

THE ROLES OF THERMAL ENVIRONMENT AND PREDATION IN HABITAT CHOICE IN THE CALIFORNIA GULL¹

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Abstract. California Gulls (*Larus californicus*) breeding in the Great Basin may encounter diurnal temperatures sufficient to cause chick mortality. Although nesting may occur in a variety of habitats, at Mono Lake, California, and elsewhere gulls prefer fairly open areas with irregular terrain near the shore of islands. These areas are relatively cool, but their major advantages seem to be promoting the isolation from and early detection of predators, providing hiding places for small chicks, and offering escape routes for large young and adults. Predation is a continual danger, whereas periods of high temperatures sufficient to cause mortality are too brief and irregular to have a dominant influence on long-term breeding success and thus on habitat selection.

Key words: Thermal environment; habitat selection; heat stress; predation; California Gull; *Larus californicus*; Mono Lake.

INTRODUCTION

"The crucial first step to survival in all organisms is habitat selection" (Wilson 1984:106). Colonial seabirds typically select islands or other inaccessible places for breeding, safety from terrestrial predators being the prime criterion for the choice of a nesting area. Factors involved in their subsequent choice of nesting habitat or nest sites, however, may vary from among localities or species.

We studied nesting areas used by California Gulls (*Larus californicus*) at Mono Lake, California (elev. 1,993 m), which is at the southern extreme of the species' breeding range at the edge of the Great Basin in east-central California. During this century the colony has increased from 3,000 to 50,000 birds (Jehl et al. 1984). This event, combined with changes in the quantity and availability of nesting areas owing to changes in the lake level, has necessitated redistribution of the colony and has required gulls to select among areas of varying physiography and microclimate, ranging from open nest sites on barren sandy or lava islets to enclosed and concealed sites on densely shrubbed islets (Fig. 1).

In most studies habitat preference is inferred from studies in areas in which a species has been

established, often for some time. Such post facto determinations, however, show little more than habitat *acceptability*, because historical factors that affect availability, or social factors that contribute to coloniality, are rarely understood well enough to be factored out. To demonstrate habitat *preference*, it is necessary to determine which areas are selected as colonies are forming, when a variety of options is available.

Using historical data (Jehl et al. 1984) and our own observations during a recent period of colony expansion, we examined attributes of present and past nesting areas at Mono Lake (Table 1), including susceptibility to predation (Jehl and Chase 1987), that may have made them attractive. In particular, we compared thermal characteristics of several areas during the chick-rearing period, because heat stress has been implicated in chick mortality in that colony (Chappell et al. 1984). Temperatures experienced by gulls at Mono Lake in the breeding season may reach 50°C. We reasoned that if heat stress is an important selective force gulls should select shaded or cooler nesting sites.

METHODS

THERMAL MEASUREMENTS

In June and July 1983 and 1984 we measured thermal environments in two major areas where gulls currently or formerly nested (Table 2). One

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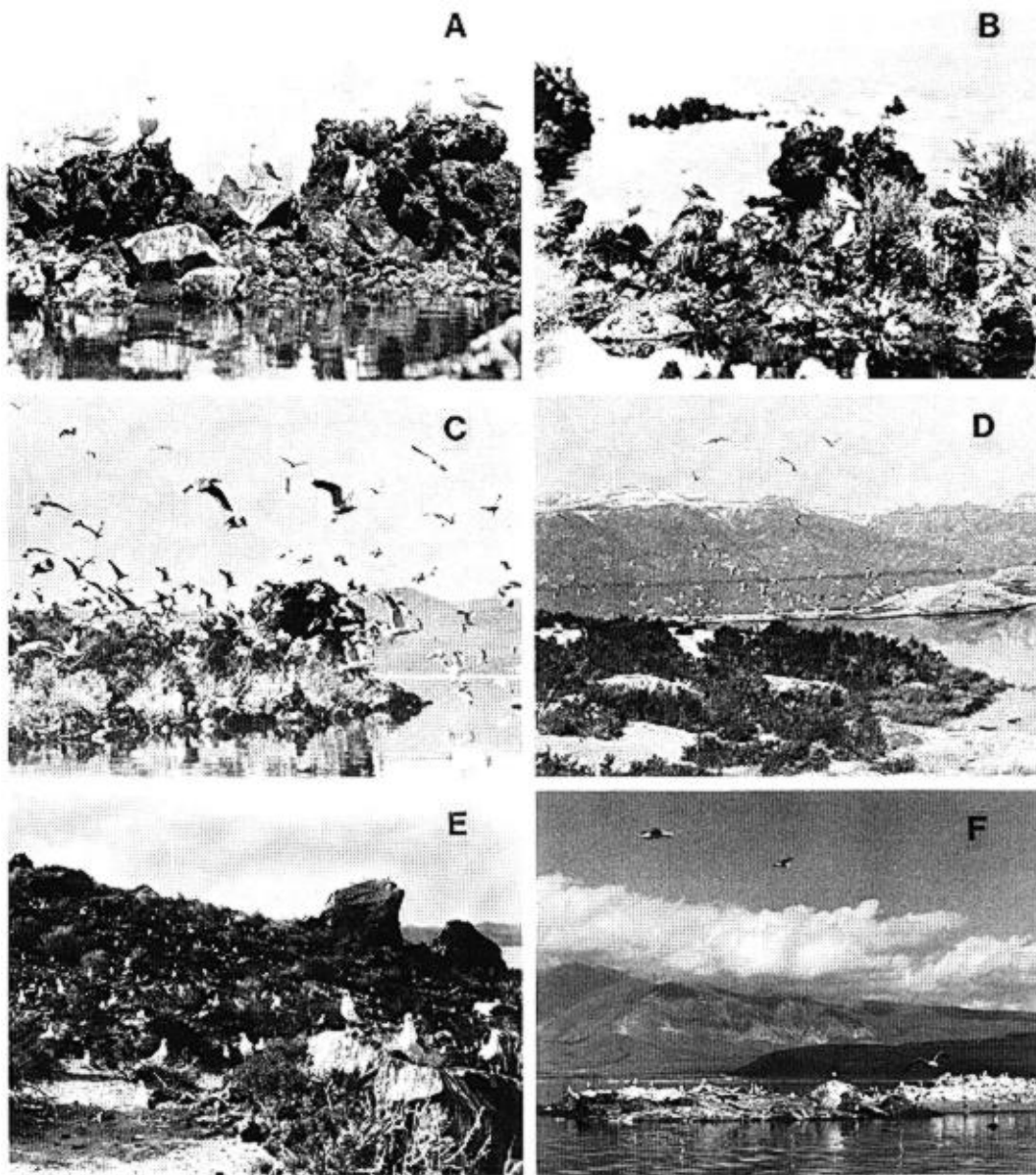


FIGURE 1. Current or former nesting areas at Mono Lake, California (A) Little Tahiti Islet (Negit Islets), 1919; (B) "Black Rocks" colony on Paoha Island, 1919; (C) Colony at shore of Negit Island, 1919; (D) "Lagoon" colony on Paoha Island, 1919; (E) Negit Island colony, 1930; (F) Coyote Islet (Paoha Islets), 1983.

was a major former site now on the southeastern crest of Negit Island but at the waterline in 1919 (Fig. 2A). (For details of localities at Mono Lake, see Jehl et al. 1984, or Jehl and Chase 1987.) Occupied almost continuously from 1919 to 1979, the area has a substrate of gray pumice sand with scattered black lava boulders and is vegetated with a moderately dense stand of

greasewood (*Sarcobates vermiculatus*) up to 1.5 m high. The second area, first occupied in 1979, was a typical site on barren Coyote Islet, where 1,100 to 1,500 pairs of gulls nested during this study (Fig. 2B). The site was 6 m from and 1 m above the eastern shore of the islet and consisted of light-colored lakebed sediments, which are irregularly covered with a broken crust of tufa.

TABLE 1. Nesting locations of California Gulls at Mono Lake, California.

Year	Site	Description	Source
1863	Poaha Island, on southeastern shore		Brewer 1930
1865	Poaha Island	"Open spaces between rocks."	Browne 1865
1916	Poaha Island	On two lava ridges that enclose a "long narrow bay, chiefly on the eastern one which bears a rather dense growth of a shrubby plant." Nests on beach shingle, under bushes, and on top of rocks. (This is the Black Rocks colony of Dawson 1923; see below.)	Grinnell and Storer 1924
1919	Poaha Island (Lagoon Colony) (Fig. 1D)	"Sloping banks of small lagoon . . . [in the] scanty cover of atriplex and artemisia . . ."	Dawson 1923:1406
	Poaha Island (Black Rocks colony) (Fig. 1B)	"Exceedingly rough lava field," most nests "along a strip within twenty feet of the water on a ridge which projected itself into the water."	Dawson 1923:1407
	Negit Island (east point) (Fig. 1C)	Sloping volcanic rocks colony "running from the water's edge up to forty feet"; scattered shrubby vegetation.	Dawson 1923:1409
	Negit Islets (Fig. 1A)	"An outlying ridge of rock" (crest of Little Tahiti Island); no vegetation.	Dawson 1923
1928-1930	Negit Island (Fig. 1E)	From shore to crest of island on southeast side. Most nests apparently in relatively open habitats, some on barren rocks, others in moderately dense vegetation.	B. Frasher photographic collection. Pomona, California, Public Library
1938	Negit Island	Whitish rocks on side of island; little or no vegetation (same area as 1976).	Nichols 1938
1950-1951	Negit Island (southeast side)	"Colony occupies a restricted area, possibly 600 by 80 meters, on the southeast side . . ."	Young 1952:206
1953	Negit Island	Nests about 2 m apart mostly "in the sandy pumice under the partial or complete shade of greasewood plants."	Johnston 1956:137
1972	Negit Islets	White rocks, no vegetation. Gulls on islets "apparently outnumbered those on Negit."	Jurek 1972
	Negit Island	Nesting primarily along 400 m of shore on east side; some "higher up . . . among black rocks."	Jurek 1972
1976	Negit Island (shore, north, east, and south side)	Whitish rocks on side of island; little or no vegetation.	Winkler 1977
	Negit (top)	Dense greasewood scrub.	Winkler 1977
	Negit Islets	White rocks, no vegetation.	Winkler 1977
1979-1986	Negit Islets	From waterline to crest (ca. 13 m elevation); white rocks, no significant vegetation.	Winkler 1983; Jehl, pers. observ.
1979-1986	Poaha Islets (Fig. 1F)	On small islets, mainly near waterline in areas of broken tufa crust; no significant vegetation.	D. Babb, pers. comm.; Jehl, unpubl.
1986	Negit Island	Mostly on whitish rocks near shore, extending in one location to margin of shrubby vegetation.	Jehl, pers. observ.
	Paoha Island	On sandy peninsula, near waterline, in area of irregular substrate, tufa crust; no significant vegetation.	Jehl, pers. observ.

We made thermal measurements at several other former nesting sites, including: the "Black Rocks" colony on Paoha Island; an area of black lava on the eastern side of Negit Island; and on

white tufa-encrusted boulders near the southeastern shore of Negit Island (Table 2). The latter area is similar to that used by the majority of the present colony.

TABLE 2. Environmental conditions in California Gull nesting areas at Mono Lake, California.

	Major study areas		Additional areas		
	Negit Island	Coyote Islet	Negit Island	Negit Island	Paoha Island
Exposure	southeast	east	east	southeast, lower rim	east, south
Elevation above lake level in 1984	20 m	1-3 m	10 m	3-5 m	12 m
Physiography	open areas of pumice sand, black rocks, amid dense vegetation	smooth, silty sediments with rough tufa crust; no vegetation	rough, lava, black rocks, no vegetation	white, tufa-encrusted lava boulders; no vegetation	black lava; no vegetation
Previous condition	immediately adjacent to waterline, 1919; colony area 15-25 m above waterline in 1970s	submerged until mid-1960s	colony near waterline in 1920s	colony in 1970s	"Black Rocks" colony of 1919
Condition in 1984	deserted	gulls nesting since 1979	deserted	deserted	deserted

From early June to late July, the major hatching and fledging period of young gulls, we made continuous measurements in the two major study areas. We used Dickson 7-day thermometers to record shade and sun temperatures. The shade probe was placed ca. 6 cm above ground (chick height): on Coyote Islet it was shaded by tufa encrustations that were open to abundant air circulation; on Negit Island it was under a greasewood bush. We added additional shading (driftwood and burlap) to insure that the probes were shaded continuously. The sun probe was wrapped in black electrical tape, to approximate black bulb temperature, and was placed 13 cm above ground (adult gull height) in a relatively spacious open area (ca. 4 m in diameter), so that neither sunlight nor air flow was impeded. Before installation, all four probes were calibrated with a Wescor thermocouple. At each site in 1984 we recorded windspeed continuously with a Windwatch/Met One cup anemometer that yielded windspeed averaged over 60-min periods. The anemometers were also positioned at approximate adult gull height in open areas. Daily solar radiation was continuously recorded on Coyote Islet with a Belfort pyroheliometer.

In addition, on several occasions we measured: direct and reflected short-wave radiation with a Licor silicon sensor; ground and sky long-wave

radiation with a Mikron 25 infra-red thermometer; humidity with a sling psychrometer. We compared substrate temperatures and short-wave reflectivity of typical nesting substrates, including: black rocks, pumice sand, tufa-encrusted boulders, and abandoned nests on Negit Island, and tufa crusts, silty ground, and extant nests on Coyote Islet. We also gathered continuous data on temperature and windspeed on Coyote in 1985. Data on daily air temperature and windspeed obtained from a weather station 4.8 km SW of Mono Lake (Cain Ranch, elevation 2,033 m) allowed us to compare thermal conditions during the breeding seasons of 1981 through 1985. We arbitrarily designated days when air temperatures at Cain Ranch exceeded 26.7°C (80°F) as "hot" days. Windspeeds averaging less than 1.9 m/sec (4 mph) per day were considered "low."

EQUIVALENT TEMPERATURE

Equivalent temperature (T_e) (Mahoney and King 1977) is an index of the external heat load that an animal experiences and is the same as operative temperature (Bakken 1976). It is calculated from:

$$T_e = T_a + r_e/\rho c_p(R_{ab} - LW_o)$$

where T_a is air temperature (°C), r_e is equivalent resistance (sec/m), R_{ab} is total absorbed radiation

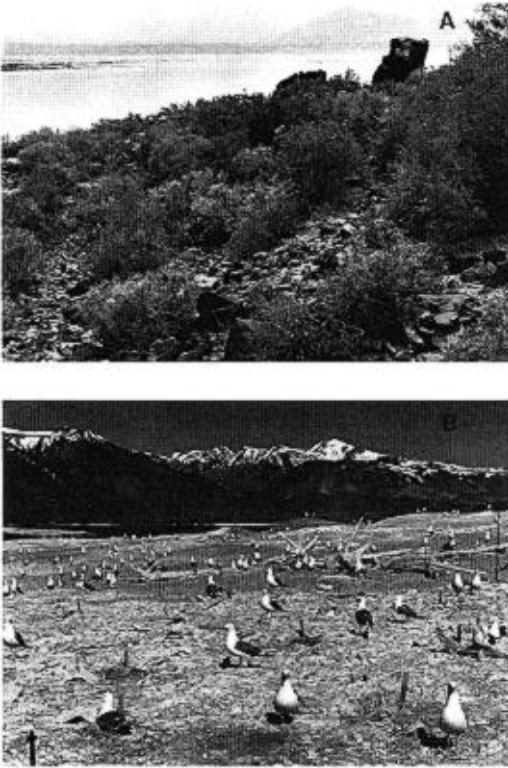


FIGURE 2. (A) Greasewood scrub near the crest of Negit Island, where gulls nested in late 1970s. (B) Broken tufa crust at the southeastern end of Coyote Islet, 1982–1985; experimental area where driftwood was introduced is in back center.

(W/m^2), LW_0 is long-wave radiation lost from the animal surface (W/m^2), and ρc_p is the product of the density and specific heat of air ($1,200 \text{ Jm}^{-3}\text{K}^{-1}$ at 20°C). The term r_e incorporates data from windspeed and size as measured by the animal's linear body dimensions parallel to the wind (characteristic dimension).

In theory equivalent temperature more closely approximates an animal's actual heat load than

does black bulb (sun) temperature because it uses the animal's actual surface properties, such as size and absorptivity to solar radiation, in the calculation. A taxidermic model of the animal (Bakken 1976) can also be used as an equivalent temperature thermometer. Neither taxidermic models nor calculated $T_{e,s}$ incorporate data on the animal's metabolic heat production, its ability to cool off through evaporation or by using postural adjustments, or on wind-dependent differences in feather and body conductance. The T_e index is advantageous because it provides a way of integrating a complex thermal environment into a single temperature, which is the thermal gradient against which the animal must maintain its body temperature.

We calculated $T_{e,s}$ for adult gulls, small chicks, and large chicks in each of the sites noted above. To ensure comparability, paired data were obtained within 15 min at any two sites. We compared T_e with sun temperatures and T_e obtained from taxidermic models of chicks that had been used in earlier studies at Mono Lake (Chappell et al. 1984). Values of T_{sun} and T_e were closely similar and usually fell between T_e of the models, which varied greatly. Thus, T_{sun} could be used to approximate T_e (unpubl. data). Relevant properties of the birds and the models are listed in Table 3.

HABITAT STUDIES

To study habitat preference, we observed the growth and occupancy pattern of nesting areas on the Paoha Islets, Paoha Island, and Negit Island from 1982 to 1986. To investigate the influence of substrate on nesting activity, at the end of the 1983 and 1984 breeding seasons we introduced pieces of driftwood into several featureless sandy areas on Coyote Islet where nesting had never occurred (Fig. 2B) and observed the occupancy of those areas in subsequent seasons. Data on nesting habitats in other colonies

TABLE 3. California Gull characteristics used in calculation of T_e .

	Chicks*		Adults	Taxidermic models†	
	Small	Large			
Body weight (g)	100–200	450–500	500–600	120	<100
Characteristic dimension (m)	0.1	0.21	0.26	0.1	0.08
Dorsal absorptivity	0.82	0.83	0.83	0.83	0.82
Ventral absorptivity	0.71	0.84	0.56	0.77	0.77

* Small chicks, still in natal down; large chicks, near fledging, and covered with contour feathers.

† Body weights of taxidermic models were estimated by comparison with healthy chicks of similar size.

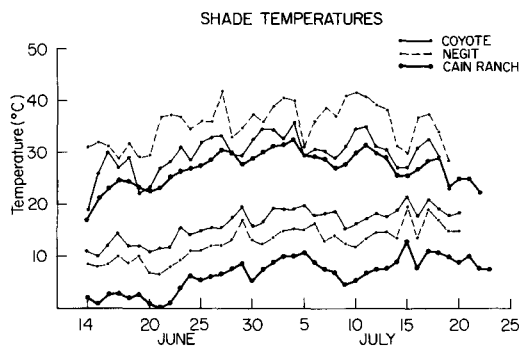


FIGURE 3. Daily maximum and minimum air temperatures in the shade on Negit Island, Coyote Islet, and Cain Ranch in June and July 1984.

throughout the species' range were derived from the literature and personal observations in Alberta, Oregon, Nevada, Wyoming, Utah, and California.

PREDATION

Nesting areas at Mono Lake are usually inaccessible to terrestrial predators, but are visited regularly by Great Horned Owls (*Bubo virginianus*) and Golden Eagles (*Aquila chrysaetos*), whose impact was documented by regular visits to the colony from 1982 through 1985 (see Jehl and Chase 1987 for details).

RESULTS

METEOROLOGICAL MEASUREMENTS

Meteorological measurements in 1984 at a local weather station (Cain Ranch) and major study areas on Negit Island and Coyote Islet are summarized below. Similar data were obtained at all three areas in 1983 and at Coyote Island and Cain Ranch in 1985 and are not presented in detail. Data from Paoha Island in 1983 are also included.

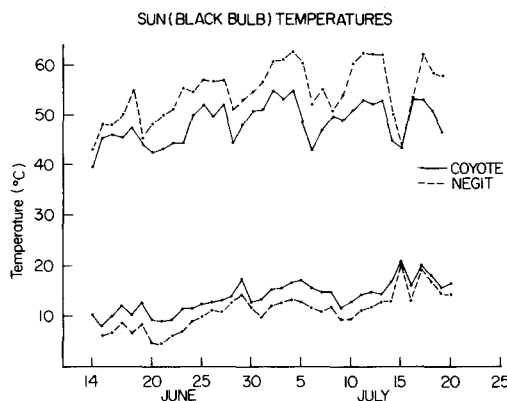


FIGURE 4. Daily maximum and minimum temperatures in the sun (black bulb temperature) on Negit Island and Coyote Islet through June and July 1984.

Temperature. From 12 June to 18 July 1984, air temperatures in the shade (T_{shade}) at the major site on Negit (pumice sand substrate, with interspersed black lava amid greasewood scrub) were more extreme than those on Coyote Islet (gray diatomite substrate, broken white tufa crusts) (Fig. 3). Sun temperatures (T_{sun}) measured in the open showed the same trends (Fig. 4).

Shade temperatures on Negit Island averaged 4.4°C warmer than Coyote Islet during the day and 3.4°C cooler at night (Table 4); the former site is higher in elevation and farther from the water. Sun temperatures on Negit averaged more than 5°C warmer than Coyote during the day and nearly 3°C cooler at night. At Cain Ranch, which is 150 m higher than Mono Lake, temperatures averaged cooler than on the islands during the day (2.5°C lower than Coyote) and at night (5 to 7°C cooler than Coyote).

Wind. Coyote, lower and more exposed, was considerably windier, with windspeeds often double those on Negit (Fig. 5). Typically, sum-

TABLE 4. Daily maximum and minimum air temperature (°C) in study sites on Negit Island and Coyote Islet, Mono Lake, California, 14 June to 14 July 1984.

	Maximum			Minimum		
	\bar{x}	SD	Range	\bar{x}	SD	Range
Shade						
Negit	34.8	4.8	22.0–41.8	12.7	3.1	6.8–19.6
Coyote	29.4	4.0	19.0–35.8	16.1	3.2	10.5–21.6
Sun						
Negit	54.0	5.7	43.0–64.0	11.0	3.6	6.0–20.3
Coyote	48.4	4.1	39.5–54.8	13.7	3.1	8.0–20.9

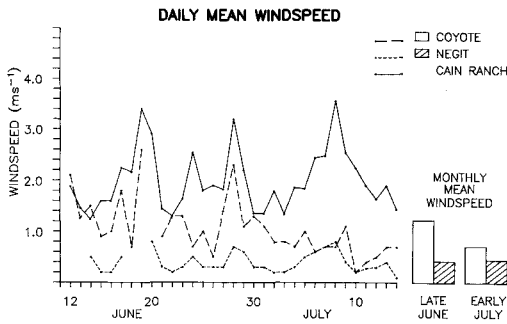


FIGURE 5. Mean windspeed each day in June and July 1984 on Negit Island, Coyote Islet, and Cain Ranch. Mean monthly windspeeds are shown by histograms at the lower right.

mer mornings on Negit and late mornings on Coyote (08:00 to 12:00) were calm, but strong southwest winds developed in the afternoon (12:00 to 18:00) (Fig. 6). In early July 1984, unlike June, afternoon winds were similar on Negit and Coyote because wind direction became more easterly and impinging directly on the Negit site.

Daily temperature range. Clear days are typical in summer at Mono Lake (21 of 30 days clear; nine partly cloudy in June to mid-July 1984). A plot of hourly sun and shade temperatures on the two islands on a clear day (Fig. 7) shows that high temperatures ($T_{\text{sun}} > \text{ca. } 40^{\circ}\text{C}$) occurred from 09:00 to 18:00, and that sun temperatures exceeded shade temperatures by 17 to 22°C for several hours. However, on days when afternoon winds averaging stronger than 2.6 m/sec developed, maximum sun temperatures were only 10 to 15°C higher. Negit temperatures in the day-

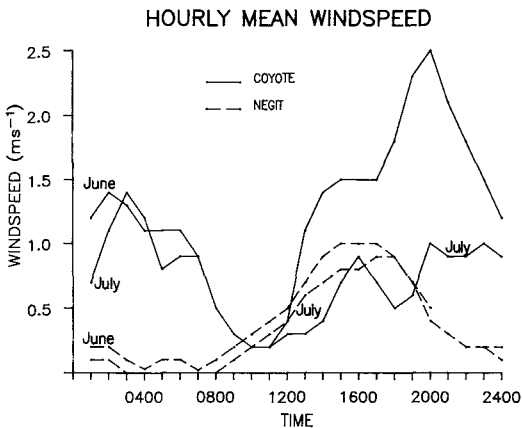


FIGURE 6. Hourly mean windspeed on Negit Island and Coyote Islet in June and July 1984.

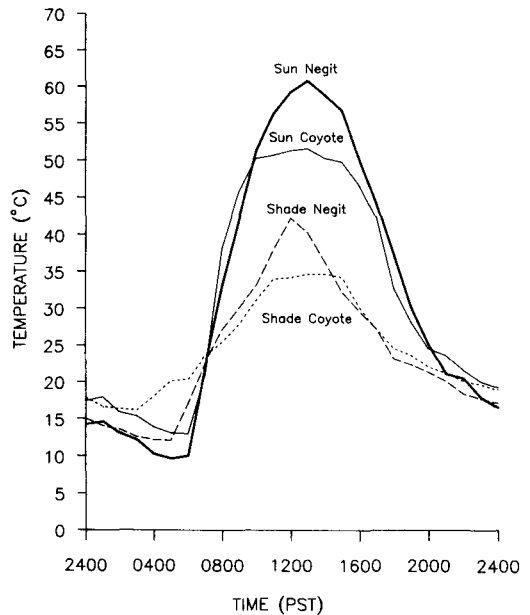


FIGURE 7. Air temperatures in the shade and sun on Negit Island and Coyote Islet on a clear day, 10 July 1984.

time were almost always higher than those on Coyote.

Equivalent temperatures in microhabitats. Equivalent temperatures (T_e) were calculated for small chicks, large chicks, and adults in full sun at the major study sites as well as at several former nesting areas on Negit Island. As was the case for sun temperatures, T_{e} s at most Negit sites averaged 3 to 7°C hotter than on Coyote (Fig. 8). Also on Negit long-wave radiation from the ground was greater, and wind speeds were lower (Table 5), owing to the sheltering effect of the high vegetation and rocks. Both black lava and white tufa were much cooler (37 to 49°C) than other Negit substrates (59 to 70°C) and were thermally similar to the "Black Rocks" site on Paoha Island (43°C) and the Coyote substrates (43°C). However, equivalent temperatures in the grease-wood area and a gravel-filled, old nest in white tufa on Negit Island were the warmest of all measured localities for gulls of any size, despite the pale color of the substrates.

Thermal stress. From 1981 to 1985, based on average daily temperatures at Cain Ranch, the pre fledging periods for gull chicks (16 June to 16 July) were hottest in 1981 and 1985, closely followed by 1984. As the differences among the 3

years are not statistically significant, we considered 1984 a representative hot year.

Chappell et al. (1984) attributed very high chick mortality (ca. 80%) in 1981 to overheating and posited that it would have been lower had the gulls bred in the shady former colony site on Negit Island rather than on the barren islets. We compared thermal stress in those habitats, which are matched by our two major study sites, using criteria of Chappell et al. (1984) who found that: chicks pant and assume a droop-wing posture to promote heat loss when temperatures exceed 37°C; panting is an effective thermoregulatory mechanism at $T_{e,s}$ up to 47°C; and (p. 212) "the maximum tolerable environmental temperature [duration unspecified] for gull chicks appears to be about 47°C and thermoregulation at any temperature above 39 to 40°C requires high rates of evaporative water loss." We found that in 1984 thermal conditions sufficient to either initiate heat stress ($T_{shade} > 37°C$) or lead to mortality ($T_{sun} > 47°C$) were realized more frequently in the greasewood site (Table 6).

A comparison of several microhabitats on Negit and Coyote, using windspeeds at each site and typical midday sun conditions, shows that in full sun when T_a is 25°C (a common, not "hot," temperature), large chicks at all but one Negit location, as well as adults and small chicks in the greasewood and in a nest in white tufa, would be exposed to temperatures causing high evaporative water loss; birds on Coyote would not (Fig. 8). At T_a of 35°C chicks at some Negit sites, including greasewood vegetation, would experience intolerable $T_{e,s}$; birds on Coyote would not. Although sun temperatures at the greasewood

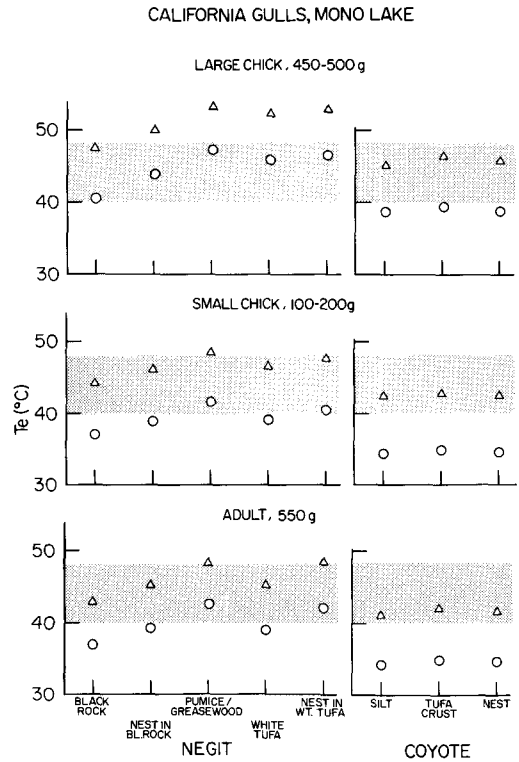


FIGURE 8. Equivalent temperatures in full sun on a clear day in different microhabitats on Negit Island and Coyote Islet for three different-sized gulls. $T_{e,s}$ are calculated for typical conditions when $T_a = 25°C$ (O) and hot conditions when $T_a = 35°C$ (Δ). Direct short-wave = 1,030 W/m²; diffuse short-wave = 100 W/m²; sky long-wave = 210 W/m². All other values used in the calculations are from Tables 2 and 3. The stippled area is the range of $T_{e,s}$ in which gulls would need to increase evaporative water loss but could survive (from Chappell et al. 1984).

TABLE 5. Typical thermal characteristics of Negit, Coyote, and Paoha islands on clear* days in early July, 1984, 11:00–11:30.

Site	Negit Island					Coyote Islet			Paoha Island
	Black rocks	Nest in black rocks	Pumice/greasewood	White tufa	Nest in white tufa	Silt	Tufa crusts	Nest	Black rocks
Reflected short-wave radiation (W/m ²)	71	85	171	476	206	222	241	201	74
Reflectivity	0.08	0.09	0.19	0.51	0.23	0.25	0.26	0.22	0.08
Ground long-wave radiation (W/m ²)	597	675	725	513	769	528	549	560	549
Substrate temperature (°C)	49°	59°	65°	37°	70°	53°	43°	44°	43°
Windspeed (m/sec)	0.95	0.95	0.93	1.38	1.38	2.10	2.10	2.10	0.1

* Perpendicular short-wave radiation equals 1,030 W/m². Diffuse short-wave radiation equals 100 W/m². Sky long-wave radiation equals 210 W/m². Air temperature at 6 cm above substrate ranged from ca. 25–35°C.

TABLE 6. A comparison of "heat stress" days on Negit Island and Coyote Islet (mean \pm 1 SD) in 1984.

14 June-14 July	Negit Island	Coyote Islet
Fraction of days when $T_{\text{sun}} \geq 47^{\circ}\text{C}$	28/30 (93%)	19/30 (63%)
Duration in hours when $T_{\text{sun}} \geq 47^{\circ}\text{C}$ (range)*	4.2 \pm 2.0 (0.25-7.0)	2.8 \pm 2.1 (0.5-6)
Fraction of days when $T_{\text{shade}} \geq 37^{\circ}\text{C}$	15/30 (50%)	0/30 (0%)
Duration in hours when $T_{\text{shade}} \geq 37^{\circ}\text{C}$ (range)*	2.0 \pm 1.2 (0.25-4.0)	0

* Based only on those days when temperatures actually rose to at least 47°C , or 37°C .

site on Negit are largely irrelevant, because the dense vegetation would have provided shade to gulls of any size, we have included those data for the sake of completeness.

Whether thermal conditions will actually lead to mortality depends upon duration of exposure as well as T_c . In 1984 at the Negit site shade temperatures sufficient to cause thermal stress ($\geq 37^{\circ}\text{C}$) occurred on 50% of the days during the chick-rearing period and lasted up to 4 hr (Table 5). That temperature was never reached in shade at the Coyote site. Periods when $T_{\text{sun}} \geq 47^{\circ}\text{C}$ in 1984 averaged 2.8 hr at Coyote and 1.3 hr in 1985. In neither year was there evidence of heat-related mortality.

OCCUPANCY OF NESTING AREAS

By observing the expansion of the colony since 1982 and the establishment of nesting areas on the Paoha Islets each year from 1983 to 1986, we found that gulls first occupied the most rugose islets or areas and subsequently occupied those with plainer topography. Slightly elevated areas near the waterline where the tufa crust had been broken into irregular blocks were used first. Flat, sandy areas of uniform topography were avoided, as were depressions where lateral visibility was impaired. As prime sites became unavailable, late-nesters would accept sandy areas or hollows, if these were adjacent to established territories. Vegetation on the Paoha Islets consisted of a few isolated greasewood bushes and scattered clumps of *Bassia hyssopifolia* that grow to approximately the height of an adult gull. Gulls sometimes nested near vegetation, but rarely within its confines, and then only after other sites had been claimed. On the Negit Islets, also sparsely vegetated, gulls nested mostly on the

sandy pumice substrate that is interspersed among the tufa-covered boulders.

Through 1984 gulls had no safe access to greasewood habitats on Paoha or Negit islands, because of the presence of coyotes. In 1984, however, rising water began to isolate a peninsula of Paoha Island and in 1986 over 100 pairs nested there. Various sites were available, but the gulls nested only on tufa-covered hillocks adjacent to the shore. They avoided an intervening sandy area that contained *B. hyssopifolia* and did not use or even make scrapes in areas of scattered greasewood scrub only 30 to 50 m distant. In 1985 a few gulls resumed nesting on Negit Island. In 1986 most nests were made in open, barren habitats and the few near dense shrubbery were among the latest to be occupied.

SUBSTRATE

We experimentally confirmed the importance of irregular substrates by introducing driftwood to a sandy area on Coyote Islet where gulls had never nested. These were occupied rapidly and in densities similar to those in adjacent tufa-encrusted substrates (Fig. 2B). Nests seemed to be placed without regard for wind direction, but we could not show this because the wood's configuration influenced its acceptability: gulls preferred to nest in a fork or within the arc of a curved piece.

HISTORICAL DATA

Historical data (Table 1) seem generally consonant with occupancy patterns described above. In 1916 to 1919, when the population approximated 3,000 birds, nesting occurred on Negit and Paoha islands and on at least one rocky islet. Although some nesting locations included shrubby vegetation (Figs. 1C, D), all were relatively open and near the waterline, and two were barren (Figs. 1A, B). By the late 1920s or early 1930s, gulls had left Paoha Island, the nesting area on Negit Island expanded from the proximity of the water into adjacent areas higher on the island. Nesting evidently remained concentrated in relatively open habitats (Fig. 1E), although sites farther from the lake contained moderate vegetation. Gulls nested in this general area into the 1950s, but as the population increased and the lake level dropped, owing to water diversions, new sites were developed. Many gulls moved downslope and nested along the barren and newly-exposed rocky shoreline in topography iden-

tical to that used on the Negit Islets; others moved higher into dense greasewood scrub on a plateau atop Negit Island (Winkler 1977). When Negit became a peninsula in 1979, some gulls shifted to the adjacent and already-occupied Negit Islets; others moved to the vacant Paoha Islets, approximately 2 km to the southwest. As gulls reoccupied Negit and Paoha islands in 1985–1986, barren areas near shore were occupied first.

PREDATION

Great Horned Owls raided parts of the gull colony almost nightly, from the time territories were being established in April until after young had fledged in early August. Diurnal visits by Golden Eagles were less frequent and mostly ended by early June. The impact of these predators, from direct as well as indirect mortality, could be high (Jehl and Chase 1987). On the Paoha Islets in 1984, for example, owls killed an average of one adult per night from mid-April to mid-June (0.9% of the adults); raids and disturbance later in the season resulted in high chick mortality and the failure of more than 10% of all nests. And in 1983 eagles killed 16 adults and nine juveniles.

Hunting patterns of the predators were well defined and were influenced by several factors (see Jehl and Chase 1987 for details). On the Paoha Islets, owls seemed to make kills of adult gulls without regard to the presence or absence of vegetation, but vegetation was so sparse and the number of kills so small that no conclusions were possible. However, in 1985 when ca. 15 pairs of gulls were enticed (by decoys) to nest amid dense greasewood shrubbery on Negit Island, nine adults were quickly dispatched, in several cases obviously having been trapped at their nests, and nesting was completely disrupted. For Golden Eagles, physiographic conditions played the overriding role in hunting success, with 40 to 41 kills occurring in hollowed out areas where the gulls' line of sight was obscured by plants or topography.

DISCUSSION

California Gulls breeding in the Great Basin encounter extreme temperature changes. At Mono Lake chicks are not usually stressed by cold because they are brooded at night, but high daytime temperatures are regular events. Overheating of small chicks is probably inconsequential because they are shaded by adults (Beck 1942, Behle 1958) or can find shelter in the irregular terrain. Large

chicks thermoregulate effectively, are better insulated, and gain heat slowly. Nevertheless, they are more likely to be stressed than small chicks because there are few large shaded areas available.

California Gulls sometimes nest near low vegetation or next to or under bushes and these shady locations might appear to enhance chick survival (Pugesek and Diem 1983, Chappell et al. 1984). Yet, Baird (1976:143) reported that nesting success had "nothing to do with vegetation" in a Montana colony. Pugesek and Diem (1983), in Wyoming, reached a similar conclusion. Using multivariate analysis they showed nest location and vegetative cover appeared to enhance productivity, but that those factors were important only because of the age of the parents at those sites. Salzman (1982) also showed that cover was not correlated with chick mortality (up to 90%) in Western Gulls (*L. occidentalis*) in a brief but intense heat wave. Furthermore, throughout the range, California Gull colonies are usually in relatively open situations, where vegetation is not much higher than a standing gull (Chappell et al. 1984; Jehl, pers. observ.; see also Palmer 1916, Willett 1919, Sugden 1926, Decker and Bowles 1932, Gabrielson and Jewett 1940, Marshall and Giles 1953, Johnston and Foster 1954, Behle 1958). Indeed, several authors have specified that California Gulls "prefer to nest where vegetation is low and sparse . . . avoiding nesting in dense herbaceous cover" (Vermeer 1970:21; see also Hayward et al. 1982) and only rarely, and sometimes as a last resort (Findholt 1985), use thick shrubbery. Others had noted that "the open and more barren areas are the first selected" (Beck 1942:94, this paper), or that gulls pluck and trample plants near their nests, so that few plants remain intact by hatching time (Kennedy 1973; Findholt, pers. comm.; Jehl, pers. observ.). Clearly, the presence of vegetation per se is not essential to colony siting.

Another feature common to most colonies is moderate roughness in the nesting substrate, which may be achieved in several ways (rocks, plants, or driftwood). We think that this condition and the use of open situations are responses to predation and cannibalism, which are major and persistent sources of mortality (Vermeer 1970, Kennedy 1973, Butler and Janes-Butler 1982, Pugesek and Diem 1983). Irregular terrain provides cover and camouflage for small chicks, which are cryptically colored. Open areas allow

adults to detect intruders and predators, but preserve an adult's ability to flee rapidly (Kruuk 1964, Vermeer 1970, Lemmetyinen 1971, Burger and Shisler 1978). For other advantages see Parsons and Chao (1983). These conclusions have been anticipated by others (e.g., Buckley and Buckley 1980). Burger and Gochfeld (1981:308) noted that preferred habitats for Kelp Gulls (*L. dominicanus*) "usually contained potential cover for chicks but were not heavily vegetated"; "rocks seemed to provide more suitable cover . . . because chicks could easily hide under them and rock size did not change during the season whereas vegetation grew taller and thicker"; and, "tall, dense vegetation made it difficult to observe predators and to fly immediately from the nest."

Conflicting selection forces associated with predation and thermal stress may pose a dilemma for gulls nesting in hot regions (Hand et al. 1981). For temperature to exert a dominant influence, reduced survivorship from heat stress must occur with sufficient frequency to override any increased risk of predation from nesting in enclosed habitats. This does not seem to be the case at Mono Lake, where avian predation is a continual and significant risk, but very hot conditions are brief and infrequent.

Howell et al. (1974) showed that Gray Gull (*L. modestus*) chicks weighing 150 g, in full sun in the Atacama Desert, Chile, could endure conditions similar to Mono Lake extremes for about 6 hr. That duration was exceeded only once (6.8 hr) at Mono Lake in 1984–1985, and at a time when chicks were small and easily shaded. American White Pelicans (*Pelecanus erythrorhynchos*) and Caspian Terns (*Sterna caspia*) often nest with California Gulls in the Great Basin, but always in the open. We doubt that they are more effective in dealing with hyperthermia than gulls, and suggest that while heat may be a challenge it is not an insurmountable problem for any of these species.

Gulls in the Great Basin, nevertheless, are subjected to heat stress each year and would be expected to nest in cool areas when possible. Historical data are usually uninterpretable because one can rarely know the condition of the habitat, where or whether alternative nesting sites were available, the intensity of predation, the age and status of nesting birds, epizootics, or other factors that affect choice, or a colony's continuous use. Nevertheless, at Mono Lake in 1919, the

four nesting areas were not restricted to, or concentrated in, brushy areas, which would have been expected if shade were a dominant factor; all were at the waterline. While shoreline sites were probably relatively cool, it does not follow that they were selected for their thermal characteristics. Indeed, the Negit Island site was on the warmer (SE) side of that island. We suspect it was open and, therefore, safer than other locations; certainly, it was far more open than the same area is today (cf. Figs. 1E, 2A), which suggests that the presence of the gulls themselves helps create or maintain acceptable habitat.

Of current nesting areas, those on the low-lying and barren Paoha Islets are the coolest overall, because of their open terrain and exposure to the wind. They also provide large chicks with access to the water, which allows them to cool off (Bartholomew et al. 1953, Behle 1958:43, Hand et al. 1981), and also to flee if terrestrial predators appear. Those advantages would not have been available to gulls nesting atop Negit Island; while vegetation there would have provided shade to chicks of any size, it would also have interfered with escape behavior (as in 1985).

We consider the risk of predation to be the major factor influencing both location of California gull colonies and the choice of nesting habitat. Colonies are usually on islands lacking terrestrial predators. Adult gulls cannot elude avian predators, but can maximize (1) their own survival by nesting where approaching predators can be detected and evaded, and (2) their reproductive success by selecting nesting substrates that camouflage and hide small chicks. Thermal conditions seem secondary, at best.

We acknowledge that factors affecting the use of nesting habitat may vary geographically or temporally (O'Connor 1985) and that under some circumstances thermal conditions may take on added importance (cf. Burger and Gochfeld 1986). The degree to which climatic conditions may affect the distribution of the California Gull colonies, however, remains to be shown.

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