RAPTOR PREDATION ON WINTERING SHOREBIRDS

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Although high mortality rates have been demonstrated for shorebirds by the analysis of band recoveries and studies of marked birds (Martin-Löf 1961; Boyd 1962; Holmes 1966; Soikelli 1970), there is little information on the causes of shorebird mortality. Goss-Custard (1970) theorized that flocking by some shorebirds on the wintering grounds is a protective response against avian predators. However, there exists no information demonstrating the extent to which raptors affect wintering shorebird populations. Consequently, it was our purpose in this study to examine in detail the relationship between raptors and shorebirds and determine the impact of the raptors on the size of winter shorebird populations. Although the raptors we studied were mainly the Merlin (*Falco columbarius*) and Short-eared Owl (*Asio flammeus*) and the shorebirds were mainly the Dunlin (*Calidris alpina*) and Least Sandpiper (*Calidris minutilla*), we have described all the raptor-shorebird interactions that we saw. The study was conducted during the winters of 1971–72 and 1972–73 on Bolinas Lagoon, Marin County, California.

STUDY AREA

Bolinas Lagoon is a 570-ha estuary at the southern edge of Point Reyes Peninsula on the central California coast (fig. 1). The entire east side of the estuary is bordered by Bolinas Ridge, which rises 460 m above sea level. The west side of Bolinas Lagoon is bordered by wooded hills, pastures, and the steep, 40-m high, wooded face of the Franciscan Mesa. To the south, a low sand spit separates the estuary from the ocean, except for a narrow opening at the estuary's southwestern corner. On the north, the estuary is bordered by the lower slopes of the Bolinas Ridge and the wooded floor of the Olema Valley. Kent Island lies close to the southwestern edge of Bolinas Lagoon, separated by a narrow channel from the Franciscan Mesa and Pine Gulch Creek delta (fig. 1). The majority of the island's 40 ha is salt marsh (*Salicornia virginica, Spartina foliosa,* and *Distichlis spicata*), but a small area on the southwestern corner is a few feet higher than the rest and is covered by grass and several Monterey pines (*Pinus radiata*) and Monterey cypresses (*Cupressus macrocarpa*). A narrow row of sand dunes extends east from this high area 460 m along the southern edge of the island and provides cover for roosting Short-eared Owls. A few hundred hectares of tidal sand and mud flat border Kent Island, the Pine Gulch Creek delta, the north and south ends of the estuary, and the sand spit on the estuary's southern boundary. These sand and mud flats form the major feeding habitat for large numbers of shorebirds that winter on the estuary.

METHODS

Using a spotting scope and binoculars, we watched many diurnal raptors while they hunted on Bolinas Lagoon. When we saw a raptor eat prey, we collected the remains and identified the prey to species by comparing the remains with study skins. We also searched for piles of feathers and other remains of shorebirds eaten by raptors and identified these in the same manner. We counted the number of primaries in each pile of feathers, and if 11 or more primaries were present, we considered the remains to represent one bird. If fewer than 11 primaries were present, we considered the remains to represent part of a bird. To estimate the number of birds represented by the partial remains, the total number of left wing primaries contained in all the partial remains was divided by the average number of primaries per wing in the remains representing an entire bird.

We studied the composition of the owls' diets by analyzing pellets collected regularly at their roosts. We removed all the bones from each pellet and determined the species to which they belonged by comparison with known skeletons. In both winters we found many bones from either Robins (*Turdus migratorius*) or Varied Thrushes (*Ixoreus naevius*) in the pellets of Short-eared Owls. Although we could not separate the bones of these two species, there was strong evidence that most were from Varied Thrushes. The lengths of the humeri, ulnae, and tarsometatarsi from the pellets were significantly different ($P < 0.05$), from the lengths of the corresponding bones of Robins, but were not significantly different ($P > 0.05$) (Steel and Torrie 1960:74) in length from the corresponding bones of Varied Thrushes. During the two winters of study, we found the feathers of 11 Varied Thrushes and 2 Robins at the Short-eared Owls' roost. In this paper, therefore, we have referred to all these bones as Varied Thrush remains. The presence in a pellet of one or more identifiable bones of an animal we considered to represent one prey item and bones from two individuals of the same species in a pellet to represent two prey items, even if major skeletal elements were missing. We calculated the proportion of each prey species in the owls' diet by converting the number of individuals of each species in the pellets to a percentage of the total prey represented in the pellets.

During February and March 1973, we kept a Short-eared Owl in captivity to obtain an estimate of the number of pellets produced daily by an owl under natural conditions. The Short-eared Owl was a wild bird that had been found with a broken wing. The wing had recently mended when we received it. The bird was kept in an outdoor cage, where it was relatively inactive except when it ran over the cage floor or flew between two perches. We fed it dead California voles (*Microtus californicus*) and deer mice (*Peromyscus maniculatus*) and recorded the total

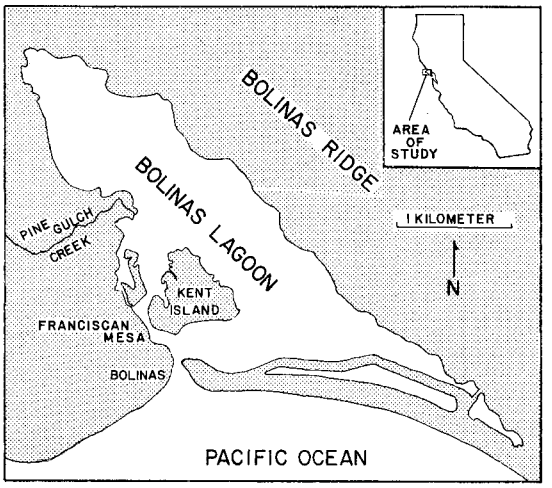

FIGURE 1. Map of Bolinas Lagoon.

weight of rodents eaten in each meal. We varied the number of rodents in each feeding, the number of feedings per night, and the time intervals between feedings. Weight of the owl was monitored throughout the experiment.

To estimate the weight of prey consumed daily by the raptors on the estuary, we calculated the average weight of each prey species. These averages were based on the weights of 12–30 individuals from Point Reyes Bird Observatory banding records and from study skin data. To estimate the number of shorebirds available to raptors, we took six censuses per month of the shorebirds on Bolinas Lagoon in the winter of 1971–72, and three censuses per month in 1972–73. The estuary was divided into three areas and the birds in each area were counted or estimated simultaneously. On some censuses small sandpipers [Least Sandpipers, Dunlins, and Western Sandpipers (*Calidris mauri*)] could not be separately identified. These birds always made up less than 20% of those that were identified and were incorporated into the census totals as Least Sandpipers, Dunlins, and Western Sandpipers according to the relative abundance of these species on the census. The average number of shorebirds from each month's censuses from October through February was calculated and the highest of these averages was used as an estimate of the winter population of each shorebird. To measure the abundance of California voles during the winter, we trapped voles in three areas on Kent Island in 1972–73, using live traps made after the pattern of Brown et al. (1969). Trap stations were 9 m apart in a grid covering 5680 m^2 on the grassy portion of Kent Island, in a smaller grid of 1670 m^2 in an isolated segment of the dunes, and in a line running for 457 m through the narrow strip of dunes on the south margin of Kent Island. Voles were trapped for 3-day periods at bimonthly intervals in each area. We put a numbered ear tag on each vole and weighed it. We estimated the size of the vole populations by means of the Lincoln Index (cf. Leopold 1933), using the first 2 days of each trapping as the capture period, and the 3rd day as the recapture period.

MERLIN

In 1971–72 a Merlin wintered on Bolinas Lagoon but we spent little time watching it. An adult female Merlin wintered there from early September 1972 to April 1973. After examining many study skins of Merlins, we were confident that the bird was an adult female and that it was of the subspecies (*F. c. bendirei*). Between 21 September 1972 and 28 February 1973, we watched the Merlin on 119 days and saw her eat 131 vertebrate prey items, of which 109 were shorebirds, and collected 12 additional shorebird remains from her eating perches. During her stay, she hunted shorebirds on Bolinas Lagoon almost every day. The falcon usually arrived early in the morning and spent the entire day on the estuary, although she sometimes left after an early afternoon meal. Her nocturnal roost was not located but it was at least 0.8 km from the estuary. On six occasions we saw her chase other Merlins away from the estuary.

The Merlin selected hunting perches in response to the distribution of her major prey, small sandpipers. At low tide, Least Sandpipers, Western Sandpipers, and Dunlins fed on the mud flats and the Merlin hunted them from perches nearby. When the tide was high and the small sandpipers came into the salt marsh to feed or to roost, she hunted them from perches in the salt marsh. During very high tides, Least Sandpipers and Dunlins congregated in pastures adjacent to the estuary and she hunted them from fence posts bordering the pastures. In mid-November heavy rains and high tides flooded the estuary and much of the adjoining pastures. Many Dunlins and some Least Sandpipers left Bolinas Lagoon and moved to pastures on Bolinas Mesa, 1.2 km west of the estuary. The Merlin followed and hunted the sandpipers there. When an opportunity arose, she often attacked other prey between hunts at shorebirds, and occasionally, instead of hunting shorebirds, she remained on the margin of the estuary and hunted passerines. She sometimes caught flying grasshoppers and lepidopterans when they were available in the fall and spring. The largest birds that we saw the Merlin kill were Sanderlings (*Calidris alba*) and Red-winged Blackbirds (*Agelaius phoeniceus*). Many times we saw her fly at American Coots (*Fulica americana*), Willets (*Catoptrophorus semipalmatus*), Marbled Godwits (*Limosa fedoa*), and Black-bellied Plovers (*Pluvialis squatarola*). She never struck them but often grabbed at them, causing them to fly off screaming. The Merlin made similar attacks on blackbirds and Killdeers (*Charadrius vociferus*) throughout the winter but in late February and early March, when the number of

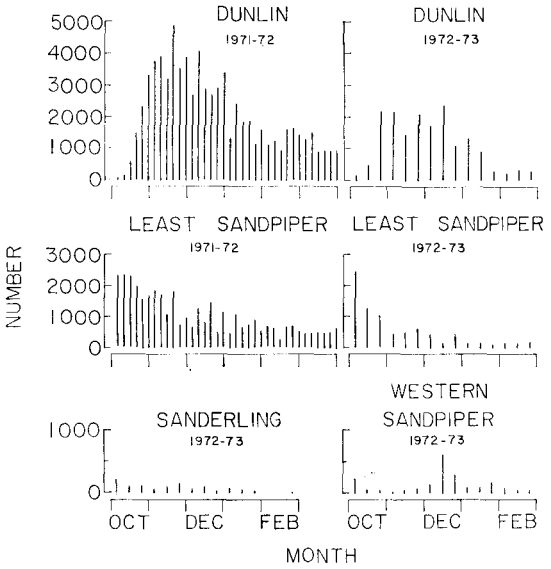

FIGURE 2. Number of shorebirds on Bolinas Lagoon during two winters, 1971–72 and 1972–73.

small shorebirds on the estuary was low (fig. 2), we saw her eat two Red-winged Blackbirds and pursue a Killdeer vigorously.

Surprise was the most important element of the Merlin's hunting. We observed 343 Merlin hunts, of which 278 were directed at quarry initially on the ground, 49 at flying birds, and 16 at birds on buildings or in trees. Her characteristic attack was a fast, low, horizontal flight from a perch, culminating in a glide at less than a meter above the ground. When the quarry was on sand or mud flats, the falcon continued her glide until she reached it, then grabbed at it, whether it was still on the ground or had just sprung into the air. Quarry which were in the salt marsh were attacked somewhat differently. When the Merlin had glided almost to the prey, she usually spread her wings and tail, lofted upward about 45 cm and then abruptly forced herself down, grabbing at the quarry as she passed low over it. It appeared that this bounce tactic startled the prey into flight, in which case she often captured it as it left the ground. If the quarry did not spring into the air, it usually escaped the falcon. When the quarry detected the Merlin's approach and was well in the air before her arrival, she sometimes chased it vigorously, mounting above and stooping at it once or many times. Just as frequently she swerved half-heartedly and attacked another quarry or flew to a perch. We saw the Merlin chasing or stooping at flying birds on 82 occasions, but we never saw her make a kill this way. Once, the Merlin caught a small sandpiper that was flying, but it escaped a few seconds after the falcon captured it. Although the Merlin may have killed a few flying birds by chasing or stooping at them, as a Merlin was seen to do on two occasions during the previous winter, she was much more successful when she surprised prey on the ground. A Merlin preying on wintering Dunlin on the Nisqually River delta, Washington, usually hunted by stooping at flying flocks of Dunlin, chasing and catching in flight individuals which left the flocks (Whitacre, Shanewise and Herman, unpubl. data).

To determine the Merlin's hunting success, we condensed Rudebeck's (1950) definition of a hunt by a bird of prey and considered that a hunt consists of one or more completed attempts to seize an individual or group of individuals of a species that the raptor is known to eat. Several attempts at a particular individual or group of prey were considered as one hunt unless they were interrupted by the Merlin's perching or attacking other prey. The Merlin captured prey in 12.8% of the 343 hunts we observed on Bolinas Lagoon. This compares to a success rate of 5% for 139 Merlin hunts observed by Rudebeck (1951) in Sweden. On Bolinas Lagoon in 17 observations of successful hunts by the Merlin at flocks of sandpipers on the ground, we were able to determine the position of the individual captured in relation to the rest of the flock. In two instances, it was 1–3 m from the main body of the flock; in three instances, it hesitated after the rest of the flock had taken off; but in the remaining 12 instances, it was taken from the main body of the flock. Of all the sandpipers which we saw the Merlin kill on Bolinas Lagoon, 76% were taken from flocks.

In order to estimate the Merlin's average daily food consumption, we watched her all day on 20 days distributed throughout the 5 months of study. On 4 days she killed one bird; on 9 days, two birds; and on 7 days, three birds; giving a mean of 2.2 birds per day. The total weight of prey killed per day ranged from 20.5 to 128.6 g and averaged 71.0 g per day. The difference between the total weight of prey captured on "2 bird days" (mean = 79.3 g) and "3 bird days" (mean = 76.2 g) was small, suggesting that when small prey were taken first, there was a greater chance of another prey being taken than if the initial prey were large. The Merlin did not always eat the entire prey in one meal. On four occasions we saw the falcon cache food and on one occasion saw her return to eat the prey the next day. The number of each prey species that we saw the Merlin eat during the study is presented in table 1. Using the average

TABLE 1. Number of vertebrate prey observed and estimated eaten by a Merlin on Bolinas Lagoon, 1 October 1972 to 28 February 1973. See text for method of calculating estimated numbers.

Species	Observed	Estimated
Least Sandpiper (*Calidris minutilla*)	51	112
Dunlin (*Calidris alpina*)	49	108
Western Sandpiper (*Calidris mauri*)	12	26
Sanderling (*Calidris alba*)	8	18
Yellow-rumped Warbler (*Dendroica coronata*)	4	9
Water Pipit (*Anthus spinoletta*)	3	7
Savanah Sparrow (*Passerculus sandwichensis*)	3	7
Northern Phalarope (*Lobipes lobatus*)	2	4
Red-winged Blackbird (*Agelaius phoeniceus*)	2	4
Red Phalarope (*Phalaropus fulicarius*)	1	
House Finch (*Carpodacus mexicanus*)	1	
Brown Creeper (*Certhia familiaris*)	1	
Western Bluebird (*Sialia mexicana*)	1	
Ruby-crowned Kinglet (*Regulus calendula*)	1	
Song Sparrow (*Melospiza melodia*)	1	
California vole (*Microtus californicus*)	2	4
Unid lizzard (*Gerrhonotus* sp.)	1	

TABLE 2. Mortality of shorebirds due to raptor predation as determined from the remains of shorebirds found on Bolinas Lagoon, 1 October 1972 to 28 February 1973.

Shorebirds	Total remains	Winter prey population	% shorebird mortality
Dunlin (*Calidris alpina*)	183	1912	9.6
Least Sandpiper (*Calidris minutilla*)	111	1582	7.0
Western Sandpiper (*Calidris mauri*)	16	348	4.6
Sanderling (*Calidris alba*)	9	133	6.8
Dowitcher (*Limnodromus* spp.)	16	103	15.5
Common Snipe (*Capella gallinago*)	2	100	2.0
Marbled Godwit (*Limosa fedoa*)	2	210	1.0
Willet (*Catoptrophorus semipalmatus*)	29	470	6.2
Greater Yellowlegs (*Tringa melanoleucus*)	1	10	10.0
Long-billed Curlew (*Numenius americanus*)	0	43	0.0
Black Turnstone (*Arenaria melanocephala*)	0	109	0.0
Killdeer (*Charadrius vociferus*)	5	72	6.9
Black-bellied Plover (*Pluvialis squatarola*)	0	325	0.0

weights of each prey species, we calculated that the total weight of prey we saw the Merlin eat was 4843 g. By multiplying the number of days during the study (151) by the average weight of prey taken per day (71.0 g), we estimated that the total weight of prey that the Merlin killed was 10,721 g or 2.2 times the total weight of prey we had observed being eaten. By multiplying the factor 2.2 by the number of individuals of each prey species we saw the Merlin eat, we estimated the number of birds of all species the Merlin killed during the study (table 1). This represented 5.6% of the Dunlins, 7.1% of the Least Sandpipers, 7.5% of the Western Sandpipers, and 13.5% of the Sanderlings that wintered on Bolinas Lagoon in 1972–73 (see table 2 for numbers of winter prey species). This estimate of the Merlin's total consumption is similar to that predicted using the average number of 2.2 prey items per day which were taken during the 20 full days of observation.

AMERICAN KESTREL (*Falco sparverius*)

American Kestrels hunted shorebirds on Bolinas Lagoon during both winters of the study. On 1 February 1972, Page saw a male kestrel eating a Least Sandpiper on Kent Island. By the following day we had found the very old remains of eight additional Least Sandpipers and one Western Sandpiper under two perches that the kestrel used. From 1 October 1972 to 28 February 1973, we often saw kestrels hunting on the margins of Bolinas Lagoon, but not until 29 November did we see this species hunting shorebirds. Subsequently, between 4 December 1972 and 21 January 1973, we saw at least three different male kestrels eat 11 Least Sandpipers and two unidentified small shorebirds. We saw no female kestrels hunting shorebirds. The kestrels hunted Least Sandpipers, Water Pipits (*Anthus spinoletta*), and Savannah Sparrows (*Passerculus sandwichensis*) in the salt marsh, but they did not hunt shorebirds on the mud flats. They approached their prey in a low glide similar to

TABLE 3. Observed prey of American Kestrels on Bolinas Lagoon, 1 October 1972 to 28 February 1973.

Species	No. eaten
Least Sandpiper (*Calidris minutilla*)	12
Scolopacidae unid.	2
Water Pipit (*Anthus spinoletta*)	1
Savanah Sparrow (*Passerculus sandwichensis*)	1
Townsend's Warbler (*Dendroica townsendi*)	1
White-crowned Sparrow (*Zonotrichia leucophrys*)	1
California vole (*Microtus californicus*)	7
Insecta	6

the Merlin's, but after lofting upward, they plummeted to the ground, whereas the Merlin usually did not take the quarry on the ground, but captured it only if it flew up. The quarry often did not leave the ground, and the kestrels seemed more adept than the Merlin at catching birds in the thick vegetation. The kestrels were successful in 3 of the 15 attacks we saw them make at prey in the salt marsh. Occasionally, they hovered over birds in the vegetation and chased them when they flew up, but we never saw them capture any in this manner. Between 1 October 1972 and 28 February 1973, we saw kestrels with 31 prey items on Bolinas Lagoon (table 3). There appeared to be a change in the kestrels' diets between November and December. In October and November, we saw kestrels eating 5 insects and 2 California voles, and in December and January, 17 birds and 4 voles.

MARSH HAWK (*Circus cyaneus*)

We did not see any Marsh Hawks hunting on Bolinas Lagoon during the winter of 1971–72, although we found a dead one on the highway bordering the estuary. On 40 days between 1 October 1972 and 28 February 1973, we saw at least one Marsh Hawk hunting on the estuary and on 2 days we saw at least two. During an additional 12 exceptionally cold days from 4 to 15 December, as many as four Marsh Hawks hunted shorebirds in the salt marsh. They hunted in typical harrier fashion and sometimes chased prey they flushed. Sometimes Marsh Hawks that were perched on the ground flew up and chased a passing bird. Three times we saw immature Marsh Hawks stoop from an altitude of over 30 m at Willets on the ground, and once we saw an immature Marsh Hawk try to intercept a flying Marbled Godwit. We observed 55 attempts of Marsh Hawks to catch prey on Bolinas Lagoon and at least 39 of these were at shorebirds. They caught three Least Sandpipers, one unidentified shorebird, and one Savannah Sparrow in these hunts. We saw Marsh Hawks eating one additional Least Sandpiper, one Dunlin, one Willet, one American Coot, and one Western Meadowlark (*Sturnella neglecta*). We also saw them partially pluck but not eat one meadowlark and one coot which were carrion.

ACCIPITERS

We put little effort into looking for Cooper's Hawks (*Accipiter cooperii*) and Sharp-shinned Hawks (*Accipiter striatus*) during the winter of 1971–72 and saw these raptors very infrequently. In the following winter we looked more intently for accipiters and saw Cooper's Hawks and Sharp-shinned Hawks on Bolinas Lagoon on 27 of the 151 days of the study in 1972–73. These hawks usually stayed on the wooded face of the Franciscan Mesa, but occasionally we saw them in the salt marsh. On 23 March 1972, a Sharp-shinned Hawk seized a Dunlin from a flock of sandpipers on a mud flat, but the hawk dropped the Dunlin and the shorebird escaped. On 10 October 1972, an immature Sharp-shinned Hawk killed a Pectoral Sandpiper (*Calidris melanotos*) in the salt marsh and then ate the bird beneath a tree on the Franciscan Mesa. On 27 September 1973, an adult Cooper's Hawk knocked a Willet to the ground from a flock of Willets that was rising from the salt marsh. When the hawk lifted it from the ground and began to fly with it, the bird escaped. We saw what we believed to be the same adult Cooper's Hawk eating two Willets on Kent Island later in the winter. It ate one of these in two meals on consecutive days, under the pines on Kent Island. The second was partially eaten in the salt marsh and was then carried to the same pine where the first had been eaten. We flushed the Cooper's Hawk and it carried the remains to the Franciscan Mesa. The remains of other Willets found under the Kent Island pines in 1971–72 may also have been victims of this hawk. Our only other observation of a Cooper's Hawk with shorebird prey was that of one eating a Dunlin at the foot of the Franciscan Mesa on 28 November 1972.

BUTEOS

Although Red-shouldered Hawks (*Buteo lineatus*) and Red-tailed Hawks (*Buteo jamaicensis*) hunted in the vicinity of Bolinas Lagoon during the entire study, we found very little evidence that they preyed on shorebirds. Between 1 October 1972 and 28 February 1973, we saw Red-tailed Hawks with six coots and one Willet, but Red-shouldered Hawks were never observed with prey.

TABLE 4. Percent composition of prey found in Short-eared Owl pellets on Bolinas Lagoon during the winters of 1971–72 and 1972–73.

Species	1971–72	1972–73
Dunlin (*Calidris alpina*)	21.0	51.3
Least Sandpiper (*Calidris minutilla*)	3.4	8.5
Other Scolopacidae		1.8
Red Phalarope (*Phalaropus fulicarius*)		0.4
Killdeer (*Charadrius vociferus*)	0.8	
Rallidae	1.5	
Saw-whet Owl (*Aegolius acadicus*)		0.4
Varied Thrush (*Ixoreus naevius*)	18.4	11.2
Other Turdidae	0.4	1.3
Icteridae	2.7	1.8
Fringillidae	2.3	7.1
Other Passeriformes	1.2	4.0
California vole (*Microtus californicus*)	42.9	10.7
Other Rodentia	5.4	1.3

WHITE-TAILED KITE (*Elanus leucurus*)

White-tailed Kites were not seen preying on shorebirds on Bolinas Lagoon. Kites were not present there during the winter of 1971–72 but two hunted on the estuary throughout the winter of 1972–73. We observed the kites killing or eating rodents 17 times, and when we were able to identify the prey, it was invariably a California vole. All of the 50 kite pellets found beneath the kites' perches between 1 August 1972 and 28 February 1973 contained remains only of the California vole.

SHORT-EARED OWL

One to four Short-eared Owls roosted in the dunes on Kent Island at various times during the winters of 1971–72 and 1972–73. At dusk they left the dunes to hunt east toward Bolinas Ridge, west toward Bolinas Mesa, or over the sand dunes and salt marsh of the estuary. On an overcast afternoon in December 1972, we watched a Short-eared Owl hunt in a wet pasture adjacent to Bolinas Lagoon. During 20 min of flight, the owl plunged to the ground 16 times and on the last plunge captured a Dunlin. This was unusual since the owls did not often hunt in daylight. They must have obtained most Dunlins in the salt marsh where the Dunlins roosted at night.

We determined the winter prey of the Short-eared Owls in 1971–72 by examining 207 pellets collected at the owls' diurnal roost (table 4). As can be seen in figure 3, the proportion of Dunlins in the owls' diet dropped from 28% in December and January to 14% in March and early April. At the same time the number of Dunlins on the estuary fell from an average of 3100 birds in December to 1100 in March. The owls' intake of Varied Thrushes and California voles also changed markedly during the winter (fig. 3). The following winter, between early November 1972 and 21 January 1973, the prey in 171 pellets were examined (fig. 3). Dunlins made up a higher proportion of the prey in 1972–73 than during the comparable period of the previous winter (fig. 3) even though the number of Dunlins wintering on Bolinas Lagoon in 1972–73 was about half that of the previous year (fig. 2). Varied Thrushes and voles constituted a lower proportion of the owls' prey than in 1971–72. During the first 21 days of January 1973, approximately 38 cm of rain fell at Bolinas and the owls' roosts were flooded several times. The number of Dunlins on the estuary dropped from 1000 to less than 300. The number of California voles in three plots on Kent Island had dwindled to an estimated 33 individuals at the end of January from an estimated 177 voles in late October. After 21 January, we could not find Short-eared Owls at their former roost in the dunes.

The winter diet of Short-eared Owls on Bolinas Lagoon was made up of 51.7% birds in 1971–72 and 87.9% in 1972–73. In three other coastal situations, birds made up between 15% and 33% of the Short-eared Owl's diet (Tomkins 1936; Ticehurst 1943; Johnston 1956; Fisler 1960). In studies of the winter diet of Short-eared Owls at inland locations, rodents made up between 95% and 100% of the owls' diet (Cahn and Kemp 1930; Errington 1932; Hendrickson and Swan 1938; Snyder and Hope 1938; Baumgartner and Baumgartner 1944; Kirkpatrick and Conway 1947; Stegeman 1957; Reed 1959; Graber 1962; Short and Drew 1962; Munyer 1966; Maser et al. 1970). Most studies on the winter diet of the Short-eared Owl have been at inland locations where the density of one or two species of rodent was high. This has led to the statement that the Short-eared Owl's winter diet consists primarily of rodents (Earhart and Johnson 1970), but our studies show that the Short-eared Owl sometimes eats large numbers of birds in the winter, at least on the coast.

Guèrin (in Chitty 1938) found that there are at least two daily pellet ejections in the Barn Owl (*Tyto alba*): "pelote nocturne" and "pelote diurne." It is likely that Short-eared Owls also frequently have more than one daily pellet ejection. In addition to the pellets found in the owls' diurnal roost, we found seven pellets that were similar in size and composition in the salt marsh where the owls were not present during the day. All these

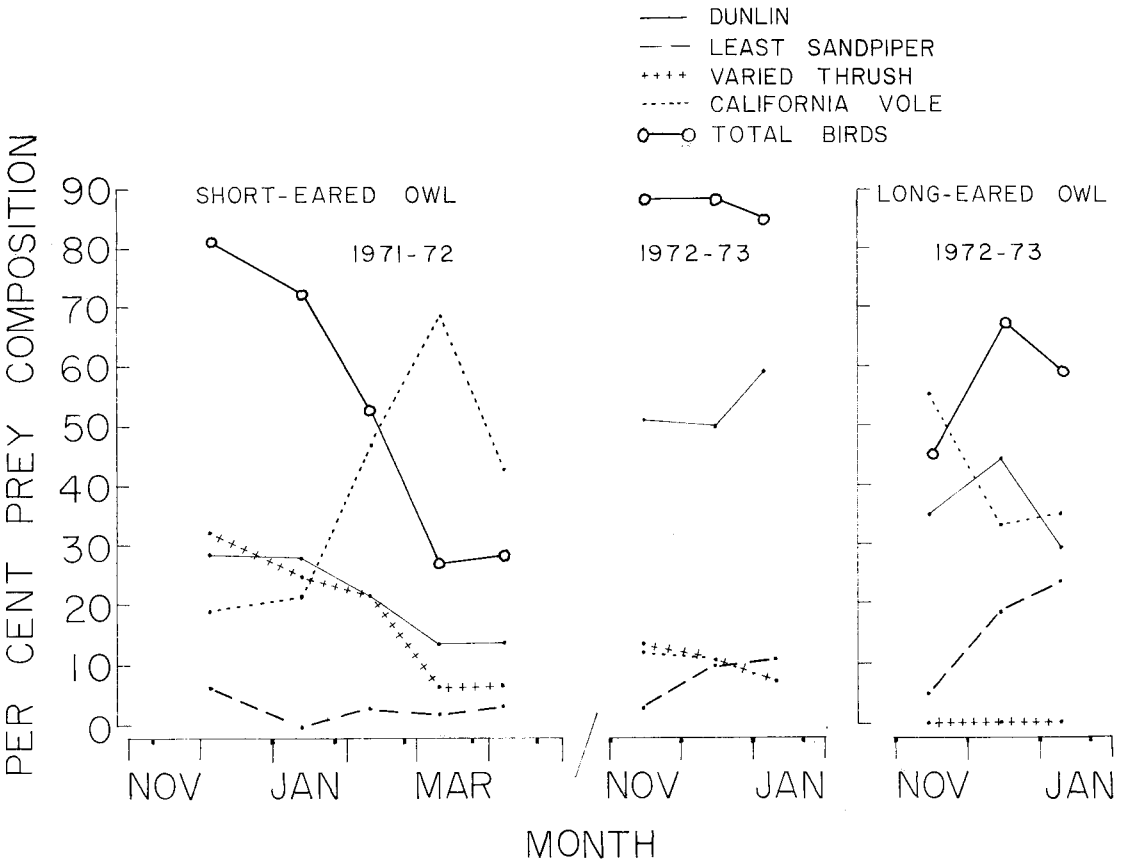

FIGURE 3. Composition of prey in pellets of two owl species during the winter. The minimum sample is 14 pellets for the Long-eared Owl and 28 pellets for the Short-eared Owl per period. Extreme dates of pellet collection are indicated by thickened areas on abscissa.

pellets contained the remains of single birds, and five were found associated with piles of shorebird feathers. The remains of the birds in four of the pellets were not as well digested as the remains in the majority of the pellets from the owls' diurnal roost. Because we found these pellets in wide expanses of salt marsh that were often covered by the tide, we must have discovered only a very small proportion of the pellets that were regurgitated away from the owls' diurnal roost.

To see how many pellets a captive Short-eared Owl is capable of producing in a day, we kept a Short-eared Owl from 15 February to 8 March 1973, feeding it California voles and deer mice at different hours of the night. On eight occasions when we gave the owl a single mouse at dusk and another at 04:00 the following morning, it produced two pellets. On only one occasion did it produce a single pellet under similar conditions. On the 4 days that we offered the owl three mice at 4–5 hr intervals during the night, it produced three pellets, each containing the remains of one mouse. At the second and third feedings each night, a pellet was usually produced within a few minutes after the mouse was offered and always before the owl began to eat the mouse. On 2 nights we gave the owl four mice at 3–4 hr intervals and it produced three pellets. Some of the pellets contained considerable amounts of undigested muscle. On 2 nights the owl was given six mice in a single feeding, with a combined weight of over 100 g. On both occasions it ate all the mice during the course of the night although it rejected the entrails from some. The owl disgorged two pellets one night and three the next. Under the feeding conditions imposed on this owl, it often produced more than one pellet from one night's feeding. We believe that similar feeding conditions often exist in nature and conclude that multiple daily pellet ejections are commonplace if not the rule with the Short-eared Owl.

The captive Short-eared Owl maintained a constant weight of 385 g for 14 days during which it ate an average of 51.9 g (range 40.4–75.6 g) of mice per day. Ignoring one pellet which contained the remains of a coot and

two which contained the remains of a Willet, because the presence of only vertebrae and feathers in these pellets indicated that much of these prey was not eaten, we found that the average weight of prey in the pellets collected from the dunes in 1971–72 was 63.0 g and in 1972–73 it was 62.7 g. Since it apparently requires about 50 g of mice to maintain a Short-eared Owl at a constant weight in captivity and considerably more energy is required by an active as compared to an inactive bird (LeFebvre 1964; Pearson 1964; Raveling and LeFebvre 1967; Craighead and Craighead 1956), we feel that considerably more than 50 g of prey per day are required to support an active Short-eared Owl. This contrasts with the ideas of Graber (1962) who felt that one owl pellet represents one "owl day" and that the average weight of prey in a pellet, which he found to be about 50 g, was sufficient to support an active Short-eared Owl. Although we do not know what the content of each pellet represents in terms of a night's forage, we feel that most pellets represent only part of a night's forage. We have assumed that pellets containing two or more prey items represent an entire night's forage and pellets containing only one prey item represent only half a night's forage. Pellets containing two or more prey items made up 23.1% of the pellets collected during the two winters of our study and represented an average of 95 g of prey. The average weight of prey in pellets containing only one item was 53.2 g and, according to our assumption, represented half of a total night's intake of 106 g. Consequently, we have assumed that an average of 100 g of prey per night was taken by each Short-eared Owl on Bolinas Lagoon.

From 9 November 1971 until 6 April 1972, one to four Short-eared Owls spent an estimated 391 owl days on Bolinas Lagoon. The total weight of prey estimated from all the pellets we found in the dunes was 13,072 g. By multiplying 391 owl days by 100 g per day, we estimated that the owls ate a total of 39,100 g. The prey represented in the pellets was 13,072/39,100 or a third of the owls' total estimated take. By applying this ratio to the number of shorebirds in the pellets, we estimated that the owls ate 165 Dunlins and 27 Least Sandpipers. This represents 4.3% of the Dunlins and 1.3% of the Least Sandpipers wintering on the estuary in the first year of study (fig. 2). In the following winter one to three Short-eared Owls roosted on Kent Island from early November 1972 to 21 January 1973. The total weight of prey found represented in their pellets was estimated to be 10,605 g compared to a total estimated take of 20,700 g. Using the same conversion technique, the total estimated take included 224 Dunlins and 37 Least Sandpipers, or 11.7% of the Dunlins and 2.3% of the Least Sandpipers, that wintered on the estuary in 1972–73 (table 2).

LONG-EARED OWL (*Asio otus*)

In late January and in February 1972 a Long-eared Owl roosted in a grove of pines on Kent Island about 90 m from the Short-eared Owls' roosting area. On 18 February, we collected 19 pellets which contained the remains of 6 Dunlins, 1 Least Sandpiper, 1 *Catharus* sp., and 14 California voles. During the following winter, between 9 November 1972 and 19 January 1973, one Long-eared Owl roosted in the same pines. The owl disappeared by 19 January following the disappearance in mid-January of most Dunlins from the estuary (fig. 2). We collected 49 pellets in which 34.8% of the prey were Dunlins; 14.5%, Least Sandpipers; 5.8%, other birds; 42.0%, California voles; and 2.9%, other rodents (fig. 3). Of all the pellets collected during the two winters of study, 29.4% contained two or more prey, or an average of 78.8 g of prey. The weight of prey in pellets containing only one item averaged 40.1 g. We assumed, as we did for the Short-eared Owl, that Long-eared Owl pellets containing two or more prey items represented the owl's total nightly take and pellets containing only one prey item represented half of the owl's nightly take. We estimated the owl was present for 82 days during the second winter, and took 6560 g of prey during this period. The pellets collected under the pines represented 2752 g of prey. Our estimate of the number of individuals of each prey species taken was 6560/2752 or 2.4 times the number in the pellets. This then included 58 Dunlins, or 3.0% of the winter population, and 24 Least Sandpipers, or 1.5% of the winter population.

GREAT HORNED OWL (*Bubo virginianus*)

During both winters, we often heard one or two Great Horned Owls calling at dusk, and on 24 November 1973, we heard five Great Horned Owls calling around the estuary. We were able to find only seven Great Horned Owl pellets from two different roosts bordering the estuary. These pellets contained the remains of three Dunlins, two Killdeers, two American Coots, one large unidentified bird, three California pocket gophers (*Thomomys bottae*), and five insects. Great Horned Owls may have had considerable impact on the size

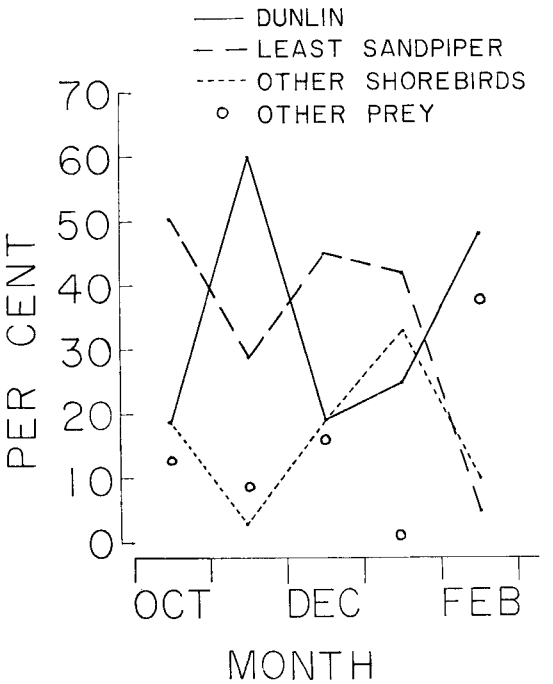

FIGURE 4. Monthly composition of prey taken by a Merlin on Bolinas Lagoon, 1 October 1972 to 28 February 1973.

of the winter shorebird population on Bolinas Lagoon.

INCREASED RAPTOR PREDATION DURING COLD WEATHER

There was evidence that during cold weather raptor predation of some shorebirds increased. During a 12-day period of extremely cold weather and high tides between 4 and 15 December 1972, there was a dramatic increase in the number of raptors hunting shorebirds on Bolinas Lagoon. During this period, the number of Marsh Hawks hunting over the salt marsh increased abruptly from two to four birds and the number of kestrels increased from one to three birds.

Changes in the behavior of the shorebirds appeared to increase their vulnerability to raptors. During the cold period, many shorebirds foraged very intently and allowed us to approach them more closely than at other times of the year. Dunlins, which usually fed in relatively compact flocks on the mud flats, dispersed into ill-defined flocks along the tideline. Least Sandpipers, which sometimes fed in the salt marsh under normal conditions, moved into the salt marsh to an unprecedented degree during the cold weather. The increase of shorebird predation during this period was directed primarily at the Least Sandpiper, apparently because of this species' increased availability in the salt marsh where the kestrels and Marsh Hawks hunted. In what also appeared to be a response to the increased availability of Least Sandpipers in the salt marsh, the Merlin adopted the kestrels' hunting techniques and began dropping into the vegetation after prey. Before the cold weather, we had only once seen the Merlin attack birds in this way. During the cold period, Least Sandpipers were eaten by the Merlin in larger numbers (68% of prey) than at any other time during the study, even though Least Sandpipers were outnumbered by about four to one by Dunlins on the estuary (fig. 2). Prior to the cold weather in December, the Merlin's diet reflected the relative numbers of her major prey on the estuary (fig. 4).

DISCUSSION

During this study, hawks and owls killed a substantial proportion of the wintering shorebirds on Bolinas Lagoon. The total numbers of shorebirds represented by all the shorebird remains we found are shown in table 2. By totaling the numbers of shorebirds which we estimated were taken by the Merlin, Short-eared Owls, and Long-eared Owl and the number that we saw other raptors eating, we calculated that raptors took 395 Dunlins, 189 Least Sandpipers, 26 Western Sandpipers, and 18 Sanderlings between 1 October 1972 and 28 February 1973. These estimates represent 20.7% of the Dunlins, 11.9% of the Least Sandpipers, 7.5% of the Western Sandpipers, and 13.5% of the Sanderlings wintering on Bolinas Lagoon in 1972–73. Our estimates of the proportions of wintering shorebirds eaten by raptors are conservative because in calculating the total number killed by raptors other than the Merlin, Short-eared Owls, and Long-eared Owl, we have included only the birds we saw kestrels, accipiters, and Marsh Hawks eating, and only the shorebirds represented in the seven Great Horned Owl pellets. Obviously, these raptors ate more shorebirds than we credited to them.

Goss-Custard (1970) proposed that the factor promoting the formation of compact flocks in shorebirds is predation. He suggested that in waders, flocking may increase the birds' awareness of the approach of predators and deter attack by certain aerial predators. If flocking does deter the attack of predators, it should result in the predators having a lower success rate in taking birds from flocks than in taking single birds or result in fewer attacks on birds in flocks as compared to single birds. Because we never saw the Merlin on Bolinas Lagoon kill a bird in the 82 cases in which she chased or stooped at flying sandpipers, we

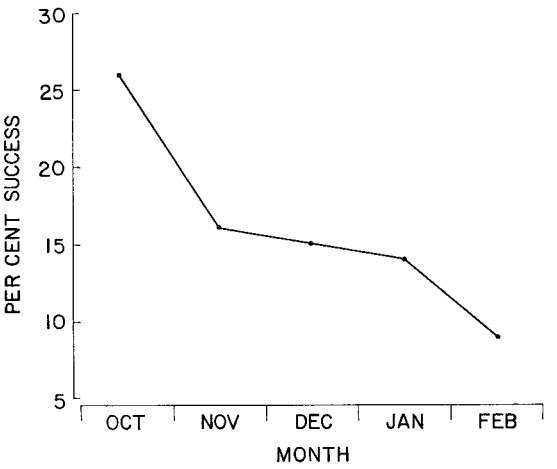

FIGURE 5. Seasonal change in rate of success of a Merlin's hunts at sandpipers on the ground in 1972–73.

felt that it would be most useful to analyze her hunting success using only those 234 hunts which were made at small sandpipers initially on the ground. The Merlin's success rate in capturing such birds was 25.6% in 39 attacks at single birds, 6.9% in 27 attacks at groups of 2 to 10 birds, 8.3% in 36 attacks at flocks of 11–49 birds, and 21.4% in 98 attacks at 50 to several hundred birds. The differences in success rates observed between the attacks at singles as compared to attacks at groups of 2 to 10 birds and 11 to 49 birds were significant at the 0.05 level (Sokal and Rohlf 1969:607–608); the differences in success rates in attacks at flocks of 2 to 10 and 11 to 49 birds were significant ($P < 0.05$) from the success rate at flocks of 50 to several hundred birds. It appeared that the Merlin's hunting success varied according to the size of the flock it attacked. As the shorebirds decreased in number (fig. 2), the Merlin's success rate also decreased (fig. 5), indicating that the availability of prey may also affect success rate.

The likelihood of a particular bird being taken on a hunt by the Merlin, comparing a single bird versus one in a flock, was calculated from the ratio of $(S^1 \times P^1)/N^1$ to $(S^2 \times P^2)/N^2$ where S^1 (0.256) is the success rate in attacks on single birds, S^2 (0.172) is the success rate in attacks at birds in flocks of two to several hundred birds, P^1 (0.193) is the proportion of hunts on single birds, P^2 (0.807) is the proportion of hunts on birds in flocks, N^1 (0.1) is the estimated proportion of small sandpipers occurring as single birds on the estuary, and N^2 (0.9) is the estimated proportion of birds present in flocks. From these data, we calculated that the likelihood of a shorebird being preyed upon as a single bird as compared to a bird in a flock was 3.2:1. Therefore, under the conditions that existed on Bolinas Lagoon, small shorebirds in flocks had less chance of being eaten by the Merlin than did shorebirds which occurred singly.

CONCLUSION

Our study indicates that raptors killed a substantial proportion of the shorebirds wintering on Bolinas Lagoon. Therefore, an important factor in shorebird mortality is predation by raptors on the wintering grounds. This has not been demonstrated previously. The data collected on the predator-prey relationship between a Merlin and a winter population of small sandpipers support the hypothesis that raptor predation is a major factor selecting for the formation of flocks in shorebirds. Finally, the different success rates observed for the Merlin in hunts at shorebird flocks of different sizes present an intriguing problem for further study.

SUMMARY

Raptor predation of shorebirds by a Merlin, American Kestrels, Marsh Hawks, Cooper's Hawks, Sharp-shinned Hawks, Red-tailed Hawks, Short-eared Owls, Long-eared Owls, and Great Horned Owls was documented on Bolinas Lagoon during the winters of 1971–72 and 1972–73. Shorebirds were the Merlin's major prey. Other diurnal raptors generally hunted shorebirds sporadically; however, during a cold snap in December 1972, Marsh Hawks and kestrels hunted shorebirds as persistently as the Merlin. Shorebirds were important prey of Short-eared Owls, Long-eared Owls, and Great Horned Owls. The number of shorebirds eaten by all the raptors during the winter of 1972–73 represented 21% of the Dunlins, 12% of the Least Sandpipers, 8% of the Western Sandpipers, 13% of the Sanderlings, and 16% of the dowitchers wintering on Bolinas Lagoon. Evidence is presented supporting the hypothesis that raptor predation is a major force selecting for flocking behavior among shorebirds.

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