NEST-SITE TENACITY AND PATTERNS OF ADULT MORTALITY IN NESTING CALIFORNIA GULLS (*LARUS CALIFORNICUS*)

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ABSTRACT.—Mortality among breeding adult California Gulls (*Larus californicus*) was low and spread throughout the breeding season in five years of a six-year study. In one year, nesting habitat decreased by 65%, mortality was 3–11 times higher and was concentrated during the period of intense territorial defense. Apparently, some displaced gulls that attempted to reclaim territories near their previous nest sites encountered resistance from territory holders. This resulted in death from trauma, especially among relatively small birds. In general there was a tendency for deaths among females to predominate in the first half of the breeding season and among males, in the latter half. Unlike the situation in British Herring Gulls (*Larus argentatus*), I found no indication of increasing adult mortality at the end of the nesting season. *Received 18 January 1988, accepted 24 August 1988.*

THE number of adult birds that die of unspecified causes in nesting colonies during the breeding season, although typically considered to be very low, is rarely quantified (Kennedy 1973, Coulson and Wooller 1976, Wanless 1983, Spear et al. 1987). I documented the extent, timing, causes, and sex distribution of mortality among adult California Gulls (*Larus californicus*) at Mono Lake, California (1983–1988). I suggest that an anomalous pattern of relatively high mortality in 1984 was associated directly with a major reduction in nesting habitat in the study area, and was promoted by the gulls' strong tendencies toward philopatry and nest-site tenacity.

METHODS

California Gulls begin to arrive at Mono Lake in early March and begin to establish territories in mid-April. Laying commences in late April, peaks in mid-May, and ends in early June. Fledging starts about 6 July and is almost complete by the end of that month. I observed adult mortality on the Paoha Islets (a series of low, sandy, barren islets; described in Jehl et al. 1984, Jehl and Chase 1987), which contained from 12 to 32% of the Mono Lake colony. I measured mortality by walking through the colony at approximately 14-day intervals in early April through late August and removing all dead adults. I recognized 3 causes of death: avian predation (Jehl and Chase 1987), fishing gear, and unspecified. Because unspecified mortality was high in 1984, I skinned freshly dead gulls in 1985–1986 and checked for wounds on the head and body, disease of internal organs, or evidence of parasitism. Sex was determined by direct examination of gonads, when possible, or by external measurements (Jehl 1987). To detect mortality away from the colony, I made beached-bird censuses along the lake shore (Jehl 1988a, b), emphasizing creek mouths and other areas where large numbers of gulls congregate.

RESULTS

In all years except 1984 the timing and extent of unspecified adult mortality were similar. Small numbers of deaths were noted throughout the nesting season (Fig. 1), although few occurred before the middle of May. Mortality was low and averaged 0.34% of the number of breeding birds (Table 1). These unspecified deaths were usually much fewer than those from predation (Table 1). A similar pattern was apparent in 1982, although quantitative data were not taken. In 1984, by contrast, unspecified deaths prevailed and totaled 1.16% of the nesting population, or 3.5 (in 1987) to 11.3 (in 1983) times greater than in other years. In addition, most of the mortality (62%) occurred before the peak of laying.

From 1983 through 1988 losses to predators accounted for 0.3–0.9% of the population. Losses to fishing gear, acquired at lakes 10–50 km away (Mono Lake is fishless), were insignificant.

In all years gulls dead from unspecified causes showed no external signs of injury and none was egg-bound or heavily parasitized. In 1983, 1985, and 1986 (data unavailable for 1987 and 1988), 20–25% were thin and had stained vents, indicating death from disease. In 1984, only 2 of 56 gulls (3.6%) that died in the first half of the season (prior to 15 May) showed similar

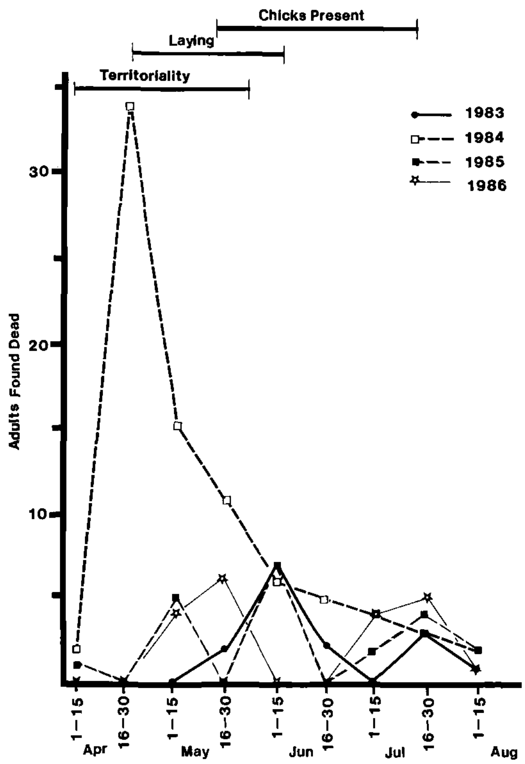

Fig. 1. Timing of deaths from unspecified causes among adult California Gulls on the Paoha Islets, Mono Lake, California, 1983-1986. Data for 1987 and 1988 (not plotted) are similar to years other than 1984.

symptoms. Virtually all had died quickly, as their plumage was in excellent condition and body mass was within normal limits for healthy birds.

Early in 1984, 25 freshly dead adults were salvaged for museum specimens. When they were prepared a few weeks later, several were noted to have suffered cerebral hemorrhages. Unfortunately, no systematic observations of trauma were recorded. Postmortem examinations in 1985 showed that trauma was involved in several deaths in the first half of the season. Four of 10 birds (2 males, 2 females) found prior to 14 June had suffered blows to the head, abdomen, or neck (2 birds showed small fractures of the cervical vertebrae). One male was fat, the other lacked fat deposits, and both females had moderate to heavy fat. No deaths from trauma were recognized in subsequent years.

The overall and annual (except 1984) sex ratios of adults dying from unspecified causes did not differ from 1:1 (Table 2). There was, however, a tendency in all years for female deaths to exceed those of males early in the season ($\chi^2 = 8.10, P < 0.01, \mathrm{df} = 1$) and for male deaths to predominate later ($\chi^2 = 5.13, P \approx 0.025$). This was especially evident in 1984. The trends remain, but are not significant, if 1984 data are excluded. Female gulls in this colony comprise 70% of the adults lost to owl predation, most of which occurs early in season (Jehl and Chase 1987).

Culmen, wing, and tarsus dimensions of gulls that died in the first half of 1984 did not differ from those obtained by collecting (all years; Jehl unpubl.). Masses of freshly dead birds, however, averaged lighter: for 11 males found dead, $\bar{x} = 652$ g vs. $\bar{x} = 735$ g for 18 males collected (student's t-test, $P < 0.05$); for 23 females found dead, $\bar{x} = 547$ g vs. $\bar{x} = 578$ g for 26 collected (student's t-test, $P < 0.02$).

DISCUSSION

During this study major changes occurred in the availability of nesting habitat in the Paoha Islets. The islets began to emerge in the 1960s as the result of a declining lake level. These were colonized in the late 1970s. In 1982 approximately 25 islets covering 13.8 ha were occupied by 4,400 pairs of gulls. A slight rise in lake level decreased islet area to 12.9 ha by the start of the 1983 season, when 8,001 pairs occupied virtually all suitable nesting habitat. By the start of the nesting season in 1984, the lake's

TABLE 1. Mortality of adult California Gulls on the Paoha Islets, Mono Lake, California, 1983-1988.

	1983	1984	1985	1986	1987	1988
No. breeding adults	16,002	7,982	6,302	7,392	6,416	5,666
Total dead (%)	59 (0.37)	147 (2.07)	64 (1.01)	42 (0.57)	65 (1.01)	58 (1.02)
Killed by avian predators (%)	44 (0.27)	64 (0.90)	38 (0.60)	20 (0.27)	52 (0.81)	45 (0.79)
Dying of unspecified causes (%)	15 (0.10)	82 (1.16)	21 (0.33)	20 (0.27)	12 (0.18)	13 (0.28)
Ensnared in fishing gear	0	1	5	2	1	0
Area of colony (ha)	12.9	4.5	4.5[a]	4.3[a]	4.3[a]	4.5[a]

[a] Does not include ca. 0.5 ha on Paoha Island, where 2 pairs nested in 1985 and 102 in 1986.

TABLE 2. Sex of adult California Gulls dying of unspecified causes on the Paoha Islets, Mono Lake, California, 1983–1988.

	10 Apr.–15 June			16 June–15 Aug.		
Year	M	F	U	M	F	U
1983	3	5	1	4	2	—
1984	22	45	1	9	4	1
1985	6	6	1	5	1	2
1986	4	5	1	5	5	—
1987	1	3	—	6	1	1
1988	4	7	—	1	1	—
Total	40	71	4	30	14	4

rapid rise (over 2.5 m), combined with severe erosion, left only eight islets covering 4.5 ha. The number of nesting pairs dropped to 3,546. This produced a net 26% increase in nesting density in the study area. A greater increase was realized in some prime locations. Subsequently, from 1985–1988, when changes in lake level and islet area were minor, the population varied between 2,833 and 3,698 pairs.

Philopatry and nest-site fidelity are well-known in adult gulls (Tinbergen 1953, Chabrzyk and Coulson 1976, Graves et al. 1986), which typically return annually to their former nesting colonies and often nest sites, although they will shift if previous breeding areas become unavailable (McNicholl 1975, Burger and Shisler 1980). After the 1983 season, nesting areas in the study area (though not elsewhere at Mono Lake) were greatly reduced. I suspect that some gulls that attempted to return to their former haunts in 1984 became involved in severe, and sometimes fatal, conflicts as they tried to reclaim territories that no longer existed or to defend territories in areas that had suddenly become overcrowded. These conflicts even involved females, which in closely-related species rarely participate in intense fights (Pierotti 1981, Burger 1984, Hand 1986).

This explanation is consistent with several observations. First, high mortality was restricted to the period of territorial establishment, and territorial interactions and severe fights, though unquantified, were much more conspicuous in 1984 than in any other year from 1982–1986. In addition, cadavers were found only in areas where nesting had occurred in 1983, but not in marginal areas that were occupied later in the season or were being occupied for the first time. The deaths occurred rapidly and at least some early deaths involved trauma. Finally, similar mortality patterns have not occurred subsequently, when nesting space has remained about the same size.

Alternative explanations are less persuasive. Because cadavers were in excellent condition and deaths evidently occurred rapidly, it seems unlikely that disease was involved; furthermore, no sick or dying gulls were recovered early in 1984. While a rapid die-off could result from poisoning—and this could affect sexes differentially if they fed in different areas (Jehl and Mahoney 1983)—neither disease nor poisoning can explain why high mortality was restricted to previous nesting areas. Furthermore, high mortalities were not detected at locations along the shore where thousands of gulls spent long periods each day. Avian predation was slightly greater in 1984 than in other years, but kills are easily recognized (Jehl and Chase 1987) and cannot be related to the unspecified mortality discussed here.

The benefits of philopatry and nest-site fidelity have been widely documented (e.g. McNicholl 1975, Buckley and Buckley 1980, Shields 1982) and need no elaboration. My observations suggest, however, that when established nesting habitat suddenly becomes limited, birds that would rather fight for traditional sites than switch to new territories can incur a heavy cost. Because larids that occupy stable habitats show higher site-tenacity than those that nest in less stable situations, and because site-tenacity increases with age, the conflicts in 1984 may have been experienced mainly by older birds as they attempted to sort out territorial boundaries (McNicholl 1975 and pers. comm.).

Whether increased adult mortality is a predictable consequence of rapid habitat reduction in colonial birds remains to be determined. I note, however, that high but unquantified mortality was recorded in a colony of Laughing Gulls (*L. atricilla*) when habitat reduction caused nesting density to double (Schreiber et al. 1979). Tuck (1960: 125) also observed mortality in Thick-billed Murres (*Uria lomvia*) that seemed related to competition for nest sites: "At Quaker Hat [Labrador], no sites were available except several small, narrow ledges. On each ledge were found nine or ten dead thick-billed murres which appeared to have been killed by sharp jabs on the head."

Territorial contests that occur on the ground favor larger individuals (Jehl and Murray 1985). The relatively low weight of gulls found dead early in 1984 is consistent with this view, as is the high proportion of females (67%), which average 6.5% smaller than males in body dimensions (Schnell 1985) and 16% lighter (Jehl 1987). Porter and Coulson (1987) showed that recruits in a Black-legged Kittiwake (*Rissa tridactyla*) colony were significantly heavier than, and accordingly gained a competitive advantage over, birds that investigated the colony but did not breed.

As noted above, the overall 1:1 sex ratio among dead California Gulls was achieved through temporal changes in which female deaths predominated early in the season and male later. Comparative data are too few to suggest whether this is a general pattern, although a temporal shift is suggested in the Western Gull (*L. occidentalis*). Deaths of adult female Western Gulls exceeded those of males by 1.7:1 from March through May, but not from June through August (1:1) (Spear et al. 1987). The sex ratio of Black-legged Kittiwakes dying in the nesting season (April–August) was also 1:1 (Coulson and Wooller 1976: table 1); these data, as presented, cannot be used to test for temporal shifts. During territorial establishment and nest-site defense (January–March), deaths (attributed to "stress") among male Kittiwakes outnumbered those among females by 14:2.

The annual peak of gull mortality is still unclear, but it does not occur at breeding. In Britain, 50% of the annual mortality among adult Herring Gulls (*L. argentatus*) occurred at the end of the breeding season, from July to September, when body mass was at its lowest point for the year; this pattern was also ascribed to stress (Coulson et al. 1983, Coulson and Butterfield 1986). In California Gulls at Mono Lake, however, adult mortality did not rise as nesting ended. Moreover, adults migrate several hundred miles immediately after the young fledge, an unlikely behavior for birds in poor condition. In the Black-legged Kittiwake, 71% of the annual mortality among breeding adults is thought to occur between September and December, when the birds are at sea (Coulson and Wooller 1976). In adult Western Gulls, 40–50% occurs in winter (December–February), with a smaller peak in fall (September–November) (Spear et al. 1987).

Clarifying patterns and causes of mortality at different points in the annual cycle is difficult because data from band recoveries are often highly biased in favor of recoveries during the breeding season, which are mainly obtained in or near the colony under study (Coulson and Wooller 1976, Spear et al. 1987). Typically, mortality is then associated with phases of the annual cycle and then attributed to "stress," which can be postulated as necessary to explain any observed results. The exemplary broad-based and long-term study of Western Gulls by Spear et al. (1987), in which causes of mortality were determined with high accuracy, illustrates how these biases and ad hoc explanations can be overcome.

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