EFFECTS OF NINE YEARS OF FOX PREDATION ON TWO SPECIES OF BREEDING GULLS

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ABSTRACT.—Ring-billed Gulls (*Larus delawarensis*) and Herring Gulls (*L. argentatus*) nesting on South Manitou Island in Lake Michigan were subjected to at least 9 yr of intense fox predation. Both gull species experienced total or nearly total reproductive failure during all but 1 yr between 1975 and 1983. The number of active nests declined significantly during this period, with Ring-bills showing a more regular rate of reduction. These gull species are unlikely to produce progeny when subjected to regular fox predation. Persistence of the colonies may be the result of a nucleus of experienced, site-tenacious breeders returning to the site year after year. *Received 11 March 1985, accepted 12 April 1985.*

LARUS gulls generally breed on islands free of terrestrial mammals. Such islands usually are too distant from mainland areas to permit regular visitation by mammals and too small to provide alternate food supplies for predators while gulls are seasonally absent. In some instances, mainland sites may suffice for nesting because they are spatially isolated from terrestrial predators by broad expanses of habitat (e.g. industrial developments) unsuitable for predators.

Mammalian predators cause juvenile and adult gull mortality as well as decreased productivity (Emlen et al. 1966, Vermeer 1970, Blokpoel 1971, Morris 1976, Patton and Southern 1977, Southern et al. 1979, Southern 1980, Petersen 1982). Yet, few studies have recorded the fate of gull colonies raided by predators during more than one breeding season. Kruuk (1964), Patterson (1965), Kadlec (1971), Patton (1979), and Petersen (1982) reported the effects of foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), and other mammals on nesting gulls. These authors determined that predators killed more prey than they consumed (surplus killing, Kruuk 1972), contributed to reduced colony size (Patterson 1965, Kadlec 1971), and lowered breeding success (Patterson 1965, Emlen et al. 1966, Petersen 1982). Sekora et al. (1979) found that Glaucous-winged Gulls (*L. glaucescens*) abandoned colony sites on the Aleutian Islands once foxes were successfully established. These authors, however, did not have information on the history of gull-fox interactions on these islands. Other researchers (e.g. Sargeant et al. 1984) have clearly demonstrated that red foxes also severely reduce duck production in mid-continental North America.

In this paper, we provide data for a Ring-billed Gull (*L. delawarensis*) colony and a Herring Gull (*L. argentatus*) colony during 9 consecutive years of coexistence with red foxes.

METHODS

During 9 nesting seasons (1975–1983), we monitored adjacent Ring-billed and Herring gull colonies, each of which was raided regularly by red foxes that resided on the island. The colonies were located on South Manitou Island within the boundaries of Sleeping Bear Dunes National Lakeshore (Leelanau Co., Michigan, 45°02'N, 86°08'W). Gulls have nested on a sandy peninsula at the northeast end of the 2,040-ha island since at least 1940 (Hatt et al. 1948). Shugart (1977) attributed a 72% decline in the Ring-bill population between 1971 and 1972 to human disturbance early in the 1972 nesting cycle rather than fox predation. His data suggest that fox predation first occurred in 1973, at an intensity lower than we report for the years 1975–1983.

During 6 of 9 breeding seasons between 1975 and 1983, a team of 1–3 investigators lived on South Manitou to conduct gull studies. During the other 3 years (1980, 1982–1983), we periodically visited the island to conduct censuses during key portions of the breeding cycle. Weekly visits were made from mid-May through early July in 1980; in 1982–1983, 2–3 visits were made to the island annually. One trip coincided with the onset of hatching at the Calcite Colony near Rogers City (Presque Isle Co.), Michigan, and the others were timed to document chick survival. Colony size, clutch size, hatching success,

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and breeding success were determined by direct-count methods. To calculate the area of occupancy, we mapped the perimeter of the colonies each year and used a planimeter on the resulting maps.

Censuses conducted annually between 17 and 24 May were used for between-year comparisons of colony and clutch sizes. This period encompasses the time when most pairs have nests with eggs in Great Lakes colonies at about 45°N latitude. Direct counts of nests and eggs provided an accurate indication of the number of pairs nesting and their clutch sizes on the count day. Day-to-day variation, however, was high because foxes removed eggs from nests nightly in most years, and consequently many gulls attempted to renest. Comparative data for the Rogers City colony, which was not subjected to fox predation, are provided to confirm that the declines recorded at South Manitou were not occurring region-wide (also see Southern and Southern 1981).

During 1975–1978, we entered the colony daily to determine hatching success and to collect dead adults and chicks and broken eggs. These visits during daylight hours were kept as short as possible to minimize our disturbance of the gulls. Under this regime in 1977, a year when fox predation was less intense, nesting success was close to normal, indicating that the much poorer nesting success in other years was not attributable to investigator-induced disturbance.

From 1975 to 1978, we collected 13,638 dead chicks, of which 9,872 (72%) were autopsied to determine the cause of death. Fox activity also was monitored by direct observation during crepuscular and nocturnal hours (including 28 overnight sessions), and by track counts on groomed perimeter sand strips. Dune sand surrounding the colonies was checked daily for fox tracks during 1975–1977. In 1978, sand strips along the western border of the Ring-billed Gull colony and northern border of the Herring Gull colony were swept with a broom following the daily check for tracks, which provided a more accurate indication of the number of fox movements into and out of the colonies each night.

During 1975–1978, crepuscular observations of foxes and records of fox tracks indicated that up to 5 foxes (3 adults and 2 pups) raided the colonies on some nights. During winter 1976–1977 and spring 1977, the National Park Service attempted to control foxes on the island. Two adult foxes were killed, and a trapping program was continued near the colonies until after nesting began.

RESULTS

PATTERN OF FOX ACTIVITY AND GULL RESPONSES

During each year except 1977, foxes regularly visited the colonies at all stages of the gull reproductive cycle. In 1977, foxes did not enter the colonies until 1 July, by which time most chicks were large and highly mobile. The pattern of fox activity in 1975 also varied from the norm because foxes did not raid the colonies for 8 straight nights during the late incubation and early hatching periods. Foxes generally visited the colonies between 2300 and 0430, but occasionally (6 observations) they remained in the area until after dawn. Periods of prey capture were interspersed with rest periods, during which foxes either consumed prey under cover of vegetation or cached prey near the colonies.

In 1975–1978, some Ring-billed Gulls left the colony as foxes entered. As our study progressed, there was an increasing tendency for Ring-bills to completely abandon the colony site during fox raids. As foxes entered the colony, departure began closest to immediate fox activity and progressed in a wavelike fashion. Airborne gulls joined in panic flights wherein they called in alarm and circled over the colony in unison. During nights of intense fox activity, adult gulls abandoned the colony site and roosted on the nearby harbor. On nights when fox activity was most persistent, adult gulls remained away for the entire night. Groups of gulls occasionally returned to the site and settled on their nests during lulls in fox activity.

By 1979, and throughout the remainder of the study, Ring-bills regularly abandoned the colony site as soon as foxes arrived. Adults then spent most nights roosting on the harbor and did not resume incubation until near dawn. Similar tendencies for nocturnal desertion were exhibited by Herring Gulls, but it was difficult to monitor their presence because most nests were surrounded by tall grass.

FOX PREDATION ON ADULT GULLS

Of all adult gulls found dead at the colonies in 1975, 1976, and 1978, foxes killed at least 71.9% (n = 196), 88.7% (n = 177), and 93.4% (n = 196), respectively (Table 1). In 1977, only 23 dead gulls were found, 1 (4.3%) of which was fox-killed (Table 1). Foxes consumed only a small fraction of the gulls they killed. For example, in 1978, portions of only 16 (15.4%) of the Ring-bills were consumed; 3 other gulls were cached but were not used later by foxes.

Foxes were most successful at preying on adult gulls during the hatching period. For ex-

TABLE 1. Evidence of fox-caused mortality at South Manitou Island, 1975–1978.

Year	Eggs out of nests	Dead chicks	Chicks autopsied		Autopsied chicks killed by foxes		Total dead adults	Adults killed by foxes	
			n	%	*n*	%		*n*	%
Ring-billed Gulls									
1975	279	8,324	5,136	61.7	2,357	45.9	172	128	74.4
1976	949	959	685	71.4	326	47.6	144	136	94.4
1977	34	856	856	100.0	421	49.2	18	1	5.6
1978	224	2,825	2,825	100.0	645	22.8	114	104	91.2
Herring Gulls									
1975	24	372	68	18.3	36	52.9	24	13	54.2
1976	57	<50[a]	<50[a]	100.0	—[b]		33	21	63.6
1977	4	166	166	100.0	—[b]		5	0	0
1978	43	136	136	100.0	83	61.0	82	79	96.3
Total[c]	1,614	13,638	9,872				592	482	

[a] Fewer than 50 chicks hatched this year (exact number not determinable). Estimates excluded from totals.
[b] All birds too badly decomposed to allow determination of cause of death.
[c] Totals exclude Herring Gulls in 1976.

ample, during 7 nights in 1978, foxes killed 71 adult Ring-bills. This was 68.3% ($n = 104$) of the adult Ring-bills killed by foxes during that nesting season. Fox predation on adult gulls was negligible after 1978 because the birds regularly abandoned the colony sites during fox forays.

Predation Effects on Colony Size and Reproduction

Ring-billed Gulls.—The number of Ring-billed Gulls nesting on the island declined fairly consistently over the 9-yr study period, from 5,479 in 1975 to 879 pairs in 1983 (Table 2). This was an 84% decrease in the number of breeding pairs. In two years, 1978 and 1982, slight increases occurred in colony size, but in each instance the downward trend resumed the following year. The increase of 264 nests (10%) in 1978 followed a year in which fox predation was interrupted by control attempts. The fact that gulls had fairly normal reproductive success in 1977 (Table 2) was reflected in the 1978 colony size. The effect of foxes is demonstrated by comparing changes in colony size at South Manitou with those at Rogers City (Table 3). Between 1974 and 1983, the number of Ring-billed Gull pairs nesting at Rogers City increased 153%.

TABLE 2. Annual data on colony size, clutch size, and success for South Manitou Ring-billed Gulls (U = unknown).

Year	Nests with eggs[a]	Empty nests	Total nests	Percent cumulative change	Mean clutch size[b]	Eggs hatched (minimum)		Young fledged/ pair	Colony area		Date first chick hatched
						n	%		m^2	m^2/ pair	
1975	5,175	304	5,479		2.74	8,534	60.1	0.07	12,850	2.35	25 May
1976	3,935	127	4,062	−25.9	2.58	1,525	15.0	0.01[c]	10,345	2.55	26 May
1977	2,686	39	2,725	−50.3	2.89	4,767	62.5	1.44	7,565	2.78	25 May
1978	2,919	70	2,989	−45.5	2.61	2,826	37.0	<0.01[d]	10,123	3.39	28 May
1979	1,815	279	2,094	−61.8	2.53	830	18.1	0	6,068	2.90	3 June
1980	1,371	262	1,633	−70.2	2.27	U	U	0	6,500	3.98	30 May
1981	910	343	1,253	−77.1	2.43	U	U	0	5,500	4.39	9 June
1982	1,095	217	1,312	−76.1	2.12	U	U	0	4,100	3.13	U
1983	725	154	879	−84.0	2.17	U	U	0	3,300	3.75	U

[a] Census conducted between 17 and 24 May.
[b] For nests with eggs; empty nests excluded.
[c] Only 9 young fledged.
[d] Only 1 young fledged.

TABLE 3. Comparative data on colony size and clutch size for Rogers City Ring-billed Gulls.

Year	Nests with eggs[a]	Empty nests	Total nests	Percent cumulative change	Mean clutch size[b]	Date first chick hatched
1974	3,924	129	4,053		2.67	20 May
1975	5,317	26	5,343	31.8	2.83	23 May
1976	6,502	66	6,568	62.1	2.79	15 May
1977	7,920	42	7,962	96.5	2.78	15 May
1978	4,918	616	5,534	36.5	2.70	21 May
1979	7,904	118	8,022	97.9	2.77	21 May
1980	7,764	292	8,056	98.8	2.66	14 May
1981	8,254	174	8,428	107.9	2.66	14 May
1982	10,017	77	10,094	149.1	2.82	17 May
1983	10,171	101	10,272	153.4	2.71	17 May

[a] Censuses between 17 and 20 May.
[b] For nests with eggs only; empty nests excluded.

Between 1975 and 1983 the nesting area used by Ring-bills at South Manitou declined to 25.7% of the original colony size (Table 2). There was a break in the pattern of declining area only during 1978. As indicated above, this followed a year of low predation and successful reproduction. Ring-bills retained their clumped nesting pattern as colony size diminished, although the amount of space occupied per gull pair increased (Table 2). The area occupied in 1983 coincided with the portion of the colony in which the first chicks hatched in both 1975 and 1976. At Rogers City, where we marked individuals and nest sites, egg-laying and hatching consistently began in the same part of the colony year after year. It appears that experienced, site-tenacious birds acted as pacesetters in the colony.

Mean clutch size at South Manitou varied between 2.12 and 2.89 (Table 2). During the first 4 years of the study (1975–1978), clutch sizes were within the range recorded at Rogers City (Table 3), but thereafter the means were consistently lower than any recorded at Rogers City. This change coincided with foxes spending more time in the colony during the incubation stage in the latter years. The clutch sizes we report represent the number of eggs remaining in nests during censuses, not necessarily the number of eggs laid.

Hatching success at South Manitou was lower than normal during all 5 years for which we have data (range 15–62%, Table 2). The highest hatching success was recorded in 1977, when no fox predation occurred during incubation. In 1977, records from a nest transect in which we monitored the fate of each egg indicated a hatching success of 88.0% (n = 1,334). After 1978, hatching was less synchronous, most eggs pipped or hatched on a particular day disap-

TABLE 4. Annual data on colony size, clutch size, and success for South Manitou Herring Gulls (U = unknown).

Year	Nests with eggs[a]	Empty nests	Total nests	Percent cumulative change	Mean clutch size[b]	Eggs hatched (minimum)		Young fledged/ pair	Colony area		Date first chick hatched
						n	%		m^2	m^2/pair	
1975	474	100	574		2.45	375	32.3	0.01	41,980	73.14	23 May
1976	281	246	527	− 8.2	1.82	50	10.4	0	41,980	79.66	25 May
1977	466	12	478	−16.7	2.98	858	61.7	1.45	41,500	86.82	21 May
1978	421	116	537	− 6.5	2.24	136	14.4	0	41,500	77.28	2 June
1979	364	277	641	11.7	2.39	291	33.4	0	41,500	64.74	29 May
1980	147	148	295	−48.6	1.46	U	U	0	31,500	106.78	U
1981	191	131	322	−43.9	2.10	U	U	0	31,500	97.83	U
1982	84	109	193	−66.4	2.10	U	U	0	27,500	142.49	U
1983	46	221	267	−53.5	1.22	U	U	0	27,500	103.00	U

[a] 17–24 May censuses.
[b] For nests with eggs; empty nests excluded.

peared that night, and it became impossible to determine how many eggs actually hatched. Hatching success for a sample of 60 nests (n = 182 eggs) at the Rogers City colony in 1983 was 92.2%.

Foxes contributed to the lower clutch size and hatching success recorded at South Manitou in three ways. First, foxes preyed on eggs, but the extent of egg predation was difficult to determine. Twenty eggs with obvious signs of fox predation (e.g. canine punctures) were found in 1978, but this accounted for only 0.4% of those eggs that failed to hatch that year (n = 4,803). Second, during nocturnal disturbances, foxes caused gulls to knock eggs out of their nests during startled flights. In 1975, 1976, and 1978, we recorded 279, 949, and 224 unbroken eggs outside of nestcups, respectively. By contrast, in the absence of fox predation in 1977, only 34 eggs were found outside nests. The third, and perhaps most important, reason for the low hatching success was embryo mortality caused by eggs cooling during prolonged periods (often more than 4 h) of nocturnal abandonment by parent gulls. For example, we recorded 77 dead embryos in pipped eggs in 1976, 0 in 1977 when no fox visits occurred during incubation, and 588 in 1978. During the late incubation and hatching phases in 1975, 1976, and 1978, low ambient nighttime temperatures ranged from 0° to 7°C. Such temperatures are sufficient to reduce the probability that gull eggs will hatch, particularly when exposure occurs late in the incubation period (Hunter et al. 1976).

Chick survival was extremely low in all years except 1977 (Table 2). During most years (1979–1983) no chicks were produced, and in two years (1976, 1978) only 1–9 chicks survived beyond 30 days. Essentially all chicks not consumed by foxes during the first night post-hatching died from prolonged exposure to low ambient temperatures that same night. In 1975 and 1977, fox activity in the colony during the early stages of the reproductive cycle was irregular or nonexistent, especially during the critical late incubation and hatching periods. In 1975, fox disturbances intensified after hatching began, and direct killing of chicks was heaviest that year, with a mean of 87.3 chicks killed per night (range 2–430, n = 17 nights, 31 May to 17 July). Many newly hatched chicks also died from other causes, presumably exposure, with total nightly chick losses averaging 225.3 (range 4–1,064). Because foxes did not raid the colony from 23 to 30 May 1975, hatching was more synchronous, and many chicks already were hatched when predation resumed on 31 May. Consequently, there was a predator swamping effect, and some chicks survived simply because foxes did not attack them. Chicks that reached several weeks of age apparently were mobile enough to disperse, thereby reducing the likelihood of foxes finding them. In 1977, foxes did not enter the colony until 1 July. Thereafter, a single fox raided the colony nightly until 17 July. As a consequence of the reduced predation in 1977, the average number of young fledged per nest (1.44) was closer to normal values for colonies subjected to the usual array of limiting factors. In 1983, for example, the mean number of young fledged per nest at Rogers City was 1.23 (n = 60 nests).

Herring Gulls.—The number of Herring Gull nests at South Manitou fluctuated between 478 and 641 during 1975–1979 (Table 4). We cannot account for the increase that occurred in 1979. The number of nests that contained eggs at census time showed a downward trend over the years (Table 4), with 1977 being the exceptional year. Beginning in 1980, after two consecutive years of complete reproductive failure, the colony showed a sharp reduction in size (1980–1983, $\bar{x}$ = 269.3; Table 4). Over the 9-yr period, the number of breeding pairs at South Manitou decreased by 53%. A comparable decline did not occur at the Rogers City colony (Table 5).

The size of the nesting area used by Herring Gulls also declined over the study period (Table 4), but the reduction was not as great as in the case of Ring-billed Gulls. Herring Gulls retained their dispersed nesting pattern and occupied most of the area used originally, with more space between nests resulting from desertions or deaths. A 49% reduction in the nesting population by 1980 was reflected in a 25% reduction in the area used for nesting. By 1983 the gulls were using about 35% less space than in 1975.

Some Herring Gulls responded to repeated egg loss by constructing auxiliary nests. Such nests varied in number within a territory and sometimes were in contact with the original nest, but in other cases were 1–2 m away. Because all or most of these nests were constructed after the birds had experienced several weeks of fox predation, they probably were not indicative of polygynous matings (Shugart and Southern 1977). This tendency may have con-

TABLE 5. Comparative data on colony size and clutch size for Rogers City Herring Gulls.

Year	Nests with eggs[a]	Empty nests	Total nests	Percent cumulative change	Mean clutch size[b]	Date first chick hatched
1974	762	40	802		2.76	20 May
1975	823	25	848	5.7	2.81	21 May
1976	786	42	828	3.2	2.68	15 May
1977	873	15	888	10.7	2.90	14 May
1978	823	104	927	16.0	2.78	20 May
1979	733	28	761	−5.1	2.81	20 May
1980	852	56	908	13.2	2.79	14 May
1981	797	39	836	4.2	2.77	13 May
1982			No census conducted			
1983	746	39	785	−2.1	2.64	15 May

[a] Censuses between 17 and 24 May.
[b] For nests with eggs only; empty nests excluded.

tributed to the high number of empty nests (Table 4), although obvious satellite nests were not counted during censuses.

Mean clutch size at South Manitou varied from 1.22 to 2.98 (Table 4). For comparison, mean clutch size for Herring G lls at Rogers City (1974–1983) ranged from 2.64 to 2.90 (Table 5). Thus, during all but one year (1977), clutch sizes were smaller on average at South Manitou than at a colony without heavy predation.

Hatching success was lower than normal during all years for which data are available (1975–1979), ranging between 10% and 62% of eggs laid (Table 4). From 1980 to 1983, essentially no Herring Gull chicks hatched or survived through the first night after hatching. With the exception of 1977, Herring Gulls experienced complete reproductive failure every year.

DISCUSSION

Ring-billed and Herring gulls are unlikely to produce progeny at colony sites subjected to regular fox predation. Our nocturnal observations during fox raids indicated that neither gull species exhibited behavior that effectively deterred or distracted foxes from their hunting. During nocturnal attacks, foxes killed small numbers of adult gulls and caused severe losses of eggs and young. They also affected hatching rates and chick survival indirectly by causing adult gulls to abandon nests, thereby exposing embryos and newly hatched chicks to low ambient temperatures. Nocturnal abandonment of a colony site following the onset of incubation is not typical of Ring-billed Gulls, although sites are regularly abandoned until about 10% of the pairs have initiated egg-laying (pers. obs.).

Because the impact of nocturnal mammalian predators on colonial ground-nesting gulls is so severe (see Southern et al. 1982), selective pressures should favor use of colony sites that are characteristically free of such predators. Indeed, most nesting sites traditionally used by these two gull species in the Great Lakes area are on small islands that are difficult for mammalian predators to reach, unsuitable for predator survival when gulls are absent, and lack habitats attractive to predators (see Scharf 1979 for colony descriptions).

If use of predator-free colony sites is essential to successful reproduction by gulls, why do they persist in using a site after predators have become established, as was the case at South Manitou? We have no evidence to suggest that the availability of nest sites was limiting for either species on the Great Lakes (particularly lakes Michigan and Huron). Gulls nested successfully on South Manitou Island prior to National Park Service acquisition around 1974 because island residents controlled foxes. The residents' efforts apparently were sufficient to allow gulls to become established as breeders and to develop site fidelity. After 1974, as fox numbers increased, the colonies declined. Persistence of the colonies from 1975 to 1983 probably was the result of a nucleus of experienced, site-tenacious breeders returning to the site annually. Limited band-recovery data from fox-killed and trapped gulls at South Manitou support this possibility. Experienced birds that returned annually probably stimulated site oc-

cupancy and some recruitment. As a consequence, the South Manitou colonies persisted even though all stages of the reproductive cycle were disrupted by foxes and complete reproductive failure was experienced repeatedly. In the short-term perspective, at least, site fidelity under these circumstances proved to be disadvantageous.

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