The Auk 116(2):513–519, 1999

BREEDING BIOLOGY OF HEERMANN'S GULLS ON ISLA RASA, GULF OF CALIFORNIA, MEXICO

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ABSTRACT.—During 1980 and 1981, I studied nest-site selection and reproductive success in Heermann's Gull (*Larus heermanni*) on Isla Rasa in the Gulf of California, Mexico. About 95% of the world population of this species nests on Isla Rasa. In 1980, about 130,240 nests were present within an area of 0.8 km^2. In the Midriff Island Region (which includes Isla Rasa), oceanic productivity is high even during El Niño events because of tidal upwelling. My results indicate that the Heermann's Gull is characterized by high nesting density (up to 110 nests per 100 m^2) and high nesting synchrony. Massive synchronized communal flights to nesting areas occurred every evening during several weeks prior to egg laying. Nesting density in valleys (71 per 100 m^2) was higher than on rocky hills (9.5 per 100 m^2). Clutch size was higher in valleys in 1981 than in 1980 and was lowest on rocky substrates on hills. Hatching success was independent of clutch size but varied with substrate and year. Fledging success among broods was independent of hatching order. Fledging success and reproductive success (i.e. the number of chicks fledged/number of eggs laid) were higher in valleys in 1981 and were lowest on rocky hills in 1980, and reproductive success was significantly higher for three-egg clutches than for one-egg clutches. The observed patterns of reproductive performance may be correlated with annual variation in food abundance and with exposure to predators in different nesting habitats and among different nesting densities. *Received 2 December 1996, accepted 30 October 1998.*

THE BREEDING BIOLOGY AND BEHAVIOR of numerous species of gulls have been well studied (e.g. Cullen 1957, Tinbergen 1959, Moynihan 1959, Beer 1966, Smith 1966, Spear and Nur 1994). However, few studies have been conducted on the "white-hooded gulls," i.e. the Gray Gull (*Larus modestus*; Howell et al. 1974) and the Heermann's Gull (*L. heermanni*). Heermann's Gulls and Gray Gulls are very closely related, they share an almost identical morphology, and they nest in desert habitats adjacent to highly productive oceans. However, Gray Gulls are inshore feeders and nest more than 50 km inland in the barren desert of northern Chile (Howell et al. 1974), whereas Heermann's Gulls nest on small desert islands in the Gulf of California in Mexico and feed mainly on small pelagic fishes (Velarde et al. 1994). Most of the previous studies of Heermann's Gulls have been qualitative (see Velarde 1989, Urrutia and Drummond 1990), and until now, no comprehensive quantitative study has been conducted on their general breeding biology.

Of the estimated world breeding population of Heermann's Gull, 95% breed on Isla Rasa (260,460 individuals in 1981; Velarde 1989) in the Midriff Islands (28°49′ N, 112°59′W). The Heermann's Gull is one of only three species of North American gulls that breed in subtropical latitudes, the others being Yellow-footed Gulls (*Larus livens*) and Western Gulls (*L. occidentalis wymani*). The areas where Heermann's Gulls nest (Islas Pomita, Cardonosa, San Ildefonso, Isabela, Trés Marietas, and others; Anderson 1983, Velarde 1989, Velarde and Anderson 1994) may be considered stable in that they are not regularly disturbed by natural events or anthropogenic factors. However, recurrent climatic phenomena, such as an increase in the frequency or magnitude of El Niño events, may influence survival and reproductive rates because of flooding of nesting areas and effects on food supplies.

My main interest was to determine how food availability, nesting density, and nesting substrate affect breeding performance in Heermann's Gulls, as has been shown for other species (e.g. Kruuk 1964, Tinbergen et al. 1967, Burger 1974, Dexheimer and Southern 1974, Hunt and Hunt 1975, Montevecchi 1978, Anderson et al. 1982, Hamer et al. 1991). In this paper, I present information on the breeding bi-

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ology of Heermann's Gulls on Isla Rasa in the Gulf of California, focusing on nesting density, nesting habitat, and food availability in relation to clutch size, hatching success, fledging success, and nesting success in 1980 and 1981. For 1980, comparison of these parameters is made between two nesting substrates with different nesting densities.

STUDY AREA AND METHODS

Study area.—Isla Rasa (ca. 56 ha) is in the upper Gulf of California, Mexico. The maximum elevation is 35 m (mean elevation of nearby islands is 500 m), and about 22% of the island (ca. 12 ha) consists of valleys; the rest (ca. 44 ha) consists of low hills of volcanic rock. Heermann's Gulls nest throughout the island except on isolated patches of cholla (*Opuntia* spp.), intertidal vegetation, and within tern colonies (see below); the latter cover 2 to 3% of the island. The lower-elevation valleys are former lagoons (Velarde 1989) and are covered by a layer of guano. The extant valleys and lagoons are almost devoid of rocks. During the study, two introduced mammals, the black rat (*Rattus rattus*) and the house mouse (*Mus musculus*), occurred on the island. In the early 1920s, harvesting of seabird eggs caused serious declines in several species in the Gulf (Bahre 1983). In 1964, Isla Rasa was declared a National Reserve and Refuge for Migratory Birds. Egg harvesting has declined substantially, although it still exists. Reliable historic estimates of numbers of nesting Heermann's Gulls on Isla Rasa do not exist.

Two other species of larids nest on Isla Rasa in large numbers during spring and early summer: Elegant Tern (*Sterna elegans*; ca. 45,000 individuals) and Royal Tern (*S. maxima*; ca. 17,000 individuals; Velarde 1989, Tobón 1992). The presence of large numbers of breeding seabirds on the island (Anderson 1983, Velarde and Anderson 1994) is due to high marine productivity (comparable to the highest on earth), particularly near the Midriff Islands, that results from upwelling. Marine productivity varies annually, but the variation is not as strong as that in the Pacific Ocean or the lower Gulf of California (Alvarez-Borrego and Lara-Lara 1991). Pacific sardines (*Sardinops caeruleus*) and northern anchovies (*Engraulis mordax*) migrate into the area in late spring and early summer (Sokolov 1974, Hammann et al. 1988, Hammann 1991). Pacific sardines constituted 60 to 97% of the diet of Heermann's Gulls in the early 1980s (Velarde et al. 1994). In the area where Heermann's Gulls from Rasa feed, the sardine fishing fleet operates year-round. Catch per unit effort (CPUE) of sardines increased from 12 metric tons in 1980 to 15 metric tons in 1981, an increase of 25% from one year to the next (Lluch-Belda et al. 1986).

Methods.—I monitored nesting Heermann's Gulls on Isla Rasa from early April to late June in 1980 and 1981. The amount of area covered of rocky hills and valleys was estimated from aerial photographs. I established 10 quadrats (each 10 × 10 m) randomly in each nesting substrate (valleys and rocky hills) during the first week of April in 1980, but only in valleys in 1981. At the end of the incubation period, nests were counted in each quadrat to determine nesting density. I also counted nests in quadrats (10 × 10 m) that were not monitored for other parameters; 26 were placed in rocky hills, and 62 were established from aerial photographs of valleys.

In 1980, data on clutch size, hatching synchrony, and chick survival were obtained from two plots of 80 nests each, one plot was established in a valley and another on a rocky hill. In 1981, a group of 58 nests was monitored in a valley. Nests were checked every other day during the incubation, hatching, and brood-rearing periods. An egg was considered lost if it disappeared or was found broken. A chick was considered to have survived if it reached the age of 20 days, which is the age when the highest mortality of chicks has passed (González-Peralta et al. 1988, Velarde 1989). Eggs were marked with a felt tip pen, using different colors according to laying sequence. Chicks were banded with numbered plastic bands to differentiate their hatching order. I used a Kruskal-Wallis test to assess differences in clutch size, hatching success (number of eggs hatched/number of eggs laid), fledging success (number of chicks fledged/number of chicks hatched), and reproductive success (number of chicks fledged/number of eggs laid) between the two nesting substrates, between years, and by hatching order. If a significant difference was found, pairwise comparisons were made using a Mann-Whitney *U*-test. Qualitative descriptions of breeding behavior and chronology were drawn from long-term observations carried out from 1979 to 1997, as well from other studies conducted on predation, stability of nesting sites, and nest-site fidelity (Velarde 1989, 1992, 1993).

Pacific sardines were the main food of Heermann's Gulls during the early 1980s when the study was conducted (Velarde et al. 1994). To estimate annual variation in food abundance, I used the reports of CPUE for sardine landings by the fishing fleet operating out of Guaymas, which is adjacent to the study area (Lluch-Belda et al. 1986).

RESULTS

General description.—Heermann's Gulls start arriving in the Midriff Islands in mid-February. Each day at dusk, they gather around Isla Rasa and perform mass flights to their breeding sites. After coming ashore, the gulls are intensely active in territorial and courtship displays. By late March, nearly 200,000 gulls join the daily flights that arrive at dusk and depart at dawn (Velarde 1989). By late March or early April, gulls remain on the island for the rest of the breeding season.

During 1980, the average nesting density was 69 ± SD of 6.7 per 100 m^2 in valleys (n = 62 quadrats, range 42 to 101 per 100 m^2) and 9.5 ± 3.6 per 100 m^2 on rocky hills (n = 26 quadrats, range 6 to 16 per 100 m^2). During 1981, the average nesting density was 72 ± 7.6 per 100 m^2 in valleys (n = 62 quadrats, range 46 to 110 per 100 m^2). The estimated total number of nests was 41,905 (32%) on rocky hills and 88,324 (68%) in valleys, and the total breeding population contained approximately 260,458 individuals.

Egg laying began almost immediately after gulls attended the breeding colony continuously during the day. Some early breeders laid their first eggs before the permanent establishment of the colony and subsequently abandoned them. These eggs were not considered in the analysis. After permanent establishment of the breeding colony, nests received constant parental attention, and pair members took turns incubating after the first egg was laid. Adults guarded their chicks constantly during the first days after hatching, and when chicks strayed from the nest area, the parents flew toward them and attempted to force them back to the territory.

Nesting synchrony, clutch size, and hatching interval.—Hatching synchrony varied between years (χ^2 = 33.57, $P < 0.001$). In 1980, 50% of the chicks hatched within 24 days after the first chick hatched, and in 1981, 50% hatched within 5 days after the first chick hatched (Fig. 1). The peak of hatching was later in 1980 than in 1981 (Fig. 1).

Clutch size varied significantly among plots (Kruskal-Wallis test, H = 10.65, n = 218, $P <$ 0.005). In 1980, clutch size was similar in nests in the rocky hill plot ($\bar{x}$ = 1.56 ± SD of 0.07, n = 80) and in the valley plot ($\bar{x}$ = 1.66 ± 0.06, n = 80; Mann-Whitney test, U = 1.35, $P > 0.05$). In the valley plots, however, clutch size was significantly higher in 1981 ($\bar{x}$ = 2.05 ± 0.09, n = 58) than in 1980 (U = 3.5, $P < 0.001$). The average hatching interval between siblings was 1.4 ± 1.5 days (n = 72 sibling pairs).

Hatching, fledging, reproductive, and nesting success.—Hatching success did not vary significantly with clutch size but varied significantly among plots (H = 10.09, n = 218, $P < 0.01$).

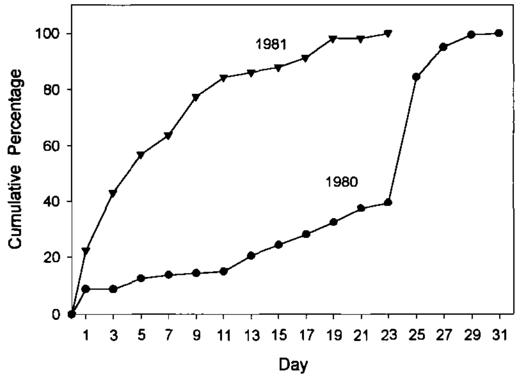

FIG. 1. Hatching distribution for Heermann's Gull chicks at Isla Rasa during 1980 and 1981, showing the cumulative percentage of chicks hatched since day 1 (day of first recorded hatching on study plots).

Hatching success was highest in the valley plot in 1980 ($\bar{x}$ = 0.93 ± 0.03, n = 80) and lowest in the valley in 1981 ($\bar{x}$ = 0.78 ± 0.05, n = 58). Fledging success did not vary significantly with clutch size or hatching order, but it was significantly higher in the valley plot ($\bar{x}$ = 0.24 ± 0.04, n = 80) than in the rocky hill plot ($\bar{x}$ = 0.06 ± 0.02, n = 80) in 1980 (U = 3.81, $P <$ 0.001) and was significantly higher in the valley plot in 1981 ($\bar{x}$ = 0.41 ± 0.06, n = 58) than in 1980 (U = 2.48, $P < 0.01$). Reproductive success (number of chicks fledged/number of eggs laid) also varied among plots (H = 35.84, n = 218, $P < 0.001$) and was significantly higher in the valley plot ($\bar{x}$ = 0.24 ± 0.04, n = 80) than in the rocky hill plot ($\bar{x}$ = 0.06 ± 0.02, n = 80) in 1980 (U = 3.95, $P < 0.001$) and was significantly higher in the valley plot in 1981 ($\bar{x}$ = 0.38 ± 0.05, n = 58) than in 1980 (U = 2.20, $P <$ 0.05). In addition, reproductive success was higher in three-egg clutches ($\bar{x}$ = 0.29 ± 0.06, n = 23) than in one-egg clutches ($\bar{x}$ = 0.16 ± 0.04, n = 82; U = 3.06, $P < 0.005$).

Extrapolating nesting success (i.e. number of chicks fledged/number of nests with eggs) to the entire island for 1980 resulted in an estimated production of 70,660 chicks in the valleys ($\bar{x}$ = 0.80 chicks per pair) and 7,540 on the rocky hills ($\bar{x}$ = 0.18 chicks per pair), for a total of 78,200 chicks ($\bar{x}$ = 0.60 chicks per pair).

DISCUSSION

Reproductive performance and food availability.—Many studies of seabirds have demonstrated a relationship between food availability and breeding parameters such as nesting date, clutch size, breeding synchrony, and reproductive success (e.g. Ashmole and Ashmole 1967, Immelmann 1971, Nisbet 1977, Anderson et al. 1982, Anderson and Gress 1984, Burger and Cooper 1984, Cairns 1987, Bukacińska et al. 1996). The higher mean clutch size of Heermann's Gulls in 1981 may reflect the lower abundance of their main food, sardines, in 1980 compared with 1981 (Lluch-Belda et al. 1986). In addition, laying and hatching were more synchronous in 1981 compared with 1980, and they also occurred earlier in the season. Sardines concentrate in the Midriff Island Region during late spring and summer (Sokolov 1974, Hammann et al. 1988, Hammann 1991), which coincides with the brood-rearing period in Heermann's Gulls. Given that food appeared to be more abundant in 1981 than in 1980, a larger proportion of the gull population would have been able to produce eggs in a shorter period of time.

Nesting synchrony could reduce predation by Yellow-footed Gulls on Heermann's Gull chicks by narrowing the window of time when the highest proportion of young is available, i.e. "predator swamping" (Kruuk 1964, Tinbergen et al. 1967, Hamilton 1971, Hoogland and Sherman 1976, Velarde 1992). Nesting synchrony in Heermann's Gulls also may be an important defense against Peregrine Falcons (*Falco peregrinus*), which often prey on adults and fledglings (Velarde 1993).

The lower nesting success in 1980 than in 1981 resulted from smaller clutch sizes in 1980, as opposed to reduced fledging or reproductive success. This result indicates that factors affecting food availability during the prelaying period, when females are accumulating energy reserves that determine clutch size (see Murphy et al. 1984), were responsible for reduced nesting success. This idea is reinforced by the fact that fledging success did not vary significantly with respect to clutch size or hatching order.

Interestingly, the average reproductive success increased with clutch size. Nest attendance and hatching success have been observed to increase with clutch size in other seabird species (Schreiber 1970, Harper 1971, Morris and Wiggins 1986, Verbeek 1988, Bollinger et al. 1990), and clutch size and breeding success have been found to increase with age in a variety of species (Furness 1984, Reid 1988, Partridge 1989, Fowler 1995, Martin 1995).

Evidence for effects of nesting density and substrate on reproductive performance.—Fledging success and reproductive success were higher among gulls that nested in higher densities. This difference was probably related to predation by Yellow-footed Gulls, which is higher on Heermann's Gull chicks in low-density nesting areas (Velarde 1992). At low nesting densities, the probability of predation per chick is higher than at high densities because defense through communal mobbing is reduced.

Predation by black rats on eggs and newly hatched chicks might be responsible for lower hatching success in some areas, as indicated by the presence of egg shells in the stomachs of rats trapped on the island (E. Velarde unpubl. data). Thus, lower hatching success in the rocky hills compared with the valleys might be explained by the higher numbers of rats in the hills where they have suitable habitat for burrow construction. Lower reproductive success in rocky substrates in the hills, compared with the valleys, might also be related to reduced visibility among rocks (see Spear and Anderson 1988). These authors concluded that reduced visibility in rocky substrates caused Yellow-footed Gulls breeding on the Midriff Islands to be more vulnerable to surprise attacks by avian predators such as Common Ravens (*Corvus corax*).

The low hatching success in the valley in 1981 might be explained by a single instance of disturbance caused by several people who carelessly wandered in the area during the incubation period. Disturbance during incubation can cause predation by conspecifics and by Yellow-footed Gullss (E. Velarde pers. obs.).

The nesting density of Heermann's Gulls on Isla Rasa (up to 110 nests per 100 m^2) is among the highest reported for any species of gull. Some of the highest nesting densities reported for other species are 100 per 100 m^2 for *Rissa tridactyla* (Coulson and White 1960) and *Larus atricilla* (Noble and Wurm 1943), 123 per 100 m^2 for *L. ridibundus* (Burger 1977, Hutson 1977), and 500 per 100 m^2 for *L. bulleri* (Beer 1966). However, in two of the *Larus* species, the highest nesting densities occurred in areas with a high degree of visual obstruction from vegetation. *Rissa tridactyla* nests on cliffs, so sometimes little visual contact occurs between neighbors. The only other gull that nests in the absence of visual obstructions and at higher densities than Heermann's Gull is *L. bulleri*, which is a highly gregarious species.

Although valleys constitute only 22% of the surface of Isla Rasa, more than two-thirds of the population of Heermann's Gull nested in the valleys. Due to lower nesting density and lower chick survival on rocky hills, only about 10% of the chicks were produced there. All potential nesting space appeared to be occupied, so space for expanding the colony was probably limited on the island. High nesting density has been shown to be an adaptation for scarce nesting sites (Noble and Wurm 1943, Beer 1966, Hutson 1977). Islands in the Gulf of California generally are steep and rocky owing to their volcanic origin. Large islands with flat areas have large terrestrial predators such as raccoons (*Procyon lotor*), ring-tailed cats (*Bassariscus astutus*), coyotes (*Canis latrans*), and snakes (Lawlor 1983, Murphy 1983, Velarde and Anderson 1994), against which mobbing by gulls may be ineffective. Not surprisingly, the most important seabird nesting colonies in the region are on islands that, until recently, have been free of medium to large terrestrial predators (Anderson 1983, Bahre 1983, Velarde and Anderson 1994). Nesting in a dense colony is advantageous to Heermann's Gulls as a defense against predation on small chicks by Yellow-footed Gulls (Velarde 1992). For this reason, it is important to keep seabird nesting islands free of terrestrial predators.

Acknowledgments

This study began while I was a graduate fellow in the Programa de Superación del Personal Académico at the Instituto de Biología of the Universidad Nacional Autónoma de México (UNAM) and was completed under a research position at this same institution. Field work was supported by Instituto de Biología-UNAM, Consejo Nacional de Ciencia y Tecnología, International Council for Bird Preservation through the Arizona-Sonora Desert Museum, International Federation for the Conservation of Birds, National Wildlife Federation, The Nature Conservancy, the Mexican Navy, and Expediciones Bajacalifornianas. I thank the personel of the Dirección General de Conservación Ecológica de los Recursos Naturales from the Secretaría de Desarrollo Urbano y Ecología for granting permits to do field work in the Reserva Especial de la Biosfera of Isla Rasa. I am also grateful to the following people for support and/or critical review of the project and different stages of the manuscript: D. W. Anderson, G. A. Bartholomew, S. B. Beebe, R. Dirzo, H. Drummond, E. Ezcurra, F. Feekes, R. S. Felger, G. de la Garza, J. D. Hair, T. H. Howell, J. M. León Cázarez, G. López Lira, T. E. Lovejoy, K. Martin, D. Piñero, J. Sarukhán, G. L. Schulman, C. G. Sibley, L. Spear, F. S. Todd, B. Villa-R., and two anonymous reviewers. Assistance in the field and office was provided by many people, particularly F. Eccardi, A. Esquivel, L. González, B. Morales, E. Tobón, M. Tordesillas, J. Vega, and L. Vieyra.

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Associate Editor: K. Martin