SPACING OUT AT MONO LAKE: BREEDING SUCCESS, NEST DENSITY, AND PREDATION IN THE SNOWY PLOVER

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ABSTRACT.—Snowy Plovers (*Charadrius alexandrinus*) nesting on the exposed lake bed surrounding Mono Lake, California lose up to 40% of their clutches. Most are destroyed by predators, predominantly California Gulls (*Larus californicus*). In 1978 Snowy Plover reproduction was estimated at 0.49–0.70 fledged young per female. Population stability was estimated to require 0.80 fledged young per female. A series of experiments with artificial clutches placed at different densities in the nesting area demonstrates that the predators can have an effect on the plovers' nesting success that is dependent upon their nest density. The maintenance of low nesting density is an important antipredator adaptation. We consider predation on clutches and broods to be the major limiting factor on the Snowy Plover population at Mono Lake. *Received 18 January 1982, accepted 27 May 1982.*

MANY workers have hypothesized that shorebird mating systems, territorial behavior and nest-dispersion patterns evolving together have increased the species' ability to exploit food resources or thwart predators, thereby enhancing the chances of successful breeding (e.g. Holmes 1966, 1972; Oring and Knudson 1972; Graul 1973; Pitelka et al. 1974; Safriel 1975). The effect of food resources and predators on shorebird breeding success has largely gone unmeasured. In fact, few workers have measured breeding success, because shorebirds' precocial young are almost impossible to relocate after they leave the nest.

Tinbergen et al. (1967) conducted the first experiments demonstrating that the dispersion of birds' nests may affect their survival. They found that the rate at which Carrion Crows (*Corvus corone*) took camouflaged, scattered chicken eggs increased with increasing egg density. Goransson et al. (1975) exposed camouflaged dwarf hen eggs to Carrion Crows and Herring Gulls (*Larus argentatus*) and obtained similar results, except when the eggs were in an area defended by Lapwings (*Vanellus vanellus*), which drove the predators from the area. Gottfried's (1978) experiments with imitation landbird nests in old-field habitat showed no relationship between the rate of nest loss and nest density. He suspected that the differences between his and the previously mentioned experiments may have been related to the types of predators. Snakes were responsible for most losses at his study site. The results of these and other experiments (Andersson and Wiklund 1978) indicate that a wide dispersion of nests may be the best strategy for birds unable to defend their nests against visually cued avian predators.

We have measured breeding success of the Snowy Plover (*Charadrius alexandrinus nivosus*) at several localities in California as part of a larger study of the species' breeding status in the state. Noting a particularly wide spacing of nests and a high level of nest loss to predators at Mono Lake, we undertook experiments with artificial nests to determine the value this wide spacing might have in reducing the predators' effects on nesting success.

This paper describes how we estimated breeding success, how the estimated success relates to the level of production needed for maintenance of population size, and how predators limit nesting success and possibly regulate the size of the breeding population.

STUDY AREA AND METHODS

Study area.—The study was conducted at Mono Lake, Mono County, California. This nearly elliptical, 15-km by 20-km, alkaline lake lies in a closed

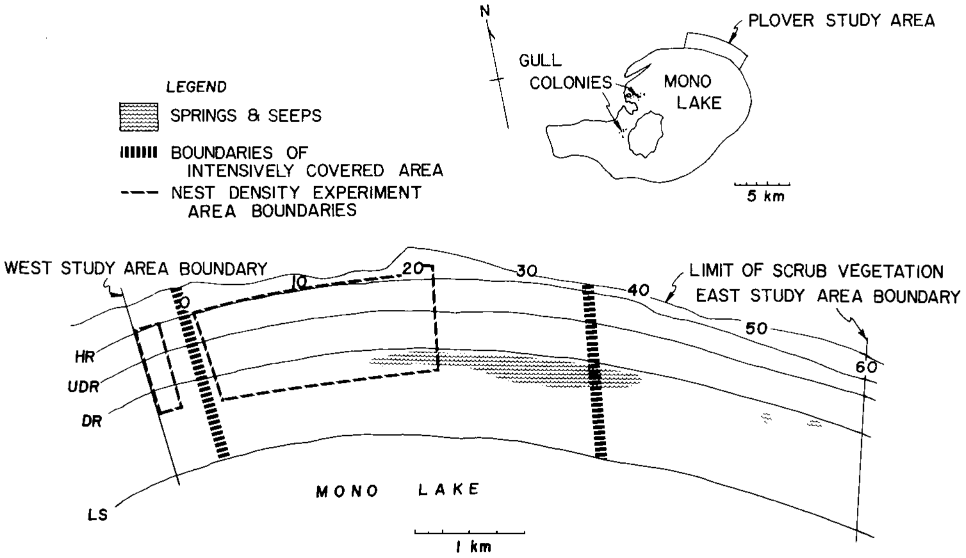

Fig. 1. Map of the Mono Lake study site showing the area of experimental plots. HR is High Ridge, UDR is Upper Drift Ridge, DR is Drift Ridge, and LS is Lake Shore. Numbers above HR are of our reference stakes.

basin about 1,940 m above sea level at the eastern base of the Sierra Nevada. The climate is typified by cold, predominantly dry winters and hot, dry summers with occasional thunderstorms and high winds.

Our study area is a 6.5- × 1.5-km section of the northeast shore of the lake (Fig. 1). The terrain consists of old beach ridges and alkaline flats. The three most prominent ridges, High Ridge (HR), Upper Drift Ridge (UDR), and Drift Ridge (DR), ran parallel to the shore 1,400 m, 1,100 m, and 750 m, respectively, from the water's edge in 1978. The distances increase by 30–100 m per year as Mono Lake's level declines due to municipal diversions of fresh water from tributary streams. Above UDR the substrate consists of coarse sand sprinkled with dark-colored basalt pebble. Below UDR it consists of alkali-encrusted sand overlaid in places by loose drifted sand. The study area is barren except for an accumulation of driftwood along DR and UDR and patchy vegetation consisting of a few scattered greasewood bushes (*Sarcobatus vermiculatus*) and a sparse cover of salt grass (*Distichlis spicata*) on a small portion of the gravel ridges. Rows of 0.3-m-high stakes placed 100 m apart along the lake shore (LS) and the three prominent ridges (DR, UDR, HR) provided references for the locations of birds and nests.

Shallow puddles of brine up to 150 m wide form along about 2.5 km of the south edge of DR where water seeps onto the lake bed. Two small springs approximately 0.5 ha in size occur within 200 m of DR in the southeastern 1 km of the study area (Fig. 1). Feeding plovers often congregate at these areas and at the lake shore.

Few birds and mammals occur in the study area. Other than the Snowy Plover, the only nesting birds were a few Horned Larks (*Eremophila alpestris*) and an occasional American Avocet (*Recurvirostra americana*). A colony of about 40,000 California Gulls (*Larus californicus*) nests on islands in Mono Lake approximately 7 km southwest of the study plot (Fig. 1). The gulls, a few Common Ravens (*Corvus corax*) and coyotes (*Canis latrans*) often forage in the area.

The study area was almost devoid of human disturbance except for our activities. Two to 6 people conducted the study from 3 April to 23 September 1978, 2 people from 11 May to 16 August 1979, 1 to 3 people from 30 May to 24 August 1980, and 1 to 4 people from 20 May to 15 August 1981.

Determination of productivity.—Before finding any nests in 1978, we trapped 22 adult plovers, snaring them by the feet on strips of noose-covered hardware mesh placed in feeding areas. Using these mats we trapped additional adults at their nests: 44 in 1978, 70 in 1980, and 15 in 1981. We gave each bird a unique combination of two bicolored bands in 1978 and four unicolored bands in later years. Birds were released within 5 min of capture.

In 1978, two to four observers each spent at least 5 h almost every day searching for all nests from 0.5 to 3.5 km east of the western boundary of the study area. From 1979 to 1981 one or two observers located a sample of nests within this area (hereafter referred to as the area of intensive nest search). In 1981 this area was extended by 1.2 km to the west. In all years we also located a sample of nests throughout the rest of the area. In 1978 we marked nests with 0.3-m-high stakes placed 10 m to the south. Afterwards we marked nest locations by a variety of naturally occurring objects placed in various directions from 1 to 10 m from the nest. In all years we described each nest by its distance and direction from the nearest reference stake, substrate type, and distance to objects and vegetation.

Most nests with incomplete clutches were checked daily to determine the laying date of the last egg. Hatching dates were predicted for these nests based on the date the last egg was laid and the average 27-day incubation period (Warriner et al. unpubl.). For nests found after clutch completion, hatching dates were estimated using the egg flotation method (Hays and LeCroy 1971) with data from a coastal Snowy Plover population. This method was accurate to within ± 3 days.

We checked most clutches at least once every 5 days until about 4 days before the predicted hatching date, when we normally began checking them one or two times daily. Nests were considered destroyed when eggs disappeared well before the projected hatching date or when remains or predator tracks were found at the nest site. Destruction dates for clutches were considered to lie midway between the date the nest was last known to be active and when it was first found destroyed, except in a few instances when the date could be more accurately approximated by evidence at the nest.

We estimated the number of nests initiated in early and late parts of the nesting season using a modification of Mayfield's (1961) method. We modified his technique to take into account the seasonal variation in clutch hatching rate at Mono Lake (see Results). The goal of our modification was to estimate the risk to predation experienced by cohorts of clutches inititated during each 7-day period throughout the nesting season. For each 7-day cohort we considered the block of time from its first date to its latest potential hatching date. The best estimate of predation risk is gained by computing the total number of clutch exposure days (N) and clutches destroyed (D) in this block of time, regardless of the cohorts to which these clutches belong. Once these values are computed, calculation of the number of nesting attempts is straightforward using Mayfield's equation: $X = Y/(1 - r)^{31}$, where X is the number of nesting attempts, Y is the number of clutches observed to hatch, and r (the quotient D/N) is the daily per clutch probability of a clutch being destroyed. The exposure period (egg-laying plus incubation periods) used in the equation is 31 days. An estimate of r for the early and late parts of the nesting seasons is $\Sigma D/\Sigma N$.

We attempted to band all chicks from each nest in 1978 but not in later years. In 1978 each brood received a unique color combination, but we used only one color combination for all broods in later years. In all years chicks received a single bicolored band. In 1978 we expended considerable effort searching for banded chicks and fledged juveniles. In all years we searched feeding areas for color-banded adults.

In this paper, clutch-hatching rate is the proportion of clutches hatching at least one chick, and brood-fledging rate is the proportion of broods fledging at least one juvenile.

Nest density experiments.—In 1979 we experimented with imitation clutches to study the effect of predators on the survival of eggs grouped at different densities. Imitation clutches consisted of three eggs of the Japanese Quail (*Coturnix coturnix*) set in shallow scrapes. Quail eggs closely resemble those of Snowy Plovers in size, shape, and color. Clutches were set out in a grid at coordinate points chosen from a table of random numbers and were checked after 5 days. When a clutch was destroyed, we replaced it at a new, randomly chosen location in the grid; if not, we left it for another 5 days. We scattered groups of imitation clutches at densities of approximately 1, 20, and 40 per 6 ha. One Snowy Plover nest per 6 ha is the maximum density found at Mono Lake in 1978, while about 20 nests per 6 ha is the maximum density reported for any site in California (Warriner et al. unpubl.). Imitation clutches were set between the western boundary of the study site and 2.7 km east (Fig. 1), in an area that was being used simultaneously by nesting plovers. We conducted seven experiments, varying the spacing of clutches and number of 5-day trials (see Fig. 4). For the first two experiments we used 0.3-m-high wooden stakes to mark the artificial clutches but later switched to natural markers to avoid possibly assisting predators in finding nests. In the first six experiments random placement of clutches did not necessarily result in the same number of clumped and dispersed clutches being placed in the six nest-site types described in the Results. In the final experiment, while grid points for all clutches were randomly chosen, equal numbers of dispersed and clumped clutches were placed in each of the six nest-site types in each trial to eliminate any bias that might arise due to differences in success of clutches among different types of sites.

RESULTS

BREEDING BIOLOGY

Snowy Plovers do not winter at Mono Lake. In 1978 we first saw them on 5 April, two days after we began observations. Egg laying began about 18 April and continued until 15 July. The incubation period varied between 25 and 32 days ($\bar{x} = 26.9$, $n = 9$). Earliest clutches hatched on 21 May and latest on 16 August in 1978. We

TABLE 1. Causes of nest loss for Snowy Plovers at Mono Lake.

Cause	1978	1979	1980	1981	Total
Unknown	35	21	4	11	71
Predation by					
California Gull	15	3	9	1	28
Common Raven	3	2	1	—	6
Canine	3	1	3	—	7
Human	1	—	—	—	1
Wind	1	—	—	—	1
Desertion	1	3	2	2	8

saw the first fledged chick (juvenile) at Mono Lake on 6 July 1978 but did not determine fledging dates of the last chicks.

Over the 4 yr at Mono Lake, the observed hatching rate of clutches varied in the intensively searched area from 39.5 to 68.2%. Predators were responsible for most nest loss. Their tracks were found at 41 of the 122 nests destroyed during the study; they probably also took the majority of nests lost to unknown causes (Table 1). The only evidence predators left at nests was tracks in the sand, and these were often blown away before we checked the nests. At many sites the substrate was too hard to show any tracks.

At Mono Lake Snowy Plovers nest on rolling sand-pebble ridges marking old shorelines and on alkali-encrusted sand flat more recently exposed by the dropping lake. Nests may be in the open or beside or under an overhanging object such as a tumbleweed, piece of tufa (precipitate of calcium carbonate), or driftwood. By considering the two substrate types and three nest positions in relation to an object, we identified six nest-site types. A preliminary analysis of data from work still in progress indicates that there may be differences in nesting success of birds using different nest-site types.

In 1978 the observed clutch-hatching rate varied during the summer, with the highest rates occurring for early and late nests (Fig. 2). Observed clutch-hatching rates for nests outside the intensively searched area were consistently lower than for those inside (Fig. 2). This indicates that our activities did not increase egg loss. With the exception of coyotes, which were deterred, other predators were indifferent to our presence. We spent little time searching the peripheral area where we probably found the most conspicuous nests; these were probably the same ones that predators found most easily. Thus, variation in our searching effort may account for the observed differences in hatching rates between the two areas.

Mayfield (1961) pointed out that observed hatching rates are usually overestimates of the true hatching rate, because clutches that are destroyed and never found are excluded from the calculations. Using Mayfield's methods (1961, 1975), we corrected our estimates of hatching rates in the intensively searched portion of the study area in 1978. Calculated hatching rates show the same trend as observed rates; clutches initiated in mid-breeding season have lower hatching rates than those initiated earlier and later (Fig. 2).

In 1978 the proportion of broods fledging young was highest for those from clutches initiated mid-season (Fig. 3). A possible increase (sample sizes are too small for certainty) in brood-fledging rate from early to mid-season parallels the increase in the clutch-hatching rate of nests being incubated at about the same time (Fig. 3). Because predators are responsible for most egg loss, the parallel rates indicate that they also may be responsible for considerable brood loss. In 1981 Swarth saw a gull catch and eat a chick. The distressed reactions and distraction displays of male plovers when gulls approach their broods are further evidence that gull predation on chicks may occur regularly. The possible decline in brood-fledging rate from mid- to late season is not easily explained by increased predator activity, because gulls are migrating from the area at this time. We suspect a waning of parental attentiveness may be a factor in the late-season decline.

The estimated mean number of chicks fledged per successful brood in 1978 was 1.64, a figure derived from the mean number of chicks, 80–90% adult size, in 22 broods. We assumed that mortaility was negligible in the short time from when the chicks reached this size until fledging.

PRODUCTIVITY AND POPULATION MAINTENANCE

The data on hatching and fledging success from the intensively searched area can be used to calculate the productivity of the Snowy Plov-

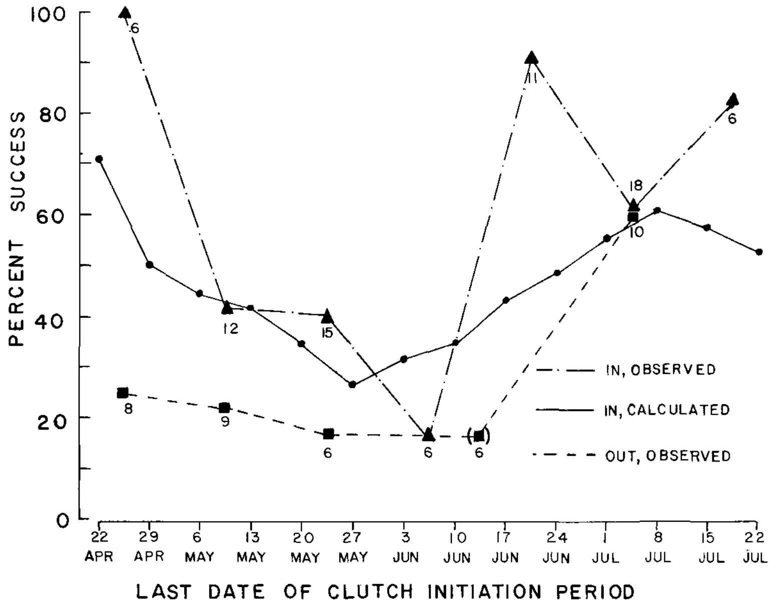

Fig. 2. Observed and calculated hatching rates of clutches initiated over successive time intervals at Mono Lake in 1978: calculated rates are plotted weekly, observed rates biweekly (see Table 2). Symbol in parenthesis indicates a 4-week period grouped to increase sample size. Sample sizes for observed rates are noted next to symbols. "In" refers to nests within and "out" to nests outside the area of intensive search.

er at Mono Lake in 1978 expressed as number of young fledged per breeding female. We divided the nesting period into two parts and assumed, for ease of analysis, that all nests initiated on 3 June or earlier represented first attempts and that all renesting attempts occurred thereafter. (Eleven of 12 known renesting attempts were initiated after 3 June.) Using our modification of Mayfield's methods and data presented in Table 2, we estimate that the 46 early- and 65 late-nesting attempts were made in the intensively searched area. We estimated the numbers of females making first and second nesting attempts in the intensively searched area during the late period (Table 3). Based on additional calculations, we estimate that 0.49 young were produced per nesting female in 1978 (Table 3).

Using estimates of annual adult (S_a) and juvenile (S_j) survival rates, we can estimate the mean number of fledged young (Z) that females should produce to maintain the breeding population size. We derived S_a from resightings of individually marked plovers on Monterey Bay from one breeding season to the next. There and at Mono Lake, return rates to a specific breeding site were higher for males than females (Table 4). The difference in detection rates between the sexes is considerably less, however, when birds not returning to their former breeding sites are taken into account. We have found some of the alternative sites frequented by coastal but not by Mono Lake females; thus, we must use the coastal data for our calculations. We pooled data for the two years and sexes, assuming no real difference between them, and estimate S_a to be 0.743 (Table 4). This estimate is minimal, as some surviving birds may have gone undetected. The survival rate for juveniles is based on 14 birds fledging in 1977 at Point Reyes, Marin County, California and that (with one exception) wintered there in 1977–1978. Nine returned the following winter, so minimal annual survival rate, S_j, equals 0.643. Because juveniles disperse in summer and fall and often disappear from the natal area, we were fortunate to obtain any information on juvenile survival rate. From the equation $Z = 2(1 - S_a)/S_j$, we calculated that 0.80 young per breeding female were required annually for population maintenance. This equation assumes that all birds breed every year from the summer following their fledging until death. We know that many do, but whether or not all do is not known. The more this assumption is violated, the greater our calculated necessary production level will be an underestimate. On the other hand, because resightings of live birds give a minimum estimate of survivorship, the calculated production level for population maintenance may be an overestimate.

Assuming that our estimated maintenance requirement level of 0.80 young per female is reasonably accurate, it is apparent that the 1978 production of 0.49 young per female is not adequate to maintain a stable local population. This discrepancy may be overestimated, however, because some female Snowy Plovers probably breed elsewhere either before or after their attempt at Mono Lake. This commonly occurs in females nesting on Monterey Bay. We can avoid this problem by considering only females that made both early- and late-nesting attempts at Mono Lake. From Table 3 we can calculate that these 30 females produced 21 young [(0.28 × 30) + (0.42 × 30)] for a production of 0.70 young per female. This is much closer to the 0.80 required for population stability and suggests that second broods must be produced commonly if this population is maintaining itself.

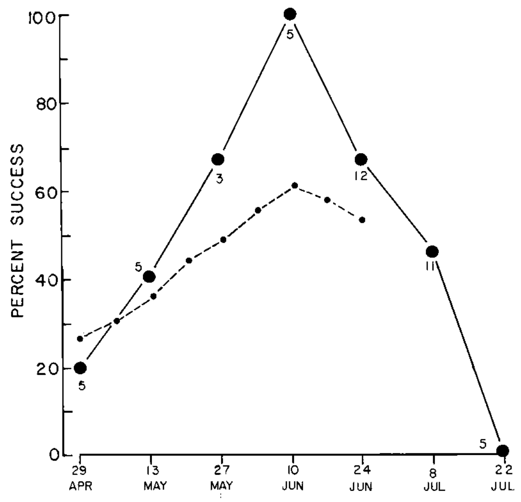

Fig. 3. Seasonal change in brood fledging rate at Mono Lake in 1978 for broods from clutches initiated for 2-week intervals by the dates indicated. Calculated clutch-hatching rates for nests at risk at about the same time (from Fig. 2) are superimposed and connected by a broken line.

DENSITY-DEPENDENT EFFECTS OF PREDATION

Imitation clutch experiments.—Factors that diminish breeding success of a species can effectively limit breeding population size if the rate at which success is diminished is sufficiently high and is positively correlated with breeding density. Experiments with imitation plover clutches at Mono Lake in 1979 demonstrate that predation causes an inverse relation between clutch survival and nest density. The null hypothesis in all the following experiments is that there is no difference between survival rates of nests at different densities. In none of the alterations of experimental design did we introduce a bias toward rejection of this null hypothesis. In the first experiment (Fig. 4), pooling results of the two 5-day trials, we found no difference between clutch survival rate in nests dispersed at 1 per 6 ha and those clumped at 20 and 40 per 6 ha ($P > 0.1$, G-test). Suspecting that predators were reacting as if there were only one dense concentration of nests, we removed two of the closely spaced groups for the second experiment, and closely spaced nests experienced lower survival (Fig. 4). In the third experiment, with nests marked by natural objects and only one area of high nest density, the survival rate was insignificantly higher for dispersed than for closely spaced nests ($P > 0.05$, G-test) (Fig. 4). At this point we became concerned that the high number of nests in the area might have attracted more gulls than normally hunt there, reducing all survival rates and obscuring differences between rates in dispersed and closely spaced nest groups. Therefore, no clutches were placed at high densities in the fourth experiment to restore the survival rate throughout the study area to "normal" levels. In the last three experiments, closely spaced and dispersed nests were separated by 300 m (Fig. 4), and survival rates of dispersed nests were significantly greater than survival rates of closely spaced nests. This difference is significant despite a potential bias favoring higher survivorship in clumped nests, because these had been moved to an area where no experiments had previously been conducted, while dispersed nests remained in the same area throughout the seven experiments. In each

TABLE 2. Hatching rate of clutches initiated during 7-day periods in 1978 and the number of nesting attempts early (before 4 June) and late (after 3 June); calculations are based on Mayfield (1961), and $r = D/N$.

Clutch initiation cohorts	Latest predicted hatching date	Number of clutches in cohort	Clutch exposure days (N)	Observed clutches destroyed (D)	Calculated clutch hatching rate $(1 - r)^{31}$	Observed clutches hatching (Y)	Number of nesting attempts $X = \Sigma Y/[1 - (\Sigma D/\Sigma N)]$
16–22 April	23 May	3	273	3	0.71	1	
23–29 April	30 May	6	405	9	0.50	6	
30 April–6 May	6 June	8	512	13	0.45	3	
7–13 May	13 June	4	609	17	0.42	0	
14–20 May	20 June	8	596	20	0.35	5	
21–27 May	27 June	8	511	21	0.27	2	
28 May–3 June	4 July	5	402	15	0.31	1	
Early period totals			3,308	98	0.39	18	$X = 18/0.39 = 46$
4–10 June	11 July	3	374	12	0.36	0	
11–17 June	18 July	5	382	10	0.44	6	
18–24 June	25 July	7	400	9	0.49	8	
25 June–1 July	1 August	9	428	8	0.56	5	
2–8 July	8 August	9	449	7	0.61	7	
9–15 July	15 August	5	407	7	0.58	6	
16–22 July	22 August	1	295	6	0.53	1	
Late period totals			2,735	59	0.51	33	$X = 33/0.51 = 65$

TABLE 3. Calculation of reproductive success in Snowy Plovers at Mono Lake in 1978. We assume that all early nests were attempted by different females and that we accounted for all nests that hatched.

	Early nests (before 4 June)	Late nests (after 3 June)
Calculated nesting attempts	(b_1) 46	(b_2) 65
Calculated clutch-hatching rate	(c) 0.39	0.51
Marked broods fledging one or more young	(d) 6	15
Broods marked	(e) 14	30
Brood-fledging rate (d/e)	(f) 0.43	0.50
Young fledged per successful brood	(g) 1.64	1.64
Young per nesting attempt (c × f × g)	(h_1) 0.28	(h_2) 0.42
Females marked before 4 June		(i) 32
Marked females definitely renesting		(j) 12
Additional marked females probably renesting		(k) 9
Renesting rate (j + k)/i		(l) 0.66
Total females laying two clutches (b_1 × 1)		(m) 30
Total females laying only an early clutch (b_1 − m)		(n) 16
Total females laying only a late clutch (b_2 − m)		(o) 35
Total females nesting in area (m + n + o)		(p) 81
Total young fledged (b_1 × h_1) + (b_2 × h_2)		(q) 39.8
Young fledged per female (q/p)		0.49

of the four trials for experiment 7, when the number of nests situated in each of the six nest types was identical for closely spaced and dispersed nests, clutches in dispersed nests had a higher survival rate than in closely spaced ones. Survival rates of clutches in dispersed nests apparently were reduced by the presence of associated groups of closely spaced nests: 58% of the dispersed nests survived in experiment four when no sets of closely spaced nests were present, compared to only 25% of dispersed nests in experiments two and three with associated groups of closely spaced nests ($G = 14.02$, $P < 0.001$).

Annual variations in survival rates of plover clutches provide further evidence that nest survival is density-dependent. In 1978, before the experiments with imitation clutches, the observed clutch-hatching rate within the area of intensive search was 59.5% of 74 clutches, compared to 39.5% of 43 clutches in 1979, the year of the experiments. With no experimental clutches present, the hatching rate of 42 clutches in 1980 was 64.3%, and of 44 clutches in 1981 was 68.2%. The significantly reduced hatching rate in 1979 ($G = 8.60$, $P < 0.05$) probably resulted from increased predator activity due to the presence of imitation clutches.

Predators' behavior.—Tinbergen et al. (1967)

TABLE 4. Minimum annual survival rates of Snowy Plovers. Numbers of marked birds potentially detectable are in parentheses.

	Return to breeding site in consecutive years		Alive from one breeding season to the next	
	Males	Females	Males	Females
Mono Lake 1978–1979	0.778 (18)	0.449 (49)		
Monterey Bay 1978–1979	0.750 (16)	0.529 (17)	0.895 (19)	0.727 (22)
Monterey Bay 1979–1980	0.522 (23)	0.292 (24)	0.679 (28)	0.719 (32)
Monterey Bay: both years combined	0.615 (39)	0.390 (41)	0.766 (47)	0.722 (54)
Monterey Bay: both years and sexes combined			0.743 (101)	

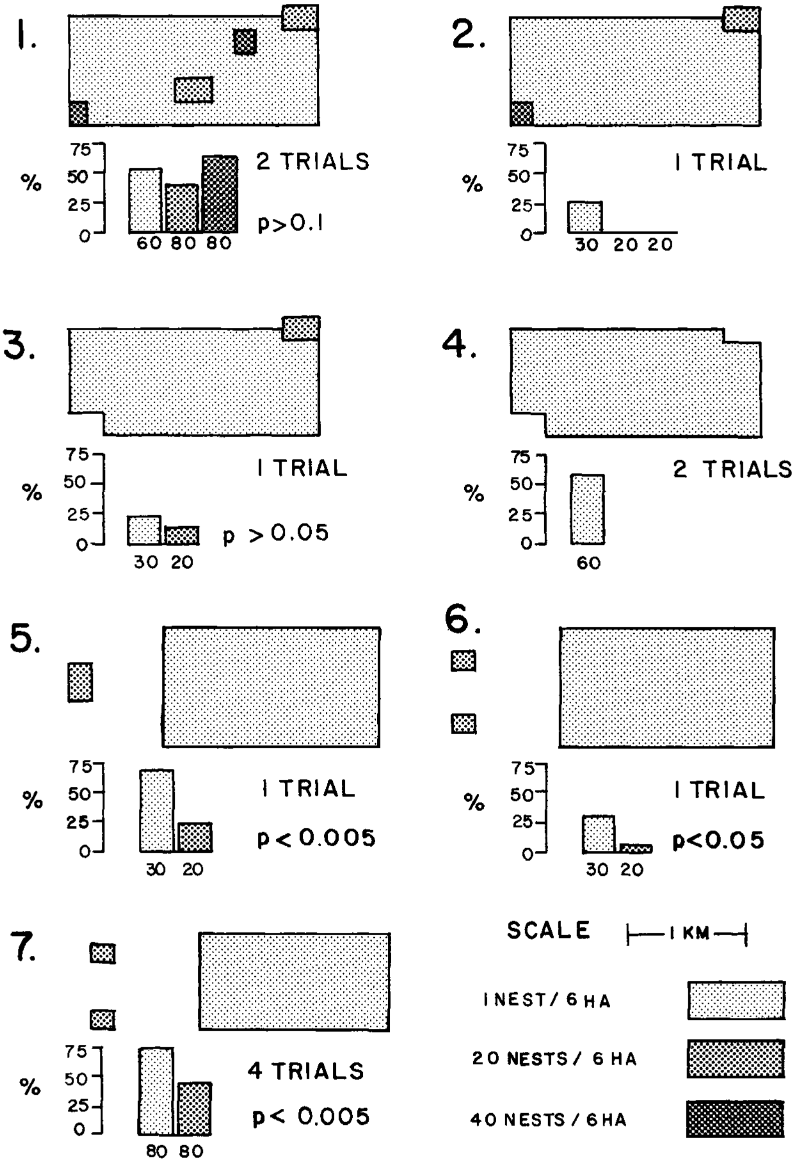

Fig. 4. Diagrams illustrating the arrangement of plots and results of the experiments with artificial clutches. For all seven plot arrangements, the left-hand (western) edge of the plot of dispersed nests is at reference stake 1 on our study site. The bar graph below each diagram gives the percentage of nests surviving for 5 days at different densities (see legend). Sample sizes are below each bar. The *G*-test was used to compare results.

mention two mechanisms by which avian predators can secure a higher proportion of clumped than scattered nests: (1) by reacting to the discovery of prey with an intensive effort around the first find and restricting their search image to the type of prey already discovered; and (2) by returning repeatedly to the area of an initial find. Both these mechanisms appear to be involved at Mono Lake, with the ravens relying on at least the former and the gulls on the latter tactic.

One incident typifies the ravens' tactics. On

27 June 1979, Page found, by checking beside and under driftwood, an unusually high number of previously undiscovered nests along DR and UDR. Three weeks later, in another part of the study area, he encountered raven tracks on DR. These tracks wove for 500 m between pieces of wood and led to three destroyed clutches under driftwood that we had not previously discovered. It appeared that the raven had used the same technique that Page had used successfully 3 weeks before to locate these nests.

On the few occasions that we saw a gull discover an imitation clutch, the gull dropped to the ground and swallowed every egg whole within a few seconds. After eating the eggs, the gull wandered about the area briefly, then flew out of sight. Gulls regularly flew back and forth over our entire study area, but, in one location where we had set a dense concentration of nests early in the experimental period, we frequently encountered one or two of them circling. It was our impression that gulls frequented this location more than the study area as a whole during the time of the experiments. As the gulls were not marked, we do not know if the individuals involved had previously taken eggs there. When one gull discovered an imitation clutch, other gulls quickly landed by it. This observation indicates a third response that can lead to a density-dependent effect of predators on their prey: predators aggregating at a site where a prey item has been discovered.

The behavior of the third predator, the coyote, cannot be characterized by these three responses. We suspect that coyotes simply stumbled upon plover nests while walking along the current lakeshore and old lakeshore ridges, which were their favored routes across our study site. Many nests were located on these low ridges.

DISCUSSION

Food supply, nest-site availability, and predators are the environmental factors most likely to affect the nest density of the Snowy Plover. We found no evidence that lack of nesting or feeding space was limiting the size of the breeding plover population at Mono Lake. The distribution of adequate food supplies undoubtedly plays a role in determining the general distribution of nesting areas; most feeding, however, occurs outside the nesting territory in undefended areas. Because plover nests occur almost anywhere in open habitat and nesting territories are frequently separate from feeding areas, potential nesting territories are practically unlimited. A few nonbreeding marked birds are always present in the area, but these are almost invariably found to be preparing for or between nesting attempts. Plovers are known to breed on Monterey Bay at densities 20 times greater than those at Mono Lake. Indeed, the nesting density of *C. a. alexandrinus* in western Europe can reach hundreds of times that at Mono Lake (Ritting-haus 1975). Thus, space appears to be available for increased nesting density, and nonbreeding birds are probably not prevented from nesting at Mono Lake because of limited space. Most feeding occurs along the shore of Mono Lake or at seeps on the dry lake bed (Fig. 1), locations that are up to 1.5 km away from some nests. Despite the fact that some individuals can frequently be found in the same feeding areas, we found no evidence of feeding territories either at Mono Lake or on the coast (Warriner et al. unpubl.). Marked individuals with nests at Mono Lake feed at the seeps and along the lake shore on the same day or on consecutive days. They also feed at different locations along the seeps or the lakeshore. Males often feed together, and aggressive interactions are infrequent unless males are accompanied by a female or a brood. If extremely high densities of males accompanied by broods or females occurred along water margins, the remainder of the plover population might be excluded from the insect food resource, but densities were not nearly high enough for this to happen. Considerable unoccupied feeding habitat occurs along the seeps and the lake shore, and plovers are often found roosting, evidence that individuals are not pressured to feed continuously.

Like all small shorebirds, the Snowy Plover cannot defend itself or its nest from predators, and it must rely on subterfuge rather than defense. Antipredator adaptations include the cryptic coloration of the adult, eggs, and young, a skulking retreat from the nest at a predator's approach, and extreme mobility and elusiveness of the nidifugous young. The placement of nests beneath objects may also be an antipredator adaptation: A preliminary analysis of our nest site data suggests that nests under objects are more likely to survive than exposed nests. The results of the artificial clutch experiments suggest that, under the conditions occurring at Mono Lake, a plover nesting too close to other birds will decrease the chances of success of its own nest and of its neighbors' nest. Thus, one might expect low nesting density to be maintained through territorial defense by established pairs and through the avoidance of high-density nesting by pairs initiating nests.

Social behavior away from feeding areas is difficult to study at Mono Lake. Such behavior is limited mainly to the crepuscular hours, perhaps in response to mid-day heat and predators. Territorial defense in a coastal population with a higher density and lower predator activity can frequently be observed throughout the day (Warriner et al. unpubl.). There is a strong possibility that the low nesting density at Mono Lake is not the direct result of social interaction, but merely the consequence of reduced population size, the ghost of predators past.

We have no way of evaluating mortality due to competition or predation away from the breeding grounds as a limiting factor, but it is difficult to imagine that they exert a stronger deleterious effect on plover numbers than does the high level of egg and chick predation observed on the breeding grounds. Although we observed a significant difference in the rate of nest predation between two levels of nest density (1 and 20 nests per 6 ha), the question might be raised as to whether or not a density-dependent relationship exists between smaller density differences. There is evidence that it may; when closely spaced nests were removed in experiment 4 (Fig. 4), leaving only dispersed nests, the rate of survival of dispersed nests increased significantly, even though the overall decrease in artificial nest density, when closely spaced and dispersed nests are considered collectively, was from about 3 to 1 nest per ha. Thus, we feel that density-dependent predation of nests currently limits numbers of Snowy Plovers at Mono Lake.

Predators affect plover nesting success widely in western North America. Ravens destroyed several coastal nests under observation in 1977 at Point Reyes, California (Page and Stenzel unpubl.); Henderson (pers. comm.) saw a raven feeding on Snowy Plover and avocet eggs at Owens Dry Lake, Inyo County, California; and Wilson (1980) reports that Common Crows (*Corvus brachyrhynchos*) took substantial numbers of plover nests in coastal Oregon. In contrast to the corvids, gulls' impact on nesting plovers appears to be less widespread. They have taken only 1 of 175 nests followed at Monterey Bay and Point Reyes. During our observations of these nests, incubating plovers showed no reaction to gulls overhead but ran far from the nest as soon as a raven came into view. This leads us to suspect that the high rate of gull predation on plover nests at Mono Lake may be an atypical phenomenon resulting from the close proximity of a large gull colony.

Mammalian predators also affect nesting plovers. Coyotes took some nests at Mono Lake (Table 1) and skunks (*Mephitis mephitis* and/or *Spilogale putorius*) were responsible for considerable plover nest loss at Wilder Beach, Santa Cruz County, California in 1980 (Bidstrup and Frederiksen pers. comm.).

Predators are not active in all breeding sites every year, and productivity levels may vary annually. For example, in 1977 plovers fledged about two young per female in a predator-free environment at Monterey Bay (Warriner et al. unpubl.). The following year production there was down to the level reported for Mono Lake, because many chicks were drowned when high tides inundated restricted feeding areas. In 1979 production was again low: this time chicks drowned or were preyed upon by Loggerhead Shrikes (*Lanius ludovicianus*). Other factors that affect plover nesting success on the coast are accidental and deliberate destruction of nests by humans and nest losses to strong winds and high tides.

The impact of predators on the entire western North American breeding population of the Snowy Plover is difficult to assess, because there have been relatively few studies of breeding success. Although the impact of predators is dominant in some locations (e.g. the Oregon coast and Mono Lake), in others (e.g. Monterey Bay) it is not. Therefore, it appears that an aggregate of factors, with intensities that vary annually and geographically, limits the breeding success and survivorship of the Snowy Plover and ultimately the size of its breeding population in the West.

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