BEHAVIOR AND POPULATION ECOLOGY OF THE BURROWING OWL, *SPEOTYTO CUNICULARIA*, IN THE IMPERIAL VALLEY OF CALIFORNIA

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The Burrowing Owl, *Speotyto cunicularia hypugaea*, is a common resident throughout much of arid North America. The conspicuous diurnal activity of these owls, in combination with their fossorial habits, has attracted the attention of many observers since the middle of the nineteenth century. Yet the accumulated knowledge of the biology of this species is surprisingly sparse, and widely scattered. Bent (1938) assembled most of the basic information to date concerning the life history and biology of Burrowing Owls.

The only detailed study available for any New World species of small owl (Ligon 1968) presents a contrast of adaptive patterns to hot, arid environments between Burrowing Owls and Elf Owls (*Micrathene whitneyi*) and has provided a point of departure for this presentation.

Burrowing Owls are a conspicuous feature of the irrigated farm lands of the Imperial Valley of southeastern California, where pairs are commonly seen along canal banks throughout the year. Although this area generally represents an environment highly modified by the activities of man, several relatively natural areas of habitat can be found for this species and its vertebrate associates in nearby parts of the undisturbed Colorado desert. The Burrowing Owl represents a species uniquely amenable to a study designed to integrate the roles of physiology, ecology, and behavior with respect to energy exchange in a natural population.

Field studies of Burrowing Owls in the Imperial Valley were pursued on 61 days, November 1962–May 1968. During this period observations were made on population dynamics, activity patterns, and behavior; data also were collected on food habits and on the physical parameters of the microclimate occupied by the owls. Field observations of these owls were complicated by their visual acuity. Undetected approach of a burrow site is frequently hindered by the scarcity of natural or artificial cover in their preferred habitat. However, in many areas the owls live near roads and pay little attention to an automobile parked 50 m or so distant. Owls were conveniently observed from an automobile or from some other concealment with 7× binoculars or a 20× spotting scope, and photographed with a 35mm camera equipped with a 400 mm (ca. 8×) telephoto lens.

HABITAT

Grinnell and Miller (1944:203) list the habitat of the Burrowing Owl of California as "open, dry, nearly or quite level, grassland; prairie; desert floor." These authors comment on the conspicuous dependence of the Burrowing Owl upon the larger burrowing mammals (notably *Citellus beecheyi*). Although Bent (1938:384) states that the Burrowing Owl prefers habitats unmodified by man, in much of southern California this species occurs in the vicinity of human activity, e.g., urban San Diego (Abbott 1930), Los Angeles International Airport (pers. observ.), and U. S. Naval Ordinance Supply Depot, Seal Beach (L. Kiff, pers. comm.). One feature these isolated colonies share is the persistence of ground squirrel (*C. beecheyi*) populations.

Relatively undisturbed habitat in the Imperial Valley exists at Greeson Slough (fig. 1), which is a side branch of the New River, situated 3 mi. W and 5 mi. S of El Centro, California. Although most of the surrounding area is under cultivation, the slough is for the most part unexploited. It is gouged from the surrounding flat bottomland of the Salton Sea Sink, and the margin is usually well-defined by a steep bank which has been modified by a perennial composite (*Crysothamnus* sp.) around the margins of the dry area, with mesquite (*Prosopis* sp.) growing near the areas of subterranean moisture. Shadscales (*Atriplex* spp.) grow in many areas, and dense stands of palo verde (*Cercidium* sp.) scrub, reeds, and tules grow in the areas of periodic standing water.

The climate ranges from many nights below freezing temperature during the winter, to occasional summer recordings of over 50° C in

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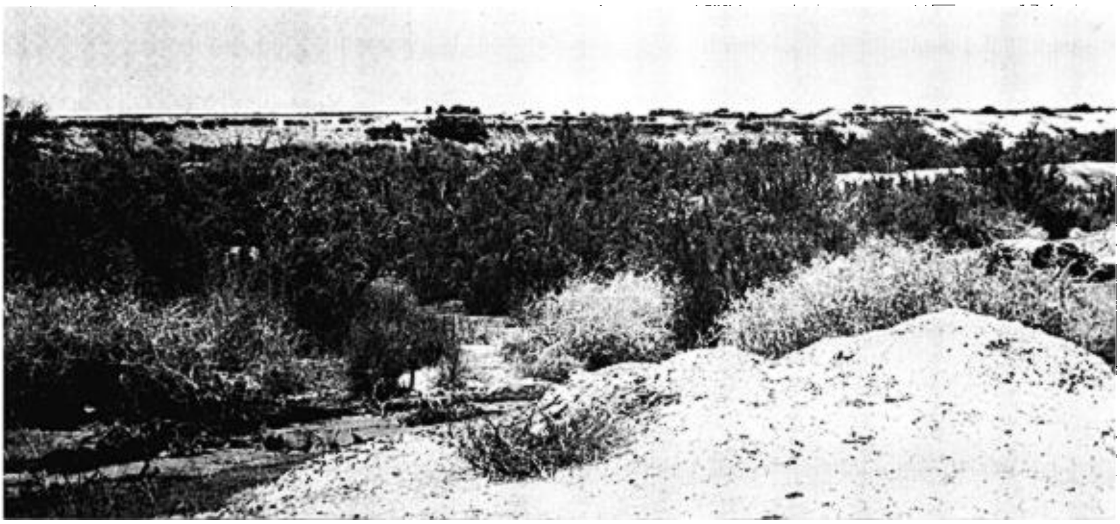

FIGURE 1. Habitat at Greeson Slough, Imperial County, California (sec. 4, T. 17S, R. 13E): 1 June 1963.

the shade. The rainfall is normally less than 6 inches per year. The irrigation system in the Imperial Valley has highly modified the environment by supplying large quantities of moisture to the air, as well as providing green plant growth through all seasons. Telephone poles provide perching posts for the Burrowing Owl and also for other birds of prey.

The drain canal system has provided many new banks which are suitable for habitation, both by the owls and their constant associate in the Imperial Valley, the round-tailed ground squirrel, *Citellus tereticaudus*. The ground squirrels provide many possible "starts" for the Burrowing Owls to utilize for their own nest sites after sufficient enlargement of the tunnels. It is not known whether Burrowing Owls construct their own burrows or modify existing holes for their own use. In the Imperial Valley I have always found evidence of past or present activities of the round-tailed ground squirrels where Burrowing Owls were observed. I have seen ground squirrels active within several feet of alert Burrowing Owls, with no apparent signs of interaction. The smaller burrows shown in figure 2 were those of an active colony of round-tailed ground squirrels at Greeson Slough on 1 June 1963. On one occasion the remains of a ground squirrel were discovered in the midden at the entrance of a Burrowing Owl burrow, which probably represented carrion rather than prey. On a few occasions Burrowing Owls were noted in sites along drainage banks that appeared to be modified from muskrat (*Ondatra zibethicus*) burrows, along an earlier high water mark.

Burrows are found in a variety of situations, and may be oriented to any point of the compass. The majority of burrows I have found in the Imperial Valley (86 of 104) are located between firm, eroded sandstone and a softer layer of silt beneath. The usual burrow is about 20 cm in diameter at its surface opening, but can be as large as 80 cm. Most burrows slant downward at an angle of about 15°, but the first segment of a tunnel rises at a similar angle in 10–15 per cent of the bur-

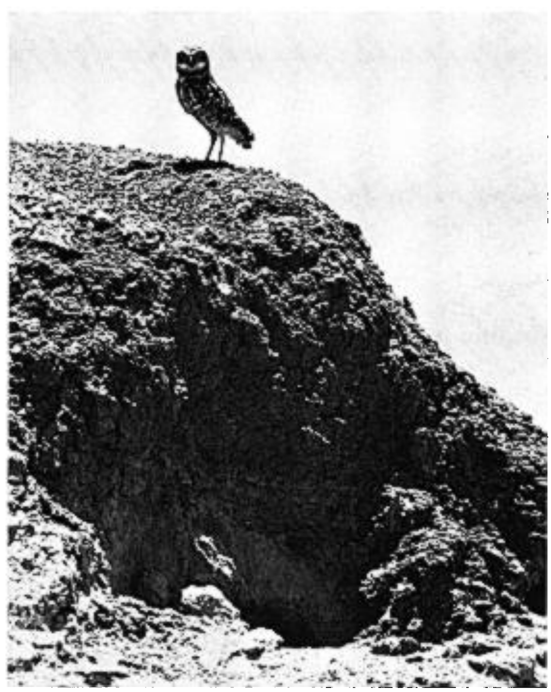

FIGURE 2. Nesting site at Greeson Slough, June 1963. An adult female Burrowing Owl is perched above entrance to burrow.

rows examined. All burrows have a left or right turn within about 1 m of the surface. Walker (1952) describes the internal structure of a Burrowing Owl burrow.

FOOD HABITS

Most of the literature on Burrowing Owls has been concerned with their food habits in various locations and seasons (see Robertson 1929; Bond 1942; Longhurst 1942; Carson 1951; Glover 1953). Like the Elf Owl, the Burrowing Owl feeds mainly on arthropods. Many of the arthropods (including scorpions) listed by Ligon (1968:38) as taken by Elf Owls have been reported from Burrowing Owl pellets (Glover 1953, from Mesa Valley, Arizona).

In surveying pellets collected in the Imperial Valley, I found that earwigs (Dermoptera) were the major food item during both winter and early summer months. Other arthropod exoskeleton parts were noted in fresh pellets at these times, including crayfish, crickets, tiger beetles, and various tenebrionid beetles. Pellets containing fur seemed to be preserved longer in the midden around owl burrows than were pellets containing chitin. In addition to the ground squirrel noted earlier, the following vertebrate remains found in pellets and/or middens of Burrowing Owls in the Imperial Valley were: *Perognathus* spp., *Peromyscus* spp., *Mus musculus*, *Thomomys bottae*, *Agelaius phoeniceus*, *Sonora semiannulata*, *Hyla regilla*, and *Bufo cognatus*.

A dead Burrowing Owl of unknown age was seen in the midden at one of the burrow sites on 22 November 1962. This carcass did not appear to have been fed upon, though cannibalism has been reported in the species (Robinson 1954). Dead juveniles are found about the burrows during the summer months. In captivity it was not uncommon to find one member of an adult pair partially devoured by its mate; no evidence of aggressive cannibalism was detected in these instances.

Burrowing Owls are primarily crepuscular in their foraging, as are Elf Owls (Ligon 1968: 36). During the daylight hours Burrowing Owls may capture prey and feed on ground squirrel carrion. While searching for prey, Burrowing Owls characteristically hover for periods of several minutes at heights of 8–15 m. When prey is captured it is devoured on the ground before hovering is resumed. During the night the foraging behavior changes to suit the reduced visibility of the small food items. Burrowing Owls may pursue arthropods on the ground by walking and running. They also may glide about 1 m above the ground; rodents seem to be the object of this foraging pattern. Earwigs and crickets occur abundantly in occupied burrows, providing a food source for the owls through a possible symbiotic relationship. The microclimate of the burrows offers shelter and favorable breeding conditions for these arthropods, as well as for their predatory co-habitors.

ACTIVITY PATTERNS

Burrowing Owls demonstrate a unique daily activity cycle among nearctic strigiforms. Their conspicuous diurnal behavior centers around the burrow sites, and patterns of activity are related to the season. Four classes of daily patterns can be recognized: winter, incubation, fledgling, and post-breeding. Pair-bonds are sometimes maintained throughout the year, as evidenced from banded pairs. Although solitary individuals may be found at any time, single owls are more frequent during the winter months.

In the winter months, both members of a pair of owls are generally observed together at the entrance of their burrow during the early morning hours and again in the late afternoon. During the day, one member of the pair is usually below ground, with the other remaining near the burrow entrance. The owl above the burrow remains alert during the day, and may be observed to visually follow small birds flying nearby. Site attachment for the burrow is reduced during the winter; at this time banded owls generally did not return to the same burrow when disturbed by trapping or by partial excavation of the burrow.

As the breeding season arrives (about early March) the attachment of the owls to the burrows increases, reaching a maximum during the incubation and fledgling periods. Both members of a pair are rarely seen together at the burrow entrance, except briefly at dawn and dusk. Bendire (1892) states that "both parents assist in incubation, which lasts about three weeks." Howell (1964) noted that, in captivity, a male Burrowing Owl did not develop an incubation patch (as did its mate) and presumably did not participate in incubation. During the breeding season, the male will occasionally enter the burrow during the day for short intervals.

In early summer, when the young owls are in an advanced state of development, the adults have a different cycle during the day. At this time a pair under observation could be behaviorally sexed, and differences in plumage, color, and pattern made it possible to keep individual track of this pair's activities.

During most of the day only one owl remains near the burrow, usually the female, and the male occupies a sentry perch in the surrounding area. He occasionally returns briefly to the nest site, but apparently never to enter the burrow. When both the adults are in the immediate vicinity of the burrow, the female enters the burrow occasionally for a moment or two if the unfledged owls are not outside. The young owls frequently are outside during the morning and afternoon, but rarely during the midday. Entire broods were not commonly observed together outside the entrances.

At the end of the breeding season, environmental temperatures are at a maximum; the fledglings are grown and the adults spend a reduced amount of time at the burrow site. Secondary burrows in the vicinity may be used by the adults at this time. Adults and young spend little time outside the burrows during the midday hours. By early October dispersal and migration are initiated, and site attachment for a specific burrow is reduced. As the weather cools the owls spend greater periods abroad during the daylight hours.

Few systematized observations have been made on the nocturnal activity of Burrowing Owls. Burrowing Owls are frequently seen flying through the path of car headlights at night, usually at an altitude of 10 m or less. Owls are also frequently flushed from the ground along the road shoulders or in the fields at night. Owls are most frequently seen this way from dusk to about 04:00.

SOCIAL BEHAVIOR

Bent (1938:391) and Howell (1964) are essentially the only references available on social behavior of Burrowing Owls. My observations include alerting and alarm behavior, decoy behavior, threat response, courtship behavior, and relations with young.

Alerting and alarm behavior. Burrowing Owls show two distinct patterns of behavior associated with general communication and the approach of predators to the burrow. When an observer approaches a burrow, the owl on "guard duty" gives the six-note alert call when the approaching "predator" is more than about 40 m away. Captive owls will give this response to an approaching dog or cat. The call is of medium pitch, and of a musical quality, roughly tempoed as "chip—chip—chi chi chip-chip." It is not accompanied by a unique display or posture; several positions may be associated with this call.

The alarm behavior occurs when an owl is steadily approached. The owl turns slightly and becomes erect (fig. 2). It gives a single-noted call, of a higher pitch than the alert call and of a somewhat more harsh quality: "cheed." The call is issued as the owl "bobs" up and down, as described by Witherby et al. (1943:324) in the Little Owl (*Athene noctua*). The entire pattern is repeated about every 15 sec until the owl flies from its perch. If young owls are out, or the other member of the pair is in the vicinity of the burrow entrance, hasty retreat occurs with the first alert call.

Decoy behavior. If an owl is approached closely, it flies to one of a limited number of secondary perches (usually two) located about 35–80 m from the burrow. The alarm behavior is frequently continued at the secondary perch. When the same burrow is approached from different directions within the same 180° sector upon different occasions, an owl flies to the same secondary perch. If the owl is pressed it will circulate back and forth among the secondary perches. On several occasions owls attempted to elude me rather than make themselves conspicuous. Owls at Site A frequently retreated to a small depression out in the open about 40 m SE of the burrow.

The decoy behavior appears to be an effective device to divert a terrestrial predator. An owl calls attention to itself through a ritualized pattern, and then retreats to a preferred post. The direction of this retreat to the sentry perch is usually in the direction opposite to that of the most frequent approach by humans.

Threat behavior. When a human or a dog comes too close to a caged Burrowing Owl, a typical strigiform response occurs. The feathers are fluffed out, the wings opened and rotated forward; while crouching the owl weaves back and forth, issuing a piercing, hissing scream of about 5 sec duration followed by "bill clicking" (Haverschmidt 1946); the call is repeated until danger ceases to threaten. When young owls give this response from within a burrow, the effect is said to be very reminiscent of an agitated rattlesnake (Bent 1938:388).

Courtship behavior. The male owl displays to the female a posture reminiscent of the threat display, except that he does not weave and the wings are drawn closer into the body, giving the appearance of greater size than the female (fig. 3A). While in this posture the male utters a distinctive five-noted call of a mellow, flute-like quality: "Whea—woo-who-woo-who." The last four notes are slurred together, and the call is generally given only once every few minutes. This call was frequently given by captive owls in the early morning hours, particularly during the spring.

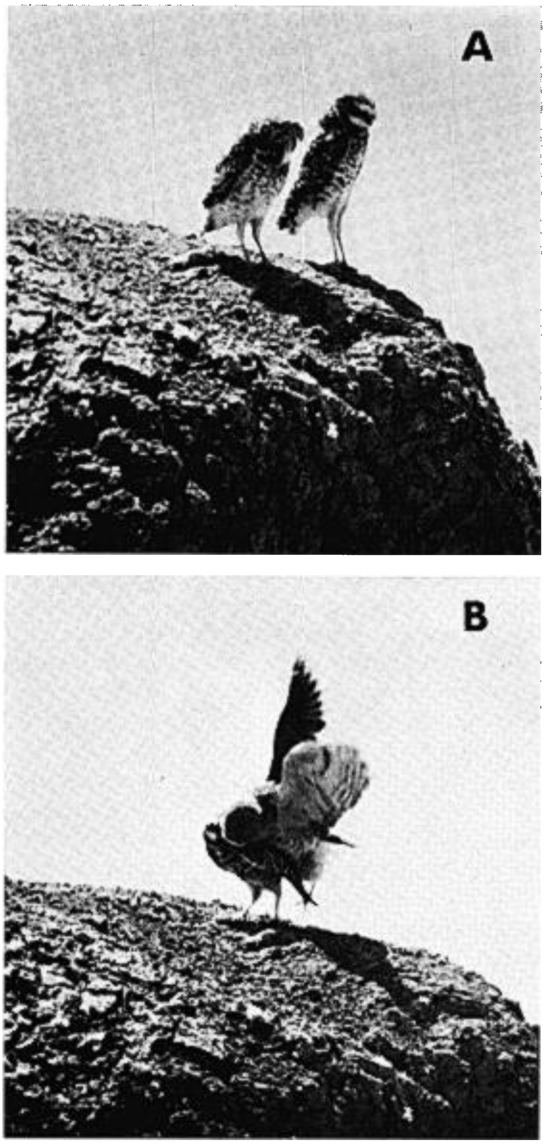

FIGURE 3. A. Courtship display with vocalization by male, Greeson Slough, 1 June 1963. B. Copulation by Burrowing Owls, Greeson Slough, 1 June 1963. At this date the pair was rearing a brood of six young owls.

On 1 June 1963 the owls at Site A were observed to copulate twice, each time preceded by the five-noted call and display by the male. The copulating pair had six young, almost to the postjuvenal molt stage. At 10:15 the female was at the burrow entrance and the male was on the sentry perch. The courtship display and call were given. Because of the overhang at the burrow entrance, the female could not see this display; she responded to the call by flying up to the perch, and copulation followed (fig. 3B). At 11:00 the male went through the courtship ritual after arriving at the burrow entrance from a distant perch. Both owls then flew to the sentry perch and copulation immediately took place. The coitions lasted about 4 sec each. I was too far away to hear any soft vocalizations which may have been associated with courtship or coition, as described in Little Owls (Haverschmidt 1946).

On several occasions the male returned from the distant perches and gave a courtship display and call at the front of the burrow entrance. The female answered from the burrow entrance with a slightly softer, higher pitched version of the six-note alert call. Then the female entered the burrow for a minute or two while the male remained at the entrance. The male soon returned to the perch away from the burrow area. On one occasion the female repeated the modified six-noted call, when the young were inside and she was at the entrance and the male was not in sight. The female did not enter the burrow unless the male was present at the site. Howell (1964) described similar courtship patterns in captivity. These patterns appear to be involved with both pair bond formation and maintenance in this species.

Relations with young. The young owls gave a distinct rasping call of about 1 sec duration when begging food from either parent. This begging behavior was noted between 09:00 and 11:00, but the adults did not respond by feeding them at this time.

Young owls retreated down the burrow when the six-note alert call was given by a parent. On several occasions young owls retreated following a display by an adult owl very similar to a threat display, but without weaving or vocalizing.

THERMOREGULATORY BEHAVIOR

The reradiation of heat from the earth's surface is very intense from bare ground such as the area around Greeson Slough. Perch selection helps Burrowing Owls avoid much of the heat that is present during the middle hours of summer days. In the early morning most of the owls are seen on the ground, facing into the sun, at times with plumage slightly fluffed if the air is cool. As the day warms, the owls move to perches several meters above the ground, such as bushes, mesquite trees, tractors, fence posts, buildings, and a variety of other elevated perches. By late morning owls generally are oriented with their backs to the sun, forming their own shade for the thinly feathered legs (fig. 4A). During the midday, owls not in the shade of a burrow entrance are usually

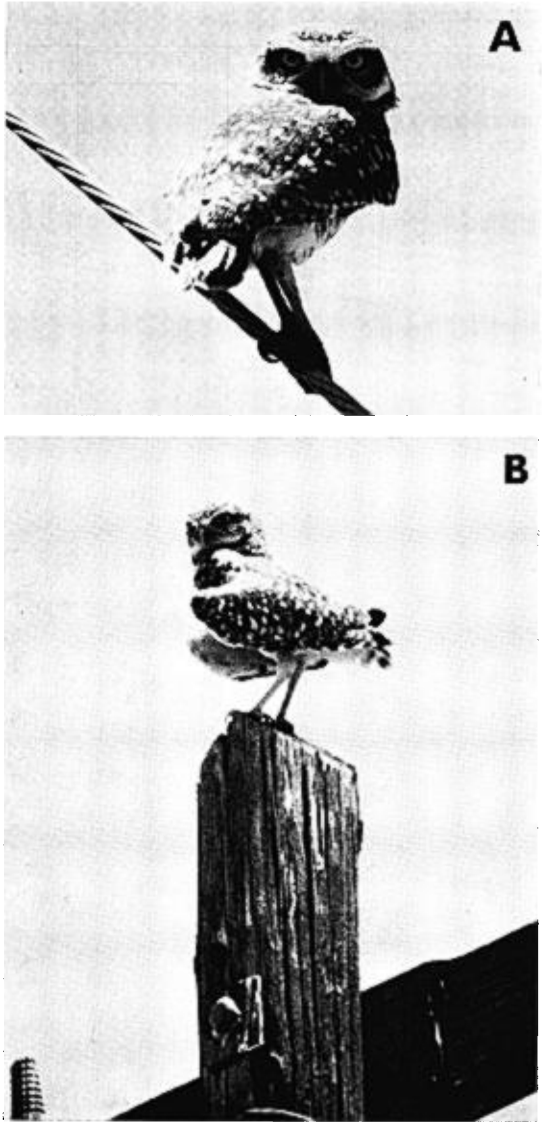

FIGURE 4. A. An afternoon perch, June 1963. Note the position of the legs relative to the body's shadow. B. Heat-stress posture of Burrowing Owl perched on a telephone pole. Note the uncovered areas under the wings, and the shaded legs.

perched on high objects, such as telephone lines, guy wires, and poles (fig. 4B).

During the midday heat the owls frequently assume the posture shown in figure 4B, with the wings extended forward, outward, and drawn slightly over the back. This posture could permit reradiation of heat from the underbody to the north sky, and also utilize the feathers of the wings as "heat shields." When the owls are in the shade, this posture is frequently assumed, and may permit the radiation of heat from the body to the shaded ground. On one occasion an owl returned to the shade of the burrow entrance from direct exposure to the sun and assumed this posture facing down the mouth of the burrow, which should provide a radiational heat-sink.

As they mature, juvenile Burrowing Owls appear at the entrances of their nests with increasing frequency during the day. During the morning hours the young owls may orient so that their shadows provide shade, which could permit radiation of body heat from their legs. As the sun reaches its zenith, the juveniles retreat into the cool burrows; by early afternoon the burrow's entrance may provide natural shade that is utilized by the young birds. Seven burrows that faced west in the Greeson Slough did not have young owls in evidence during the midday, although they were known to be present.

Thus, both adult and immature Burrowing Owls have considerable behavioral control over the thermal regimes that they occupy. The elevated perches selected by the adults place them in a favorable position for reducing conductional and thermal radiational heat gain. The use of the burrow as a thermoregulatory mechanism (a favorable ecoclimate) is a behavioral alternative utilized by both young and adult owls. Similarly, the utilization of shade, either their own or that of another object, is a behavioral feature of both age groups (note fig. 4B). The role of the legs in control of heat loss has been demonstrated in several orders of birds (see Steen and Steen 1965) and is probably important to Burrowing Owls.

When a Burrowing Owl becomes heat stressed it may resort to evaporative cooling, facilitated by gular flutter. Owls were not observed to utilize gular flutter for temperature regulation for periods of more than an hour or two a day in the field.

BURROW TEMPERATURES AND HUMIDITIES

Microclimatic measurements of five burrows were made at different times of year along canal banks in the study area.

Dry- and wet-bulb temperatures were taken with an Atkins thermistor psychrometer. Burrow temperatures and humidities were measured with a flexible extension of the psychrometer barrel inserted into their openings. Readings were converted to relative humidities (RH) with psychrometric tables (Marvin 1941); absolute humidities (AH) were calculated with the equation given by Coulombe et al. (1965).

The results show that although temperatures are not significantly different from the entrance into the depth of the burrows, the

TABLE 1. Burrow[a] temperatures and humidities at different times of year.

Date	Time	Ambient T (°F)	Ambient RH (%)	Burrow entrance T (°F)	Burrow entrance RH (%)	Burrow depth T (°F)	Burrow depth RH (%)
16 Dec. 66	10:50	67.0	30	67.5	38	66.0	58
	11:10	72.5	25	73.0	29	72.5	38
	11:20	73.5	48	74.5	51	74.5	56
	11:25	74.0	36	74.0	39	74.5	51
	11:35	75.0	37	74.5	37	74.5	49
	12:00	75.5	38	72.0	51	74.5	54
	12:15	74.5	39	73.5	47	74.0	58
14 Sept. 66	10:55	93.5	39	93.0	46	94.5	64
	11:03	96.2	39	93.5	45	95.0	50
19 May 67	10:35	72.0	45	73.0	55	72.0	88
	10:45	73.5	44	74.0	97	72.0	98
	13:25	83.0	16	82.0	17	82.0	33
	13:40	81.0	13	79.0	27	77.0	29
	14:45	82.0	21	81.0	39	81.0	83
23 June 65	11:20	86.4	51	87.0	54	88.6	86
	11:40	88.0	66	87.9	69	89.6	81
	12:00	90.0	66	90.0	65	91.0	80
	13:35	92.8	63	93.5	67	100.2	80
7 June 66	11:00	86.8	30	88.0	39	88.1	60
Mean		80.9 (27.0°C)	39.3	80.5 (26.9°C)	48.0	81.1 (27.3°C)	62.9
		AH = 10.4 g H_2O/m^3		AH = 12.6 g H_2O/m^3		AH = 16.9 g H_2O/m^3	

[a] Ambient conditions were taken 5 cm above ground at burrow entrance; conditions at burrow entrance were measured 5 cm inside; and burrow depth conditions at 30 cm inside. See text for details of methods. Measurements from five burrows.

amount of water vapor in the air increases (table 1). At 5 cm into the burrows, mean AH was 21 per cent greater than for ambient air; at 30 cm depth, mean AH was 63 per cent greater than ambient air (table 1). No correlation was noted between the direction that a burrow faced and the temperatures in the depth of the burrows.

Soil water and evaporation by the owls tend to keep the water vapor concentration in the depths of the burrow close to saturation (at minimal burrow temperature during the day). The relatively high AH in the burrows will lower the amount of water lost through evaporation while the owl is in the burrow as opposed to in the open. In the laboratory, Burrowing Owls commence gular flutter at an ambient temperature of 40°C, with an AH of 18.2 g H_2O per m^3 air (Coulombe 1970).

LABORATORY BEHAVIOR

The activity patterns of these birds during the breeding season place them in the severest of the daily heat stresses. Field observations indicate that Burrowing Owls meet these problems in a number of behavioral (and physiological) ways. Laboratory experiments were conducted to assess the role of free water in temperature regulation and the relation of the circadian activity patterns to temperature change.

On 23 June 1965 an adult Burrowing Owl was observed to fly from its perch on a telephone wire down to the edge of the drain canal near its burrow. The air temperature was 30.6°C at the time (11:20), and the owl spent several minutes drinking water from the canal. Subsequently I observed captive owls drinking water, particularly at ambient air temperatures above 30°C. Two naive owls (raised from about four weeks to maturity in the laboratory) drank water even when maintained at room temperature. An experiment was designed to quantify aspects of drinking behavior in relation to level and patterns of general activity at selected air temperatures.

Methods. Owls captured for physiological studies were also used for behavioral observation in the laboratory (for details of capture and maintenance, see Coulombe 1970). Owls in the laboratory were kept on a controlled photoperiod, in a windowless room equipped with an observation port of one-way glass. Several aspects of daily activity patterns were investigated in the laboratory. Daily activity patterns and water consumption were investigated at 35°C and 41°C by keeping a mated pair of owls in a temperature-controlled room.

The normal photoperiod of the first week of July (when the experiments were begun)

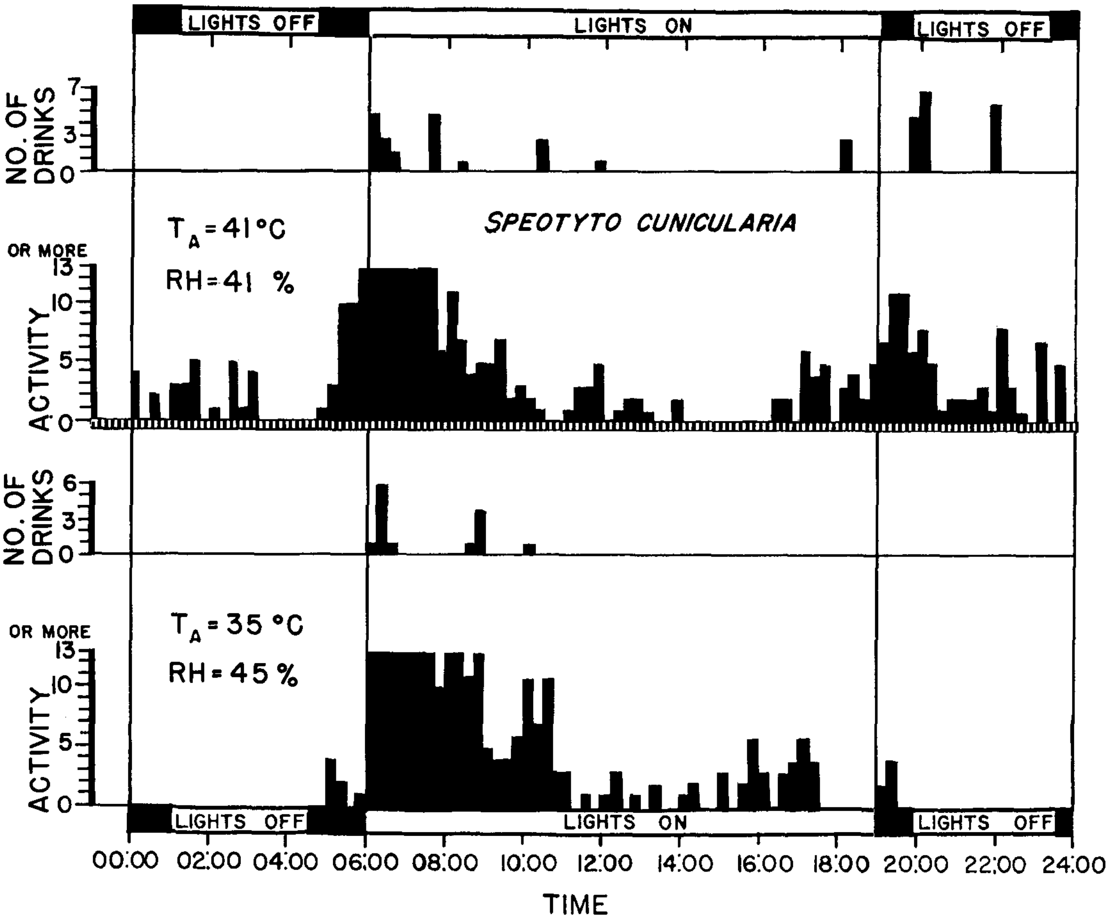

FIGURE 5. Drinking and activity patterns in the laboratory. Number of drinks and activity on perch switches are averaged over three days, and reported in 15-min intervals for a mated pair of Burrowing Owls. The experiments were conducted starting the first week of July.

was provided both by diffuse fluorescent lighting and a directional infrared lamp in the room. Food (*Tenebrio* larvae and canned dog food) and tap water were available ad libitum. Activity was monitored using an Esterline-Angus event recorder, with microswitches connected to perches in the cage. Drinking was registered by the completion of an electrical circuit between the water and the cage floor whenever an owl attempted to drink. When this circuit was completed, a current of 10 μa at 15 mv was amplified to trigger a sensitive relay, which in turn activated the event recorder. The owls gave no indications of detecting or avoiding the electrical current associated with their water source.

Results. A mated pair of Burrowing Owls was maintained at 35°C, (mean RH, 45 per cent; range, 41–48), which is a temperature within thermoneutrality (Coulombe 1970). Activity and the number of drinks recorded during each 15-min interval (averaged over three consecutive days) are given in the lower part of figure 5. General activity was at the highest level during the 4–5 hr following the onset of the photoperiod; drinking corresponded to maximum levels of general activity. No nocturnal activity was recorded except during the first hour preceding the photoperiod and during the first hour after the lights were off.

Subsequent to the preceding experiment, the ambient temperature was raised to 41°C (mean RH, 41 per cent; range, 39–43), which represented mild heat stress as judged from metabolic response (Coulombe 1970). After several days of adjustment, activity and drinking during 15-min periods were each averaged over three days (fig. 5). Nocturnal activity became pronounced at this higher air temperature.

The frequency of drinking increased at 41°C (fig. 5) and nocturnal drinking occurred. The periods of drinking behavior correspond to high levels of overall activity, as in the previous experiment.

TABLE 2. Burrowing Owl population census, 1965–1967, total census route, Imperial Valley, California.

Date	Time	No. owls seen	No. active burrows	No. adults per burrow	Est. no. owls[a]	% observed[b]	Est. no. owls/mi.[2]
5 Apr. 66	10:00–12:00	15	11	1.36	20	75	6.7
23 Apr. 67	10:00–11:15	22	20	1.10	33	67	11.0
1 May 66	9:00–11:00	25	22	1.14	39	64	13.0
18 May 67	8:30–10:00	27	23	1.18	38	71	12.7
6 June 66	11:00–12:25	21	17	1.24	30	70	10.0
23 June 65	8:00–10:00	35	25	1.40	49	71	16.3
6 July 67	7:30– 8:45	25[c]	18	1.39	35	72	11.7
14 Sept. 66	10:30–12:45	3	12	0.25	6	50	1.0
30 Sept. 66	12:00–13:30	7	13	0.54	11	63	3.7
11 Dec. 65	6:00–12:00	9	10	0.90	15	60	5.0

[a] Estimated by adding twice the number of pairs observed to 5/3 times the number of single owls seen.
[b] Calculated from actual no. of owls seen divided by estimated no. of owls.
[c] An additional nine juveniles were seen.

Discussion. A shift to crepuscular activity and increased nocturnal activity at air temperatures above thermoneutrality may have adaptive value to Burrowing Owls. In the field, such a shift in activity pattern would reduce their exposure to excessive environmental heat stress.

Drinking may be of significance to populations of Burrowing Owls where free water is available. Utilization of free water could permit these owls to maintain normal body temperatures, through increased use of gular flutter in environments of severe heat stress. This may permit the species to occupy areas where there would not be sufficient water (preformed and metabolic) available in their food to sustain a breeding population.

POPULATION DYNAMICS

Population stability. I banded a total of 14 adult and 10 juvenile Burrowing Owls (USFWS metal bands provided by C. H. Trost) near El Centro, Imperial County, California, June–December 1966. No determination of sex was attempted in the field. Burrowing Owls were easily captured by placing unbaited single-doored Tomahawk live-traps (48 × 16 cm) in a manner that blocked the entrance of occupied burrows. When owls were outside the burrow, they could be captured trying to reenter the burrow during the breeding season. At other times, success was limited to trapping owls attempting to exit from their burrow.

No recaptures other than my own have been reported. Of these owls 19 were banded along one-half mile of continuous habitat (Dahlia Drain Canal SE¼ sec. 24, T. 16S, R. 14E). In this local population, none of eight juveniles banded in June 1966 was subsequently recaptured during the fall and winter of 1966, and none bred there in 1967. During the fall and winter of 1966, seven additional immigrant adults were banded at this location. Only one of these immigrants remained in the 1967 breeding population at this site; however, the total breeding population there remained approximately the same from 1966 to 1967, the additional members being recruited from spring immigrants. It appeared that 20–25 per cent of the breeding population remains in the Imperial Valley during the winter months, with probable immigration from the north and emigration to the south in this period.

Population census. Roadside censuses were made of Burrowing Owls 1965–1967 southwest of El Centro, Imperial County, California. A driving route was established that included Greeson Slough and an area along the New River. The route was 6.0 miles long, through an area of 3 square miles of potential habitat for Burrowing Owls.

The result of the population counts of 1965–1967 are given in tables 2 and 3. The banded owls along Dahlia drain canal provide a partially-marked population for comparative purposes.

Population estimates from these data are difficult since several simultaneous variables are involved. Census data were collected at different seasons and different times of day. The seasonal and daily patterns of Burrowing Owls influence the probability of observing one or both individuals of a pair at any given moment. The actual number of unmated owls in the population also influences these estimates, since one member of a pair of owls may be below ground at a given moment. If the absolute population size varies from year to year to a significant extent, the estimates will be further complicated. However, a number of these variables can be factored from the census data, and meaningful estimates can be made.

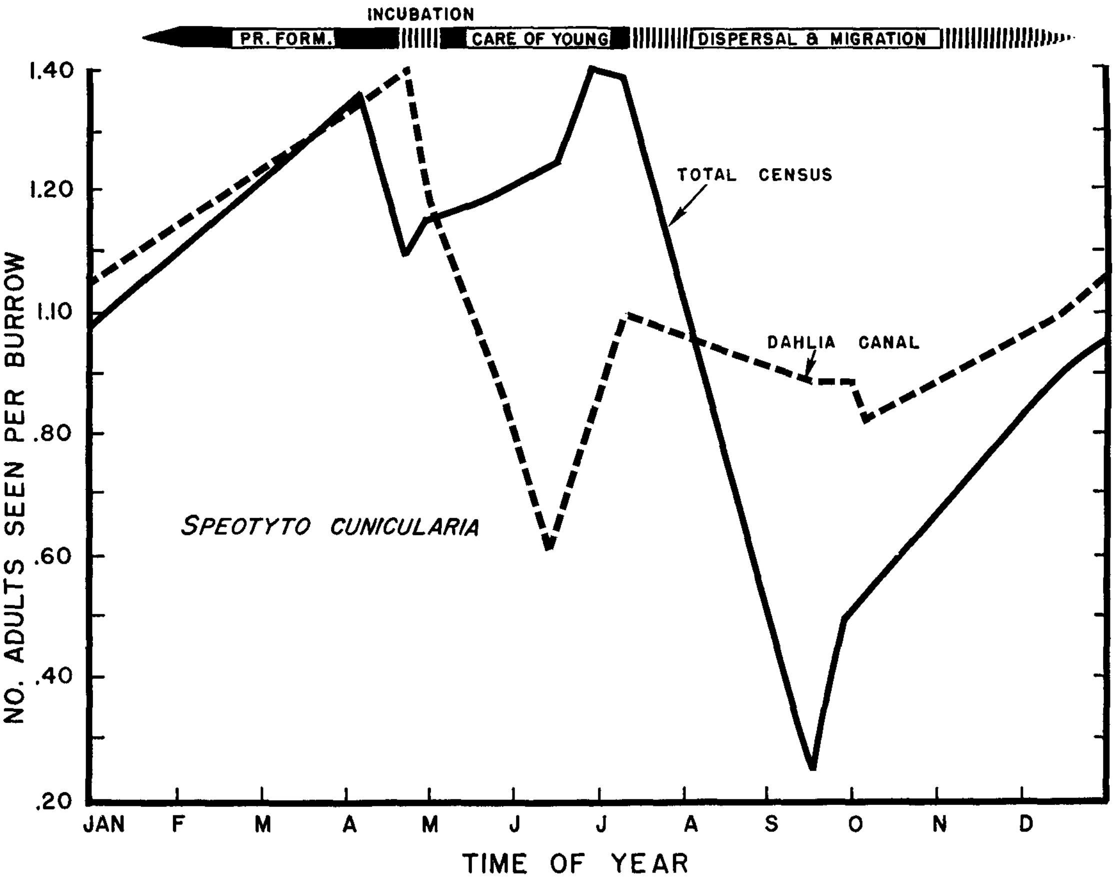

FIGURE 6. Number of adult owls seen per burrow, Imperial Valley, California, 1965–1967.

The number of owls estimated in the census population was calculated by adding an arbitrary proportion of single owls to the number of pairs counted (see table 2). It was assumed that two-thirds of the single owls counted were actually paired, and that the remaining one-third were unmated. This assumption of a constant proportion of unmated birds may not be valid; however, as the actual percentage of such birds in the census population changes, the relative estimates change correspondingly. This can be seen in the calculation of "per cent observed" in tables 2 and 3; this parameter was derived by dividing the actual number of owls counted by the number estimated to be present. Although the average per cent observed was similar between the total census figures and the Dahlia canal numbers (66.3

TABLE 3. Dahlia drain canal Burrowing Owl census, 1966–1967.[a]

Date			Time	No. owls seen	No. active burrows	No. adults per burrow	Est. no. owls[b]	% observed[b]	Est. no. owls/mi.[2]	No. owls trapped	Proportion of banded owls[c]	Actual no. owls/ mi.[2d]
23	Apr.	67	10:00–11:15	14	10	1.40	18	78	24.0			
1	May	66	11:45–12:10	12	11	1.18	19	68	25.4			
18	May	67	8:30–10:00	8	9	0.89	12	66	24.0			
6	July	67	7:30– 8:45	6	6	1.00	10	60	20.0			
14	Sept.	66	10:30–12:45	7	8	0.88	12	58	24.0			
30	Sept.	66	12:00–13:30	7	8	0.88	10	70	20.0			
6–7	June	66	17:00–20:00	6	10	0.60	10	60	20.0	7		18.0
1–2	Oct.	66	17:00–20:00	9	11	0.82	13	69	26.0	7	0.29	18.0
15–16	Dec.	66	16:00–20:00	10	10	1.00	14	65	20.0	10	0.33	25.0

[a] See text for details on trapping and banding procedures, and location.
[b] See table 2 for explanation.
[c] Calculated from number banded owls captured divided by total number of banded owls in population.
[d] Number of owls trapped divided by area of suitable habitat.

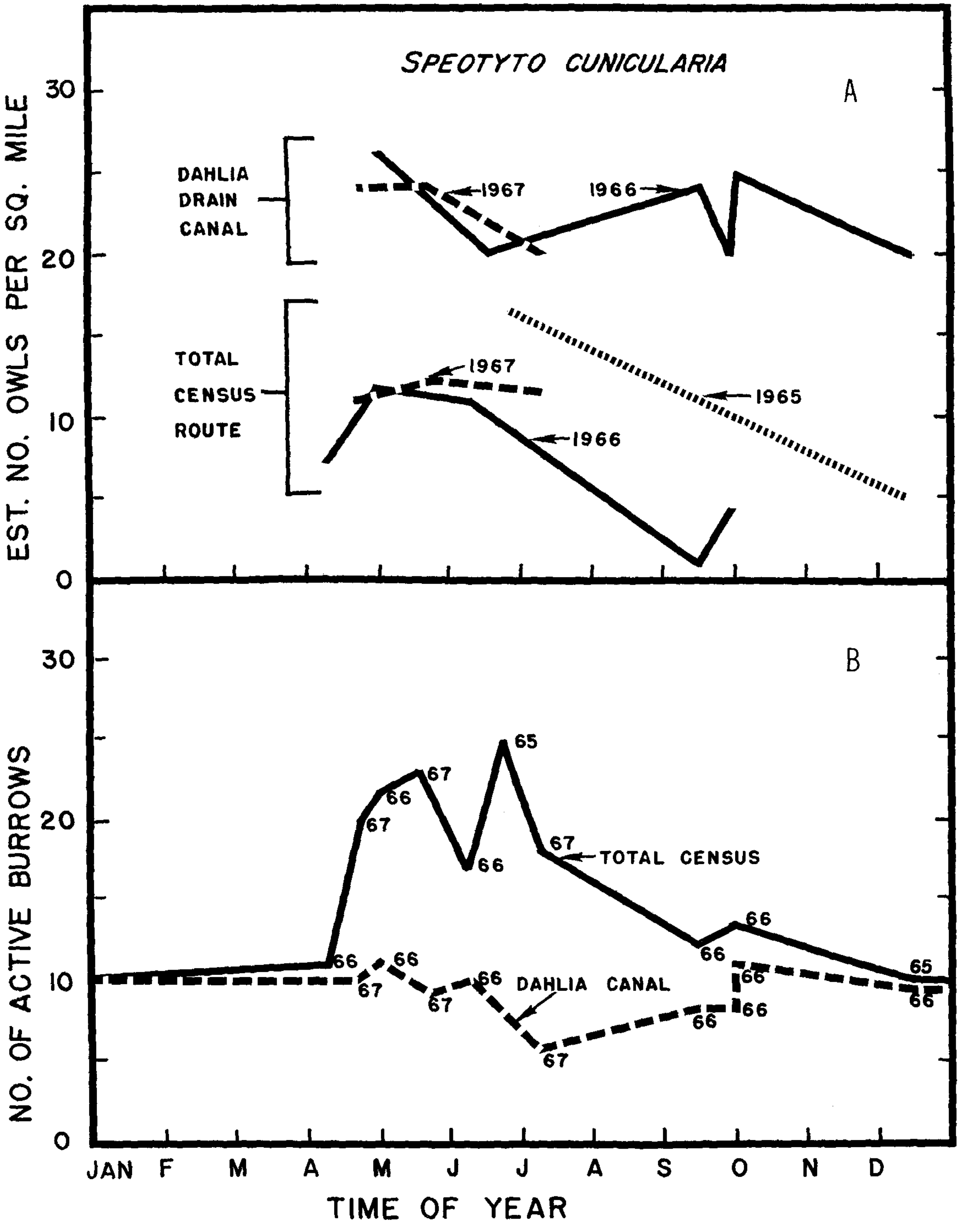

FIGURE 7. A. Estimated number of owls per square mile. B. Number of active burrows observed, Imperial Valley, California, 1965–1967.

and 66.0 per cent, respectively), there were specific trends in each case. The percentage of owls observed was lowest in the fall and winter months for the total census population (table 2), indicating fewer pairs in the population and/or dispersal. The percentage of owls observed along the Dahlia canal does not show this trend, perhaps because the owls were easier to see in that area. However, the fall and winter tendency towards fewer pairs and a greater number of single Burrowing Owls can be seen in both census groups, in the number of adults observed per burrow (fig. 6).

Seasonal and yearly trends of estimated

population numbers in the two census groups show contrasting patterns. The Dahlia canal colony averaged an estimated 22–23 owls per square mile through all seasons in both 1966 and 1967 (fig. 7A). The total census population averaged an estimated 12–13 owls per square mile during the breeding seasons of 1966 and 1967; in the fall and winter months of 1965 and 1966 the total census estimates declined to about 3–4 owls per square mile (fig. 7A). Apparently the Dahlia canal habitat is capable of supporting a greater number of Burrowing Owls at all times of year. In 1965 there was a larger total population of owls along the census route (fig. 7A), which coincided with the general observation of more owls present throughout the entire Imperial Valley that year.

The seasonal trends in estimated numbers of owls were also reflected in an independent estimate of population size by observing the number of occupied burrows. A burrow was considered to be "active" when fresh pellets, tracks or other evidence of current occupancy were noted. As seen in figure 7B, the number of active burrows remained essentially constant along the Dahlia drain canal through 1966 and 1967; the increase in spring and early summer numbers is reflected along the total census route.

The actual number of owls present along the Dahlia canal during 1966, as determined by trapping, ranged from 18 to 25 owls per square mile (mean, 20.3); census estimates during the same period ranged from 20 to 26 owls per square mile (mean, 22.0), indicating a close correspondence of these two methods (see table 3). The fact that about one-third of the trapped owls had previously been captured indicates that in many cases only one member of a pair was captured and banded. Also, the specific trap locations at active burrows remained static, so that an interchange of members in the local population was reflected in these results.

The impact of winter migrants on the Imperial Valley population is unknown. Burrowing Owls are more or less migratory throughout the northern parts of their range (Bendire 1892; Brenckle 1936); however, some owls may remain on their northern breeding ground all winter (Agersborg 1885). Coues (1874) states that both Burrowing Owls and Prairie Dogs are abroad on "pleasant days" in December and January on the plains of western Kansas, although night temperatures "often fall to nearly zero (Fahrenheit)."

DISCUSSION

Behavior. In general the patterns of behavior observed in Burrowing Owls remarkably parallel observations on the Palearctic Little Owl, as described by Witherby et al. (1943) and Haverschmidt (1946). Both of these species tend toward crepuscular feeding and diurnal activity; both species form pair bonds of lasting duration, accompanied by frequent copulations prior to and well past the reproductive period; and the female of both species appears to perform most, if not all, incubation.

The only apparent divergences in behavioral characteristics between these two species are associated with the strictly subterranean nesting habits of the Burrowing Owl. Little Owls also nest in tree cavities (Haverschmidt 1946), or in buildings, as well as terrestrial sites (Witherby et al. 1943:324), and are not closely associated with the nesting site during the non-breeding season (Haverschmidt ibid.). Hopping while in search of prey occurs (Haverschmidt 1946), although running has been observed in Little Owls (Witherby et al. 1943:323). Burrowing Owls always run in pursuit of prey, and frequently grasp prey in their talons to devour them. Little Owls grasp small prey in their beak, and devour them without using their feet (Haverschmidt 1946).

The arboreal habits of some Little Owls seem to increase the amount of avian food in their diets (Haverschmidt 1946; Witherby et al. 1943:324); Burrowing Owls rarely have evidence of small birds in their diets. In the Imperial Valley, Burrowing Owls may nest within a few meters of extensive breeding colonies of Redwinged, Tricolored, and Yellow-headed Blackbirds, with no apparent interactions.

Population control. Adult Burrowing Owls do not have many predators in the Imperial Valley. However, the eggs and young may be particularly vulnerable. I have observed large gopher snakes (*Pituophis catenifer*) in active burrows during the spring months; certainly large snakes take a toll of eggs and nestlings. Mammalian predators take a number of young before they fledge. Striped skunks (*Mephitis mephitis*) were observed entering owl burrows, and feral house cats may enter some of the larger burrows on occasion. I observed a badger (*Taxidea taxus*) in the process of digging out a burrow containing young owls which I had been attempting to band. Perhaps the relatively large brood size of Burrowing Owls (three to six young) may be an adaptation to a high rate of predation on the young, and/or to scarcity (in many areas) of nest sites.

Food did not appear to operate as a limiting factor on the Imperial Valley owl population, at least in a quantitative sense. Since insects and arthropods were active at all times of year along the canal banks, and many of these utilize owl burrows as shelter or breeding sites, the burrows provide the owls with a potential food resource.

The major factor controlling the abundance of Burrowing Owls in the Imperial Valley seems to be the availability of burrow sites. Although at least 1000 miles of canal banks are present in the Imperial Valley, only a fraction of these are suitable habitat at any given time. The canals which supply water are not suitable due to periodic rises in water level. Some of the major arterial canals have banks for the owls to occupy. About one-third of the canal mileage is in drain canals, which usually have very little water flow. These canals are subject to dredging operations every few years, which destroy the established burrow sites. If the vegetation grows above the top of these canals, or becomes moderately dense along the banks, they are no longer occupied by Burrowing Owls. Along four miles of drain canal near the town of Westmoreland, I counted 13 pairs of Burrowing Owls in June 1966. In early July this canal was dredged, and on 14 July no owls could be found along the same canal. Thus, the only stable habitat exists in areas where agriculture is not in progress, such as Greeson Slough or along the New or Alamo Rivers.

Role of the burrow. Certainly a unique and conspicuous feature of the Burrowing Owl is its burrow, which is apparently the key to the ecology of this species. The overall distribution of *Speotyto cunicularia* in western North America coincides with the occurrence of colonial burrowing rodents of the genera *Citellus* or *Cynomys*, which provide suitable burrow "starts" from which these owls construct their burrows. The burrow provides the center of activity throughout the year for these owls, and plays an important role in the social and thermoregulatory behavior, food supply, and population dynamics.

All owls studied have demonstrated territoriality, at least during the breeding season (see Ligon 1968). Burrowing Owls did not appear to defend territories other than the immediate vicinity of their burrows. Several pairs were observed foraging over a field adjacent to Dahlia canal with no signs of aggressive interactions; all owls freely passed each other in the different areas on this field. Burrowing Owls were not observed to defend their burrow sites against other species except potential predators.

As in the hole-nesting Elf Owl, the nest site is the center of activity for Burrowing Owls. Social behavior centers around the burrow, and although site attachment for a particular burrow may be very low during the fall and winter months, I have never observed a Burrowing Owl that was not utilizing a ground-hole for shelter. Territoriality in this species probably centers around the burrow. Copulation occurs at the burrow site and acts in pair-bond maintenance, as in the Elf Owl (Ligon 1968) and the Little Owl (Haverschmidt 1946).

The number of active burrows in the two census areas changed little from year to year. This parameter appears to be the best basis for estimating the population size of the species. Differences between the two census areas in estimated density are probably due to burrow spacing rather than to the proportion of paired owls to unmated individuals. However, pair formation appeared to occur earlier in the fall and winter along the Dahlia canal than in other areas, which perhaps is related to the greater carrying capacity of that particular habitat.

The role of the burrow in the population ecology and thermoregulation of Burrowing Owls reaffirms the conclusions of Bartholomew (1966) that "an ecologically relevant understanding of physiology requires a knowledge of microclimate and is heavily dependent upon concurrent integration of the behavior of the species in question." The quantification of factors of physiology and their integration with the ecoclimates occupied by a local population of Burrowing Owls can provide new insights as to the adaptations of these diurnal owls to their particular environment (Coulombe 1968).

SUMMARY

The natural history and population dynamics of Burrowing Owls (*Speotyto cunicularia*) were studied near El Centro, Imperial County, California. Discussions of the distribution, habitat, food habits, activity patterns, and various aspects of the behavior of this species are presented.

A conspicuous and unique feature of this small diurnal owl, its burrow, provides the key to the ecology of the species. The distribution of Burrowing Owls coincides with the occurrence of colonial burrowing rodents (*Citellus* or *Cynomys*), and local occurrences of these birds appear to be governed more by the suitability of burrow sites than by any other single factor.

The burrow provides the center of activities throughout the year; it plays an important role in the food supply and in the social and thermoregulatory behavior of these owls. The social behavior of Burrowing Owls is remarkably parallel to the behavioral patterns of the Palearctic Little Owl (*Athene noctua*); divergence in some aspects of behavior seem to be correlated with the greater "terrestriality" of Burrowing Owls. Owl populations resident in the Imperial Valley of southern California encounter temperatures near freezing during the winter and are active during periods of intense environmental radiation during the summer. Burrows were found to provide a buffered ecoclimate for these owls throughout the year. Absolute humidity in the depths of the burrows averaged 16.9 g $H_2O \cdot (m^3\ air)^{-1}$, about 70 per cent greater than that of ambient air. The accumulation of water vapor, from both biotic and abiotic sources, reduces the saturation deficit of the burrow air. Thus pulmocutaneous evaporation should be reduced while the owls are in their burrows.

Laboratory experiments suggest that Burrowing Owls undergo a shift in general activity patterns at ambient temperatures above 40°C. The total amount of activity remains about the same as at lower ambient temperatures, but crepuscular and nocturnal activity are increased while diurnal activity decreases.

Burrowing Owls were observed drinking free water in the field and in captivity. The response of consuming free water appears to be innate rather than acquired. The frequency of drinking in the laboratory increased with ambient temperature. Drinking may not be confined to a local population where free water is available throughout the year.

Owl populations were stable at about 20 owls/mi.^{2} in optimal habitat; in other areas the number fluctuated seasonally, with the highest densities occurring during the breeding season. Availability of burrow sites appears to be the critical factor in the prediction of Burrowing Owl numbers. Predators seem to play a significant role in controlling the number of young owls recruited; however, an exceptionally large clutch size in this species tends to offset the effects of predation, particularly in the agricultural areas.

The role of the burrow in the population ecology and thermoregulation of burrowing owls reaffirms the conclusions of Bartholomew (1966) that an ecologically relevant understanding of physiology requires a knowledge of microclimate and is heavily dependent upon concurrent integration of the behavior of the species in question.

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Editor's Note: The preceding article by Coulombe was submitted somewhat earlier than the following one by Thomsen, but editorial processing of the two overlapped in time. Each is an independent study and the similarity in subject matter and in timing is coincidental. In view of this coincidence and of the complementary nature of many of their results it seemed advisable to publish both together.