

NEST-SITE SELECTION BY YELLOW-FOOTED GULLS¹

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Abstract. In 1977, we studied nest-site selection and breeding success of Yellow-footed Gulls (*Larus livens*) at Bahia de los Angeles, Baja California. Seventy-five percent of the population nested colonially, a habit facilitating defense against egg and chick predation by Common Ravens (*Corvus corax*). The majority of these pairs selected beach-berm substrate where they obtained optimum visibility of surroundings. Beach-berm substrate also provided conditions that enabled them to place nests close to the water (advantageous for maintaining predator defense while practicing thermoregulatory activities necessary in a hot climate). The remaining 25% of the population nested noncolonially, probably in response to the threat of egg collecting by man. The majority of these pairs nested on talus-boulder substrate, a terrain difficult for man to negotiate, but which also provided suboptimum visibility of surroundings, and suboptimum conditions for nesting close to the water. Low reproductive success (0.12 young/pair) on Islas Coronado and La Ventana was attributed to predation by man on gulls nesting colonially, and ravens on gulls nesting noncolonially.

Key words: *Nest-site selection; predation; Baja California; Yellow-footed Gull.*

INTRODUCTION

The more important features that provide favorable nesting habitat for larids include substrate stability, proximity of feeding areas, adequate spacing from aggressive neighbors, absence of mammalian predators, and shelter from climatological factors (reviewed by Buckley and Buckley 1980, Burger 1985, Burger and Gochfeld 1985). Although nest-site selection has been studied extensively in many species, little information is available for the Yellow-footed Gull (*Larus livens*), a species endemic to the Gulf of California, Mexico (Anderson 1983). Nest-site selection in *L. livens* is of additional interest because this is the only large, white-headed gull that breeds in the subtropical zone; all other species breed in temperate or arctic regions (see Hand et al. 1981, Harrison 1983).

There is evidence suggesting that breeding success of *L. livens* is strongly affected by avian (Common Ravens, *Corvus corax*) and mammalian predators, e.g., humans (Hand 1980, Hand et al. 1981), which act as opposing forces on nest-site selection in gulls. For example, where avian predators are the major selective force, gulls have relatively short internest distances, thus facilitating predator diversion through group defense

(reviewed by Götmark and Andersson 1984). On the other hand, dense nesting arrangements likely increase the foraging efficiency of large mammalian predators, against which group defense is usually ineffective (see Tinbergen 1952, Kruuk 1964, Lack 1967, Tinbergen et al. 1967, Kadlec 1971, Southern et al. 1980). Therefore, greater internest distances are expected where large mammalian predators are the most serious threat, as found by Tinbergen (1960), Boekelheide (1980), Burger and Lesser (1980), Hand (1980) and Hand et al. (1981) did, in fact, observe *L. livens* nesting both colonially and noncolonially, although selective factors affecting these alternate choices were not studied.

In this study we examined nest-site selection of *L. livens* breeding at Bahia de los Angeles, Baja California (29°00'N, 114°00'W), with emphasis on nest spacing between conspecifics, nest exposure to climatological factors, predator avoidance, foraging behavior, and breeding success.

STUDY AREA AND METHODS

During 1977, we studied *L. livens* nesting on seven nearshore (<15 km from the mainland) islands—Islas Bota, Cerraja, Coronado, Mitlan, Pata, Rasita, and La Ventana. These islands are dry and rocky, are not inhabited by large mammals, and have no vegetation suitable for use as cover by nesting gulls. *Larus livens* is known to nest only within 30 m of the high-tide line (Hand et al. 1981, this study); therefore, we considered

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all shoreline as potential nesting habitat. Two shoreline substrates were discernable: beach-berm and talus-boulder. Beach-berms were at least 10 m wide, and consisted of rounded rocks and coral mostly < 30 cm wide at the level uppermost area of beaches. Talus-boulder substrate lacked a level berm and consisted mostly of nonuniformly shaped rocks > 30 cm wide. The 29.2-km total of island shoreline consisted of 82% talus-boulder, 17% beach-berm, and about 1% sheer bluff. There were 20 beaches within the study area; each island had at least one beach.

We evaluated nest exposure to wind/sea waves relative to two factors. The first was aspect: north, south, east, or west exposures (prevailing winds at Bahía de los Angeles are from the west-northwest during the breeding season). Second was degree of exposure to the sea, or visibility of seaward surroundings from the nest (i.e., "seavista"), and included three categories: (1) sea exposure > 180°; (2) exposure 180° to 90°, including nests partially protected by island contours or nearby islands; and (3) exposure < 90°, including nests positioned in coves, small bays, or along narrow channels separating islands. Visibility of landward surroundings from the nest was evaluated relative to nest distance to the nearest bluff (i.e., a bank with 45° to 90° slope rising > 5 m above its base); gulls with nests < 50 m distant from the nearest bluff were categorized as having "poor" landward visibility, and those with nests > 50 m distant from the nearest bluff were categorized as having "good" landward visibility. These classifications were considered as indicators of the gulls' ability to detect approaching ravens (see Results: Predation). Bluffs, or shoreline with bluffs < 50 m distant, composed 93% of the available nesting habitat; the remaining shoreline was > 50 m from bluffs.

To examine nest-site selection, we mapped all nests during April and May, noting terrain characteristics within 5 m, distance to nearest neighbor's nest, distance to nearest bluff, distance to highest high-tide line (HHTL; defined here as the highest level of surf-deposited debris), and aspect and degree of exposure to the sea. We observed no predation resulting from our disturbance, and we were careful to avoid it.

We defined a breeding pair as two adults that defended a well-constructed nest. Although studies typically quantify breeding populations of seabirds by counting or estimating numbers of pairs that lay eggs, we used this alternative meth-

od because of the high rate of egg loss during our study, and because in many cases we did not visit nests often enough to determine if eggs had been laid. We considered pairs with nests of nearest neighbors ≤ 25 m as colonial, and those with internest distances > 25 m as noncolonial. These classifications were based on the tendency for internest distances to fall within two distinct categories: 92% of the colonial pairs were separated from nearest neighbors by 20 m or less, and 81% of the noncolonial pairs were separated by > 50 m.

To examine nest-site selection as related to foraging and predation, we observed breeding pairs on Islas Coronado and La Ventana between 30 April and 1 June, using 8× binoculars and a 20× spotting scope at distances > 200 m from nests. Observation positions were on bluffs and hillsides 20 to 100 m above nesting gulls, and with a wide view of the surrounding land and sea. Observations included 204 nest hours of 23 colonial pairs at four colonies (a maximum of three pairs was observed simultaneously), and 54 hr of eight noncolonial pairs. Colonial pairs included 17 nesting on beach-berm and six on talus-boulder, while noncolonial pairs included two nesting on beach-berm, five on talus-boulder, and one atop a bluff. We only observed pairs with eggs or young. Because of the high rate of loss of eggs and young, 121 hr (59%) of our observations on colonial pairs, and 40 hr (74%) of our observations on noncolonial pairs, were of only seven, and four pairs, respectively.

We estimated breeding productivity of gulls nesting on Islas Coronado and La Ventana as the number of young per breeding pair that reached an age of approximately 2 weeks (i.e., the minimum age of young at the time we left the study area). We counted young during late May and early June by observing nest sites from distances (> 200 m) great enough so that we did not disturb the gulls. No eggs were being incubated; if no young were observed at a nest site after two or more observation sessions totaling at least 6 hr we concluded that none were present. Although young older than 2 weeks sometimes moved up to 20 m from the nest site (see also Hand et al. 1981), locating them was not difficult. Generally they were inactive and often hid if both parents were off territory, but usually became active when a parent returned.

Statistical analyses follow Zar (1974), and variation about means are given as the standard deviation (SD).

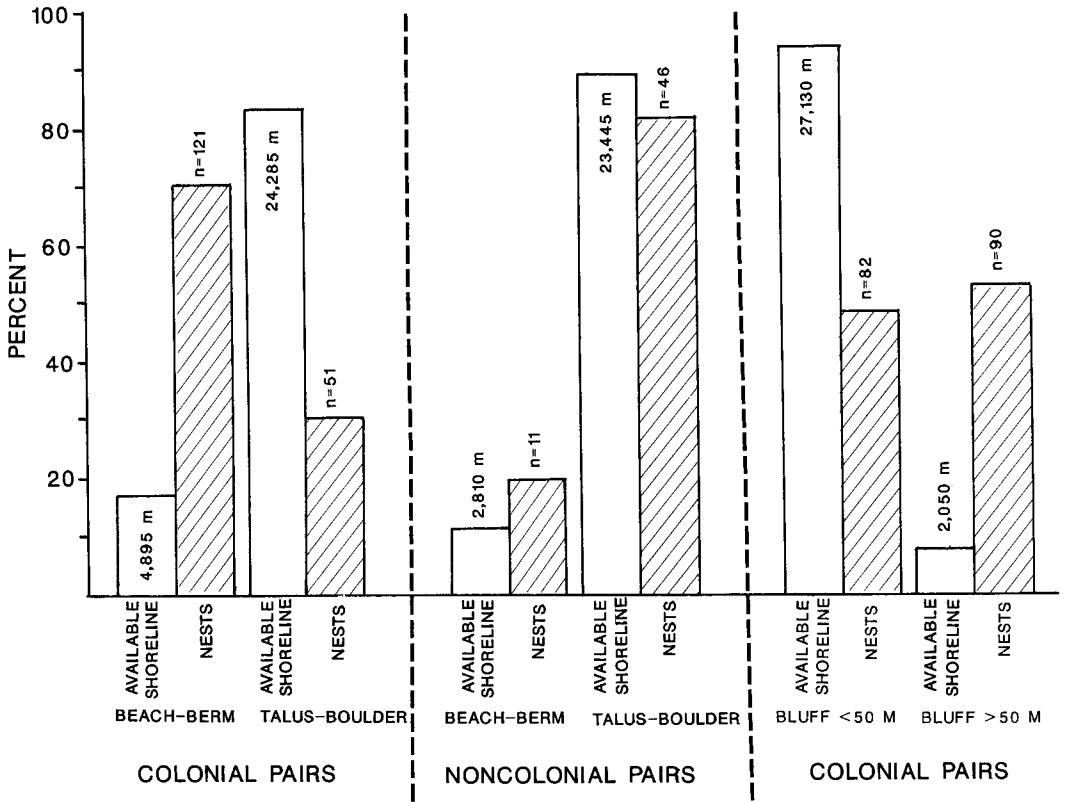


FIGURE 1. Nest-site location of colonial and noncolonial Yellow-footed Gulls at Bahia de los Angeles, Baja California: bars are shown as the percent of nests located on beach-berm and talus-boulder substrate, relative to availability of respective substrates (in percent); and percent of nests positioned on shoreline with nearest bluff <50 m, or nearest bluff >50 m, relative to availability of respective shoreline (in percent). Shoreline available to noncolonial pairs does not include that in use by colonial pairs.

RESULTS

GENERAL NESTING PATTERN

We found 172 (75%) colonial and 57 (25%) noncolonial pairs. By island these included: Bota, 26 colonial/6 noncolonial; Cerraja, 6/6; Coronado, 84/25; Mitlan, 13/6; Pata, 9/3; Rasita, 21/0; and La Ventana, 13/11. Colonies averaged 12.5 ± 3.35 pairs ($n = 13$, range = 3–36 pairs). All except 16 (9%) colonial pairs built nests in a single row (i.e., linearly) along the shoreline. It appeared that the territories of each of the pairs with non-linearly positioned nests were separated from a waterfront position by the territories of just one other pair. These findings are similar to those of Hand et al. (1981) for *L. livens* breeding on offshore islands.

The first eggs of colonial and noncolonial pairs

were found on 3 and 4 April, respectively. Because we examined gulls' nests every day on one or more islands during the pre- and early egg-laying periods, we believe these first-egg dates are reasonable. Peak egg laying occurred in mid-April; this is similar to that observed by Hand (1980) for gulls breeding on offshore islands in 1976. At Bahia de los Angeles, laying of first clutches by both colonial and noncolonial pairs extended through at least 28 April.

SUBSTRATE AND VISIBILITY OF LANDWARD SURROUNDINGS FROM NESTS

Colonial pairs nested on beach-berm more often than expected considering the composition of all the shoreline ($G = 106.07$, $df = 1$, $P < 0.001$, Fig. 1). Yet, 52% of the beach shoreline was not used, including large sections of most beaches

TABLE 1. Nest-site location of colonial and noncolonial Yellow-footed Gulls relative to degree of seaward exposure/sea vista.

	Degrees of seaward exposure/sea vista		
	180°	180°-90°	90°
Colonial pairs:			
Available shoreline (%)	47.9	37.8	14.3
Pairs observed (<i>n</i> = 172)	111	40	21
Pairs expected (<i>n</i>)	82	65	25
Noncolonial pairs:			
Available shoreline (%)	45.4	41.1	13.5
Pairs observed (<i>n</i> = 57)	28	26	3
Pairs expected (<i>n</i>)	26	23	8

where gulls nested. Noncolonial pairs used habitats no differently than expected if choice was random ($G = 1.75$, $df = 1$, $P > 0.1$). Ten (18%) of the noncolonial pairs nested atop bluffs, 6–8 m above sea level. These nests were positioned above talus-boulder substrate, and, unless otherwise noted, are included in that category in the following analyses.

Colonial pairs selected shoreline with good landward visibility, i.e., bluffs > 50 m distant ($G = 93.11$, $df = 1$, $P < 0.001$, Fig. 1). Nests of all of the 90 pairs > 50 m from bluffs were, in fact, > 300 m from bluffs, and all were on beach-berm substrate. We could not compare nest-site selection related to quality of landward visibility in noncolonial pairs using the same criteria employed for colonial pairs (i.e., nest distance to nearest bluff) since the 10 noncolonial pairs nesting atop bluffs were < 50 m from bluffs but still had good landward visibility. Nevertheless, the 47 noncolonial pairs not on bluffs all had poor landward visibility. A greater proportion of co-

lonial pairs had good landward visibility (52%, $n = 172$) than did noncolonial pairs (18%, $n = 57$) ($G = 22.77$, $df = 1$, $P < 0.001$).

NEST EXPOSURE TO SEA WAVES/SEA VISTA OF GULLS FROM NEST SITES

Colonial pairs selected shoreline with the widest angle of sea exposure/vista ($G = 11.15$, $df = 2$, $P < 0.01$, Table 1), but aspect of exposure was an unimportant factor ($G = 0.34$, $df = 3$, $P > 0.5$, Table 2). In contrast, noncolonial pairs selected shoreline with southern aspects, while avoiding those with a northern aspect ($G = 12.18$, $df = 3$, $P < 0.01$), but did not select nest sites relative to degrees of sea exposure/vista ($G = 2.62$, $df = 2$, $P > 0.1$).

VISIBILITY OF INCUBATING GULLS TO PREDATORS

The percent of incubating gulls that could be seen by men in boats varied significantly between nesting categories ($G = 68.93$, $df = 5$, $P < 0.001$, Table 3); pairs nesting linearly on beach-berm were most visible, while pairs nesting nonlinearly in talus-boulders were least visible. Visibility of incubating gulls to men at sea varied little between colonial and noncolonial pairs ($G = 0.58$, $df = 1$, $P > 0.25$). Only five pairs built nests not visible to birds passing overhead: one colonial and four noncolonial pairs.

NEST DISPERSION AND NEST DISTANCE TO HHTL

Inter-nest distances of colonial pairs ranged from 3–25 m, although 66% were separated by 6–15 m. Colonial pairs nesting nonlinearly on beach-berm positioned nests significantly closer to nearest neighbors' nests than other colonial pairs (Table 3). Inter-nest distances between noncolon-

TABLE 2. Nest-site location of colonial and noncolonial Yellow-footed Gulls relative to aspect of seaward exposure.

	Aspect of seaward exposure			
	West	North	South	East
Colonial pairs:				
Available shoreline (%)	32.9	27.1	12.2	27.8
Pairs observed (<i>n</i> = 172)	59	48	22	43
Pairs expected (<i>n</i>)	57	47	21	48
Noncolonial pairs:				
Available shoreline (%)	33.8	28.3	9.0	28.9
Pairs observed (<i>n</i> = 57)	20	5	16	16
Pairs expected (<i>n</i>)	19	16	5	17

TABLE 3. Incubating Yellow-footed Gulls visible to humans at sea, and nest distance (m) to highest high-tide line (HHTL) and nearest neighbor's nest (NN), with respect to breeding habit and nesting substrate (L = linear nests, NL = nonlinear nests).

	Nests <i>n</i>	Incubating gulls visible to humans at sea		Distance to NN ^a $\bar{x} \pm SD$	Distance to HHTL ^b $\bar{x} \pm SD$
		<i>n</i>	(%)		
Colonial pairs:					
L/Beach-berm	114	113	(99)	11.2 ± 5.7 ^c	6.4 ± 2.2 ^s
L/Talus-boulders	42	33	(79)	12.3 ± 6.2 ^c	7.7 ± 2.2 ^t
NL/Beach-berm	7	3	(43)	6.4 ± 2.8 ^d	13.9 ± 3.0 ^{x,y}
NL/Talus-boulders	9	0	(0)	9.8 ± 3.7 ^{d,c}	16.1 ± 4.0 ^y
Noncolonial pairs:					
Beach-berm	11	11	(100)	118.2 ± 167.0 ^e	7.2 ± 1.9 ^{s,t}
Talus-boulders	46	37	(80)	143.5 ± 186.7 ^e	9.1 ± 4.0 ^x
All colonial pairs	172	149	(89)	11.2 ± 5.7	7.6 ± 3.4
All noncolonial pairs	57	48	(84)	138.6 ± 182.0	8.8 ± 3.8

^a Distance to nearest neighbor; means which do not share a common superscript (c, d, e) are significantly different ($P < 0.05$, by Student-Newman-Keuls [SNK] multiple comparison test).

^b Distance to HHTL; means which do not share a common superscript (s, t, x, y) are significantly different ($P < 0.05$, by SNK multiple comparison test).

ial pairs and nearest neighbors ranged from 29–1,210 m. Only four noncolonial pairs built nests within 100 m of colonies, these being 33, 58, 69, and 77 m from the nearest colonial neighbors' nests.

Nests of colonial pairs were significantly closer to the HHTL than nests of noncolonial pairs ($t' = 2.27$, $df = 227$, $P < 0.05$, Table 3; range for the population = 0.5–24 m). Among colonial pairs nesting linearly, beach-berm pairs placed nests closer to the HHTL than pairs nesting on talus-boulder substrate. Nests positioned nonlinearly were farther from the HHTL than nests positioned linearly. Nest distance from the HHTL, as a function of degrees of exposure to the sea, did not vary significantly among pairs nesting on beach-berm ($t' = 1.01$, $df = 130$, $P > 0.20$, Table 4); however, pairs nesting on talus-boulders, with exposure $> 180^\circ$, positioned nests farther from

the HHTL than pairs nesting on talus-boulders having lesser degrees of exposure. For gulls nesting on beach-berm, nest distance from the HHTL as a function of aspect was significantly greater among birds with nests exposed to the west (i.e., into prevailing winds), compared to those with nests exposed to the east (Table 5). For gulls nesting on talus-boulders, nest distance from the HHTL was greater among birds with nests exposed to the north or west, compared to those with southern exposure. These findings are similar to those of Hand et al. (1981) for *L. livens* breeding on offshore islands.

BREEDING PRODUCTIVITY

Although we were unable to determine clutch size, the observations of Hand (1980) at a colony less disturbed than those at Bahia de los Angeles suggest that *L. livens* probably produce a three-

TABLE 4. Nest distance (m) of Yellow-footed Gulls from the highest high-tide line (HHTL) relative to degree of seaward exposure/sea vista.^a

	Degrees of seaward exposure/sea vista		
	180°	180°-90°	90°
Beach-berm:			
Nest distance	(<i>n</i> = 82)	(<i>n</i> = 50)	—
From HHTL ($\bar{x} \pm SD$)	7.1 ± 3.0	6.6 ± 2.3	
Talus-boulder:			
Nest distance	(<i>n</i> = 57)	(<i>n</i> = 19)	(<i>n</i> = 21)
From HHTL ($\bar{x} \pm SD$) ^a	10.3 ± 4.5 ^c	7.7 ± 2.7 ^t	7.4 ± 2.6 ^f

^a Means which do not share a common superscript (e, f) are significantly different ($P < 0.05$, by Student-Newman-Keuls multiple comparison test).

TABLE 5. Nest distance (m) of Yellow-footed Gulls from the highest high-tide line (HHTL) relative to aspect of seaward exposure.

	Aspect of seaward exposure			
	West	North	South	East
Beach-berm:				
Nest distance	(n = 45)	(n = 23)	(n = 21)	(n = 43)
From HHTL ($\bar{x} \pm SD$) ^a	7.6 \pm 2.7 ^c	6.9 \pm 2.6 ^{c,d}	6.8 \pm 1.9 ^{c,d}	6.2 \pm 3.1 ^d
Talus-boulder:				
Nest distance	(n = 33)	(n = 30)	(n = 18)	(n = 16)
From HHTL ($\bar{x} \pm SD$) ^b	10.0 \pm 4.2 ^e	10.2 \pm 4.9 ^e	7.0 \pm 1.1 ^h	8.1 \pm 2.8 ^{e,h}

^a Means which do not share a common superscript (c, d) are significantly different ($P < 0.05$, by Student-Newman-Keuls [SNK] multiple comparison test).

^b Means which do not share a common superscript (g, h) are significantly different ($P < 0.05$, by SNK multiple comparison test).

egg clutch typical of large *Larus* gulls. It follows that an annual fledging rate of one to 1.5 young per pair would be expected (see Coulter 1973; Ainley and Bockelheide, in press, and references therein). Yet, we observed only 0.12 young (all approximately 2 weeks of age or older) per breeding pair ($n = 133$ pairs) on Islas Coronado and La Ventana. Only 10 pairs were raising young, and there were no eggs at the time of our observations. This low productivity is similar to that observed by Hand (1980) among *L. livens* breeding on offshore islands during 1974 through 1978. At Bahia de los Angeles, the productivity rate in colonial pairs was 0.11 young/pair ($n = 97$) and 0.14 young/pair ($n = 36$) in noncolonial pairs; the difference was insignificant ($G = 0.12$, $df = 1$, $P > 0.5$). The seven successful colonial pairs had 1, 1, 1, 1, 2, 2, and 3 young per pair, and the three successful noncolonial pairs had 1, 2, and 2 young per pair. A greater proportion ($G = 6.35$, $df = 1$, $P < 0.05$) of the seven colonial pairs with nonlinearly placed nests were raising young (43%) than that of the 90 colonial pairs with linearly positioned nests (4%). Moreover, the three successful nonlinear nesting pairs had nests within 10 m of one another. All colonial pairs breeding on the two islands nested on beach-berm, thus precluding comparison of productivity among colonial pairs with respect to nesting substrate. All the successful noncolonial pairs nested in talus-boulders.

Productivity was probably higher for colonial pairs nesting at two other islands. In early June, while banding young gulls on Isla Rasita and Isla Bota we found 0.71 young/pair ($n = 21$), and 0.31 young/pair ($n = 26$), respectively. These are minimum values because we probably missed young hiding among the talus-boulders where the majority of nests were located.

PREDATION

During 204 hr of observation of colonial pairs we observed men take eggs from a beach-berm colony once. We also observed humans eating gull eggs in the town of Bahia de los Angeles where residents told us that each year they collected and ate gull eggs, primarily during peak laying in April (see also Hand 1980). This would explain the abrupt egg loss at large beach-berm colonies; e.g., an Isla Coronado colony with 36 nests containing 82 eggs on 18 April, had only four eggs on 24 April. The four eggs were in two adjacent nests at one end of the colony.

Four pairs of ravens nested on Islas Coronado and La Ventana; all hatched young during the egg-laying period of the gulls. We never saw ravens preying on gulls in colonies, but frequently observed them flying or perched nearby, and saw them being mobbed on five occasions during 204 hr of observation on colonial gulls. During 54 hr of observation on noncolonial pairs, however, ravens took two eggs and two young (1 to 3 days old) during three raids on three different gull pairs: one pair nesting on talus-boulder substrate, one pair atop a bluff, and one pair on beach-berm. On seven other occasions we saw ravens carrying gull eggs and young. We do not believe our presence as observers affected the rate of raven predation because: (1) we observed from distances such that, with the exception of the period of our arrival at observation positions, the gulls' behavior was not discernably affected; and (2) all three instances of raven predation occurred at least 2 hr after we had begun observations, and in each case a gull was brooding eggs or young when ravens arrived.

Pairs of ravens worked as a team and were successful on each predation attempt we ob-

TABLE 6. Territorial defense by colonial and noncolonial Yellow-footed Gulls during incubation and chick-rearing periods.

	Incubation period		Chick period	
	Colonial pairs	Noncolonial pairs	Colonial pairs	Noncolonial pairs
Pairs observed (<i>n</i>)	16	5	9	3
Hours of observation (<i>n</i>)	129	34	75	20
Pursuits/hour/pair ($\bar{x} \pm SD$)	0.09 \pm 0.062	0.35 \pm 0.115	0.16 \pm 0.075	0.80 \pm 0.366
Species pursued				
Conspecifics:				
Neighbor (<i>n</i>)	2	—	5	—
Non-neighbor (<i>n</i>)	5	5	5	8
Common Raven (<i>n</i>)	3	1	2	5
Other ^a (<i>n</i>)	1	6	0	3

^a Other species included: Red-tailed Hawk (*Buteo jamaicensis*), colonial pairs—one pursuit; Osprey (*Pandion haliaetus*), noncolonial—four pursuits; Heermann's Gull (*Larus heermanni*), noncolonial—two pursuits; Turkey Vulture (*Cathartes aura*), Brown Pelican (*Pelicanus occidentalis*), and Great Blue Heron (*Ardea occidentalis*), each pursued once by noncolonial gulls.

served. When attacking, they flew towards nesting gulls from the inland side of bluffs, thus concealing themselves as long as possible. Wind appeared to be an important factor increasing their maneuverability; all predations occurred during afternoons when winds were 25–40 km/hr.

No overt attempts or successful conspecific predation were seen; however, intrusion by conspecifics on territories of colonial pairs was frequent (Table 6) and usually resulted in immediate repulsion of the intruder (see also Hand 1980, Hand et al. 1981).

TERRITORY DEFENSE

Noncolonial gulls had higher rates of defense, either of territory or of eggs or chicks, than colonial gulls during both incubation (Mann-Whitney $U = 79.5$, $P < 0.001$, Table 6) and chick-rearing ($U = 27$, $P < 0.001$) periods. A greater proportion ($G = 4.03$, $df = 1$, $P < 0.05$) of pursuits by colonial pairs were directed toward conspecifics (74%, $n = 23$), compared to that of noncolonial gulls (46%, $n = 28$). All pursuits of conspecifics by colonial gulls, but only two out of 13 pursuits by noncolonial gulls, resulted from conspecific landing intrusions in territories. Other pursuits of conspecifics by noncolonial gulls occurred when conspecifics flew past territories. Pursuits of conspecifics were made by only one member of a pair whether they were colonial or noncolonial ($n = 30$). Colonial gulls, however, attacked ravens and a Red-tailed Hawk (*Buteo jamaicensis*) in groups of two to four ($\bar{x} = 2.5$, $n = 6$), while noncolonial gulls pursued other bird species singly in 11 of 15 instances. Three of the

four exceptions occurred when a gull, already in pursuit of a single retreating raven, flew past the territory of another noncolonial pair and was joined by one of the latter. The fourth exception occurred when a pair unsuccessfully defended their young from attack by two ravens.

TERRITORY OCCUPATION AND FORAGING BEHAVIOR

At least one member of each pair was on territory during incubation and early chick periods. The amount of time that colonial gull pairs occupied territories together during the incubation period ($\bar{x} = 77 \pm 7.6\%$ of their time together, $n = 23$ pairs) was significantly greater ($t' = 2.70$, $df = 29$, $P < 0.02$) than that of noncolonial pairs ($\bar{x} = 67 \pm 9.8\%$ of their time together, $n = 8$ pairs).

Although Yellow-footed Gulls apparently searched for food while away from territories, much searching took place from the territory while the mate simultaneously attended the nest site. Colonial gulls initiated $68 \pm 10.0\%$ ($n = 7$ pairs), and noncolonial pairs $48 \pm 9.6\%$ ($n = 4$ pairs; only pairs that we observed at least 10 hr were included in these analyses), of their foraging trips towards food sources visible to them from their territories. On these occasions they took flight abruptly and hurriedly flew in a straight course 10 m to 5 km out to sea towards an intended food source. Visual cues were multispecies feeding flocks (primarily boobies [*Sula* sp.] and Brown Pelicans [*Pelicanus occidentalis*]), small schooling fish breaking the waters' surface, and fishing boats. The proportion of foraging trips directed towards food sources visible from nest sites was significantly greater in colonial pairs

than noncolonial pairs ($t' = 3.27$, $df = 9$, $P < 0.01$).

DISCUSSION

Most *L. livens* (75%) breeding at Bahia de los Angeles nested colonially, and most colonial pairs (70%) selected nest sites on beach-berm shoreline. There they obtained optimum conditions for positioning nests close to the water, as well as optimum landward and seaward visibility. Tinbergen (1960), Burger (1972, 1974), and Buckley and Buckley (1980) found that other species of Larinae also selected nest sites offering better than average visibility, and suggested that this was an adaptation facilitating predator detection and/or feeding efficiency. As suggested by Hand et al. (1981), this may be especially important in a species such as *L. livens* which, during incubation bouts, must frequently (average = once/5.6 hr of incubation; Hand et al. 1981) leave nest contents unguarded for periods averaging about 3 min while they stand or float in the water to relieve heat stress. Short distances between nests and the water, and good landward visibility, enabled these gulls to practice thermoregulatory activities while simultaneously detecting ravens at distances facilitating effective mobbing activities before ravens arrived. Good visibility of the sea also facilitated the locating of food sources from the territory. Increasing the amount of time that mates could simultaneously attend nest sites may have been an additional factor reducing the chance of predation by ravens and conspecifics. The markedly greater amount of time that *L. livens* occupied territories together (76%, $n = 163$ hr of observation), compared to *L. occidentalis* (43%, $n = 4,182.5$ hr of observation; Pierotti 1981), and *L. marinus* (27%, $n = 1,877$ hr of observation; Butler and Janes-Butler 1983), is probably not surprising. The latter two species breed in more temperate climates, and, unlike *L. livens*, generally do not leave eggs and young unguarded while mates are away foraging (Pierotti 1981, Butler and Janes-Butler 1983).

The existence of large sections of unused beach-berm shoreline at Bahia de los Angeles, especially that adjoining sections where gulls nested, suggests that gulls nesting on talus-boulder substrate did so by choice. It is especially interesting, therefore, that 81 percent of the noncolonial gulls nested on talus-boulder substrate. Besides precluding advantages gained from group defense, nonco-

lonial gulls selected nest sites providing reduced landward visibility due to bluff proximity, reduced protection from sea waves as indicated by greater nest distances from the high-tide line, and lesser degrees of sea vista, compared to gulls nesting on beach-berm. The positioning of nests farther from the shoreline, and in areas affording lesser vista, may have been related to the higher spray zone, relative to the high-tide line, associated with talus-boulders compared to beach-berm (Spear and Anderson, pers. observ.). All of these factors apparently reduced the gulls' defense against ravens.

We made several assumptions to estimate the effect of raven predation on the productivity of noncolonial pairs. These included: (1) that the predation rate was as we report (one predation upon noncolonial gulls/13.5 hr/pair of ravens); (2) that ravens were active predators only during the afternoon when winds were up (8 hr/day); (3) that the clutch size and incubation period of *L. livens* averaged 2.7 eggs and 27 days (i.e., similar to that of other large larids; Vermeer 1963, Schreiber 1970, Coulter 1973, and references therein); and (4) that gull chicks were not vulnerable after 7 days of age (none larger in size than corresponding to the given age were seen in possession of ravens). Based on these assumptions the four pairs of ravens nesting on Islas Coronado and La Ventana would have reduced the maximum potential productivity of the 36 pairs of noncolonial gulls by 84 percent. This would account for their near failure.

That noncolonial gulls, constituting 25 percent of the breeding population at Bahia de los Angeles, selected nest sites that were highly vulnerable to raven predation suggests that the individuals were responding to yet another selective force acting in opposition to that imposed by ravens. We believe that this threat was imposed by humans. Nests spaced widely apart on terrain difficult for humans to traverse offer a small reward compared to nests placed in a colonial situation, so it is not surprising that we observed no eggng at nests of noncolonial gulls.

In conclusion, our results support the contentions of Tinbergen (1960), Burger (1972, 1974), and Buckley and Buckley (1980), that selection of exposed nesting areas is an important adaptation for avoiding (avian) predation and increasing foraging efficiency. Furthermore, our data support the hypothesis that while avian predation selects for colonial nesting, predation by

large mammals has the reverse effect. The disadvantage of nesting where both types of predators are found is also apparent. The low productivity of *L. livens* at Bahia de los Angeles in 1977 supports Hand's (1980) conclusion that some colonies may be threatened, assuming continuation of eggging by humans. Hand (1980) noted that eggging of *L. livens* probably increased after Isla Rasa, the site of a large colony of terns (*Sterna elegans* and *S. maxima*) and Heermann's Gulls (*L. heermanni*), and a traditional eggging ground of residents of the Gulf of California, received protection in 1964.

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