PREDATION BY SHORT-EARED OWLS ON A SALICORNIA SALT MARSH

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THE Short-eared Owl (*Asio flammeus*) is a regular and common winter visitant to the San Francisco Bay region of California. It lives there in suitable habitat from August and September until about the first week in May. The winter populations of this owl leave in late April for northern or interior breeding grounds. Short-eared Owls may breed in the marshes around San Francisco Bay and elsewhere in the region (Grinnell and Wythe, 1927:85); however, none has been recorded doing so in recent years. All owls dealt with in this paper have been migrants or winter residents.

The study area was a part of San Pablo salt marsh, one mile north-northwest of Richmond, Contra Costa County, California. This marsh is a good example of a San Francisco Bay salt marsh (see Hinde, 1954); it is characterized by two plant associations. There is on low ground, subject to daily tidal coverage, the *Spartina* zone, characterized by extensive pure stands of *Spartina foliosa*. Short-eared Owls are uncommon in the *Spartina*. Higher ground is covered by the *Salicornia* association (Fig. 1). The dominant plants of this zone are *Salicornia ambigua*, *Grindelia cuneifolia*, and *Distichlis spicata*. *Grindelia* is a woody perennial growing along the tidal creeks, or sloughs, on the more elevated parts of the marsh. All the dominants of this zone may be found in the lower zone wherever the elevated slough banks produce higher marsh conditions. Other important plants of this association are *Frankenia grandifolia*, *Jaumea carnosa*, *Limonium commune*, *Triglochin maritima*, *Cuscuta salina*, and *Achillea millefolium*. It is in this area of the marsh that Short-eared Owls find conditions most suitable for foraging and concealment.

On the upper portion of the marsh where the tidal sloughs branch in intricate patterns the densest and tallest vegetation on San Pablo marsh is found. This is composed mainly of leafed-out *Grindelia*, but there is a varying admixture of *Distichlis* and *Salicornia*; the height reached is two to four feet. Short-eared Owls find roosting cover in daylight hours in these tangles, especially when there is stranded driftwood amongst the plants. Less frequently the owls are found in small, irregularly-shaped openings in the *Salicornia* mat or within clumps of arrowgrass (*Triglochin maritima*). Individuals of this plant commonly grow grouped in a ring shape and the owls easily find concealment within these clumps, in spite of the fact that the clumps are surrounded for tens of feet by pure *Salicornia* that is usually only about six inches high.

FIG. 1. A tidal slough on San Pablo salt marsh. The slough is about 25 feet wide. In the center foreground *Spartina* is evident; along the slough banks grows *Grindelia*; the remainder of the vegetation is almost wholly *Salicornia*.

Numbers of the owls.—A trustworthy method of counting these birds was not developed. The behavior of the owls in the presence of an observer was highly unpredictable. They would not necessarily flush when an observer was as close as 20 yards from them. Those that did flew variously 50 to 500 yards. It was not always possible to determine the exact spot on the marsh where the birds alighted because the marsh is flat and diagnostic landmarks uncommon. Thus, when an owl was flushed, frequently it was difficult to know whether or not it had already been counted.

The best count of owls was made on December 26, 1951, when an extremely high tide covered everything on the marsh except the topmost six to ten inches of *Grindelia* branches and pieces of wood and other flotsam. The fauna of the marsh was pushed up to these dry posts and consequently was generally ill-concealed. Under these conditions the owls foraged conspicuously up and down the *Grindelia* rows. Normally the owls are nighttime feeders in this area, but during the high tides they spent a large amount of time in the air in daylight foraging. When they alighted, they were still

exposed to view on emergent posts and floating timbers. Four, and possibly five, owls were visible simultaneously at 11:30 a.m. on the day mentioned. Sibley (1955) recorded ten Short-eared Owls during a two-mile walk along a levee in salt marshes near Alviso, at the southern end of San Francisco Bay, under similar tidal conditions. Thus, since I had about 150 acres under observation, I saw possibly only half of the owls that were present on that day. The number of owls on San Pablo salt marsh in the winter may be taken at no less than four or five and probably no higher than eight or ten.

This broad estimate may well apply to all years of the study, since there is no evidence that 1951 was any different from the subsequent years with regard to the number of Short-eared Owls on the marsh. At the beginning and end of the winter period the density of owls is definitely less than that reached in midwinter.

Feeding Relationships

Foraging behavior.—My best observations on foraging behavior were made in daylight hours during high tides, as has been indicated. Yet the owls here are nocturnal foragers in the main, and my observations may not be wholly representative. The most common foraging method used is harrying flight. Harrying flight is effected by flying slowly along the course of a tidal slough and is punctuated by sudden drops to the level of the vegetation or ground surface after prey or to alight. Also, the owls occasionally sally forth after prey from their roosting places, or, more usually, from higher prominences.

The owls become active foragers about a half-hour before sunset, or somewhat earlier on overcast days. I do not know how much of the night is spent foraging, but it is unlikely that these birds differ much from other nocturnally-foraging Short-eared Owls in this respect. Normally they cease feeding by one hour after sunrise at most. Twice I have disturbed owls in the act of eating Dowitchers (*Limnodromus griseus*) in the middle of the afternoon, two and three hours before sunset.

A possible explanation for the almost complete absence of daytime feeding in this species that is known to hunt in the daytime as a rule on its breeding grounds and in certain parts of its winter range (Errington, 1932:178) is that gulls flock around the owls and mob them in flight. Species known to fly at the owls are the Glaucous-winged Gull (*Larus glaucescens*) and Ring-billed Gull (*L. delawarensis*); other gulls also participate. When attacked by the gulls, the owls invariably increase their flying altitude. The reasons for this seem obscure, for the extra altitude is not used by the owls for aerial maneuvers. I never saw a gull actually strike an owl; either the gulls

were content merely to come close, or the erratic, bouncy flight of the owls served to throw the gulls off course. But, there is no question that the owls were disturbed by the gulls.

Pitelka, Tomich, and Treichel (1955:112) reported that territorial Pomarine Jaegers (*Stercorarius pomarinus*) harried Short-eared Owls on the breeding grounds near Barrow, Alaska. The chasing was so severe that these observers were not certain just when the owls found time to forage unmolested, but they thought it was probably in the twilight hours when the jaegers possibly were not as alert as in the full light of day. Certainly the situation on San Pablo marsh is not as critical to the owls, and there is no territoriality involved, but it is worthy of note that daytime foraging of owls is absent and harrying by gulls occurs.

Prey items.—Although there is a good-sized literature on the food of Short-eared Owls in the breeding season (for example, Pitelka, Tomich, and Treichel, 1955; Errington, 1937) little information is available on their food in the winter in North America. Fisher (1893), Cahn and Kemp (1930), Errington (1932), and Tomkins (1936) report the largest winter samples of food items; Huey's (1926) report is the only one listed in Bent (1938) for western North America. It is, coincidentally, for a salt marsh locality but involves only two pellets.

On San Pablo salt marsh I picked up pellets of Short-eared Owls at irregular times and stations within an area of about 200 acres. No definite pattern was followed in picking up the pellets because the owls had no preferred casting spots and dropped pellets at random stations throughout the marsh. This made it difficult to get dates for most of the pellets. In the one instance of finding a true casting station only 32 pellets were found and these spanned a period in time of about three months.

A mammal was counted as occurring only on the basis of a skull; this avoided the possibility of duplication of individuals. Therefore, this count presents a minimum occurrence for the mammalian remains. In the case of birds, and especially small birds, occurrence of many bones and feathers in a pellet was taken to represent at least one bird, whether or not the skull was present. In point of fact, but one bird skull was found; the Short-eared Owl chops and mangles all of a bird's head except the bill, which it does not necessarily ingest. If an isolated long bone or a few feathers occurred in a pellet, the dominant remains in which were mammalian, no count was made of them. Any occurrence of insect hard parts was taken to represent one, or more, insect(s). From this it will be seen that a maximum occurrence of birds and insects is indicated in the tabulation, contrary to the situation in the mammals.

TABLE 1

FOOD ITEMS FOUND IN PELLETS OF THE SHORT-EARED OWL ON SAN PABLO SALT MARSH

	Absolute Occurrence	Frequency in per cent				
		1952	1953	1954	1955	Total
Microtus californicus	272	56.1	44.8	37.0	33.6	42.9
Rattus norvegicus	116	7.2	16.7	20.5	27.3	18.0
Reithrodontomys raviventris	56	8.4	7.0	11.5	6.9	8.6
Mus musculus	40	8.4	3.5	6.5	5.7	6.1
Sorex vagrans	17	6.1	2.6	1.0	1.3	2.6
Thomomys bottae	6	4.0	—	—	—	0.9
Scapanus latimanus	1	0.7	—	—	—	0.2
Mammals: total	508	90.9	74.6	76.5	74.9	79.8
Erolia-Ereunetes	21	1.0	6.2	4.5	3.8	3.2
Unidentified birds	17	—	3.5	4.5	1.3	2.6
Sturnella neglecta	15	1.0	0.9	3.0	3.8	2.2
Erolia minutilla	12	3.0	—	1.5	1.9	1.8
Passerculus sandwichensis	9	—	2.5	1.0	1.9	1.4
Ereunetes mauri	6	0.7	—	1.0	1.9	0.9
Erolia alpina	6	—	—	0.5	3.2	0.9
Limnodromus griseus	5	—	1.7	—	1.3	0.8
Melospiza melodia	4	—	0.9	1.5	—	0.6
Rallus longirostris	3	—	—	0.5	1.3	0.5
Anthus spinoletta	1	—	—	0.5	—	0.2
Pooecetes gramineus	1	0.7	--	—	—	0.2
Passerella iliaca	1	—	—	0.5	—	0.2
Birds: total	101	6.4	15.7	19.0	20.6	15.5
Stenopelmatus (sand-cricket)	28	2.0	8.8	4.5	3.8	4.7
Unidentified insects	3	0.7	0.9	—	0.7	0.5
Total	638	100.0	100.0	100.0	100.0	100.0

Table 1 presents the list of the occurrence of all the species and groups identified from the pellets. The gross breakdown shows about 75 per cent of the items to be mammals, 20 per cent birds, and 5 per cent insects. This is only a crude indication of the various groups as to their importance to owls as food, for the relative masses involved place the mammals as responsible for about 85 to 90 per cent of the food of the owls. Most of the mammals, and presumably also the birds, in the pellets were subadults, but this is true of most free-living populations of vertebrate animals in the period September to April.

In the discussion of the prey species, which follows immediately, I have attempted to indicate something of the relative numbers of the wild populations that are involved. I have relied on the number of occupied nests as

the major indication of mammal numbers; this type of information was gathered primarily in the spring, not in the early winter. With this as an index, none of the mammals on which I could gather data appeared to fluctuate in numbers. Probably it would be more realistic to say that the fluctuations that did occur were not large enough to be detected by my relatively crude techniques. As Table 1 shows, there were some important shifts in the occurrence of the mammals as prey items in the pellets from year to year. I would say that these shifts in occurrence reflect changes in population density possibly of similar direction and size.

As for the birds, they can be counted directly, especially in the breeding season, or otherwise simply dealt with. It has been possible to list their occurrence on the marsh as populations with some accuracy. This good fortune actually means little; in the first place, the incidence in the pellets of any one bird or group of birds is so slight that their fluctuations have little importance to the diet of the owls (see Table 1). In the second place, the density of the resident birds (mainly Song Sparrows) varies little (Johnston, MS), so that the owls have about the same number to choose from always. I cannot speak with the same assurance about the migrants.

The California vole (*Microtus californicus*) is the most numerous prey species found in the pellets. In 1952 it was also the most important animal to the owls in point of food mass furnished. In 1953, 1954, and 1955 the Norway rat (*Rattus norvegicus*) furnished the greatest bulk. The reduction of *Microtus* in the pellet samples after 1952 seems a significant trend in spite of the fact that the number of nests and fresh cuttings of the vole indicated a steady level of population density; probably there was a real drop in density. It should be noted that there may be some as yet undemonstrated relationship between the drop in *Microtus* and the rise in *Rattus* in the pellets.

Further, the incidence of *Microtus* in the pellets does not indicate this population to follow the regular and periodic fluctuations in density that have been described for microtines elsewhere. It is probable that *M. californicus* only three to four miles distant in the headwaters of Wildcat Creek shows the classic four year cycle (Robert Hoffmann, MS), yet the present data show a "high" in 1952 and a decrease every year since that time. 1955 should have been "high" again if this population were to parallel the classic cycle.

The Norway rat showed a steady rise in incidence of occurrence in the pellets. It remained, at its highest, second to *Microtus* in numbers, but was responsible for most of the food eaten by the owls. Since the rat lives successfully in the wild state on the marsh, and its numbers are constantly augmented by ingress of individuals from the nearby Richmond city dump,

it would be thought that its numbers would remain relatively constant. This is not true; at least, a four-fold increase in occurrence in the pellets seems to indicate a related increase in population density.

The occurrence of the other mammals in the pellets does not indicate annual variation in numbers. Possibly the numbers of shrews (*Sorex vagrans*) fluctuate, but the sample sizes are basically too small to make certain. However, there is little doubt that the salt marsh harvest mouse (*Reithrodontomys raviventris*) and the house mouse (*Mus musculus*) were taken by the owls at a steady rate.

The pocket gopher (*Thomomys bottae*) and the western mole (*Scapanus latimanus*) are not residents of San Pablo salt marsh but they occur nearby in cultivated fields and along San Pablo and Wildcat creeks, which flow through the marsh. The low incidence and sporadic occurrence of these mammals show that they are not important to the Short-eared Owls of San Pablo salt marsh.

About seven and one-half per cent of the items taken were migrant, charadriiform birds, and some four and one-half per cent were resident birds, mainly passerines. Within the limits of a small sample I consider these frequencies to be practically equivalent with one another. If it is borne in mind that, although the shorebirds at their peak density outnumber passerines by at times over 10 to 1, the shorebirds are transient and are never for long at a maximum density, then the practical equivalence of occurrence between them and the passerines seems reasonable. Table 2

TABLE 2

ESTIMATED NUMBERS OF RESIDENT AND MIGRANT BIRDS ON SAN PABLO SALT MARSH IN MIDWINTER[1]

RESIDENT BIRDS	
Clapper Rail, *Rallus longirostris*	about 30
Marsh Wren, *Telmatodytes palustris*	about 30
Western Meadowlark, *Sturnella neglecta*	possibly 50
Savannah Sparrow, *Passerculus sandwichensis*	about 150
Song Sparrow, *Melospiza melodia*	very near 450
Total	710
MIGRANT BIRDS	
Short-billed Dowitcher, *Limnodromus griseus*	up to 1000
Western Sandpiper, *Ereunetes mauri*	up to 1000
Red-backed Sandpiper, *Erolia alpina*	up to 1500
Least Sandpiper, *Erolia minutilla*	up to 5000
Total	8500

[1]The resident birds occupy about 200 acres; the migrants use this and in addition 500 to 1000 acres of intertidal mudflat.

presents a rough estimate of the density of these two groups of birds on 200 acres of salt marsh.

For the resident birds I arrived at the figures in the following manner: I know there are about 150 pairs of Song Sparrows in the breeding season and that these will produce about four fledglings per pair to make a total of about 900 birds at the late spring maximum. Of these, about 450 ought to be available to the owls in mid-December. Winter estimates (Table 2) based on 50 breeding pairs of Savannah Sparrows, 10 pairs of Clapper Rails, and 10 pairs of Marsh Wrens are 150, 30, and 30 individuals, respectively. About 50 Western Meadowlarks should be added to make a total of 710 birds. Earlier in the season there would be more, later in the season fewer, birds.

The migrant shorebirds occur sometimes in numbers as large as I have indicated, but I think usually the occurrence would be somewhat less. Certainly one-quarter to one-half of my estimate of 8500 would be a conservative indication of mean occurrence. These relatively vast numbers probably adequately account for the number of individuals taken by the owls. But, it must be remembered that on San Pablo marsh the Short-eared Owl is a nocturnal feeder; accordingly, it would be the roosting shorebirds on the high marsh that would be prey for the owls, and presumably these birds would be easy to catch. Therefore, it seems a little unusual that more were not taken. Perhaps this is further evidence of the already known preference of the Short-eared Owl for small mammals as food.

It should be mentioned that the Western Meadowlark does not live on the marsh but large numbers of them every day venture far out on the marsh in foraging. The Fox Sparrow (*Passerella iliaca*) probably was taken along the nearby Wildcat Creek. All other birds found in the pellets occur normally on the marsh, either as residents or migrants.

Relationships of Short-eared Owls to the Community

An accurate perspective on the impress made by the predation of an owl population can be gotten only through placing this predation properly in the setting of the community. The Short-eared Owl is influenced by the population dynamics, movements, and indeed the mere presence of virtually every animal species on the marsh. Many of the animal interrelationships are subtle, and some are doubtless yet unsuspected. My information on community interaction is almost wholly restricted to that relating to the food situation. The food relationships outlined in Figure 2 are those that I have become aware of in the course of studies on the population ecology of the Song Sparrow. Thus, except for the owl pellet samples and counts of resident birds, the details of the pyramidal structure of the community are purely qualitative. Fortunately, this community is a simple one and

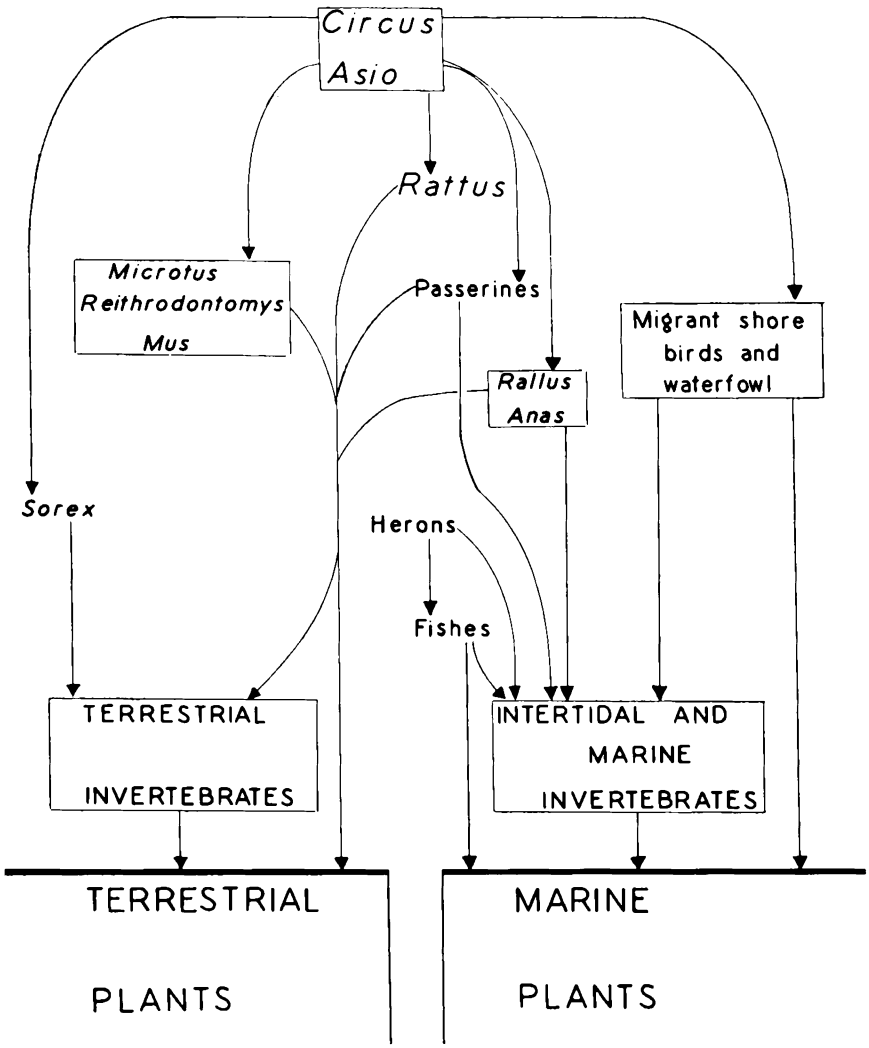

FIG. 2. The food web in winter on a *Salicornia* salt marsh.

the available information indicates the generalization represented by Figure 2 to be valid in all respects.

Several of the groups deserve comment and listing of the animals included. The groups are considered in order as they increase in total number of individuals.

Predators.—The Short-eared Owl has been discussed. Of the hawks only the Marsh Hawk (*Circus cyaneus*) was resident and of major importance.

One pair nested in a nearby *Spartina* area, producing two to four young each year. The winter population numbered four to six individuals.

Other hawks that hunted on the marsh were the Peregrine Falcon (*Falco peregrinus*) and the Merlin (*F. columbarius*). These two were seen but rarely. More commonly seen were the Sparrow Hawk (*F. sparverius*), Red-tailed Hawk (*Buteo jamaicensis*), and Sharp-shinned Hawk (*Accipiter striatus*); but these three were never seen to hunt on the marsh.

Four herons hunted on the marsh. The Common Egret (*Casmerodius albus*) and the Great Blue Heron (*Ardea herodias*) were the most important; the Black-crowned Night Heron (*Nycticorax nycticorax*) and the Snowy Egret (*Leucophoyx thula*) were less abundant and were present only in the late winter and spring. Probably some rodents were taken by these herons.

The Norway rat is the only mammalian predator of any importance on the marsh. It is known that the rat takes eggs and young of the Mallard (*Anas platyrhynchos*), Clapper Rail, Savannah Sparrow, and Song Sparrow. Probably it preys also on the young of the other, smaller mammals.

Secondary consumers.—This group includes those animals that stand in an intermediate position in the predator-food resource sequence. The box labeled, "Rallus/Anas" refers to the Clapper Rail and the Mallard; there are two pairs of nesting Mallards on the marsh.

Passerine birds may be broken down into two groups, as per the following lists:

Resident	Winter visitant
Telmatodytes palustris	*Anthus spinoletta*
Sturnella neglecta	*Pooecetes gramineus*
Passerculus sandwichensis	*Passerella iliaca*
Melospiza melodia	*Dendroica auduboni*
	Geothlypis trichas

Migrant shorebirds and waterfowl make up the bulk of the marsh avifauna during the winter period. In the following lists those species of most importance on the marsh are marked with an asterisk. All records are based on sight identification made in the field.

Waterfowl

Branta canadensis	*Aythya americana*
Branta bernicla	*Aythya marila*
Chen hyperborea	**Aythya affinis*
Anas platyrhynchos	*Bucephala clangula*
Anas carolinensis	*Oxyura jamaicensis*
**Anas acuta*	*Mergus serrator*
Mareca americana	**Fulica americana*
Aythya valisineria	

Shorebirds

**Squatarola squatarola*	*Capella gallinago*
Charadrius vociferus	*Crocethia alba*
Numenius phaeopus	**Ereunetes mauri*
Numenius americanus	**Erolia minutilla*
Limosa fedoa	**Erolia alpina*
Totanus flavipes	*Recurvirostra americana*
**Catoptrophorus semipalmatus*	*Lobipes lobatus*
**Limnodromus griseus*	

Of the fishes only the three-spined stickleback (*Gasterosteus aculeatus*) was found to be a permanent inhabitant of the creeks and ponds of the marsh. Utilizing the tidal creeks as foraging grounds during periods of high water, and occasionally becoming stranded when the water level dropped were the following species: northern anchovy (*Engraulis mordax*), jack smelt (*Atherinopsis californiensis*), top smelt (*Atherinops affinis*), and staghorn sculpin (*Leptocottus armatus*). The striped bass (*Roccus saxatilis*) probably also should be included in this list, but I did not find it; it would prey on shrimps and smaller fishes.

Terrestrial invertebrates.—This list is far from complete; many additions could be made, most probably among the insects.

Amphipoda	Insecta
Isopoda	Coleoptera
Arachnida	Lepidoptera
	Diptera

Intertidal and marine invertebrates.—Insects are here included by virtue of those species that live part of their lives in the quiet waters of ponds and occluded oxbows; the water in these sometimes is highly saline, due to evaporation.

Nemertea	Insecta
Polychaeta: Nereidae	Dysticidae
Ostracoda	Notonectidae
Copepoda	Diptera
Isopoda	Aspidobranchia
Amphipoda	Pectinibranchia
Decapoda	Filibranchia

The relationships diagrammed in Figure 2 hold only for the fall and spring months, when all the animals indicated would be present on the marsh. Especially in the summer the relationships would be markedly different. As an example, the insects are extremely abundant and the waterfowl and shorebirds are practically absent in summer. Actually, almost all the larger and conspicuous birds use other areas for breeding; the Short-eared Owl and the herons are included here. Thus, the fullest expression

of the relationships subsumed by the intertidal and salt marsh food web and pyramid of numbers is reached in the fall-to-spring period, for which Figure 2 is valid.

Summary

The Short-eared Owl is a common winter visitant to the salt marshes around San Francisco Bay. Between four and ten owls live in the winter on the study plot of some 200 acres on San Pablo salt marsh. The owls forage mainly at night there. Of 638 items found in pellets, 75 per cent were mammals, 20 per cent birds, and 5 per cent insects. Mammals were responsible for about 90 per cent of the mass consumed, *Microtus* and *Rattus* being the most important kinds. The relationship of Short-eared Owl predation to the community food web is indicated by means of a diagram.

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