Cooperative feeding interactions involving two or more avian predators have been described for a number of species (Christman, Condor 59:343, 1957; Parks and Bressler, Auk 80:198, 1963; Meyerriecks and Nellis, Wilson Bull. 79:236, 1967; Dusi, Auk 85:129, 1968; Emlen and Ambrose, Auk 87:164–165, 1970; Haverschmit, Wilson Bull. 82:99, 1970; Mueller et al., Auk 89:190, 1972; Anderson, Wilson Bull. 86:462, 1974); however, only one account of a cooperative feeding interaction between an avian predator and a mammalian predator is given in the literature. Welty (*The Life of Birds*, W. B. Saunders Co., Philadelphia, 1975:396) described a cooperative feeding interaction which involved a Rough-legged Hawk (*Buteo lagopus*) that fed upon rodents dislodged by a hunting Arctic fox (*Alopex lagopus*).

The tendency for birds to follow mammalian predators in a situation which does not involve nest site defense has been reported for several avian predator species. Berger (Auk 73:288, 1956) gave an account of a Marsh Hawk pursuing a domestic cat (*Felis domestica*). A pair of Mountain Choughs (*Pyrrhocorax graculus*) were reported by Lane (Ibis 99:116, 1957) to follow a hunting stoat (*Mustela erminea*). Holland (Br. Birds 67: 212–213, 1974) observed an attraction and following tendency among Long-eared Owls (*Asio otus*) for a dachshund (*Canis familiaris*). Therefore, the tendency to follow mammalian predators may exist independently of the cooperative feeding phenomenon among Marsh Hawks and other avian predators. However, the tendency also could serve as the behavioral basis for cooperative feeding between avian and mammalian predators when the opportunity arises.—LeRoy W. Bandy and Barbara Bandy, *Rt. 1, Box 75, Stetson, Maine 04488.* *Accepted 4 March 1977.*

Predation ecology of coexistng Great Horned and Barn owls.—Food habits of the Great Horned Owl (*Bubo virginianus*) and the Barn Owl (*Tyto alba*) are well studied (e.g., Wilson, Auk 55:187–197, 1938; Graber, Condor 64:473–487, 1962), but an emphasis on feeding ecology and niche segregation is fairly recent (Marti, Condor 76:45–61, 1974). This paper details some of the mechanisms facilitating coexistence of these owls during the summer at Tule Lake National Wildlife Refuge, Siskiyou County, California.

Methods.—Observations extended from 17 June to 12 July 1975. Of the 107 km^2 study area, about half consisted of open water; the remainder included the eastern slope of a large ridge where both owl species roosted on rock cliffs, a region of natural vegetation along the base of the ridge, and agricultural fields to the east. The onset of owl activity at 2 rock cliffs (northern and southern, 5.3 km apart) was recorded on alternate evenings. Small rodents were trapped and tethered (with brass wire wrapped at the base of the tail) on 2 dirt roads, 1 with telephone poles and 1 without, to test the importance of high perches in the hunting patterns of the owls. Identity of predators was determined either from direct observation with a night scope or observation of wing marks and footprints around the kill. Kills of questionable identity were excluded. The presence of car and observer did not constitute a new or unusual feature at either site, since parked farm equipment is common along the roads. Habitat preferences and hunting patterns were studied by driving through the area in a non-systematic pattern between 22:00 and 04:00 PDT. Twenty-six h of these observations were recorded over 17 nights.

Pellets were used to determine food habits and were collected at weekly intervals at known owl roosts. Barn and Great Horned owl pellets were separated on the basis of size, shape, firmness, and exact location of collection, as suggested by Moon (Trans. Kans. Acad. Sci. 43:457–466, 1940); those of questionable origin were discarded.

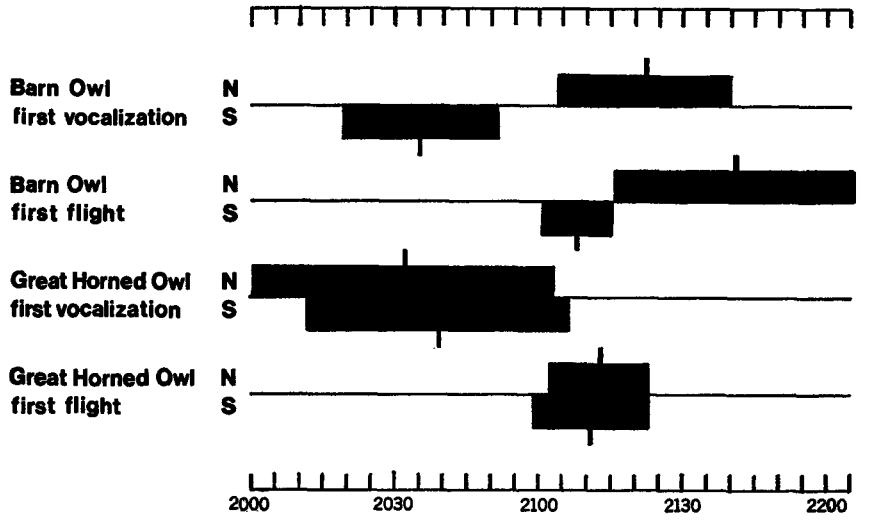

FIG. 1. Activity onset in Great Horned Owls and Barn Owls roosting on 2 cliffs at Tule Lake National Wildlife Refuge, measured by initial vocalization and initial flight from the cliff. Vertical line = mean, horizontal bar = 95% confidence limits of the mean, top bar = northern cliff, bottom bar = southern cliff.

Statistical tests follow those described by Snedecor and Cochran (Statistical Methods, Iowa State Univ. Press, Ames, 1967).

Food habits.—I analyzed 250 whole pellets and numerous pellet fragments containing 1003 prey items. Great Horned Owls averaged 3.83 and Barn Owls 2.42 prey items/pellet. A significant difference existed between proportions of different prey taken by the 2 species ($\chi^2 = 13.41$, df = 2, $P < 0.005$), although extensive overlap was evident (Table 1).

Activity at roosting sites.—Four Great Horned Owls were resident at each of the 2 cliffs; Barn Owls numbered 25 at the southern cliff while 5 was the maximum heard at any one time at the northern cliff. Initial vocalization and initial flight from the roost were recorded as indicators of activity onset. Great Horned Owl activity onset, though somewhat variable with respect to time (Fig. 1), was not significantly different at the 2 cliffs for initial vocalization (2-tailed t-test, $t = 0.311$, $P > 0.60$) or initial flight ($t = 0.338$, $P > 0.60$). Barn Owl activity, however, began significantly later at the northern than at the southern cliff (Fig. 1) for initial vocalization ($t = 4.684$, $P < 0.001$) and for initial flight ($t = 4.845$, $P < 0.001$). Although data were limited, Barn Owls also appeared to return to the roost earlier than Great Horned Owls over 4 mornings of observation. Generally they had left exposed perches for more protected roosts and their vocalization level had dropped noticeably by the time Great Horned Owls arrived at the cliffs.

Roosting sites of individual owls were divided into 3 categories based on extent of exposure. Barn Owls chose less exposed roosts significantly more often than Great Horned Owls ($\chi^2 = 13.20$, df = 2, $P < 0.005$). Barn Owls typically roosted far back in protected crevices or in deep holes where they were invisible from the road, while Great Horned Owls perched on exposed rocks or ledges, or in large open holes.

TABLE 1

PREY ITEMS IDENTIFIED IN OWL PELLETS COLLECTED AT KNOWN OWL ROOSTS WITHIN THE STUDY AREA[1]

Prey species	Great Horned Owl		Barn Owl	
	Number of items	Percent of total	Number of items	Percent of total
Microtus	404	66.7	241	60.6
Peromyscus	167	27.6	147	36.9
Dipodomys	7	1.1	3	0.8
Sylvilagus	2	0.3	1	0.2
Euphagus cyanocephalus	2	0.3	0	0
Sorex	1	0.2	1	0.2
Tadarida brasiliensis	1	0.2	0	0
Mustela frenata	1	0.2	0	0
Unidentified bird	8	1.4	2	0.5
Unidentified small mammal	4	0.7	0	0
Insect	8	1.3	3	0.8

[1] Includes 107 Great Horned Owl pellets, 143 Barn Owl pellets, and numerous pellet fragments from both species.

Direct interspecific interactions were observed only twice; these consisted of single Barn Owls harrying or diving at single Great Horned Owls at the southern cliff. Indirect interactions occurred on at least 8 occasions when either the arrival of a Great Horned Owl at one of the cliffs or the beginning of its vocalizations was accompanied by a decline or brief cessation in Barn Owl activity and vocalizations. In addition, remains of at least 4 Barn Owls were found near the southern cliff under perches used by Great Horned Owls. Thus not only competitive interactions, but also predator-prey interactions were occurring.

Hunting behavior.—Twelve kills of tethered prey were observed on the road having telephone poles; of these, 8 were by Great Horned Owls and 4 by Barn Owls. All 6 kills occurring on the road without poles were by Barn Owls. The difference between numbers of kills by the 2 species at the 2 sites was significant (χ^2 corrected for continuity $= 4.640$, $df = 1$, $P < 0.05$), with Great Horned Owls favoring the road having telephone poles.

Great Horned Owls made extensive use of telephone poles and to a lesser extent other perches, while Barn Owls spent more time on lower perches, on the ground, or in flight (Table 2). This necessarily limited the hunting habitat used by the larger species: Great Horned Owls were never sighted in areas where perches were not present. Barn Owls showed a more uniform distribution throughout the area, although few were sighted along the road at the base of the cliffs where the majority of Great Horned Owl sightings were concentrated.

Search and attack behavior also varied between the species. Generally, Great Horned Owls moved regularly and directly from one telephone pole to the next along a road, spending from 1 to 59 min on a pole ($\bar{x} = 7.3$, $n = 38$). When prey was sighted, a steep downward flight was made, with the owl sometimes banking just before landing. Usually the wings were flapped briefly on landing, after which no movement was seen for a period of ½ to 3 min until the owl took off again, flying directly up to one of the poles nearby. Great Horned Owls were most often observed hunting alone, although groups of 2 or 3 owls

TABLE 2

RECORD OF BARN OWLS AND GREAT HORNED OWLS SIGHTED DURING 26 H SPENT DRIVING THROUGH THE STUDY AREA BETWEEN 22:00 AND 04:00[1]

	Great Horned Owl	Barn Owl
In flight	1	13
On perches:		
Telephone poles	30	2
Signposts	7	11
Ground	3	17
Other	3	5
Total	44	48

[1] Observations before 22:00 or after 04:00 were excluded so that owls emerging from roosts or returning in the morning would not bias data.

were twice seen moving from pole to pole together. In both cases vocalizations occurred almost continuously between members of the group.

Barn Owls hunted primarily on the wing and occasionally from low perches. Hunting flight was usually low, with a quick erratic wingbeat or, less frequently, a fast direct flap, as described by Wilson (1938). This species was most often observed flying along irrigation channels or over strips of natural vegetation on the levee paralleling the road. Sudden steep banking drops into the vegetation were common, and owls often emerged several seconds later when unsuccessful.

Discussion.—Differences in hunting methods and habitat preferences result in reduced spatial overlap, giving Barn Owls access to areas not normally used by Great Horned Owls. These differences in hunting habits are probably physically based: the smaller size and lighter wing loading of the Barn Owl may make hunting on the wing profitable in spite of the energy expenditure, while the larger Great Horned Owl with its heavier wing loading may be constrained to hunting primarily from perches (Earhart and Johnson, Condor 72:251–264, 1970; Marti 1974).

Balancing this is the interactive dominance of the Great Horned Owl and its status as a potential predator on the smaller owl. Inhibition of Barn Owl activity by Great Horned Owl arrivals at the cliffs, a lack of Barn Owl sightings where Great Horned Owl sightings were concentrated, and remains of Barn Owls found below Great Horned Owl perches all point to the importance of this interaction. The selection of protected roosting sites by Barn Owls is consistent with this, as is the delayed Barn Owl activity onset at the northern cliff where Barn Owls were much less numerous and Great Horned Owl activity was more prolonged and conspicuous.

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