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THERMAL STRESS AND PREDATION: INFLUENCES ON THE STRUCTURE OF A GULL COLONY AND POSSIBLY ON BREEDING DISTRIBUTIONS

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ABSTRACT.—The arrangement of nesting territories of *Larus occidentalis livens* on beaches is commonly linear, and most territories are adjacent to water. This arrangement differs from clustered colonies typical of most gulls. Two hypotheses are advanced to explain this unusual arrangement: it may provide access to the intertidal zone for foraging or access to water for thermoregulation. Foraging activity in the intertidal zone is of only modest or secondary importance. In contrast, thermal stress is great and access to water for thermoregulation appears to be essential. Due to the organization of the nesting colony, adults can leave their nests and go to the water during long incubation and brooding bouts and still return quickly to prevent nest predation by ravens or other gulls. The linear arrangement of nests is less pronounced on broad beaches or peninsulas, although close proximity to the water persists. The absence of gulls as breeding species on most tropical islands, which may be related to heat stress and associated problems of predation or overexposure of eggs to the sun, rather than to shortage of food, is discussed. Adaptations by which some species may avoid the heat stress/predation dilemma in any thermally stressful environment are listed.

Two of the three recognized subspecies of Western Gull (*Larus occidentalis*) closely resemble each other. They breed on offshore islands along the west coast of the United States and Baja California. The third subspecies, *L. o. livens*, differs from the other two in a number of characteristics, one of which is colony structure—the subject of this investigation. *L. o. livens* is virtually restricted to the Gulf of California (approximately 23–32°N, 113°W; Devillers et al. 1971) and appears to be fully isolated geographically from the Pacific Coast subspecies (Devillers et al. 1971, Hand 1979). Because this subspecies differs in several respects from the other two (reviewed in Hand 1979), several investigators have suggested that it should be recognized as a separate species (Dickey and van Rossem 1925, Devillers 1971, LeValley 1975, Hand, in press).

In appearance and behavior (Hand 1979), all three subspecies are kin to other large, white-headed gulls of both hemispheres (Moynihan 1959), typified by the Herring Gull (*L. argentatus*) in the northern hemisphere and the Kelp Gull (*L. dominicanus*) in the southern hemisphere. Most gulls breed at latitudes above 30°, in boreal, subantarctic, and arctic habitats. *L. o. livens*, in contrast, breeds on desert islands under extremely hot and dry conditions.

A striking feature of its colony structure is that nests are nearly always placed on beaches or low-lying peninsulas, usually in a roughly linear manner slightly above the high-tide line. These gulls may also nest in semi-isolation: a single pair may be the only gulls occupying the beach of a small cove. Thus, the territories of most pairs are “on the waterfront” and their owners have unimpeded access to the water without having

TABLE 1. Colony size and distance to nearest neighbor's nest for *Larus occidentalis livens* in the Gulf of California.^a

Island	Number of nests	Distance (m) to nearest neighbor's nest		Substrate
		Mean	SD	
Refugio	20	8.65	2.99	Grass
Angel de la Guarda	45	7.15	6.34	Sand beach
San Esteban (E side)	12	10.67	5.38	Sand beach
San Lorenzo Sur (SW side)	139	9.08	6.00	Sand beach
Pond (N of Angel de la Guarda)	13	4.74	2.24	Brush and rock
Estanque (spit nearest Angel de la Guarda)	37	5.94	3.55	Boulder beach
San Pedro Martir (cove, SE side)	40	7.52	4.83	Boulder beach
Salspuedes (NW cove)	43	5.99	2.90	Boulder beach
Cardinosa (S cove)	29	7.55	6.66	Boulder beach

^a These censuses refer only to colonies visited and do not purport to be complete censuses of the populations resident in the Northern Gulf.

to cross other territories. Slopes or plateaus away from the water, which appear otherwise suitable for nesting, are virtually never used. Although some other species may also align their nests with respect to artificial or natural environmental features (Noble and Wurm 1945, Bongiorno 1970, Burger 1974), the nests in colonies of *L. o. livens* are not clustered as they are in colonies of most gulls, including other white-headed gulls nesting at higher latitudes.

Our preliminary observations indicated that pairs of this subspecies defend long, narrow territories from their nests to, and possibly into, the intertidal zone. Observations of birds feeding, drinking, and bathing in the intertidal zone suggested that water might be important for foraging, for thermoregulation, or both, and that one or both factors might account for the unusual structure of their colonies. This paper reports results of a study to determine 1) whether pairs defend areas extending from the nest to, or into, the intertidal region, 2) what factors cause the linear organization of the colony, and 3) what selection pressure(s) favors nesting near the water.

STUDY AREA

The Gulf of California contains 45 fairly large islands and many smaller ones; only nine exceed 20 km in length (Anderson et al. 1976). They are of barren or desert-like aspect, and their coastlines are often irregular, rocky, and steep. Most, however, have beaches that range in composition from large boulders (>1 m in length), to cobbles of various sizes, to sand.

Hunt and Warner visited islands listed in Table 1 between 2 and 11 April 1973. Hand worked at the north and southeast ends of Isla Angel de la Guarda (15–17 June 1974; 19–23 April 1975) and at Isla Cardinosa, a small island immediately south of Angel de la Guarda (11–29 April 1976, 14–20 May 1978). All of these islands are in the northern part of the Gulf (Fig. 1).

Tidal amplitudes are large in the Gulf of California: up to 6.7 m; maximum tide for islands in the principal study area is approximately 3.4 m. Storms with strong winds (e.g., 26 km/h with gusts up to 40.8 km/h) occur occasionally during the breeding season, driving the

surf above the high-tide line, especially on windward beaches. During clear weather, however, shorelines are washed by varying but generally very mild surf. Few mammals inhabit any of the islands and on most they pose no serious threat to the gulls, their eggs, or chicks.

METHODS

Hand made some observations (35 h total) of unmarked birds on Isla Angel de la Guarda from a blind, and more extensive observations (more than 95 h) of territorial and thermoregulatory behavior at Isla Cardinosa from blinds overlooking south and northwest beaches (Fig. 1). The latter study involved marked and unmarked pairs holding waterfront sites. Four marked and two unmarked pairs were observed in 1976, and a different set of three marked and three unmarked pairs in 1978. The birds were marked by tying a fish to the dye-coated inside of a tin can; when a gull tried to extract the fish, dye spread over its head and breast in a unique pattern which remained up to two weeks. Most observations were made when nests contained eggs or small chicks (one to eight days of age). Less structured observations of territory establishment and courting involved unmarked birds, the sexes of which usually could not be determined with confidence because they were no longer courting and copulating.

In order to determine territory structure, Hand recorded the owners' responses to intruders: intruder is supplanted immediately, supplanted after an initial delay (one-half to several minutes), challenged (i.e., displayed to, but not supplanted), or tolerated (no display other than an alert posture). Hand also recorded which owner was present and, if both were present, which displaced the intruder; and noted whether these interactions occurred within 3 to 4 m of the eggs or chicks, farther away (but not at the water's edge), or at the water's edge.

Hand also examined the use of the intertidal region of Isla Cardinosa in April 1976 and May 1978: eight censuses were made from observation posts overlooking the south beach and seven from points overlooking the north beach (Fig. 1). This island has no mudflats: all intertidal regions are cobble or boulders and even at low tide little seaweed is exposed. The state of the tide (low, medium, high) was recorded and birds were tallied as foraging if they consumed a food item or appeared to be searching or probing in the water, seaweed, or cobble.

In 1976 and 1978, Hand recorded behavior associated with thermal stress. A blind was used as gulls will not voluntarily leave their nests to drink and bathe if they can see a human observer. Hand made uninterrupted daily observations (3–6 h), from mid-morning

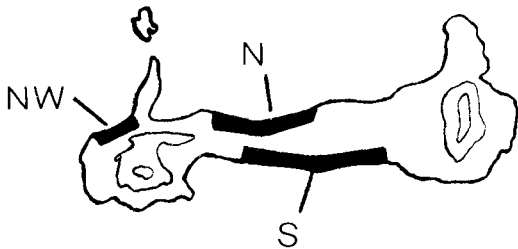
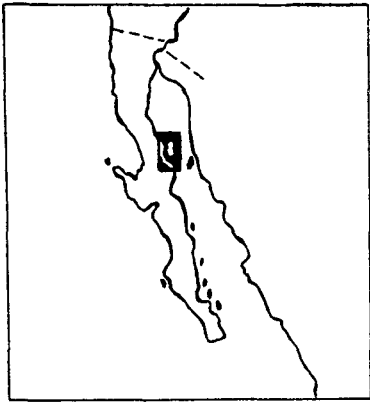


FIGURE 1. Location of study sites. The small black rectangle on the map of Baja California indicates the general location of the principal study site, Isla Cardinosa, and other islands included in the study. Beaches studied on Isla Cardinosa are indicated by letter: NW = northwest beach, N = north beach, S = south beach.

to mid-to-late afternoon, and recorded the following information: wind speed (at roughly hourly intervals—1976 only); black bulb (1978 only) and shaded air temperatures (at roughly 5-min intervals); whether or not birds (six pairs each year) were panting (at roughly 5–10-min intervals); degree of erection of scapular feathers (at 5-min intervals in 1976 and irregular intervals in 1978); duration of any period when a bird was off a nest containing eggs and the behavior of the relieved birds; any instance in which a parent attending chicks moved farther than 5 m from them and its behavior while away from them.

RESULTS

COMPARISON OF NESTING COLONIES

L. o. livens commonly breeds wherever nests can be placed far enough above the high-water mark to avoid destruction during storms. Large beaches may hold 200 or more pairs, smaller beaches two or three pairs; single pairs are found in small coves (Hand, unpubl. observ.). Nests in these colonies are characteristically arranged in a line, as illustrated in Figure 2 for the north beach of Isla Cardinosa.

To determine whether the linear arrangement of nests in these colonies is caused by

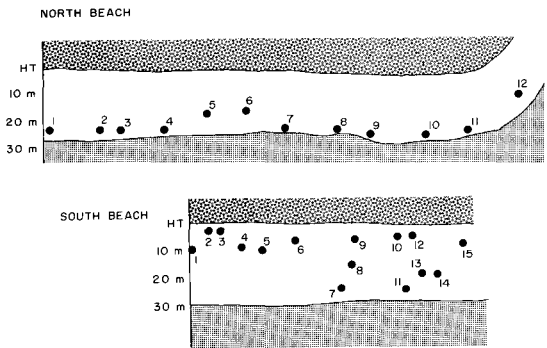


FIGURE 2. Sections of north and south beaches on Isla Cardinosa. Dots indicate nest locations. HT = high-tide line. Oval pattern = intertidal region. Stippled areas = slopes behind nests.

a preference for waterfront territories or by physical constraints of the terrain, we compared the arrangement of nests on two beaches that have similar cobble substrate, but differ in width. Locations of all 12 nests on the north beach of Isla Cardinosa were compared to those on a section of south beach with a similar number of nests (Fig. 2). The north beach is narrower (approximately 26 m maximum at high tide) than the south beach (for which many points are 30 m in width at high tide). Both are backed by low bluffs. All of the nests on the north beach were in a line; and there were no nests behind pairs 1–6 on the south beach.

Nest arrangements on the two beaches cannot be evaluated without considering differences in the protection each offers during spring storms. The north beach is more exposed, and nests on this beach were well back from the high-tide line: 75.0% (N = 12) were 20 m or more from it. On the south beach section, 66.6% (N = 15) were within 10 m of the high-tide line and only 13.3% (2 of 15) were more distant than 20 m.

Nest density was higher on the south beach (0.0054 nests/m vs. 0.0028 nests/m on the north beach in the sections shown in Fig. 2). The nests were closer together on the south beach (mean distance \pm SD, to nearest neighbor: south beach, 7.3 ± 2.6 m, N = 13; north beach 13.2 ± 3.3 m, N = 10), and many were nearer to the high-tide line, allowing room for additional nests behind waterfront territories.

TERRITORY STRUCTURE AND DEFENSE

The responses of pairs nesting on the waterfront to intruders indicated that these territories extended from the nest area into the intertidal zone. Most intruders were sup-

planted from somewhere within the territory other than at the water, but on eight occasions when the tide was substantially below mean high tide they were at the water's edge and were thus in the intertidal zone.

Boundaries were firmly established between territories of neighboring pairs in areas near their nests and in the upper parts of the intertidal zone. Interactions between neighbors at the water during medium or low tides were so few that we could not determine the nature of territory boundaries there. A few observations suggest that the territories extend into the water for short distances, but again our observations of birds interacting in the water are too few to justify conclusions.

Distances between nests in our study area are indicated in Table 1. The four most extensively observed pairs appeared to be breeding successfully with nests close together and no large barriers to visibility between them. Two of these nests were only 2.2 m apart.

Defense during incubation. Intruding gulls most often entered territories within several meters of the water, but occasionally landed in other areas, such as the bluffs behind some nests. Incubating birds never left nests to displace intruders, a behavior that would leave eggs exposed. Intrusions by other gulls were relatively rare when both members of an incubating pair were present. They evoked variable responses from the non-incubating member. Intruders who were bathing or loafing at the surf could be tolerated, supplanted, or challenged but not supplanted. Intruders were never permitted near the nest and were commonly supplanted from locations between the nest and water as well. Nesting gulls consistently defended a larger area during the courtship and post-hatching period than during incubation (Hunt and Hunt 1975).

Defense during chick stage. Intrusions occurred regularly during all observation periods, but our most systematic observations were made when most pairs had small chicks. During 21 h of observation, conspecific intruders entered territories 75 times and were supplanted 55 times (Table 2). When both parents were present, only one usually overtly challenged an intruder. Parents responded with about equal frequency, whether they were close to the chicks or some distance away (e.g., loafing near the surf).

The responses of single parents attending chicks were variable. Sometimes they

TABLE 2. Response of attendants to intruding gulls (seven pairs, 21.25 h of observation).

Response	Number of responses
I. Intruder removed ^a	55
A. Intruder not within 2 m of the water (N = 44)	
B. Intruder within 2 m of the water (N = 8)	
C. Owner returns from the water to remove intruder near chicks or nest (N = 3)	
II. Intruder challenged/displaced, but not removed	9
A. Intruder not within 2 m of the water (N = 8)	
B. Intruder within 2 m of the water (N = 1)	
III. Intruder neither challenged ^b nor removed	11
A. Intruder not within 2 m of the water (N = 11)	
B. Intruder within 2 m of the water ^c	

^a Displaced at least to the next territory.

^b The parent, which is in an aggressive or alert posture, watches the intruder carefully, but does not charge or display.

^c Value could not be determined. Owners were marked on the breast. If a bird at the surf was facing away from the observer, it was not always obvious if it was a non-attending owner that had just returned, a non-attending member of a neighboring pair, or an intruder from another location.

watched an intruder carefully, but did not supplant it. If an intruder came within 3 or 4 m of chicks, it was usually charged, although not necessarily supplanted. Single parents tended to remain near their chicks, but in some (11) cases they left them briefly to displace intruders as far as 15 m away. They also frequently went to the water while their partners were absent, but immediately returned to the nest or chicks to remove intruders.

In sum, any piece of ground around the nest or on a corridor between nest and water was defended. The focal point of defense in the early days post-hatching was centered on the chicks (Ewald et al. 1980). Parents, when alone, might leave the nest or chicks briefly, but they always kept them in sight.

FORAGING

L. o. livens is an omnivorous opportunist. Hand saw them swallow or regurgitate fish, a petrel (probably *Halocystena microsoma*, which breeds in large numbers on Isla Cardinosa), a large crustacean (crab or lobster), squid, small red crabs, pelican eggs (*Pelecanus occidentalis*), offal thrown from fishing boats, and food scraps from campsites. Groups of up to 60 individuals congregated

where professional fishermen clean their catch. In mid-May, 1978, large numbers of squid became trapped in the intertidal shallows of a bay below the territories of several pairs. Gulls gathered to feed here in groups of 10 to 45 individuals, and chicks on this island were fed squid for at least the next five days.

Gulls also forage in the intertidal zone. On Isla Mejia, a large crescent-shaped beach forms a bay on its lee side where low tides expose a mud flat partially covered with seaweed. On two consecutive days, Hand watched 30 to 40 gulls foraging there for several hours at low tide. The birds moved more or less randomly, but numerous displacements occurred. The situation resembled descriptions of defense of feeding areas by Herring Gulls (Drury and Smith 1968). Nesting territories of many of the foragers were on the windward side of the beach and were not contiguous with the mud flat.

In 10 of 15 censuses on Isla Cardinosa, no birds were foraging in the intertidal zone; this included three of the five censuses conducted at low tide. The largest number of gulls foraging during any census occurred on the south beach on 14 April 1976 during low tide. The section of the beach adjoining the intertidal area under observation had 52 nesting pairs, and both members were present at many sites so that 85 to 90 birds were on the beach. Only nine, however, displayed any interest in hunting among the rocks or debris in the intertidal zone, with little evident success. The north beach of the island had 12 nesting pairs, and the largest number of birds seen hunting among the rocks on this beach was two (during a high tide). Birds did search in the exposed cobble of these beaches at times not included in the censuses. On two such occasions, we chased them away, examined the areas, and found only small prey items (isopods, amphipods, limpets, crabs, and flatworms). During more than 90 h of detailed observations, we saw known individuals at 10 nests forage in the intertidal zone below their territories only seven times. Our evidence thus suggests that nesting adjacent to water does not occur primarily to provide access to intertidal sources of food.

THERMOREGULATION

Observations of the behavior and thermal environment of gulls on Isla Cardinosa indicate that they experience considerable heat stress. Shade temperatures on hot days were above 30°C at midday and for many

TABLE 3. Black-bulb and shade temperatures on Isla Cardinosa, 1978.

Day	Time		Shaded temperatures in blind (°C)	Black-bulb temperatures ^a (°C)
16 May	10:30 to 17:00	Range	27.5–36.0	40.5–53.5
		Mean ± SD	31.5 ± 2.5	46.0 ± 4.0
		N	16	16
17 May ^b	9:30 to 15:00	Range	23.5–27.5	40.5–51.5
		Mean ± SD	25.8 ± 1.3	45.5 ± 3.6
		N	11	11
18 May	10:00 to 14:30	Range	30.0–35.0	36.5–50.5
		Mean ± SD	32.9 ± 1.8	44.4 ± 4.1
		N	10	10

^a Black-bulb placed in direct sun, at ground level, sheltered from breeze.

^b A cloudy, overcast day.

hours black-bulb temperatures consistently exceeded 40°C (Table 3). A few gulls on the island were sometimes shaded by an adjacent rock, usually in the late afternoon, but the vast majority were fully exposed to the sun, frequently without benefit of any significant breeze. The upper critical temperature of the Herring Gull, a gull of similar size, is 30°C (Lustick et al. 1978). If the upper critical temperature of *L. o. livens* is similar, birds would acquire a heat load whenever standard operative temperatures (Bakken 1980) exceed 30°C, a regular occurrence on windless days in these colonies.

Behavior of the gulls reinforces the notion that they experience heat stress. When their mates were present, adults left eggs or chicks and went to the water to bathe, drink, or both. More significantly, they also made trips to water when their mates were absent: five incubating birds whose mates were absent made 18 trips to the water during 38.5 h of observation, and four others attending very small chicks made 13 such trips during 21.0 h of observation. Trips by lone birds were uniformly brief, usually no more than 3 to 4 min. (One bird with a chick and a hatching egg made the round trip in less than 40 s.) Thus, adults left eggs and very small chicks unprotected for only brief periods while they sought water. Physiological measurements would be required to establish unequivocally that heat stress necessitated these trips, but the gulls' behavior suggests that this is the case, particularly during incubation.

We detected no obvious evidence of belly-soaking, such as dripping wet feathers

(Maclean 1975), nor did parents provide moisture to chicks other than in regurgitated food. However, it is possible that the gulls erect their belly feathers while in the water and thereby wet the feathers which would subsequently wet the eggs. Once when a bird returned, sat, and then stood again briefly, the eggs did appear damp.

Incubating gulls on Isla Cardinosa sometimes stood over their eggs for several minutes, a behavior commonly seen in the desert-nesting Gray Gull (*L. modestus*), and believed to prevent the eggs from overheating (Howell et al. 1974:21). During 15.5 h of observation of four nests during mid-April, however, eggs were left *completely* uncovered 11 times for intervals varying between 30 s and 5 min (usually about 3 min). Since gulls lose heat through the feet at high temperatures (Steen and Steen 1965), they may receive thermal relief by exposing their legs or brood patches or both, especially if a slight breeze is blowing. It is not clear why these gulls did not *always* stand over their eggs, shading them while simultaneously exposing their legs. Perhaps rocks or other objects prevented breezes from reaching particular nests so that birds were forced to move away from the nest in order to be cooled by the breeze.

Incubating *L. o. livens* also regularly pant and elevate their dark scapular feathers to varying degrees, another indication that they are experiencing heat stress. Shade and trips to water had notable effects on the frequency of both forms of behavior. In one example (Fig. 3), male 3 and female 4 had been panting steadily for over 2 h. At 15:00, male 3 made a brief trip to the surf and during the next 15 min he did not pant and his scapular feathers were relaxed, while female 4 continued to show signs of thermal stress. Panting virtually always stopped for several minutes after a trip to water, and although the scapulars did not always return to a fully relaxed position when the bird again sat on the nest, their elevation was always reduced after such trips. In addition, exudate typically began to drip from the nostrils about 15 min after the birds drank. In a second example (Fig. 3), male 6 also initially showed signs of thermal stress until about 13:15 when his bill, and then head, became shaded by a nearby rock. Panting and feather erection then ceased and the contrast to birds still in full sun was striking, particularly since this effect occurred with shading of only the head. On three or four occasions, Hand watched birds as shade began to fall on their backs: they could have

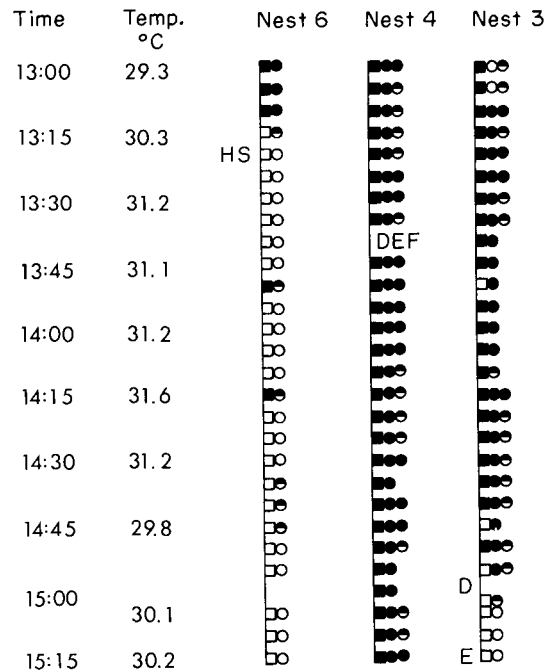


FIGURE 3. Effects of shade or trips to water on panting and erection of scapular feathers. There was no breeze during the recording period. Temperatures were recorded at 5-min intervals (one exception, the reading at 15:02) in still air in the shade of a blind. Panting: open box = not panting; closed box = panting. Scapular feather erection: open circle = scapular feathers relaxed; one filled circle = scapular feathers elevated slightly; two filled circles = scapular feathers elevated noticeably, but tips not separated. Half-filled circles indicate a state of erection intermediate between the number of filled circles depicted. HS = head shaded. DEF = defecates. D = drinking trip. E = exudate drips from nostrils.

moved their heads into the shade, but none did and they continued to pant.

Within a day or so after hatching, parents lured their chicks 2 to 4 m from the nest before feeding them. On three occasions, they lured 4- or 5-day-old chicks from a shaded hiding place near the nest to another hiding place within 1 or 2 m of the water. Since we saw other chicks at the water's edge on other occasions, "long-distance" luring probably occurred commonly. In all cases, chicks near the water were at least four or five days old. The movements occurred much as Evans (1970) described for "colony emigrations" in Ring-billed Gulls (*L. delawarensis*).

Moving chicks to water allowed the attending parent to loaf in comfort without leaving them. Nonetheless, chicks were left in or near the nest, while the parent flew to the water, until they were three or four days old. Since the water was calm on very hot days, chicks could presumably drink or

bathe. This may have been essential if they could not be shaded effectively by parents or objects near the nest. Although Hand observed chicks at the water's edge continuously for several hours on five occasions, none went into the surf or drank; all of them, however, were shaded by rocks most of the time and showed no signs of heat stress.

PREDATION

Common Ravens (*Corvus corax*) were present on all islands that we visited and virtually all gulls tending eggs or chicks gave Long Calls (Hand 1979, in press) and watched them intently whenever they appeared. Other species (Brown Pelicans, Osprey [*Pandion haliaetus*], and American Oystercatchers [*Haematopus palliatus*]) that passed low and directly over nests caused no such response. D. Judge (pers. comm.) has seen ravens steal gull eggs, and there is every reason to believe that they would pose a serious threat to eggs and chicks left exposed and unattended.

Gulls, however, are probably their own worst enemies, since they cannibalize the eggs and young of other breeding conspecifics. *L. o. livens* is no exception: adults take eggs and attack and kill conspecific young birds. For example, on Isla Cardinosa in 1978 one seven- or eight-day-old chick was mobbed and killed on its own territory, while another on a nearby territory simply disappeared (Hand 1980). Bodies of eight chicks of approximately the same age were also found on this island, which had approximately 200 nests. Given the large number of intrusions that occurred on Isla Cardinosa and the regularity with which single parents left the nest and went to the water, there seems little doubt that eggs or chicks exposed and unprotected for any extended period would be taken by other gulls.

DISCUSSION

COLONY STRUCTURE

The linear arrangement of territories in colonies of *L. o. livens* may be prevalent either because the birds prefer unobstructed access to the water or because they are constrained to such an organization by the habitat. Some beaches are narrow or backed by bluffs; others change abruptly in composition from open cobble, lacking vegetation or sand, to some other substrate. Birds may not nest behind other pairs only because there is no room to do so on a preferred substratum.

The arrangement of nests was not strictly linear on the south beach of Isla Cardinosa (Fig. 2), and nests or nest construction activities have occasionally been noted in areas other than beaches ("built at the foot of cliffs, just above high-water mark"—Bent 1921:92, and "about 9 m up from the water on steep, rocky slopes"—J. R. Jehl, pers. comm.). We do not know if the nests in these other areas were arranged linearly, but they were clearly close to the water. On Refugio (at the north end of Angel de la Guarda), where the colony occupied a low spit, Hunt and Warner found nests on grassy areas up to 30 m away from the beach. Most, however, were along the shore rather than on the central portion of the spit. This finding supports the hypothesis that *L. o. livens* prefers waterfront nest sites, even on low-lying peninsulas.

Two additional observations in our study indicate that this gull prefers to nest as near the water as weather and terrain will allow, and that it prefers unobstructed access to water. First, nests were closer to the high-tide line on the sheltered south beach of Isla Cardinosa than on the north beach, apparently as close as was possible without significantly increasing the danger of loss during storms. Second, linearity persisted on parts of south beach, even where space was available behind waterfront nests (Fig. 2). Pairs could presumably select any unoccupied beach site, but some apparently established waterfront territories on the less protected north beach rather than behind waterfront pairs on the south beach.

Since pairs do not invariably hold waterfront territories, but all territories are near water, it is theoretically possible that *unobstructed* access to the water may not be more important than simply the close proximity of water. The longer the flight distance between the water and the nest, however, the greater the potential hazards of predation to eggs and chicks. In view of the large tidal amplitudes in Baja California, which often leave nests far from the water at low tide, waterfront sites may be the best ones. Also, adults holding waterfront territories move their young to the water to tend them. If pairs that do not hold waterfront territories attempt to do the same, their chicks may face an increased risk of attack as they pass through the territories of other pairs to reach the water.

The potential for predation of eggs or chicks is unusually great in the Gulf of California because breeding adults frequently leave the nest. The primary solution to this

dilemma has apparently been behavioral: colony structure has been altered by selection (or learning) acting on nest site preferences, allowing adults to leave nests while simultaneously protecting them.

POSSIBLE EFFECTS OF THERMAL STRESS AND ASSOCIATED PROBLEMS ON THE DISTRIBUTION OF GULLS IN THE TROPICS

Gulls are widespread and very successful in temperate, boreal, and even arctic marine habitats, but notably absent throughout most of the marine tropics. A commonly encountered explanation for their absence in the tropics is that they are coastal scavengers, and that tropical islands do not provide enough food to support more than a few of them at most (Snow and Snow 1968:262). Gulls are, however, highly adaptable, omnivorous opportunists (Fordham 1964, Harris 1965, Trapp 1979). They have a remarkable range of techniques for procuring food (Tinbergen 1953, Ashmole 1971:229) and they can shift foraging patterns to take advantage of short-term fluctuations in food supply (Ingolfson 1967). Many prey on eggs and chicks, and since most suitable tropical islands support breeding colonies of other species nearly year-round, a ready food supply should be available. Although their numbers might be limited by available food, in warm marine environments or elsewhere, it seems unlikely to us that lack of food is a sufficient explanation for the frequent absence of gulls as breeding species on marine, tropical islands.

Our observations of thermal stress, predation, and colony structure in groups of *L. o. livens* suggest other factors that may contribute substantially to the exclusion of large white-headed gulls from tropical islands. The following discussion focuses on the predation of eggs and chicks and on the overheating of eggs, but these need not be the only critical thermal problems of gulls in the tropics. Kendeigh's studies (1934, 1964) show that the time and energy expended by breeding adults to cool themselves may become so great that they interfere directly with the birds' reproductive effort. G. A. Bartholomew, T. R. Howell, and their colleagues have described a variety of thermoregulatory adaptations that are clearly vital to the success of several tropical families (Bartholomew et al. 1953, Bartholomew and Dawson 1954, Howell and Bartholomew 1961a, b, c). For example, pelicaniforms are very successful in the tropics and make extensive use of gular flutter for thermoregulation. Other species, such as

the tropical albatrosses, can apparently go without drinking for long periods. These investigators stress the importance of appreciating the thermoregulatory capacities of tropical sea birds in understanding their distribution and general biology (Howell and Bartholomew 1962).

The present distribution of gulls indicates that they evolved in boreal/temperate regions of the northern hemisphere. In this regard, responses of *L. o. livens* to thermal stress are similar to those of temperate/boreal species (Steen and Steen 1965, Lustick et al. 1978). Potential gull colonists in tropical marine habitats may be faced with some problems in procuring food, but stresses imposed by high temperatures may be even more critical. If a particular island does not, for some reason, provide opportunities for gull colonists to solve heat stress problems and the associated problem of predation (conspecific or otherwise) should they leave the nest or chicks, then they probably cannot secure a foothold, even if food is abundant.

A few species of gulls do breed successfully in thermally stressful environments. Many relevant aspects of their breeding biology are still largely unknown, but the adaptations of one species, the Heermann's Gull (*L. heermanni*), to the problems of heat stress and predation have been described (Bartholomew and Dawson 1979) and differ somewhat from those of *L. o. livens*. Heermann's Gull also breeds in the Gulf of California, in dense colonies in which most territories lack ready access to the water. Many responses of this species to thermal stress are similar to those of *L. o. livens* and other gulls and include panting and feather erection. Unlike *L. o. livens*, however, incubating *L. heermanni* sit tightly and continuously on the eggs during the heat of the day. Unless relieved by a mate, they do not make trips to the water. Consequently, the eggs are protected from other gulls and, as emphasized by Bartholomew and Dawson, not exposed to the sun, which would cause injurious overheating within minutes. After sunset, many members of a colony may take flight, and sometimes depart for waters some distance from the nests (G. A. Bartholomew, pers. comm.). The eggs are then exposed, but since the sun has set, overheating is not a threat and the danger of predation by neighbors is much reduced since nearly all birds leave the area. The explanation for differences in the behavior of *L. heermanni* and *L. o. livens* may relate to differences in the color of their plumage:

TABLE 4. Possible solutions to the thermal stress/predation dilemma of gulls.

Adaptation	Species ^a
1. Nest immediately adjacent to water and utilize it for drinking/cooling: allows nest observation during quick trips to water, reducing risk of predation or overexposure of eggs to the sun	<i>L. o. livens</i> <i>L. fuliginosus</i> <i>L. hemprichii</i>
2. Nest under a cover that provides sufficient shade to reduce or eliminate thermal stress	<i>Creagrus furcatus</i> <i>L. hemprichii</i>
3. Shorten nest relief intervals	
4. Develop dark plumage to reduce thermal stress. Replenish water losses after nest relief or in the dark	<i>L. hemprichii</i> <i>L. modestus</i> <i>L. heermanni</i> <i>L. fuliginosus</i>
5. Wet the eggs (belly-soaking) to cool them	<i>L. o. livens</i> <i>L. genei</i>
6. Move chicks near water so that they can be guarded while the adult is in the water	<i>L. o. livens</i> <i>L. fuliginosus</i>
7. Depend for cooling or for replacement of body water on reliable environmental changes, such as: 1) Daily winds 2) Daily rains	<i>L. modestus</i>
8. Develop compensating physiological responses to heat stress, such as higher heat tolerance or lowered metabolic rate <i>To deal specifically with conspecific predation:</i>	
9. Cease conspecific predation	<i>C. furcatus</i> ^b <i>L. modestus</i>
10. Nest solitarily	<i>L. hemprichii</i> <i>L. fuliginosus</i>
11. Adjust trips to water to minimize danger from neighbors (e.g., go only when neighbors do or when they cannot leave their own nests)	<i>L. o. livens</i> <i>L. heermanni</i>
12. Synchronize nesting so that neighbors are busy with their own eggs/chicks	Nearly all gulls

^a References: *L. o. livens*: this study; *L. fuliginosus*: Snow and Snow (1969); *L. hemprichii*: Archer and Godman (1937), Meinertzhagen (1954), Fogden (1964); *C. furcatus*: Snow and Snow (1967, 1968); *L. modestus*: Howell et al. (1974); *L. heermanni*: Bartholomew and Dawson (1979); *L. genei*: Wallace (1964).

^b The adaptation is probably related to change in feeding habits, not heat stress or predation.

the lower neck and body of *L. heermanni* are dark grey, not white as in *L. o. livens*. Howell et al. (1974) concluded that a thermoregulatory benefit is a likely selective advantage of dark plumage, and Walsberg et al. (1978) demonstrated experimentally that in a breeze, dark plumage may be more effective than white in minimizing a heat load. The dark plumage of Heermann's Gull may facilitate breeding away from the immediate vicinity of water by prolonging the period of tolerance of the birds to heat stress—drinking can be deferred until the next nest relief or until after sunset, when neither overexposure nor predation of the eggs or chicks are likely to occur.

In the Galapagos Islands, the Lava (*L. fuliginosus*) and Swallow-tailed (*Creagrus furcatus*) gulls also breed under warm conditions. Papers discussing their colony structure (or lack of it in the case of *L. fuliginosus*) have usually implied or argued that present conditions are the result of evolutionary solutions to problems associated

with foraging and predation (Snow and Snow 1967, 1968, 1969). The breeding sites and dispersions of both species, however, can also be interpreted as adaptations to heat stress and predation. The same is true of other larids that breed in tropical marine habitats. The Sooty Gull (*L. hemprichii*) for example, sometimes nests in small colonies and sometimes solitarily (Fogden 1964); Lack (1968:132) presumed that solitary nesting occurs where food supplies are insufficient to support a colony. This species, also a bold predator of eggs and chicks and troubled by thermal stress, frequently nests on the edges of islands near the water, commonly under bushes, and incubating adults regularly leave the nest and go to the water to cool off (Fogden 1964). The habit of nesting under bushes has been attributed both to attempts to avoid heat stress (Meinertzhagen 1954) and predation (Archer and Godman 1937). Solitary nesting may reduce predation, especially conspecific predation. Fogden's descriptions of this gull's foraging

activities, while not quantitative, do not suggest that food scarcity is a problem. Clapham (1964) specifically stated that in the Red Sea, where Sooty Gulls also breed, the food supply is astonishingly rich. Thus it can be argued, in the absence of relevant data, that this gull nests solitarily or close to water in order to avoid predation, and not because of food scarcity.

Pairs of gulls may be able to nest away from the water if they can decrease intervals between nest exchanges, so that each bird can cool itself more frequently. Grant (1979) reported, for example, that the nest relief intervals of Black-necked Stilts (*Himantopus mexicanus*) and American Avocets (*Recurvirostra americana*) in the thermally stressful Salton Sea area of southern California are inversely correlated with ambient temperature, becoming shorter as temperatures rise. The same is also apparently true of Forster's Terns (*Sterna forsteri*) at the Salton Sea. Neither *L. o. livens* nor *L. heermanni* (G. A. Bartholomew, pers. comm.) appear to shorten incubation shifts in response to thermal stress, although quantitative data are lacking. Drent (1970) suggested that among Herring Gulls the duration of an incubation shift is determined by the foraging pattern of the off-duty bird. If foraging methods do not permit frequent nest reliefs, colonizing gulls must find other solutions to problems associated with thermal stress.

Terns may breed successfully in the tropics, in contrast to gulls, because they do not practice conspecific predation. Dinsmore (1972) reported that incubating Sooty Terns (*S. fuscata*), which breed in dense clusters, fly to the water to drink, leaving their nests exposed. This allows them to cool themselves, risking predation only from non-conspecific sources. Gulls in similar circumstances face an intolerably high risk of predation from their neighbors.

Table 4 is an almost entirely hypothetical list of possible adaptations (or pre-adaptations) that alone or in combination may solve the dilemma of thermal stress/egg overexposure/predation of gulls that breed in any hot habitat. The table also identifies species that breed in hot or marine tropical regions and have, or may have, such adaptations. The table is not exhaustive, and the listing of a species does not necessarily indicate that it has the trait or that the trait reduces heat stress or associated problems, only that the literature suggests that such an adaptation is present and may function in that capacity.

This study focuses attention on a crucial problem, other than food scarcity, faced by gulls—which by ancestry are temperate/boreal species—if they attempt to breed in marine tropical habitats, a problem apparently generated in large part, by their predatory habits. Future studies of gulls and terns that breed in the tropics and other thermally stressful habitats should place more emphasis on thermal stress and related phenomena. Consideration of possible adaptations such as those in Table 4, as well as data on foraging behavior, may increase our understanding of the factors that influence the geographic distribution of gulls.

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