

## FORAGING PATTERNS AND PREY SELECTION BY AVIAN PREDATORS: A COMPARATIVE STUDY IN TWO COLONIES OF CALIFORNIA GULLS

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**ABSTRACT.**—We studied the effects of avian predators, especially Great Horned Owls (*Bubo virginianus*), in colonies of California Gulls (*Larus californicus*) at Mono Lake, California, and Antero Reservoir, Colorado, in the years 1981–1985. During early gull nesting and incubation owls preyed on adult gulls. The frequency of kills varied from almost nightly in the Mono Lake study area in some years to as little as monthly at Antero Reservoir. Owls shifted to chicks as they became available. During attacks adult gulls left the colony for periods of 30 min to 3 h. This resulted in indirect chick losses caused by hypothermia at Antero Reservoir, where nocturnal temperatures often dropped below 0°C, and by subsequent predation by adult gulls at Mono Lake, where temperatures were moderate.

Losses of adult gulls to owls were negligible, whereas losses of chicks were sometimes great, and in some areas nesting was completely disrupted. Predation by Golden Eagles (*Aquila chrysaetos*) and Common Ravens (*Corvus corax*) was infrequent and had little effect on adults or young at either colony.

We also investigated factors that make gulls susceptible to avian predators. Adult size was unimportant, but females comprised 70% of the kills, probably owing to their greater attentiveness at the nest. Gulls nesting near the owls' nest or in areas in which predation had been high in previous years also risked greater mortality. Gulls in dense, central parts of the colony suffered very little mortality at Mono Lake, but high mortality at Antero Reservoir. Nesting near vegetation greatly increased the risk of owl predation in some areas; in others it had little effect. However, nesting where visibility was obstructed by plants or topography facilitated attacks by Golden Eagles.

Gull distribution within the colony changed in years following intense owl predation. Experienced birds shifted to new nest sites or left the area entirely and were replaced by birds that had nested in peripheral areas or by birds nesting for the first time.

Knowledge of the impact and history of predation in a colony is relevant to interpreting patterns of colony occupancy and habitat use.

Great Horned Owls (*Bubo virginianus*) are important predators on colonially nesting larids (Southern et al. 1982, Nisbet 1975), including California Gulls (*Larus californicus*) (Vermeer 1970). Not only do they kill adults and young, their nocturnal raids can disrupt colonies, causing adults to desert eggs and chicks (Nisbet and Welton 1984). In studies at Mono Lake, Mono Co., California, Jehl observed that these owls as well as Golden Eagles (*Aquila chrysaetos*) hunted regularly in the large California Gull colony, sometimes having a major impact on nesting success. Concurrently, Chase obtained similar results from studies at Antero Reservoir, Park Co., Colorado, where owls, eagles, and Common Ravens (*Corvus corax*) were present. In this paper, we (1) describe the behavior of predators and prey, which varied annually both within and between the two colonies, (2) compare the impact of nocturnal vs. diurnal predators on the gulls' reproductive success, (3) present information on prey selection by the owls and eagles, and (4) document distributional changes in the colonies resulting from these disturbances.

### METHODS

#### MONO LAKE, CALIFORNIA

From 1982 through 1985 Jehl studied California Gulls breeding on the Paoha and Channel islets (Fig. 1A) at Mono Lake (ML) (elevation ca. 1945 m). In 1982, these comprised ca. 15 sandy and virtually barren islets (Paoha Islets) plus many tiny satellites, and two rocky islets (Channel Islets) approximately 0.6 km to the NE. They varied in size from about 0.02 to 6 ha. In 1983, a rise in lake level and severe erosion greatly reduced the number and extent of the islets, so that in 1984–1985 only five islets and their satellites persisted in the Paoha series (Fig. 1B); the Channel Islets were submerged. In the years 1982–1985 the nesting population on these islets varied from 6200 to 17,000 gulls (14–35% of the entire ML colony).

Laying at ML begins in late April, peaks between 10–30 May, and continues into mid-June. The hatching period peaks in the first two weeks of June. In May nocturnal temperatures occasionally fall below freezing, but later in the summer, when chicks are present, they rarely dip below 10°C. Diurnal temperatures in the chick-rearing period commonly exceed 30°C.

Predation was studied opportunistically in 1982–1983 and more systematically in 1984–1985. In the latter two years, Jehl surveyed the colony regularly from the start of the breeding season in early April until all fledglings had departed in August. Because the nesting islets are low (maximum elevation 0.3–2.5 m in 1984), flat, and essentially unvegetated (Fig. 2), he could detect most dead adults from a small boat and landed only momentarily to retrieve carcasses. To determine mor-

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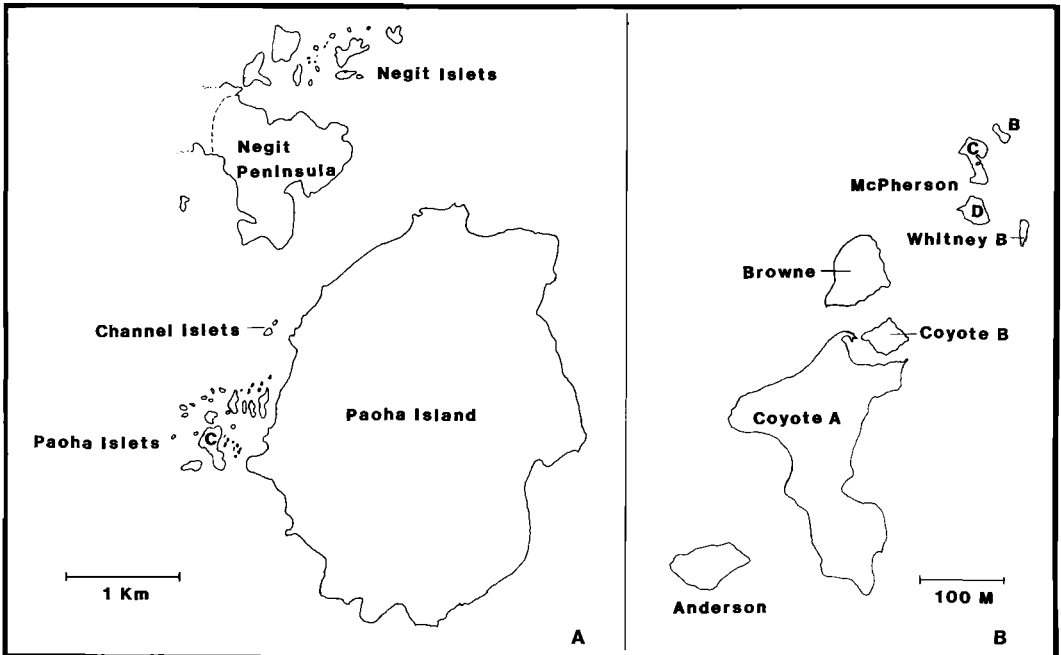


FIGURE 1. A) Configuration of the islands in Mono Lake, California, in 1982; C = Coyote Islet. B) Configuration of the Paoha Islets in 1984-1985.

tality among young gulls, he searched each islet by foot on 9-10 July, when the earliest chicks were fledging; in late July, when most young were independent; and in early August, after the islets were deserted. Other checks were made opportunistically in areas where nesting had failed, or where the brief presence of an observer would not affect chick survival.

Jehl removed all carcasses, plotted the location of those that had been killed by predators and, when possible, obtained standard morphological measurements (exposed culmen, depth of bill at gonydeal angle, chord of wing, tarsus) on remains of adults. Adults were sexed by gonadal examination if possible, or by measurements. Size differences allow over 90% of adults to be sexed correctly (Jehl 1987).

*Antero Reservoir, Colorado.*—California Gulls nest on three islands in Antero Reservoir (AR) (elevation 2770 m). These are small (0.5 to 17 ha) and moderately vegetated with grasses and low sage shrubs. This colony, which has existed for at least 30 years, increased from 643 pairs in 1981 to 1218 in 1985. Breeding chronology is similar to that at ML, although a late thaw may delay the season by 1-2 weeks. Temperatures regularly fall below freezing through the first two weeks of brooding. Snow, up to 0.2 m, is not uncommon through mid-June. High diurnal temperatures of 21-30°C in June and July are regularly reduced by daily thunderstorms. Temperature variations may exceed 22°C per hour and 30°C per day.

Chase documented the breeding on Rock and Gull islands (Fig. 3), at the western end of the reservoir and on Goose Island, at the eastern end, since 1981. He made daily visits to each island and documented mortality through the entire breeding season. From 20 to

40% of the adults in the colony were individually marked and their breeding efforts were monitored each year.

## RESULTS

### GREAT HORNED OWL

#### *Foraging patterns*

The presence of Great Horned Owls in each colony was ascertained by direct observations and could also be inferred from remains at the kill site. Owls typically dismember gulls, biting off the head, and sometimes wings and legs, and feeding mainly on the upper breast (Fig. 4). They fed at or near the point of capture, and removed very few gulls, as confirmed by surveys of their nests and roosts. Jehl twice found decapitated adults (wt. ca. 600 g) floating 100 m offshore the colony, suggesting that these were too heavy to be carried off. From these observations we think that owl foraging areas and impact on adult gulls and large chicks can be measured satisfactorily. Small chicks disappear for many reasons, including predation by adult gulls, and their losses to owls are often unmeasurable.

One or two owls foraged regularly in the study area at ML. At AR predation was infrequent and no more than one owl was present per night. The differences may reflect the existence of alternative food sources; they were not related to distance from the owls' nest or roost (2-2.5 km from the foraging areas in each case). At both localities



FIGURE 2. Typical nesting area of California Gulls on Paoha Islets, Mono Lake, California.

owls began capturing adults shortly after the gulls initiated strong territorial defense in mid-April, and continued taking them through mid-June, when they switched to chicks. Over 90% of adult kills occurred from late April to early June, predation being heaviest in the last half of May (Fig. 5). At AR an owl would fly in and make a direct kill of an adult. When preying on chicks, it would typically land on the crest of a hill and, after scaring off adults, fly into a group of chicks. We have no observations of hunting behavior at ML.

In each year at ML the owls maintained consistent and rather localized hunting ranges. They appeared to start hunting near their nest site, almost surely on Negit Island, and to work over a small area until its resources were depleted. In 1982, predation was first noted on the Channel Islets, which were deserted by 6 July after several large chicks and adults were killed. The owls then shifted to Coyote Islet and later in the season to McPherson Islet. In June 1983, although a few chicks were killed early on Coyote, the owls evidently concentrated their activity on the Channel Islets, routing all 81 pairs by 10 July. They then shifted to Whitney B; all 23 pairs deserted within three days. Subsequently, as in 1982, they hunted on Coyote and then on McPherson in late July and early August. They also continued to forage on Whitney B, killing juveniles that had arrived from other islets.

In 1984, the Channel Islets were submerged.



FIGURE 3. Nesting area on Gull Island, Antero Reservoir, Colorado.

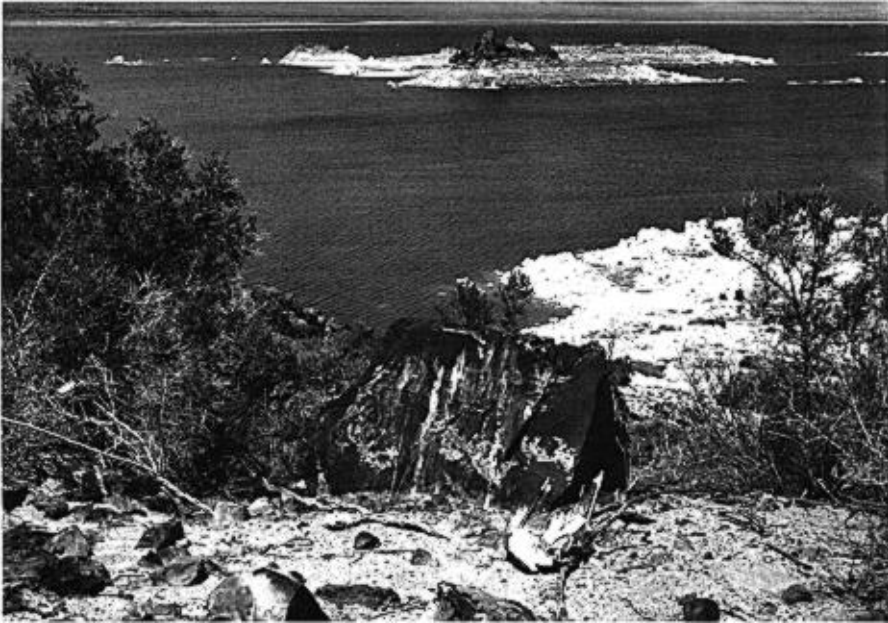


FIGURE 4. The decapitated remains of a California Gull killed by a Great Horned Owl on Negit Island, Mono Lake, California, 1985.

The earliest kills were on Browne and Coyote B islets, but from mid-June through mid-July owls hunted exclusively—and totally disrupted nesting—on the southern end of Coyote A. Subsequently, they moved to the north end of Coyote A, hunting there and on Browne Islet until mid August (Fig. 6).

In 1985, as in 1984, hunting was concentrated on Coyote A Islet (Table 1), but was less intense and more dispersed. It was first noted on 16 June, when three chicks were killed on the southern tip of the islet. Except for four large chicks killed in mid-July, there was no further evidence of predation until late July, when large chicks were taken nightly at least through 8 August, mostly on the northern half of the island.

At AR predation was confined to Gull Island until 1984, when a large aggregation of gulls moved to Goose Island (Table 1). The owl shifted its activities among areas of high nesting density on Goose Island.

In the ML study area, virtually all adults and young were dispatched in open areas on relatively high ground. However, when ca. 15 pairs began nesting among dense shrubbery near the owl's roost on Negit Island in 1985, predation was far greater than in any other area or year; at least nine adults were killed and the remainder abandoned before any eggs hatched. At AR adults were also killed on high bare ground, whereas chicks were taken without regard for topography

but always in areas of high density. In 1982 mortality was greatest in vegetation near the tip of Gull Island, whereas in 1983 it was greatest in the barren center of the island.

At ML owls avoided dense concentrations of gulls, foraged on the periphery of nesting areas, and did not shift into areas of high density until late in the season, after most young had fledged and birds were few. By contrast, at AR central nests attracted more attention.

Throughout this study there was no evidence of owl predation away from the AR colony. At ML, thousands of gulls gather daily on the deltas of small creeks. Sick or weak birds that may remain ashore there at night are killed by owls (distinct from those hunting in the colony) and coyotes (*Canis latrans*), but the numbers involved are small.

#### IMPACT

In both colonies, the impact on adult gulls was small, amounting to 0.2–1.5% (average 0.4%) of the nesting population (Table 1); nearly all mortality occurred before mid-June. At ML in 1984 observations began on 5 April but predation did not begin until mid-April (Fig. 5), presumably because gulls left the islands at night prior to the start of intense territorial defense (Vermeer 1970, Chardine and Morris 1983). Over the next 60 days 60 adults were killed (1.0/night). Mortality was not constant, however, and in late May 30

TABLE 1  
NUMBERS OF ADULT GULLS KILLED BY OWLS ON THE PAOHA ISLETS, MONG LAKE, CALIFORNIA, AND ANTERO RESERVOIR, COLORADO, 1981-1985

	1981			1982			1983			1984			1985		
	No. nesting	No. killed	No. nesting	No. killed	No. nesting	No. killed	No. nesting	No. killed	No. nesting	No. killed*	No. nesting	No. killed	No. nesting	No. killed <sup>b</sup>	
Paoha Islets															
Anderson															
Browne															
Coyote A															
Coyote B															
McPherson B															
McPherson C															
McPherson D															
Whitney B															
Total															
Antero Reservoir															
Gull	550	10 (1.8%)	584	5 (0.8%)	450	1 (0.2%)	416	3 (0.7%)	466	0	0	0	0	0	
Goose	50	0	75	0	134	0	496	1 (0.2%)	715	5 (0.7%)	5	0	0	0	
Rock	43	0	39	0	32	0	36	0	37	0	0	0	0	0	
Total	643	10 (1.5%)	798	5 (0.6%)	616	1 (0.2%)	948	4 (0.4%)	1218	5 (0.4%)	5	0	0	0	

\* 14 April-31 August, one additional adult found killed on 7 September 1984.

<sup>b</sup> 4 April-17 August; one additional adult found killed on 25 September 1985.

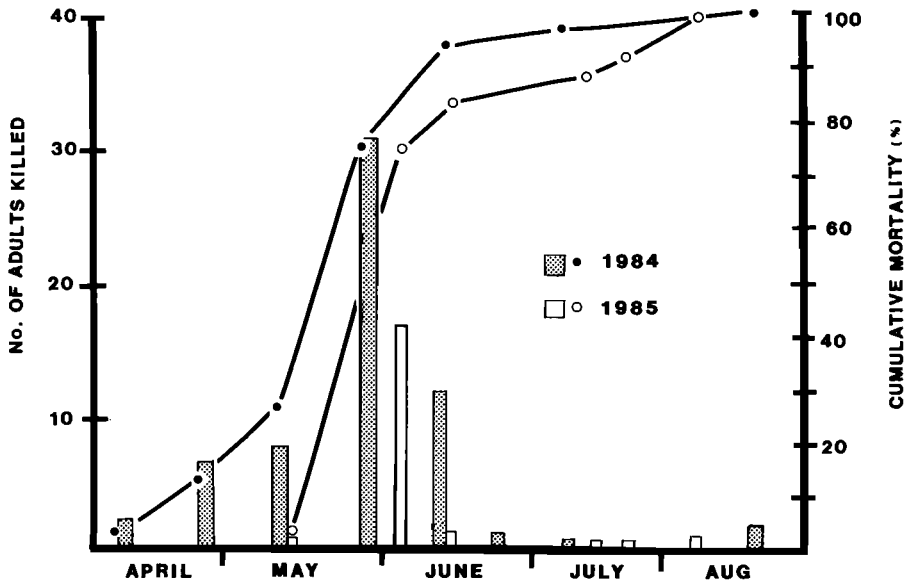


FIGURE 5. Mortality patterns of adult California Gulls killed by Great Horned Owls on the Paoha Islets, Mono Lake, California, 1984 and 1985.

adults were killed in 15 days. In 1985 owls did not appear in the study area until 14 May, and from then until 4 June 18 adults were killed (0.86/night); only six other adult kills were recorded subsequently. At AR only 26 adults were killed over five nesting seasons, all in the incubation stage.

Females suffered most of the adult losses in 1984–1985 at ML (no data for other years). Of 112 killed, 78 were females (69.6%), 18 (16.1%) males and 16 (14.3%) unsexed. This differs significantly from a 1:1 sex ratio and also from the sex ratio of gulls found dead in the colony of other causes (56 females : 42 males;  $P < 0.005$  in each case,  $\chi^2$  test). The sex ratio of kills made away from the colony was: males—4, females—2, unsexed—1. Dimensions of gulls killed by owls did not differ from those in the population at large (Student's *t*-test; Table 2).

Losses of young were higher than of adults, and much more difficult to assess because (1) small chicks disappear without a trace (some are lost to predators, and others are devoured by adult gulls); and (2) indirect effects of predation can greatly exceed those from killing, and can only be inferred.

At ML in 1982, no chicks were produced from 20 nests on the Channel Islets, and the number of young killed on the Paoha Islets (78) amounted to 2.8% of the total alive in early July; at least 33 chicks were killed in a 13-day period in late July–early August. In 1983, predation again resulted in complete failure on the Channel Islets

(81 nests) and Whitney B (23 nests) and resulted in an estimated loss of 2–3% of the chicks in the study area. The intensity of predation in late July–early August (31 kills in 14 days) was similar to that in 1983.

In 1984, direct mortality, although higher than in other years, remained low. An estimated two young were killed each night from mid-June to mid-August (120 chicks). Indirect mortality, however, was great. No chicks are known to have fledged from 377 nests on the southern end of Coyote Island, the owl's main foraging area (Fig. 6). This was 33% of the nests on that island and 10.6% of those in the study area. Further, if each of 52 adults killed prior to 23 June resulted in the loss of a nest, nest failure from owls rises to at least 12%.

TABLE 2  
MEAN DIMENSIONS (MM) OF ADULT CALIFORNIA GULLS AT MONO LAKE, CALIFORNIA

	Killed by Great Horned Owls			Collected or found dead		
	Sex	N	Mean	Sex	N	Mean
Exposed culmen	M	5	47.3	M	45	47.2
	F	17	42.9	F	85	42.7
Wing (chord)	M	6	389.8	M	47	393.8
	F	34	372.5	F	94	374.5
Tarsus	M	0		M	42	59.2
	F	10	54.0	F	82	55.1

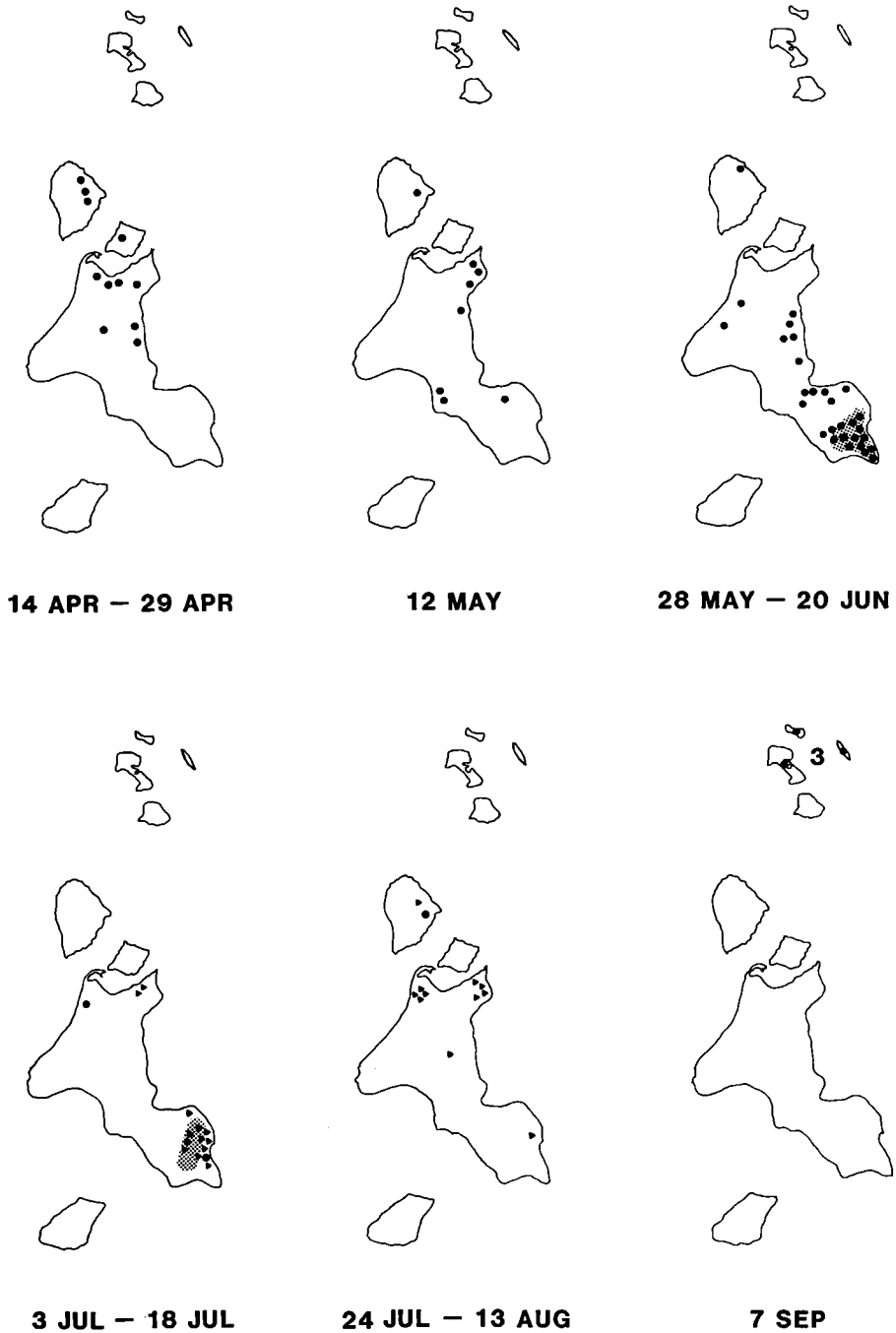


FIGURE 6. Hunting locations of Great Horned Owls on the Paoha Islets, Mono Lake, California, in 1984. Circles indicate kills of adults, triangles of young gulls. Stippled area shows major hunting area for young on Coyote A; some kills in these areas are not plotted individually.

TABLE 3

DIRECT AND INDIRECT MORTALITY OF CHICKS FROM OWL PREDATION AT ANTERO RESERVOIR, COLORADO

Year	Direct	Indirect
1981	15–20 (ca. 50%)	16 (50%)
1982	74 (72.5%)	28 (27.5%)
1983	18 (22.2%)	63 (77.7%)
1984	45 (46.5%)	54 (53.5%)
1985	38 (29.9%)	89 (70.1%)

At AR owls caused the death of 3–10% of chicks in any year. Mass killings sometimes occurred when an owl entered a dense area of the colony; although only one or two chicks were eaten, many might be dismembered (51 in 30 minutes by one owl on 21 June 1982). Nevertheless, indirect mortality sometimes exceeded direct mortality (Table 3). It resulted mainly from exposure and occurred even though chicks formed creches. Temperatures below 0°C, when coupled with rain, resulted in death from hypothermia for untended chicks (e.g., 16 on 20 June 1981). The chicks' tendency to creche when the adults were driven off led to further local increases in density, which facilitated predation.

#### *Responses to owls*

We have no direct observations from ML, although nocturnal desertion of gull nests has been noted (M. Morton pers. comm.). At AR adults left the colony as soon as a kill was made (which was as soon as the owl arrived), but usually returned within 30 min after the owl departed. On nights of intense predation, eggs and chicks might remain unattended for several hours, but adults never remained away until daylight (cf. Southern et al. 1985). In areas of persistent and localized predation at ML, adults often abandoned eggs and chicks. This did not occur at AR, where the owl's activities were more widespread.

The effects of predation extended over more than a single year and affected the use of breeding sites in subsequent seasons. At AR in 1981, predation was insignificant, and colony structure and distribution remained stable into 1982. In 1982–1984, predation became important on Gull Island, and adults began to shift to other areas on Gull Island and invaded Goose Island in 1983. By 1985 many birds had moved to Goose Island; many others, however, never reappeared and presumably joined colonies that were forming elsewhere in the western Great Plains (Chase pers. obs., Findholt 1986). Data from marked adults showed that experienced breeders were involved in shifts within the colony, and that their previous nest sites were claimed by 2–4-year-old birds new to the area, or by 4–5 year olds that

had nested on the periphery of the colony before (Chase in prep.). Local changes in distribution also occurred at ML; in the most dramatic case, an area with persistent predation in 1984 was occupied two weeks later than other areas in 1985, and the number of pairs there dropped from 377 to 109.

#### GOLDEN EAGLE

##### *Foraging patterns*

Eagles usually leave carcasses intact but eat the entire pectoral muscle mass as well as the neck and major limb muscles. Unlike owls, they can easily carry off adult gulls (Behle 1958). One or two eagles hunted regularly at ML, albeit infrequently in the study area. Kills were recorded from 24 April to 28 July; most mortality occurred by mid-June and, accordingly, was concentrated on adults. Forty of 41 kills in the study area took place on Coyote A and were made in depressions that contained some vegetation.

##### *Impact*

In all years, at both areas, the impact of eagles was small and probably restricted to direct mortality, as their disturbances were diurnal and too brief to result in the redistribution or exposure of chicks. At ML from 1983–1985, 32 adult and nine juvenile gull carcasses were attributed to eagle predation, 25 in 1983 alone. No kills were recognized in 1982, but the data are incomplete. As with owls, most eagle-caused mortality among adults was suffered by females (16 of 21 sexed kills), which did not differ in size from females in the colony at large (Jehl unpubl.). At AR eagles killed a total of three gulls in 1984–1985.

##### *Responses to eagles*

The arrival of eagles at ML caused a brief panic flight among gulls, even when the predators were as much as two km overhead. At AR eagles cannot approach undetected and were usually attacked if they approached within 0.5 km of the colonies. Indeed, one was driven into the lake and, after swimming ashore, was harried constantly as it dried off.

Jehl observed two hunting episodes. In one, an eagle flew low across ML from the southwest, intersecting Coyote Islet in an area where few gulls were nesting. Using the crest of the islet for concealment, it cruised, accipiter-like, 0.5 m above the ground, then veered sharply across the ridgeline and plunged into a hollow, which was found to contain the remains of 11 adult gulls. Nesting gulls panicked, but settled within 2 m of the eagle after it landed. When it flushed, a few gulls mobbed it briefly but most continued incubating. In another event, two eagles flushed



from an area of scattered brush on Paoha Island, where they had been chasing a sick gull. Although no more than 50 m from a group of loafing gulls, the gulls showed no reaction until the eagles flushed.

#### OTHER PREDATORS

At AR Common Ravens were harried when they approached and could capture chicks on the periphery of the colony only when adults were distracted (e.g., by the presence of humans). They accounted for the loss of 16 small (<200 g) chicks, but no eggs. Canada Geese (*Branta canadensis*) defending nests killed two adults and one chick that strayed nearby. A muskrat (*Ondatra zibethica*) entered the colony in 1981 and ate five clutches before it was attached and killed by adult gulls.

#### DISCUSSION

Southern et al. (1982) noted that “the following generalizations seem to apply with respect to nocturnal predation on colonial gulls: (1) adult gulls usually react . . . by temporarily fleeing the site, (2) fleeing exposes eggs and young to . . . weather and predation, and (3) no aspect of gull breeding biology . . . appears to be effective in decreasing the toll. Additionally, tenacity to a colony site reduced the probability that a gull will relocate in successive years following nesting failures.” Our data support points 1 through 3, but, we found that site tenacity was relinquished in years following intense predation. Studies of marked gulls at AR showed that stability was an illusion, which resulted from the replacement of previous inhabitants by new birds.

At both colonies indirect losses after periods of nocturnal disturbance exerted a higher toll on chicks than did outright killing, but the causes differed. Death at ML resulted from predation by adult gulls, whereas at AR hypothermia was the major cause. Chardine and Morris (1983) also found that “the cost of desertion at night, in terms of egg failure, was relatively small” when avian predators were involved. Much higher losses have been reported in response to mammalian disturbance (Southern et al. 1985).

The owls' exploitation patterns also differed at the two colonies. At ML they hunted rather predictably, slowly depleting prey in one area before moving on. At AR the owl hop-scotched between areas of high abundance and sometimes indulged in frenzy killing. As a result, the immediate impact at AR was greater, and this may have made it disadvantageous for the owl to return to an area visited previously. These exploitation patterns may also have affected the responses of adult gulls. At ML owls caused relatively little

chick mortality on any night, but their repeated visits caused adults to abandon eggs and chicks (cf. Emlen et al. 1966, Vermeer 1970). At AR, episodes of predation, though locally severe, were non-recurring and parents remained as long as their chicks survived.

#### THE BASIS OF PREY SELECTION

Which factors determine whether individuals will fall prey to predators? Studies of diurnal predators have indicated that very young or very old individuals, as well as those that are ill, out of range, behaving unusually, or are oddly colored are prone to high mortality (Rudebeck 1950–1951, Lack 1954, Mech 1970, Mueller 1974). How nocturnal predators select prey has received little attention, although several studies have indicated that owls are likely to catch individuals that are inexperienced or in unfamiliar terrain (e.g., Pearson and Pearson 1947, Metzgar 1967).

##### *Prey selection by owls*

Owls probably hunted entirely by sight in our colonies. Even on the darkest clear nights there was sufficient starlight to highlight roosting or incubating gulls, whose abundance made hunting by aural cues unnecessary. Owls at the Paoha Islets evidently originated on Negit Island. Because owls tended to begin foraging near their own nest before moving farther afield, nearby gulls suffered high mortality. Data showing that owls returned annually, in a regular sequence when possible, to areas that had been bountiful in the past, indicate that local knowledge plays a major role in hunting success, even when food is superabundant and conspicuous (cf. Martin 1986).

We found, as did Vermeer (1970), that owls preyed on adults early in the season but then shifted to young. The switch might indicate a preference for chicks, but more likely indicates the chicks' greater vulnerability. Adults, having no defense against nocturnal predators, have no alternative but to depart. At AR owls in a feeding frenzy took only large young, which ran and creched; they ignored nearby small chicks, which usually crouched motionless, a behavior that rendered them susceptible to exposure.

The position of a nest in a colony affects its chances of being raided by a diurnal predator; peripheral sites are more vulnerable because the predator has less chance of being detected and endures fewer attacks to reach them (Buckley and Buckley 1980). Nest position would seem of little relevance to owls, because gulls neither mob nor defend their nest against them (Kruuk 1964, 1966). Nevertheless, owls at ML avoided the center of the colony and hunted there only late

in the season, when densities had become very low. This suggests that some aspect of population size or density can impair the success of nocturnal predators as it does for diurnal predators (Burger and Gochfeld 1984). Yet, owls at AR foraged mostly where densities were greatest, and central nests attracted most attention. These differences may be related to the ease with which prey can be detected. At ML the substrate is relatively uniform, and prey are easily perceived. At AR scattered vegetation provided greater camouflage for the chicks, which may have caused the owls to hunt where chicks were most abundant.

At AR and on the Paoha Islets, many kills of adult gulls took place on high, bare ground, evidently because birds there were more quickly detected by arriving owls. We found no consistent relationship between the presence of vegetation and chick mortality at AR; vegetation on the Paoha Islets is too scarce to allow any conclusions. However, in 1985, when gulls nested among dense shrubbery on Negit Island, adults suffered high losses. By nesting in that habitat the gulls achieved concealment but, when discovered, found their escape routes blocked by plants. Thus, it is not surprising that in all locations at ML vegetated areas were consistently the last to be occupied (Jehl and Mahoney MS).

Adult females were highly susceptible to aerial predators (68% of owl kills; 76% of losses to eagles), probably owing to their greater attentiveness. Jehl and Mahoney (1983) inferred differences in the time budgets of male and female California Gulls, and Chase (unpubl.) found that 73–89% of nests were brooded by females from 2200–0400 hrs, and that males often roosted off the territory. Although females average 20% lighter than males, size did not affect an adult's vulnerability because gulls of either sex killed by owls were no smaller than those in the general population, and because even males are far smaller than the maximum size prey for Great Horned Owls. We know of no previous demonstration of differential mortality from avian predators in gull colonies.

#### *Prey selection by eagles*

Eagles are visual predators, and at ML captured prey almost exclusively in two small areas near the edge of Coyote Islet. Although our observations are consistent with the ideas that familiarity with an area is important, and that peripheral nests are more likely to be attacked, physiographic conditions seemed to play the overriding role in hunting success. All but one kill was made where vegetation or undulating terrain impaired the gulls' ability to detect arriving eagles.

#### *Consequences of predation*

Sargeant et al. (1984) reported that red foxes (*Vulpes vulpes*) (1) killed a total of 242,000 adult ducks each year in the Prairie Potholes region of North Dakota, (2) 76% of the kills in the north-central United States were females, and (3) an- atid populations are highly skewed toward males (1.2:1). In our study the number of adult gulls killed by avian predators was too small to have affected the operational sex ratio, and the number of young killed, directly or indirectly, was too small to exert a major influence on population dynamics, although local effects might be extreme. If predators imposed any significant selection on nesting gulls, it is likely to have been related to promoting synchrony and affecting the choice of nesting habitats. Early-nesting adults and late-fledging chicks have a high probability of being captured, because they are the only prey available. This is also true for adults that nest in areas previously frequented by predators or in habitats where the ability to detect or flee from arriving predators is impaired.

#### *Measuring mortality*

Predation is common in seabird colonies. Its direct effects are obvious, but its indirect effects can be hard to perceive and quantify. For example, in 1984, when gull nesting density was greater than in other years on the Paoha Islets, the effects of owls were greater and those of eagles less than in other years. We suspect that these events were interrelated; specifically, that the high density of gulls enhanced indirect losses to owls, but concomitantly made it nearly impossible for eagles to enter the study area undetected during the day.

In studying colonial birds, researchers often determine life history parameters in a "typical" area and extrapolate the results to the entire colony, even though it is impossible to judge *a priori* which study areas, if any, might provide "representative" results. As we have shown, annual variability in the local impact of predators can be large and lead to the abandonment of long-held nesting areas by experienced birds and their later occupancy by inexperienced breeders, which in turn can result in changes in the age structure of a breeding unit (Pugesek and Diem 1983) and in seemingly inexplicable changes in productivity (Chase in prep.). Students of colonial birds should be cognizant of these complications and plan their sampling procedures accordingly.

*Addendum.*—In 1986 Mono Lake gulls expanded their nesting locations on Negit Island and Paoha Island, which were reoccupied in 1985. The owls concentrated their activity near their roost on Negit Island, which lessened predation

pressure elsewhere. On the Paoha Islets and Paoha Island sixteen adults (0.2% of the adult population) were killed between 17 April and 28 May. As in earlier years, most kills (14) were made on Coyote A and females suffered most (75%) of the mortality. Chick mortality was almost unrecorded. Three eagle kills of adult gulls (two males, one female) were made in areas of reduced visibility on Coyote A and Paoha Island. Interestingly, gulls nested successfully on Paoha Island, even though at least one coyote had access to the nesting area.

Antero Reservoir was drained and nesting was disrupted. Two adult gulls killed by eagles early in the season were the only evidence of avian predation.

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