer night activities is also gratefully acknowledged.

LITERATURE CITED

Bent, A. C. 1938. Life histories of North American birds of prey. Part 2. U.S. Natl. Mus., Bull. 170.

Best, R. 1969. Habitat, annual cycle, and food of Burrowing Owls in southwestern New Mexico. Unpubl. M.S. Thesis, N. Mexico State Univ., Las Cruces.

Brenckle, J. F. 1936. The migration of the western Burrowing Owl. Bird-Banding 7:166–168.

Coues, E. 1874. Birds of the Northwest. U.S. Geol. Surv. Terr. Misc. Publ. No. 3.

Coulombe, H. N. 1970. Physiological and physical aspects of temperature regulation in the Burrowing Owl, *Speotyto cunicularia*. Comp. Biochem. Physiol. 35:307–337.

Coulombe, H. N. 1971. Behavior and population ecology of the Burrowing Owl in the Imperial Valley of California. Condor 73:162–176.

Earhart, C. M., and N. K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72:251–262.

Hartley, P. H. T. 1950. An experimental analysis of interspecific recognition. Symp. Soc. Exptl. Biol. 4:313–336.

Ligon, J. D. 1968. The biology of the Elf Owl, *Micrathene whitneyi*. Univ. Mich. Mus. Zool. Misc. Publ. 136.

LIGON, J. S. 1961. New Mexico birds and where to find them. Univ. New Mexico Press, p. 147.
MARTIN, D. J. 1971a. A trapping technique for Burrowing Owls. Bird-Banding 42:26.
MARTIN, D. J. 1971b. Unique Burrowing Owl pellets. Bird-Banding 42:298–299.
MARTIN, D. J. 1973. A spectrographic analysis of Burrowing Owl vocalizations. Auk 90:564–578.
SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco.
THOMSEN, L. 1971. Behavior and ecology of Burrowing Owls in the Oakland Municipal Airport. Condor 73:177–192.
WELTY, J. C. 1962. The life of birds. W. B. Saunders Co., Philadelphia and London.

Accepted for publication 11 January 1973.