BEHAVIOR AND ECOLOGY OF BURROWING OWLS ON THE OAKLAND MUNICIPAL AIRPORT

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Among owls, the Burrowing Owl, *Speotyto cunicularia hypugaea*, presents an unusual opportunity for study, being colonial, diurnal, and crepuscular, as well as nocturnal. These owls occur in many places around the San Francisco Bay area. Though eliminated by civilization from some sites, they have moved into others, particularly those created by bay-fill projects. One of the largest populations of Burrowing Owls in the Bay Area is on the Oakland Municipal Airport, Alameda County, California, where this study was conducted.

The major part of the study covers the period from October 1964 to August 1966. Virtually all of the airport owls were leg-banded to permit field identification of individuals, and to facilitate study of the population as a whole. Shorter periods of observation were made in March and July 1967.

STUDY AREA

The older parts of the Oakland Airport and the adjacent golf course were filled in 1928 with various materials, mostly dredgings from San Francisco Bay, sand, and dirt. The ground is vegetated with assorted annual grasses, mustard (*Brassica*), and some scattered coyote brush (*Baccharis*). Most of the owls live on the west end of the old airport, scattered out for about a mile along the junction of the airport and the golf course, and within 300 yards of the latter. This area of about 150 acres formed the major part of the study area.

The newer part of the airport was filled in 1956–1957 and presently supports a thin scattering of ice plant (*Mesembryamthemum*), coyote brush, annual grasses and forbs. Few owls live there.

METHODS

Each bird received a U. S. Fish and Wildlife Service aluminum band and a combination of three or four plastic colored bands. During the course of the study, 107 owls were captured and marked. These birds included the entire 1965 population except for three young, and nearly all of the 1966 population. Most birds were weighed, inspected superficially for ectoparasites and feather condition, banded, and released directly into the burrow. Weighing was done immediately after capture.

Since the birds were primarily active at dawn and dusk, the bulk of observations were made at those times with 7 × 50 binoculars and a 20× spotting scope. During 1965, most observations were made at dawn; during 1966, most were made at dusk. Over 1000 hr were spent on the study area.

Generally one or a very few burrows were closely observed while the owls were most active; spot checking of the entire population was done either before or after this, depending on the time of day.

Stakes about 18 inches tall were erected at many burrows. Especially during the spring and summer, owls perched on the stakes, thus effectively getting above the grass where their bands could be seen.

For purposes of trapping, collecting pellets, erecting stakes, and general inspection, burrows had to be visited periodically. Since the owls were upset by such infringements, I tried to visit the burrows when the birds were away or inside. Starting in October 1965, the burrows were avoided except when it became necessary to collect pellets or to band.

BURROWS

The burrow is an important feature in the lives of the owls, being used for nesting, retreat from enemies, storage of food, and shelter. Although during the nesting period owls were associated with only one burrow, each bird was familiar with a large number. Burrows housing owls had droppings, pellets, and bits of prey items on the mounds, especially during the spring and summer.

USE OF GROUND SQUIRREL BURROWS

Beechey ground squirrels (*Spermophilus beecheyi*) provided most of the owls' burrows. During 1965 and 1966 there were always some apparently vacant burrows, and the squirrels excavated many new ones. On several occasions owls were found to have moved into burrows occupied by squirrels, apparently having evicted the latter. Although squirrels frequently took up residence in abandoned owl burrows, a situation was never found which even remotely suggested that the squirrel had evicted the owl.

DIGGING

With the exception of the period during which nesting material lined the burrow, the owls renovated and maintained burrows by digging. This was done extensively before nesting material was brought, and to a lesser degree by both adults and young after the nesting material was removed. The bird would stand on one leg and fling the substrate back with a few strokes of the other leg. Then it would take a step forward and repeat the process, kicking back with the other leg. Sometimes

the wing opposite the leg that kicked was extended down for support. I never saw a bird progress backward out of the burrow as Bendire (1892) relates. Males and females were seen digging with about equal frequency, but the females worked longer. During one observation period of 96 min, the female of a pair dug 11 times totalling 47 min, while the male dug 11 times totalling 34 min.

Although digging was done primarily with the feet, apparently the beak was used also since sand, dirt, and stone were found in pellets with increasing frequency September–April. The greatest amount of dirt in pellets occurred January–April, after which there was a sudden drop to zero, when the nesting material was being brought. This inorganic material in the pellets corresponded to the type of substrate in which the owls were digging.

During the period of intense digging, pairs or individuals were seen to dig at several burrows, gradually concentrating their efforts on a single one. But even during the height of gathering nesting material for the chosen burrow they were occasionally seen digging at another.

The question of whether the owls dig their own burrows frequently arises. Some authors think they do not (Fisher 1893; Dawson 1923); others claim they do (Rhoades 1892; Pearson 1936; Goodrich 1945), although no one has recorded their doing it. Forbush and May (1939) say that the western Burrowing Owl does not dig its own burrow, but that the Florida sub-species does. Unquestionably the birds are able to dig, as I observed many times. From two related lines of evidence in this study, it appears that they occasionally do dig their own burrows, but from general field observations it would seem that more commonly they enlarge and improve existing holes. Also, the fact that they are so often associated with burrowing mammals suggests their dependence upon them.

First, prior to 1963, when annual burning of the airport occurred, ground squirrels were restricted to the dike along the southern end of the study area. Dr. Michael Pontrelli (pers. comm.) said that north of the area of squirrel occupation he occasionally came across a burrow which had not been there the preceding few days with owl(s) living in it. The same observation was made a few times in the present study, although the current presence of numerous ground squirrels makes it questionable whether the owls were creators of the new burrows. Second, a pair of owls was observed in the process of digging a burrow where it was almost certain there was none before. Their efforts far surpassed any of the mere renovating activities performed by other birds.

POPULATION MOVEMENTS

SEASONAL MOVEMENTS

Since the object of the study was to observe the owls with as little disturbance as possible, I did not dig up burrows or insert apparatus for the purpose of discovering owls. Experience on other areas showed that such activities often resulted in the owls moving.

The fact that in closely observed areas some birds would not be seen for a few days to a few weeks during the winter suggests that they may stay in the burrow during these times, become strictly nocturnal, or go to other burrows. Agersborg (1885) wrote of southeast Dakota that Burrowing Owls not only retreated to their burrows in bad weather, but stored large quantities of food. Ligon (1961) in New Mexico dug up a burrow in the winter and discovered an owl. He felt they did not migrate, but rather stayed in the burrows.

Seasonal movements other than migration occur. After the young learned to fly, the family groups often moved from burrow to burrow. One to three changes were made per family. Starting about September, each young owl began to stay increasingly to itself at one burrow, while the siblings usually appropriated burrows nearby.

At the same time the birds became less active. Instead of sitting in prominent locations, they remained in the grass. They confined their activities increasingly to the night.

By late February the pattern was noticeably reversed, with the owls starting their activities of preening, courtship, and foraging earlier in the evening and becoming quiescent later in the morning. As pairs formed, they investigated new burrows. Territory boundaries were in flux, but began to take form as pairs chose their burrows.

DAILY MOVEMENTS

The owls spent most of the day near their burrows. Between noon and 16:00 the owls were little in evidence. They came out in late afternoon to sit until the evening's proceedings began. An attempted census in mid-afternoon often yielded 10–25 per cent of the population, while one taken in late afternoon yielded 40–80 per cent.

Every evening, in the half-light of dusk, all the owls made their way to the golf course to forage. Adults with young to feed returned to the burrow during the night.

GENERAL HABITS

FORAGING

Birds caught before sunrise always had distended stomachs, whereas those caught in the early evening did not, indicating that they foraged at night. Murphy and Amadon's (1953) claim that the Burrowing Owl possesses only about the same ability as man to see in weak light is refuted by the above observation. Foraging took place by four methods, here discussed in order of importance.

Ground foraging. During the winter, ground foraging was the only hunting method observed. It was strongly reminiscent of the foraging behavior of the robin. The owls sometimes substituted short flights (a few flaps and a glide) for running.

In the late spring and summer, the following foraging methods were also used.

Observation foraging. In using this method, the owl perched at an elevated position and scanned the area below. When a prey item was sighted, the owl dropped from its perch, spent a few seconds to a few minutes on the ground, then returned to the perch. An owl was observed to fly 100 yards from a perch 25 ft high and retrieve a Jerusalem cricket from a taxiway.

Hovering. During early March of 1966 owls began using this method of hunting, and continued it through July. In form, it was like that utilized by the sparrow hawk. Most hovers occurred after sundown and before pitch-dark, but a few occurred before sundown; on one night with a half-moon, three hovers were observed. Hovering at night may be more common than here indicated. The capture of meadow voles seemed to be the object of hovering, and their consumption during the spring and summer increased. Males performed 98 per cent of the hovers observed.

Flycatching. Flycatching in the manner of the Tyrannidae was observed only a few times.

TEMPERATURE REGULATION

Except for puffing up their feathers in cold weather, the owls at the airport showed little signs of being affected by the weather. However, east of Livermore, Alameda County, California, at about 11:00 with the temperature at 85–90°F, owls under observation held their wings 1–1.5 inches away from their bodies. They did not go into their burrows to escape the heat.

BATHING

Dust bathing was seen five times; the substrate was either loose dirt or sand. In the typical procedure, the bird squatted, plunked its face into the sand, and turned it rapidly from side to side several times. During the process the sand flew laterally, the breast feathers were puffed up, and sometimes the wings moved slightly.

REACTIONS TO AND RELATIONS WITH MAMMALS AND BIRDS

Large mammals. This group includes dogs and man. Dogs, primarily from the nearby suburban area, were not uncommon visitors to the airport. During the nestling period in particular, the adult owls became frenzied when dogs approached the burrow, and chattered and dived at them. When the young owls could fly, both they and the adults chattered at dogs, but seldom dived at them. Dogs caused about 20 per cent of damaged burrows and humans about 65 per cent.

In response to the approach of people, an adult owl was never seen to retreat into the burrow. They either flew silently away, or chattered for a while and then flew away. An owl was never seen to dive at a human.

Small mammals. Jackrabbits (*Lepus californicus*), Beechey ground squirrels, long-tailed weasels (*Mustela frenata*), striped skunks (*Mephitis mephitis*), and house cats (*Felis domesticus*) were the only other mammals with which the owls had to deal, in other than a strict predator-prey relationship.

Jackrabbits were very abundant at the airport. Owls generally ignored them. Only once was an owl observed to chase and harass a jackrabbit by diving at it. Young owls put on a full defensive posture for rabbits, which always gave way. The defensive posture was essentially that pictured in Austing and Holt (1966:124). In this position the owl swayed from side to side. Jackrabbits, when running away from danger, served to warn the owls. As more and more rabbits ran by, the owl(s) began to look around, concentrating their attention on the direction from which the rabbits came, and eventually locating the source of danger.

Only two weasels were seen in the course of the study. One was involved in a weasel-owl interaction in which the owls harassed the weasel.

No interaction between cats and the owls was observed.

One family of skunks and several individuals were seen. In the only skunk-owl interaction seen, a male owl dived repeatedly at an adult skunk.

The owls' relationship to Beechey ground squirrels should have been particularly interesting because squirrels provided most of the

TABLE 1. Food habits of the Burrowing Owl based on pellet analysis.

Food item	% Frequency				% Volume			
	Dec.–Feb.	Mar.–May	June–Aug.	Sept.–Nov.	Dec.–Feb.	Mar.–May	June–Aug.	Sept.–Nov.
Meadow vole (*Microtus californicus*)	20.1	34.4	40.7	37.2	14.9	24.6	37.1	33.9
Jackrabbit (*Lepus californicus*)	4.8	4.6	1.4	0.9	3.5	4.1	1.3	0.2
Pocket gopher (*Thomomys bottae*)	0	2.6	2.2	0.1	0	2.1	2.8	0.1
Norway rat (*Rattus norvegicus*)	0.5	0.6	0	0.5	0.5	0.6	0	0.4
House mouse (*Mus musculus*)	0	0	0	1.2	0	0	0	1.0
Hoary bat (*Lasiurus cinereus*)	0	0	0	0.1	0	0	0	0.1
Total mammal	18.9	31.4	41.2	35.7				
Meadowlark (*Sturnella neglecta*)	0	0.2	0	0.1	0	0.2	0	0.1
Redwinged or Brewer's Blackbird (*Agelaius phoeniceus* or *Euphagus cyanocephalus*)	0	0.3	0	0	0	0.4	0	0
Shorebirds	0	0.3	0	0	0	0.2	0	0
Unidentified birds	5.2	5.3	2.2	1.4	3.9	5.1	2.0	1.2
Total birds	3.9	5.9	2.0	1.3				
Toad (*Bufo boreas*)	0	1.1	2.6	0	0	0.3	0.8	0
Jerusalem cricket (*Stenopelmatus fuscus*)	60.0	56.2	60.4	64.3	7.8	13.7	12.0	11.5
Unidentified Orthoptera	0	0.2	0	0.2	0	0.1	0	0.2
Coleoptera	84.2	60.5	47.3	64.7	22.1	14.8	11.3	16.0
Diptera	0	0.2	0	0.1	0		0	
Total insect	29.9	28.6	23.3	27.7				
Isopoda	0	0.2	0	0.3	0	0.1	0	0.1
Sand and dirt	36.8	13.5	1.1	2.8	12.1	3.3	.02	0.9
Stones	5.7	1.3	1.1	0.4	3.0	0.2	0.1	0.3
Vegetation	71.3	61.0	55.5	57.4	32.7	30.2	32.6	33.9
Total	98.5	99.9	100	99.9				
No. pellets	209	608	366	929				

owls' burrows. However, surprisingly few interactions between the two species were seen. In those situations the squirrels were always the "losers." Contact between the two species was minimized by a temporal separation; the squirrels went into their burrows before the owls became very active, and did not come out in the morning until long after the owls had become quiescent.

Birds. Although owls were observed harassing mammals, they were observed *being* harassed by birds: Robins, Redwinged Blackbirds, Cliff Swallows, Western Meadowlarks, Mockingbirds, Sparrow Hawks, and American Avocets. Of these, only Redwinged Blackbirds and Meadowlarks were known to have been eaten by the owls. Except for the incident with the avocet, all large shorebirds and ducks ignored and were ignored by the owls. Killdeer screams usually alerted the owls in a manner similar to the running jackrabbits.

Aside from Sparrow Hawks, raptorial birds were treated with caution: instead of flying away, as in response to the approach of a large mammal, Burrowing Owls either squatted down well within the burrow entrance, or went inside the burrow.

Pheasants were common inhabitants of the airport, and were generally ignored.

FOOD HABITS

The investigation of food habits involved collection and analysis of 2112 pellets, examination of remains found at the burrows, and observation of prey items captured.

Due to the owls' habit of picking at their food, pellet contents were exceedingly fragmentary. Due to their propensity for decapitating the larger food items and saving the rest for a later meal, a pellet was a poor indication of the number of food items consumed. The frequency with which an item occurred was recorded, and an estimation of pellet contents by per cent volume was made; the results are summarized in table 1. For comparison, food items found at burrows were tabulated (table 2), as were food items seen carried, captured, or eaten (table 3). The

TABLE 2. Food items found at burrows of Burrowing Owls.

Food item	Frequency				% Frequency			
	Dec.–Feb.	Mar.–May	June–Aug.	Sept.–Nov.	Dec.–Feb.	Mar.–May	June–Aug.	Sept.–Nov.
Meadow vole (*Microtus californicus*)		3	8			5.8	6.4	
Jackrabbit (*Lepus californicus*)		8	10	1		15.4	8.1	100
Meadowlark (*Sturnella neglecta*)	1	1	11		50	1.9	8.9	
Redwinged or Brewer's Blackbird (*Agelaius phoeniceus* or *Euphagus cyanocephalus*)		1				1.9		
Other Passeriformes		3	3			5.8	2.4	
Shorebirds		13	2			25.0	1.6	
California Gull (*Larus californicus*)		1				1.9		
Mourning Dove (*Zenaidura macroura*)		1				1.9		
Pigeon (*Columba livia*)		1				1.9		
Pheasant (*Phasianus colchicus*)		1				1.9		
Toad (*Bufo boreas*)		15	46			28.8	37.1	
Jerusalem cricket (*Stenopelmatus fuscus*)	1		42		50		33.9	
Bumblebee (*Bombus* sp.)		4				7.7		
Monarch butterfly (*Danaus* sp.)		1				1.9		
Total	2	52	124	1	100	100	100	100

problems involved in food studies of raptors have been discussed by Craighead and Craighead (1956).

At least 60 per cent of the jackrabbit material consumed consisted of young ones, and at least five per cent was of adults; how much was taken as carrion is unknown. Dead jackrabbits were frequently found, especially during and after stormy weather.

One of the Norway rats eaten was an adult; the others were about the size of *Microtus*.

Since Beechey ground squirrels were so abundant at the airport, their complete absence in the list of prey species attests to the owls' crepuscular and nocturnal hunting habits. However, Bendire (1892) reports Townsend ground squirrels and young prairie dogs being killed and consumed by Burrowing Owls; Scott (1940) reports the same for thirteen-lined ground squirrels. Thus Beechey ground squirrels would seem to be a potential prey species. Only one carcass was found, and although it was within 20 yards of an active owl burrow, it rotted completely without being consumed by owls.

Adult and young birds seemed to occur about equally, although only a third of the remains was sufficiently well preserved to make a judgment. The California Gull and Domestic Pigeon were probably taken as carrion, since these birds appeared too large for the owls to kill. The pheasant was perhaps two weeks old at death, and might have been killed by the owls. The major incidence of bird consumption occurred in mid-April 1965 after a week of wet weather.

Four of the six most common Coleoptera were in the family Carabidae, one was in the family Staphylinidae, and one, Curculionidae (?). Of the six most common coleopterans, only three could be identified to a point where something of their ecology could be stated. One of these, *Calathus* sp., would be expected on both the airport and the golf course; and two, *Ocypus* sp. and *Pterostichus* sp., would be expected on the golf course sod. From this slender evidence, it seems that the owls probably encountered their beetle prey while on ground foraging trips, and that they derived a substantial part of this fare from the golf

TABLE 3. Food items seen carried, captured, or eaten by Burrowing Owls.

Food item	Frequency				% Frequency			
	Dec.–Feb.	Mar.–May	June–Aug.	Sept.–Nov.	Dec.–Feb.	May June–	Mar.–Aug.	Sept.–Nov.
Meadow vole (*Microtus californicus*)		2	14			100	38.9	
Pocket gopher (*Thomomys bottae*)			1				2.8	
Jerusalem cricket (*Stenopelmatus fuscus*)			10	1			27.8	100
Other insects			11				30.6	
Total	0	2	36	1	0	100	100	100

FIGURE 1. Female (left) and male Burrowing Owls, showing heavier barring on the female.

course. Grasshoppers, frequently mentioned in the literature as a common food item (Fisher 1893; Bailey 1921; Robertson 1929), formed an inconsequential part of the diet of the airport owls.

Although remains of toads were found abundantly at the burrows in spring and summer, evidence in pellets was scanty, perhaps because little skeletal material was eaten.

Vegetation was found in large quantities in the pellets in all seasons. Somewhat over half of this was presumably food of the consumed prey. The rest occurred as large pieces of grass and other vegetation which the owls probably consumed directly.

By and large, the owls at the airport seemed to eat a considerable variety of mammals, birds, and extraneous material, but not as great a variety of insects as Burrowing Owls elsewhere reported. Only Longhurst (1942) found them to eat as many kinds of vertebrates as occurred in my sample.

SEXUAL DIMORPHISM

The weight of 12 males averaged 172.0 g, with a range of 145.0–191.3 g; 10 females averaged 168.0 g, with a range of 125.6–210.0 g. The difference in mean weights for males and females was only about 4 g, or 2.3 per cent. The high extreme for females was a bird laying or about to do so, and the low extreme, a female with dependent young. In general, since males and females weighed nearly the same, and since both lost much weight when feeding young, weight was a poor criterion of sex.

Morphologically, the only useful field criterion of sex was the more extensive barring of breast and belly of the female (fig. 1). This barring varied among individuals; some males were almost white on the belly, and others were only slightly lighter than the females. The difference did not show up well in museum specimens.

Roberts (1932) and Grant (1965) in Minnesota noted that pairs consisted of a gray and a reddish-brown bird, and thought that the former was the male. Such a difference was not at all noticeable among the airport owls immediately after the postnuptial molt, but developed gradually so that during the 2 months prior to the next postnuptial molt, the male was fairly easy to distinguish by his lighter color. The change was due to the greater wear and sun-bleaching of his feathers, particularly on the head.

Behaviorally there were great differences. One which was often diagnostic at a glance was the posture of the bird standing or perching. The female generally held her body in a more horizontal position (fig. 2a, b). This difference did not apply well to birds "sleeping" during the day, or to disturbed birds.

COMMUNICATIONS

VOCAL COMMUNICATIONS

Chuck. The chuck was used as a low-level note of excitement. This sharp, single note was given simultaneously with each profound bow after a flushed bird had landed at some distance from the observer. Presumably this functioned, in general, in drawing attention away from the burrow, yet an owl was never seen to flush, then bow and chuck for any approaching animal except man.

The chuck and bow were used in the context of locating or "inquiring about" the mate in an abnormal situation. The chuck was also a mild warning note to the young.

Chuck-chatter. This sound consisted of 2–6 chucks (each accompanied by a bow, as above), followed immediately by a chatter of 5–8 notes on the same pitch and of the same quality as the chuck. It was usually repeated; a maximum of eight was heard in a series. It

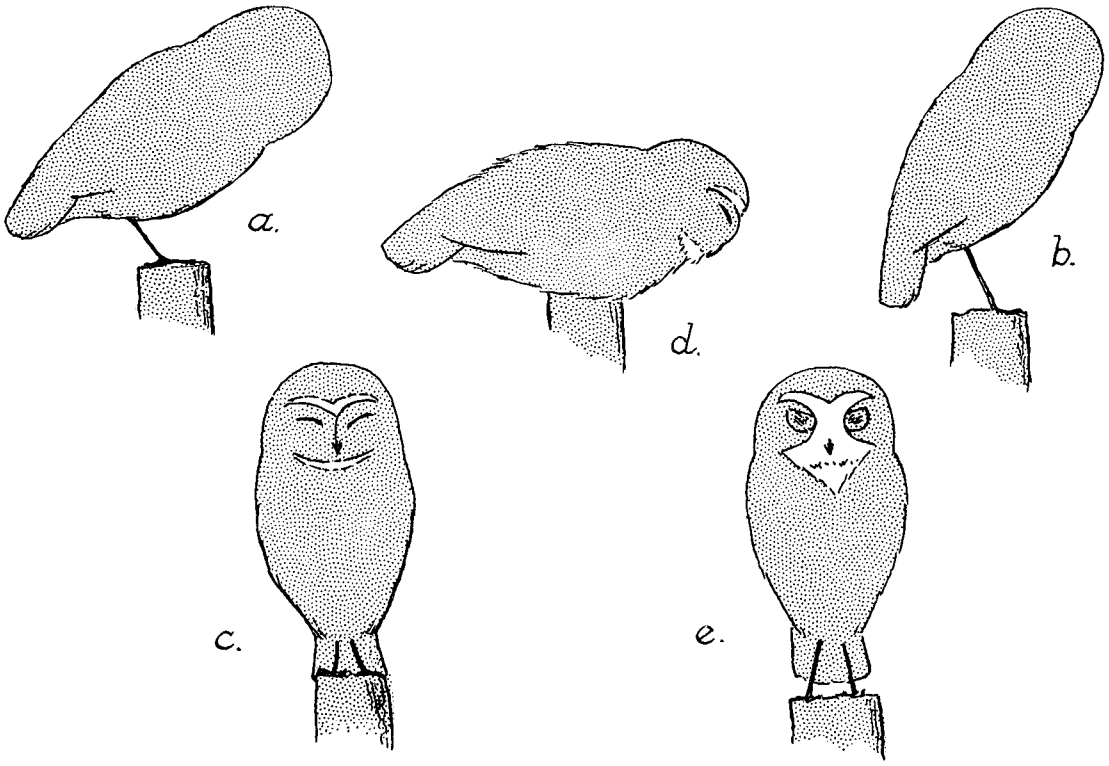

FIGURE 2. Posturing of Burrowing Owls, showing sexual dimorphism (a, female, and b, male), use of white patches (c and e), and bird calling (d).

was given under conditions of slightly greater agitation than the simple chuck.

Chatter. This call was a rapid series of chucks, given in situations of high agitation. The call varied considerably, with the pitch becoming increasingly higher and louder, within a narrow limit, as the intensity of the situation increased. Occasionally one to three quick preliminary notes were given, but these were not accompanied by a bow. Chattering frequently occurred during the day in the nesting period, and was often heard before daylight or after dark. The chatter, used extensively by both adults, warned the young of danger.

At some point in the nesting cycle the male began flying overhead and chattering at the intruder when the burrow was approached, instead of silently flying away. The timing of this change in behavior in relation to events inside the burrow varied among males.

Primary song. This call was two-syllabled, in quality like a muted California Quail, with the second syllable much longer than the first, and sometimes rising very slightly at the end. Variations noted included one bird that was slightly higher in pitch than the others, and another that had two short notes rather than one preceding the long note.

With two dubious exceptions, the song was given only by males. The song was heard at all times of the year, although only occasionally September–December. It was usually given at or near the burrow.

Primary song was used in relation to territoriality and pair formation. In this paper, the giving of the primary song is referred to as "calling."

Rasp. The rasp was a note similar to radio static, and was 1–2 sec in length. During courtship the female used the rasp, but its role was not determined. Among captive birds, the male's primary call frequently drew a rasping response from the female. The rasp was never used as a threat as indicated by Grant (1965). The female, and rarely the male, used the note to encourage the young to come out of the burrow, as an "all's clear" signal. Later, as the birds moved around in a family group, the rasp was used extensively as a location note.

Scream. The scream was given in times of crisis. It was a continuous, loud, scratchy sound, higher in pitch than the rasp. It was seldom heard in the field.

Rattlesnake. The "rattlesnake" was the precursor of the adult scream. It was so similar to the rattling of the snake that one is tempted

to regard it as a mimic of rattlers by very young owls, affording a deterrent to predators. This would be very adaptive for a burrowing animal living in rattlesnake country. However, W. C. Russell (pers. comm.) heard the same sound from young Saw-whet Owls, and Bent (1938) described a sound emitted by young Screech Owls which appears to be the same as that of the Burrowing Owls. Thus, the "rattlesnake" is perhaps a characteristic common to many owls, rather than a speciality developed by Burrowing Owls to mimic rattlesnakes.

Whine. Captive birds occasionally uttered a thin whining note repeated up to several seconds. It seemed to be a protest note.

Grunt. Captive birds occasionally made a series of small grunts; the sound was not heard in the field, and its meaning remains unknown.

Warble. The warble was a series of mellow, liquid notes similar to those of the Red-shafted Flicker. It was possibly a greeting note.

VISUAL COMMUNICATION

The posturing of the male and female (fig. 2a, b) may represent one factor in sex recognition by the owls. The white throat patches and eyebrows, in conjunction with the appropriate posture, not only played a prominent role in courtship and were used in fear situations, but probably also served in species recognition and in location. Birds displaying the white were much more easily seen (by me).

In defense of territory, mere sight of the defender by the intruder was frequently an effective deterrant.

A bird that suddenly stood upright to gain more information about a possible source of danger often became an object of close attention by the other bird(s) at the burrow.

COURTSHIP AND PAIR FORMATION

Pair formation began in early December; most pairs were formed by late February, but some did not form until mid-May. The pairs formed by late February were surprisingly synchronous in the subsequent phases of nesting and will be referred to as "on schedule." Those few pairs formed after February will be referred to as "late" pairs.

PRIMARY SONG

Primary song marked the beginning of pair formation, and seemed to be a principal component of it. The latter was not irrefutably clear to me until the middle of the courting season in 1966, when most of the females were paired and four unpaired males were competing for two unpaired females. At this point, primary song by paired males was noticeably reduced or absent, except in unusual circumstances, while the unpaired males spent as much as an hour per evening calling. Two closely watched cases revealed that the male called until the female came to him, whereupon the male she had just left began to call.

PREENING

Although self-preening did not appear to assume the highly stylized role in courtship that it does in some other birds, it frequently preceded copulation. That the male did by far the most preening (at least at dawn and dusk) perhaps indicates it was a general sort of stimulant for the female. Wing-and-leg stretching may serve the same function.

COPULATION; "WHITE AND TALL"

Copulation took place at the burrow at dawn and at dusk (frequency was at least six times greater at dusk). I did not discover whether it took place at night. It was never seen at any place other than a burrow, and generally it occurred at the pair's main burrow. It was most frequently observed only once per pair per evening, but on four occasions it occurred twice, and once, three times.

In the 1966 season, copulation was first observed on 6 December 1965; it occurred with increasing frequency through late March and mid-April. The latest copulation occurring with a pair on schedule was 23 April. It was observed among late pairs 1–20 May.

Early in the season copulation was often clumsily performed, but subsequently it was perfected. Defects noticed were: male standing upright on female; male standing nearly on female's head; female walking out from under male; male falling off female; and in one case, female on top.

Copulation was sometimes accompanied by an "exchange of food." In the 10 times this was witnessed, no food was actually seen to be exchanged.

The "white and tall" performance was closely associated with copulation. Both male and female possess the ability to display two white throat patches and eyebrows (fig. 2c, d, e). In relation to courtship, the female's white patches were seldom seen except occasionally after copulation. The male displayed white while giving the primary song (fig. 2d); before, during, and after copulation (fig. 2e); and as a general sign of sexual excitement.

At the same time the male displayed the white, he stood very tall with feathers raised, and looked down at the female. This stance was broken when the male suddenly looked

fiercely at some other object on the ground, preened briefly, or gradually relaxed, during which time the white became less prominent, and the owl less tall. Then his attention swung back to the female, and once again he became suddenly white and tall. This routine occurred once to several times per evening per pair.

At some point either before or after the white and tall stance, the female left the mound and ran a few feet away or flew a few yards away. This action usually resulted in eliciting the white and tall stance from the male. The female stayed away a few seconds to a few minutes; the male became more relaxed. As the female ran or flew back, the male again became white and tall, and when she reached the burrow, copulation occurred. Often the male then ran down the burrow, reappearing 10–30 sec later, white but not particularly tall. Both then either preened (the male doing much more), sat, or began ground foraging. A few variations of this procedure occurred.

Since the white and tall stance was so often associated with an excited male and copulation, it was usually seen in the evening. Upon returning to the burrow in the morning, copulation sometimes took place but more often did not.

CIRCULAR FLIGHT

In this rare performance the bird left the burrow and flew a circular route, returning to the burrow. The loop was up to 50 yards in diameter. I saw it performed 10 times by males and once by a female. It occurred before sunrise nine times, and after sunset twice.

HEAD-SCRATCHING

In head-scratching, one bird nibbled the other's head and face feathers with its bill, and the bird being scratched usually lowered its head. Head-scratching was sometimes solicited by one bird standing in front of the other with lowered head.

Males scratched females more, both in number of times and in length of time. Head-scratching was seen 22 February–24 May in 1965, and 1 February–4 May in 1966. Sometimes the "food exchange" gesture accompanied head-scratching but, as in copulation, no food was actually seen.

GIFTS

Six times a male brought an insect, and once a toad, to the mound and deposited it near or directly in front of the female who ate it. This activity always occurred in the evening, March–May, before the female had begun to lay.

RASPING

Occasionally during courtship, rasping (by the female in those cases where sex could be determined) was heard at dawn. It seemed to serve as a location note. Yet in one pair (newly formed, late) the female sat next to the male and rasped intermittently, sometimes until well after sunrise.

COURTSHIP ACTIVITIES OF YOUNG

Young birds performed head-scratching, "food exchange," and copulation. From those cases in which one or both birds were identified and the sex was ascertained from later observations, it was apparent that the sex of the young birds involved in these courtship patterns was not particularly important to the role they performed.

PERMANENCE OF PAIRS

Once formed, the pair-bond was not rigidly permanent, although pairs formed in the previous season tended to retain their integrity. Of the nine pairs in 1965, five retained their identity in 1966. Both members of one of the nine pairs disappeared completely; the female of another pair died; the female of a third pair disappeared; and the fourth pair split in 1966 and each member acquired a new mate.

Within a breeding season (1966) most changes were made among first-year birds, adults that had lost their previous mates, or birds that had entered the population from the outside. Of the nine new pairs constituted in 1966, possibly five contained only young birds from 1965. (Two young males and one young female were involved, as well as four unbanded females and two unbanded males whose ages were unknown.) One of the nine new pairs was made up of a 1965 adult male and an unbanded female. In each of three other pairs, an adult female marked in 1965 paired with a male hatched in 1965.

TERRITORIALITY

With the commencement of pair formation, territories began to be established. A territory consisted of the burrow and a certain amount of surrounding property and air space. It was established and maintained primarily by the male, although the female participated when the burrow itself was approached by an intruder. The burrow was well within the territory. The owls displayed territoriality only to other Burrowing Owls, although they defended the nest against other species. Territory was always considerably smaller than the home range used by the pair.

MAINTENANCE OF TERRITORY

Three methods of territorial defense employed by a defending male were apparent: primary song, the presentations of himself to the intruder, and physical contact. If, as is probably the case, primary song functions in the same manner whenever it is given (although it someitmes has the dual purpose of mate attraction), then it constitutes the major method of territorial establishment and maintenance.

To the human observer, the second method employed, that of the resident male presenting himself to the intruder, is by far the most subtle, for the birds are silent, and there is no obvious scuffle; yet on the basis of my observations, it is much more common than physical contact, although less important than primary song. The intruder usually, but not always, takes the hint and leaves.

Physical contact is rarely employed. Unusual circumstances which bring an intruder very close to the burrow (0–10 yards) elicit it. Even the female sometimes participated in driving away the intruder, but not as vigorously as the male.

In only one case was there sufficient interaction to determine the nature of the territorial boundary: it was not a precise line but rather a zone about 20 yards across. From meager evidence observed in other cases, it seemed that the boundary was located approximately equidistant between two burrows.

Territory was vigorously defended until fledging, after which defense assumed less importance. One male (see "An inexplicable case of nesting failure") exhibited territorial behavior throughout the non-breeding season.

The vertical space defended by an owl more or less corresponded to the defended surface area, but was not as scrupulously maintained.

TERRITORY SIZE

Since no pair was completely surrounded by other pairs, and most territorial activity consisted of primary song, territorial behavior at the boundary of two territories was seldom observed, and thus it was not possible to map a complete territory. Consequently, estimation of territory size is hazardous. As one approximation, the distances to surrounding burrows from a given burrow were measured, the average was found and divided by two (assuming the boundaries were in the middle), and this figure was used as the radius of a circle representing the territory. On this basis, six territories averaged 1.98 acres in size, with a range of 0.1–4.0 acres (table 4). Because virtually no territorial behavior was seen between pairs whose burrows were more than 150 yards apart, these were not included in the table. Mean territory size may therefore have been much larger than here indicated.

TABLE 4. Estimate of territory size of six pairs of Burrowing Owls.

Year	Burrow no.	Neighbor's burrow no.	Distance from neighbor (yd)	Territory size (acres)
1965	109	G2	130	2.8
1965	520	511	116.7	2.2
1966	109	214	55	1.6
		201	50	
1966	214	205	124.6	4.0
		109	55	
		201	58.3	
1966	G1	G8	20	0.6
		G7	40	
1966	G8	G1	10	0.1

The low figure in table 4 (0.1 acres) represents a pair whose nearest neighbor was only 20 yards away, and who had no neighbors on other sides. The second lowest figure (.06 acres) represents the nearest neighbor of the above pair. This second pair had a neighbor on another side. All three neighbors had other burrows from which to choose had they wanted to "hold" more territory.

PERMANENCE OF TERRITORIES

In general, it seemed that the stability of neighbors was more important than the absolute distance between pairs in determining stability of territories. Half of the pairs changed burrows one or more times in 1966. These changes, even within a pair's own territory, often made for adjustments in territorial boundaries.

SELECTION OF THE NEST SITE AND NEST BUILDING

Following pair formation some pairs were seen at only one burrow, while others were seen at more than one burrow before choosing one as the nest site. Burrow hunting was conducted at dusk and probably during the night. More than one burrow was visited, at least by some pairs, during an evening. It was not clear which member of the pair took the initiative on these investigations. A little nesting material was sometimes brought to a burrow before the pair moved to another. Males were seen carrying nesting material more than females.

By the first two weeks of April the owls had begun to gather the nesting material. In 1965 this consisted mostly of divots from the golf course. In 1966 there were several burrows containing large amounts of loose grass

from pheasant scratching sites, but many burrows still contained mostly divots. Occasional miscellaneous items such as gum wrappers were brought. Collection of nesting material dwindled in May, and ceased two to three weeks before the young emerged.

NESTING PERIOD

During the later stages of gathering nesting material, the females became highly secretive, virtually disappearing during laying and incubation. In 1966 disappearance occurred during the last week in April for most females. By the 32nd day thereafter, the females were seen again, and by a week later all the nesting material had been removed from the burrow. Young were not usually seen until about 10–14 days later.

The young of a given brood were of different sizes when they first emerged, which suggests that incubation commences with the laying of the first egg. Incubation is reported to last three weeks (Bendire 1892). That the female did not reappear until about four weeks after laying began indicates that she was incubating the eggs or brooding the hatched young. The female probably incubates most, if not all, of the night as well as the day. At one burrow she had not come off the nest by 23:00 on the nights observed, and several mornings she came out between 03:50 and 04:00, and returned 20 min later for the day.

Bendire asserts that the male as well as the female incubates. During this study no evidence was found to support his statement. On the contrary, that the male was nearly always available for observation strongly suggests that he did not incubate.

Removal of nesting material probably commences when the female again makes a diurnal appearance. The labor must occur at night, for no bird was seen transporting material. It certainly is removed, for in the one burrow dug out which contained young (dead), the tunnel and nest cavity were perfectly clean.

EMERGENCE OF THE YOUNG

For the present purposes, "nestlings" are considered young confined to the burrow entrance and immediate surroundings, and "fledglings" are young that are capable of short flights. The fledgling period is considered to end in September when the young have become independent of the adults. One burrow was closely observed 17 June–7 July 1965 in an attempt to obtain an accurate record of the feeding of nestlings. In 29 cases of the adults bringing food in which the female was distinguished from the male, 79 per cent occurred between 03:45 and 04:45. The few days on which observations were initiated before 03:45 indicated that little happened earlier. This and other sampling showed that the male brought most of the food, while the female helped distribute it.

When they first emerged from the burrow, the young stayed cautiously at the entrance. In about a week they were running about, flapping their wings, but not straying more than a few feet from the burrow. Four weeks from their emergence, they were flying quite well, although they remained within 50 yards of the burrow. They also began to forage independently, and the amount of food obtained must have been appreciable since the male brought much less than he had earlier.

TABLE 5. Productivity and mortality of the Burrowing Owls at the Oakland Airport, 1965–1966.

	1965	1966
Productivity		
No. breeding adults[a]	18	18
No. non-breeding adults[a]	3[b]	12[c]
No. young produced	40	31
Young/breeding adult	2.2	1.7
Young/adult	2.0	1.0
Mortality		
No. nestlings	7	7
No. fledglings	4	1
Sept.–April		
Juvenile	70%	
Adult	19%	
Total	35%	

[a] "Adults" included the young from the year before, since they bred the first year.
[b] I had taken a pair into the lab; when released, they formed part of the non-breeding population.
[c] One pair was constituted so that the unbanded female might have been the same as one which had "disappeared"; the minimum figure was taken.

REPRODUCTIVE PERFORMANCE

REPRODUCTIVE SUCCESS

Results pertaining to breeding success are given in table 5. Productivity was lower in 1966 than in 1965, despite a higher population of adults. There appeared to be an inverse relationship between the number of adults present on the study area in the spring and the number of young they eventually produced. The causes are no doubt complex, but seemed largely related to environmental conditions and to interactions among the birds themselves.

In 1965–66 the grass was two weeks later in sprouting than in 1964–65, and dried up more than a month earlier. Presumably the longer green season of 1964–65 was favorable for meadow vole and insect populations, but unfortunately these were not monitored.

Coupled with the length of the green season was the amount of shifting of burrows and mates. The 1964–65 population did relatively little shifting, and what was done had little effect upon neighbors, quite possibly since the pairs were fairly well separated. All pairs except one managed to hatch young. Two pairs were two weeks behind the majority due to burrow shifting, and one pair formed about 23 May was a month later than the majority in emergence of the young.

In 1966, 12 of the 30 birds failed to produce young. Territorial distribution was more clumped than in 1965, and any pair that changed burrows and/or mates tended to make their neighbors move also. They shifted around to such an extent that by the time the late pairs had formed they had wasted so much time in relation to the green season that nothing came of their efforts.

Thus, although a pair formed as late as 23 May in 1965 was able successfully to complete nesting, pairs formed earlier in 1966 (26 April, 1 May, and 20 May) were not able to do so.

Fledging success in 1965 was greater than in 1966, both in terms of numbers fledged (see table 5) and in per cent of pairs successful in fledging. In 1965, eight of nine pairs (88.8 per cent) attempting nesting were successful in fledging young. In 1966, eight of 15 pairs that attempted nesting hatched young. Of these, two burrows were destroyed by human activity and the young lost. The same pair that failed to fledge young in 1965 also failed in 1966; only remains of young were found. Thus, only five of 15 pairs (33.3 per cent) fledged young.

Four of the eight pairs that hatched young in 1966 had been together the year before; two other pairs were composed of a 1965 adult male and a female of unknown age; and in the remaining two, 1965 adult females paired with males that had hatched in 1965. By contrast, of the pairs failing to hatch young, only one had been together the year before. (The female of this pair disappeared in mid-season.) One pair came to the study area already mated (their history was unknown) and left as a pair. The remaining pairs contained at least one young of the 1965 season; these pairs accounted for much of the moving around. These data suggest that experience in living and in raising young, plus a stability both within the pair and in relation to the activities of other pairs, contributes to successful reproduction.

FOOD AS A LIMITING FACTOR

In order to test the possibility that food might be a limiting factor in the raising of young, two burrows were chosen and half-grown, dead, laboratory rats were placed on the mounds of the two burrows each two to three days. Six young were fledged from one burrow and seven dead young owls were recovered from the other. Productivity was 3.2 young per adult at these burrows, as compared with 2.2 for the population as a whole. This result is presently only suggestive. The procedure was not repeated in 1966 due to lack of rats.

NON-BREEDING POPULATION

The non-breeding population is here considered to include un-mated individuals and pairs that performed part of the courtship or nesting pattern but failed to lay eggs (or at least to incubate them).

The 1965 non-breeding population was 3/21, or 14.3 per cent, and that of 1966 was 12/30, or 40 per cent.

The three birds in 1965 had a relatively simple history. Two of them were caught as a pair on 16 March and held in captivity for observation. Upon their release on 27 April they immediately separated. The male remained in the area for the rest of the season. Within two days the female had replaced the unbanded female at a burrow about ½ mile away. Although this new pair engaged in extensive courtship, they did not bring nesting material, and did not nest.

The 1966 non-breeding population had a complicated history of burrow- and mate-shifting. Courtship activities continued until early June, and in some cases nesting material was brought, especially by pairs formed later than April.

In no year, 1964–67, were there any single females present on the study area, and in all three years there was a surplus of males. Such an imbalance could arise from differential mortality rates or from an imbalance at conception. Other avian populations exhibit imbalanced sex ratios (Mayr 1939).

RENESTING

No pairs renested after fledging young. In each of the seasons, 1965 and 1966, there were two possible cases of renesting after loss of eggs or nestlings.

AN INEXPLICABLE CASE OF NESTING FAILURE

One pair failed to rear young in all years. In 1965, their burrow was one to which the dead laboratory rats were brought. Events seemed to be proceeding normally in 1965, but seven dead owls were found at the burrow. It was thought that the parents may have

cannibalized the young since the two groups of remains which were recovered corresponded exactly with the two series of days on which rats were not left at the burrow. Why failure to leave rats might produce such a violent reaction is totally obscure. The adults made no attempt to renest.

By late March of 1966, courtship activity and other events seemed normal between the pair. However, on 23 and 24 March, when copulation occurred, the female was on top. Subsequently, copulation was normal. No such reverse copulations were observed in other pairs. In late May and early June feathers from young owl(s) were found at the burrow. No other evidence of mortality was recovered, but no young ever emerged from the burrow.

These events suggest something fundamentally wrong with one or both members of the pair and/or the pair bond. In 1967 this pair broke up and each had acquired a new mate by April. When observations were again made up in July, the male was no longer on the study area, and the female had acquired still another mate, but there were no young.

Other reports (Bent 1938; Robinson 1954) suggest that cannibalism occurs. Robinson saw four birds at the mound, one of which was feeding on a Burrowing Owl, which suggests that perhaps the victim was a member of the family group; neither the victim's age nor that of the live owls was mentioned.

MORTALITY AND SURVIVAL

MORTALITY FACTORS

The usual mortality factors of predations, starvation, diseases and parasites, and accidents presumably obtained in the owl population at the Oakland Airport. In addition, the plugging of burrows was a distinct possible cause of loss, especially of eggs and young. Whether such an event should be categorized as "accidental" is a moot point.

Starvation. The only two birds weighed in winter (February) weighed 198 g (a female) and 166 g (a male). Average weight for all birds was 170 g. If these weights were characteristic for the populations during the winter, then death by starvation at that time would seem remote.

Diseases and parasites. Diseases and parasites seemed to be insignificant in reducing the airport population, which declined from 54 in late summer 1965 to 30 in spring of 1966, and from 46 in late summer of 1966 to 33 in spring of 1967. In 1965 no parasites were found on owls, and all birds seemed healthy. However, in 1966 some birds carried a few lice, *Colpocephalum pectinatum.*

Fleas are mentioned frequently in the literature as common inhabitants of the burrows. The four owls trapped east of Livermore, Contra Costa County, California, each supported a large population of fleas. A sample of these fleas revealed 33 sticktight fleas, *Echidnophaga gallinacea*, and one human flea, *Pulex irritans.* Though diligently sought, not a single flea was discovered in owl burrows or on owls at the airport.

NESTLING AND FLEDGLING MORTALITY

In 1965, seven of 40 (18.0 per cent) young died as nestlings (table 5). They constituted one clutch whose remains were found at the burrow. A minimum figure for nestling mortality in 1966 was 23 per cent, and was probably higher, as one damaged burrow which probably contained young was not excavated. By comparison, Murie (1929) found a 50 per cent nestling mortality for Snowy Owls due to exposure. Watson (1957) found essentially no nestling mortality in the Snowy Owls he studied.

Surprisingly few young were lost as fledglings, four in 1965 and one in 1966. In 1965, three of the four died when their burrow was damaged. In each year the loss occurred well before the family group made its first change in burrow. Southern et al. (1954) also found a high survival rate during the fledgling period in the Tawny Owls they studied.

TOTAL MORTALITY

Due to the fact that the owls became so secretive during the winter, and perhaps may have moved temporarily from the study area, it was impossible to follow mortality during this time. By late April 1966 it was again possible to see the birds enough to make positive identifications. At that time 15 of the 21 adults of 1965 were present. Moreover, two birds that had been banded early in 1965 but had thereafter disappeared, were once again on the study area. Making the usual assumption that the number that immigrate into the population equals the number that emigrate, these two birds represent two adults on the study area in late August 1965, and thus 17 of the 21 adults were represented in April 1966.

Eight of the 27 banded young were still present in April 1966. Three young of unknown origin were added to the population by 1 September 1965, and in April one of these was still present. Thus nine of 30 banded young were accounted for.

From December 1965 to April 1966, seven

TABLE 6. Description of survivors of the 1965 young Burrowing Owls.

Home burrow no.	Survivor			Siblings		Breeding history 1966
	no.	sex	wt. (g)	$\bar{x}$ wt. (g)	range	
G2	LbWW	♀	168.2			late pair bond; no young
109	RWR	♂	165.5	151.5	162.5–141.3	late pair bond; no young
109	YLbLb	♂	162.5	152.3	165.5–141.3	early pair bond; 5 young; female was an adult in 1965
109	WWW	♂	155.7	154.0	165.5–141.3	disappeared in early Jan.; seen 28 Feb.–1 Mar., then not seen again
205	WRW	♂	156.5	149.6	156.2–143.0	did not pair
407	WWR	♂	160.4	153.9	156.5–152.4	seen sporadically until 19 Nov.; seen once 11 Mar.; not seen again
417	RWW	♂	144.6	144.8	148.2–141.4	normal pair bond; lost mate; paired again (late); no young
511	WLbW	♂	156.5	151.7		late pair bond; no young
901	WWDb	♂	158.5	157.4		recaptured 13 June 1966; not seen again; not looked for; young? (weight on 13 June was intermediate between that of a breeding and a non-breeding male)
?	ODbO	♂	169.2	175.5		normal pair bond; 6 young; female was an adult in 1965

unbanded birds which could not be placed in an age group were added to the population. Two came as a pair; four of the remaining five were females. It should be noted that since it was desirable to minimize disturbance to the population, only the pair and the single male were initially banded. The females did considerable moving around, and since they were indistinguishable, the most that can be said is that the maximum number of unbanded females at any one time was four, and that this was the case during most of the time from April to June.

Considering the sedentary nature of the adults on the study area, probably few of these seven additions to the population were adults in 1965. On the other hand, to consider them young suggests a large reservoir of owls outside the study area. Although there were at least two, and probably four pairs about ¾ mile away, these would probably not contribute so large a number of offspring (seven) to the study area. Another possibility is that some young may disperse a long distance, and that some or most of these seven represent birds which had come from distances of more than a mile. Also, three of the 1965 population remained unbanded. Undoubtedly a combination of the above possibilities accounts for the seven additions to the population of the study area; unfortunately, to categorize these birds is a precarious undertaking. Perhaps the most reasonable approach at this time is to arrive at a September 1965–April 1966 mortality figure (table 5) for adults ($100 \times 17/21 = 81$ per cent survival, or 19 per cent mortality), young ($100 \times 9/30 = 30$ per cent survival, or 70 per cent mortality), and overall, assuming the seven entering the population represent seven which left ($100\ [17 + 9 + 7] \div [21 + 30] = 65$ per cent survival, or 35 per cent mortality).

In 1967 the observation period consisted of only one week in April and one in July. It was thought that all birds on the study area were located and identified. Of the original 21 adults present in 1965, 17 were represented in April 1966 and 13 were present in April 1967, or 23.5 per cent mortality September 1966–April 1967. This figure agrees quite favorable with the 19 per cent mortality for the same group in 1965–1966, and suggests an age-constant mortality for adults. The owls studied by Olsson (1958) and Schifferli (1957) had adult mortality rates of 24 and 43 per cent, respectively. No account was found which indicated a first-year mortality rate as high as in the present study.

In spite of the fact that so many birds died, very little direct evidence was found as to cause of death.

SURVIVING YOUNG

Table 6 describes the survivors among the 1965 young, and gives a brief summary of the

survivors' performance in the 1966 breeding season.

Five of the nine survivors were the heaviest of their broods. One of these had two other surviving siblings, and these were the second and third heaviest of their group. The 109 clutch was the only one to have more than one survivor on the study area after 1 January 1966.

Only two survivors were not the heaviest of their group, or did not have heavier siblings represented as survivors. Both of these birds weighed, in fact, less than the average for their group. All others weighed more than the group average. Thus, on the study area, the heaviest siblings tended to be the survivors. Some of the surviving birds weighed only tenths of grams more than their non-surviving siblings. Why this small difference should confer an advantage upon the survivors is unclear.

DISPERSAL

Dispersal of young seemed to occur in two major "waves." As the family groups moved around, especially in September, a few young owls were seen outside their normal ground. Beginning in January with the commencement of calling and territorial behavior, another wave of dispersal occurred. Between September and January, dispersal was extremely difficult to follow, and the image of two dispersal periods may be an artifact of observation.

Eight 1965 young which survived on the study area, at least until 1 January 1966, traveled an average distance of 2075 ft from their home burrow. This figure, of course, ignores the birds that traveled outside the bounds of the study area and were not located. Of these eight, only one was a female. This, coupled with the fact that five of the seven new additions to the population in 1966 were females, suggests that females disperse farther than males. Their stimulus may be the calling males.

PLUMAGE AND MOLT

Newly hatched owls were not seen; Bent (1938) describes their plumage. During their first days of standing around on the mound the young birds had most of the juvenal plumage. During the following three weeks, rectrices and flight feathers grew, but the wing stripe remained (buffy middle secondary coverts). The bird remained in this plumage for a month to six weeks before the acquisition of adult plumage. During this time the lesser secondary coverts were growing and partially covering the middle secondary coverts. During the last two weeks of July the latter were molted, from innermost to outermost, and replaced with brown coverts, as in the adult.

At the same time, adult breast feathers began pushing through the creamy juvenal feathers, beginning at the upper part of the breast. In 1965 the young seen at a very early stage in mid-June had acquired plumage that seemed indistinguishable from that of the adults by early August.

This plumage was kept until early March, when at least a partial prenuptial molt occurred in both adults and young. Although contour feathers were found at the burrows, their new counterparts on captured birds were not apparent. It may be that loss of some of these feathers is one way for the males to become more lightly barred.

The postnuptial molt was complete. The non-breeding population began its molt in early June, and the breeding population began by mid-July. A pair trapped at that time showed differences in their molt pattern. The female had the entire row of greater primary and secondary coverts gone, with pinfeathers about one inch long coming in. Those over the third and fourth primaries were longest. The third and fourth primaries had molted and their replacements were nearly full-grown. Alula, tail, and contour feathers were still worn. The male had molted nothing except the alula, which was completely re-grown.

If there is a simultaneous molt of tail feathers, as suggested by Mayr and Mayr (1954), it was not apparent. Tail molting in captive birds was not simultaneous.

SUMMARY

A two year study of the Burrowing Owl was made at the Oakland Airport, Alameda County, California, on an area of about 150 acres. Most birds were color banded. Efforts were made to disturb the birds as little as possible.

Although Beechey ground squirrels provided most of the owls' burrows, one pair was seen digging a burrow, and sparse evidence suggests that a few others might have done so also.

The owls were primarily crepuscular and nocturnal, and returned to the burrow in the early morning. They went to the adjoining golf course at night. Although it was not determined if some owls migrated, many at least did not.

General habits, criteria for sexual dimorphism, and communications are discussed. Food habits were examined on the basis of pellet analysis, food items found at burrows, and food items seen carried by owls.

Pair formation began in December for 1966. Pairs that had been together the preceding year tended to retain their integrity. Males relied heavily on primary song in acquiring a mate.

Territory was established and maintained by the male, using primary song, the presentation of himself to intruders, and (rarely) physical contact. Territories within a season were permanent largely to the extent that the neighbors were permanent. An approximation of territory size was made. Territories were much smaller than home range.

During courtship, the pairs investigated several burrows for possible nesting sites. Nesting material consisted largely of divots from the golf course. Males were seen to bring most of the nesting material.

The females became secretive and remained inside the burrow for most of the period of laying and incubating. At this time nesting material was abundantly visible at the burrow entrance.

The males brought most of the food for the young, and the females helped distribute it. Two weeks to a month after the young emerged, the birds changed burrows. They usually remained together in a family group until September, sometimes changing burrows again.

In 1965, productivity was 2.2 young per breeding adult, or 2.0 per adult in the entire population. In 1966, the corresponding figures were 1.7 and 1.0. Reproductive success was largely dependent upon the length of the green season and upon the interactions among the birds themselves.

Juvenile mortality was 70 per cent September 1965–April 1966. For the same time interval, adult mortality was 19 per cent, and total mortality, 35 per cent. Surviving young tended to be the heaviest individuals of their brood. Females seemed to disperse farther than males.

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