EGG PREDATION BY TWO NESTING GULLS ON TWO NESTING TERNS AT ISLA RASA, GULF OF CALIFORNIA, MEXICO

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ABSTRACT

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Colonially breeding seabirds frequently nest in mixed colonies, which may provide advantages and disadvantages, such as interspecific egg and chick predation. We analyzed egg predation of Elegant Terns *Thalasseus elegans* and Royal Terns *T. maximus* by Heermann's Gulls *Larus heermanni* and Yellow-footed Gulls *L. livens* at Isla Rasa, in the Gulf of California. All four species nest on this island, including over 90% of the world's Elegant Tern and Heermann's Gull nesting populations. Just a few Yellow-footed Gull pairs nest here, at a ratio of ~10,000 Heermann's Gulls:1 Yellow-footed Gull, although their ratio in the study observation area was 10:1. We recorded the number of egg predation attempts, egg predations, and defense attacks by terns on gulls. We analyzed all possible interactions of gulls as predators of tern eggs and found that Yellow-footed Gulls attempted to prey on both tern species' eggs indiscriminately, while Heermann's Gulls preferentially attempted to prey on Elegant Tern eggs. Considered in proportion to their abundance, Yellow-footed Gulls performed significantly more attempts and egg predations on both tern species. For defensive attacks, Royal Terns attacked Yellow-footed Gulls more often than Heermann's Gulls, while the reverse was true for Elegant Terns. Considering their relative numbers, both tern species attacked Yellow-footed Gulls more often than Heermann's Gulls. Our study shows that only a small proportion of Heermann's Gulls engage in tern egg predation, and territorial behavior by both gull species precludes their presence in large numbers around the tern colony. The highest interaction numbers are between Heermann's Gulls and Elegant Terns, the lightest of the four possible gull-tern combinations by mass. Individual Heermann's Gull predations on Elegant Tern eggs were negligible, and considering relative population numbers, we found no significant differences in egg predation by either gull species on either tern species, which may be determining the balance of interactions between these four species at Isla Rasa.

Key words: egg predation, Laridae, *Larus heermanni*, *Larus livens*, mixed species seabird nesting, *Thalasseus elegans*, *Thalasseus maximus*

INTRODUCTION

Gulls and terns generally nest colonially, a pattern that usually helps to reduce nest predation on eggs and/or chicks under certain conditions, as well as to promote transmission of information among colony members, which favors group foraging (Burger & Gochfeld, 1994; Evans, 1982). They also frequently nest in mixed-species colonies or, at least, in single-species colonies adjoining or near other larid colonies (Quintana & Yorio, 1998). This form of nesting has been found to promote interactions that may be positive for some, or at least one, of the species that share the nesting area (Hernandez-Matías et al., 2003; Varela et al., 2007). Some classic works have identified advantages such as (1) reduction of the individual's probability of being preyed upon (Hoogland & Sherman, 1976; Kruuk, 1964); (2) greater difficulty for a predator to select a prey individual from a compact group (Humphries & Driver, 1967); (3) allowing potential prey to defend communally or mob the predator (Altmann, 1956; Crook, 1964); and (4) increased probability that the potential prey detect the predator, allowing potential prey to use their time more efficiently (some prey foraging while others are guarding) (Hamilton, 1971; Kenward, 1978; Pulliam, 1973).

Some disadvantages of colonial nesting have been shown to include (1) competition for nesting space (Lack, 1966; Hoogland & Sherman, 1976), (2) competition for a mate (Gochfeld, 1980; Vermeer, 1963), (3) intraspecific predation (Davis & Dunn, 1976; Emlen, 1956; Hunt & Hunt, 1975; Montevecchi, 1977; Parsons, 1971; Paynter, 1949), (4) greater risk of interspecific predation (Kruuk, 1964; Tinbergen et al., 1967), and (5) greater risk of parasites or diseases spreading in the nesting area (Hoogland & Sherman, 1976). In many instances, the advantages and disadvantages for each of the different species involved in the mixed-species nesting are not evident at first sight, and careful observations and data analysis are necessary to detect them.

In this work, we analyze possible advantages and disadvantages of predation interactions of two gull species on the eggs of two tern species sharing a nesting island. The two gull species, Heermann's Gull *Larus heermanni* and Yellow-footed Gull *L. livens*, are quasi-endemic (i.e., a type of endemic species that may disperse beyond its specific niche but does not scatter widely); and the two tern species are the quasi-endemic Elegant Tern *Thalasseus elegans* and the very widespread Royal Tern *T. maximus*. By studying these types of interactions among the four species, we hoped to gain some understanding of the processes that facilitate, or at least allow, the joint nesting of this particular and unique suite of seabird species.

METHODS

Study Area

Isla Rasa (28°49′24″N, 112°59′03″W), situated in the Midriff Islands region of the Gulf of California (Fig. 1), with a total surface area



Fig. 1. Location of Isla Rasa in the Gulf of California, Mexico.

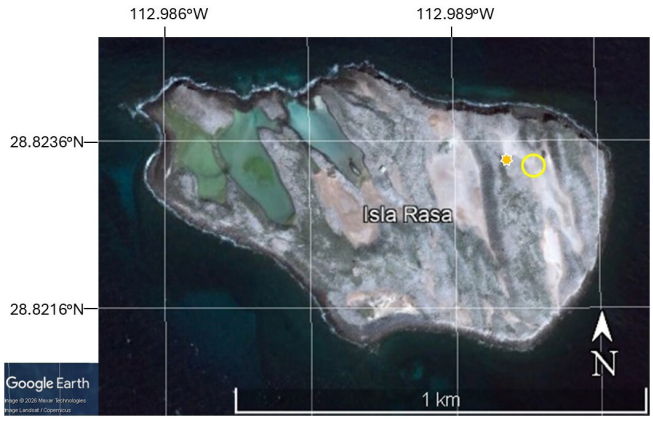


Fig. 2. Location of observers (orange star) and of the tern (Elegant Tern *Thalasseus elegans* and Royal Tern *T. maximus*) colony under observation (yellow circle) at Isla Rasa (28°49′29.71″N, 112°58′39.54″W), Gulf of California, Mexico. (Background map from Google Earth, image © 2026 Maxar Technologies, image Landsat/Copernicus.)

of about 0.6 km^2, is the nesting site of some 95% of the world populations of both Heermann's Gulls and Elegant Terns, and it has the second-largest known nesting colony of Royal Terns in the Mexican Pacific after Isla El Rancho, Sinaloa (Castillo-Guerrero et al., 2014), with average recorded total populations for these species of about 130,000, 100,000, and 8,000 nests, respectively, at this location between 2000 and 2013. However, figures may vary widely between years in each nesting site, depending on oceanographic conditions and food availability (Velarde et al., 2005; Velarde, Ezcurra, et al., 2015).

Heermann's Gulls nest on most of the island, using both valleys and rocky hills (see Velarde, 1992, for a detailed description of the island substrate and nesting distribution of Heermann's Gulls), with average densities of 1 nest/m^2 and 0.09 nests/m^2, respectively, while Elegant and Royal Terns nest in the valleys, at densities of about 14 nests/m^2 and 9 nests/m^2, respectively. Each species may form a single-species colony in some areas, but there are always sections where both species may mingle. The locations of the terns' nesting colonies vary from one year to the next, with no fixed location. Since Heermann's Gulls generally establish their nests in late March or early April, one or two weeks before terns get established, terns may invade Heermann's Gulls' nesting areas, and their colony can end up surrounded by gulls' territories. Yellow-footed Gulls are also quasi-endemic to the area. Although only some 10 Yellow-footed Gull nests can be found scattered along the small cliffs of Isla Rasa's coastal perimeter, these birds may be found on the island in higher numbers due to the fact that two neighboring sites, both about 7 km from Rasa, have important nesting colonies of this species (i.e., Isla Partida Norte and the San Lorenzo Archipelago, together hosting some 400 individuals). This proximity allows the gulls to easily commute daily to Rasa if prey are available there (Velarde, 1992). The Yellow-footed Gull is a large gull that is known to depredate the eggs and chicks of both tern species and Heermann's Gull (Velarde, 1992). This great concentration of nesting seabirds, all of them larids, including two crested terns, allows for the development of some interesting ecological interactions within the nesting colony areas.

Field Observations

We observed predation of eggs of both tern species by both gull species from a vantage point on a hill adjoining the valley where the observed tern colony was located (Fig. 2); the observers were located over 100 m from the border of the tern colony to avoid disturbing the terns. We directed observations at the border of the mixed Royal and Elegant Tern colony. Based on previous observations of the nesting behavior of Heermann's Gulls and both tern species, we purposefully chose a colony edge that lacked neighboring Heermann's Gull nesting territories (Fig. 3), as nesting Heermann's Gulls drive not only their conspecifics from their territory but also Yellow-footed Gulls. Therefore, egg predation has not been observed along this type of adjoining colony area. Gull predation on tern eggs only occurs along the tern colony border that is not contiguous to Heermann's Gull nesting territories.



Fig. 3. Aerial view of tern (Elegant Tern *Thalasseus elegans* and Royal Tern *T. maximus*) colony borders at Isla Rasa, Gulf of California, Mexico (15 May 2018): (A) area adjoining Heermann's Gull *Larus heermanni* nesting colony and (B) area not adjoining Heermann's Gull nesting colony. Photo credits: Thor Morales

The method followed was "recording all events of some behaviors" (Altmann, 1974). We recorded the following information: (1) number of attempts by both Heermann's and Yellow-footed Gulls to prey on eggs of both Royal and Elegant Terns, (2) the species and number of individuals of each tern species on which the egg predation attempts were performed, (3) the species and number of individuals of each tern species on which the egg predations were performed, and (4) the species and number of individual terns that attacked each predatory gull. Predation success was estimated as the proportion of gull attempts that resulted in an actual egg predation. This was estimated separately for each gull-tern species-pair combination—Royal and Elegant Terns, and Heermann's and Yellow-footed Gulls—thus rendering four types of interactions: Yellow-footed Gull/Royal Tern, Yellow-footed Gull/Elegant Tern, Heermann's Gull/Royal Tern, and Heermann's Gull/Elegant Tern.

To quantify the differences among the predation attempts on both tern species by both gull species, we took observations along two portions of the edge of the colony that had approximately the same number of terns of each species. During the second and third weeks of April 2012, we carried out a total of 100 hr of observation (in 2-hr periods each, between 06h00 and 19h00), 50 hr on each of the two tern species' sections of the colony. These values were added for the total observation time (2-hr period) and then added for the total time of observation (50 hr) for each of the two tern species separately. Every 30 min, starting from the beginning of each observation period, we counted the total number of Heermann's and Yellow-footed Gulls in the observation area, giving a total of five counts for each 2-hr observation period, or a total of 125 counts for each of the 50 hr of observation per tern species. These counts were used to estimate the average number of predatory gulls of each species present in the observation area.

Data Analysis

To test for deviation from randomness or from expected values, we used chi-square tests for the following comparisons.

Egg Predation Attempts

We tested whether each gull species attempted to prey on eggs of a preferential tern prey species. That is, given that tern prey availability was equal within the section of the colony we used for our study (where the relative abundance of each tern species was 50%), we tested whether the predation attempt pattern differed from an equal distribution in favor of one tern species.

Egg Predations

We tested whether the predation success rate (defined as the number of successful attacks divided by the number of attempts) was higher when one species of tern was attacked by each of the two gull species, compared to the success rate when attacking the other tern species.

Defensive Attacks by Terns on Gulls

We evaluated whether terns of each of the two species had different defense responses when they were attacked by each of the two gull species.

Predation Proportionality by Gulls

Lastly, for all three analyzed parameters (predation attempts, actual predations, and defensive attacks), to determine if one gull species was more active in the observation area than the other, and because the relative abundance of the Yellow-footed Gull was *ca*. 10% of the total gull abundance in the study site, we tested whether the number of observed parameters from each gull species was proportional to its abundance, independently of the targeted prey.

In all tests, we constructed a contingency table and calculated the expected values following the null hypothesis to be tested. If the overall χ^2 value was significant, we then calculated the Pearson residuals for each cell of the table (residual = [observed − expected]/√[expected]). Because in a frequency dataset under the null hypothesis of Poisson error the Pearson residual is expected to be distributed as a normalized deviate, the sign of the deviation and the significance of its value can be tested against the normal distribution *z*-values.

RESULTS

In the observation area, individual Heermann's and Yellow-footed Gulls were found to be in a 10:1 ratio across all observation periods. A total of 127 egg predation attempts and 83 actual egg predations by individuals of both gull species on both tern species were recorded across all observation periods (Table 1). Predation attempts and actual predations occurred only at the periphery of the tern nesting colony. When the gulls attempted to prey on the terns' eggs, some terns attacked the gulls in response to defend their eggs. We recorded a total of 67 observations of a tern attacking a gull that was attempting to prey on the tern's egg.

Egg Predation Attempts

The chi-square test showed that, when we consider interactions of each gull species individually, Yellow-footed Gulls attempted to prey indiscriminately on both tern species, while Heermann's Gulls had a significant preference for Elegant Terns ($\chi^2 = 21.41$, $df = 1$, $p < .0001$).

When both gull-tern pairs were considered in a single contingency table, we found a significant interaction between gull and tern species: Royal Terns received significantly fewer egg predation attempts from Heermann's Gulls and significantly more attempts from Yellow-footed Gulls than expected, while Elegant Terns received more attempts from Heermann's Gulls and fewer from Yellow-footed Gulls than expected ($\chi^2 = 18.31$, $df = 1$, $p < .0001$). This interaction, however, is mostly due to the preferential predation attempt pattern of the Heermann's Gulls, as shown in the first analysis.

When the analysis was carried out accounting for the relative proportion of Heermann's vs. Yellow-footed Gulls in the observation area (90% of the gulls in the study area were Heermann's Gulls), a significantly higher number of predation attempts were found to be carried out by Yellow-footed Gulls on both Royal and Elegant Terns ($\chi^2 = 318.12$, $df = 1$, $p < .0001$).

Egg Predations

The chi-square test showed that, individually, Yellow-footed Gulls preyed indiscriminately on both tern species, while Heermann's

TABLE 1
Events recorded during 100 observation hours of egg predation by Yellow-footed Gulls *Larus livens* (*L.l.*) and Heermann's Gulls *L. heermanni* (*L.h.*) on Royal Terns *Thalasseus maximus* (*T.m.*) and Elegant Terns *T. elegans* (*T.e.*) at Isla Rasa, Gulf of California, Mexico[a]

	Number and proportions of events by species pair[c]							
Types of events[b]	***T.m./L.l.***	**(%)**	***T.m./L.h.***	**(%)**	***T.e./L.l.***	**(%)**	***T.e./L.h.***	**(%)**
Attempts	41	(32.3)	10	(7.9)	32	(25.2)	44	(34.6)
Predations	23	(27.7)	6	(7.2)	21	(25.3)	33	(39.8)
Defenses	20	(29.9)	7	(10.4)	14	(20.9)	26	(38.8)
Relative attempts	41	(52.6)	1	(1.3)	32	(41.0)	4.4	(5.1)
Relative predations	23	(48.0)	0.6	(1.3)	21	(43.8)	3.3	(6.9)
Relative defenses	20	(53.6)	0.7	(1.9)	14	(37.5)	2.6	(7.0)
Predation success	23/41	(0.56)	6/10	(0.60)	21/32	(0.66)	33/44	(0.70)

[a] Approximate average mass of each seabird species: Yellow-footed Gull (*L.l.*): 1,000 g; Heermann's Gull (*L.h.*): 500 g; Royal Tern (*T.m.*): 450 g; Elegant Tern (*T.e.*): 250 g.
[b] Relative events (attempts, predations, and defenses) refer to the number of events scaled according to the proportion of each gull species present in the area: 10 Heermann's Gulls: 1 Yellow-footed Gull.
[c] Percentages for all event types except predation success were calculated by dividing the number for each species pair by the total number of events of that type across all species pairs. Percentages for predation success were calculated by dividing the number of predations by the number of attempts for a given species pair.

Gulls had a significant preference for Elegant Terns ($\chi^2 = 18.69$, $df = 1$, $p < .0001$).

When both gull-tern pairs were considered in a single contingency table for egg predations, we found a significant interaction between gull and tern species: Royal Terns received significantly more egg predations from Yellow-footed Gulls than expected, while they received fewer from Heermann's Gulls. By contrast, Elegant Terns eggs were significantly less preyed upon by Yellow-footed Gulls than expected, and more by Heermann's Gulls ($\chi^2 = 13.29$, $df = 1$, $p = .0003$). Again, this interaction is mostly due to the preferential predation pattern of the Heermann's Gulls on Elegant Tern eggs.

When the analysis was carried out accounting for the relative proportions of Heermann's vs. Yellow-footed Gulls in the observation area, a significantly higher number of egg predations were found to be carried out by Yellow-footed Gulls, on both Royal as well as Elegant Terns ($\chi^2 = 170.61$, $df = 1$, $p < .0001$). The highest success rate was attained when predation was attempted on Elegant Tern eggs by Heermann's Gulls (75%), followed by Yellow-footed Gulls (66%), while predation attempts on Royal Tern eggs by Heermann's Gulls had a success rate of 60%. The lowest success rate was that of Yellow-footed Gull attempts on Royal Tern eggs (56%). However, we found that these predation success rates were not significantly different among the four pairs of species ($\chi^2 = 3.4872$, $df = 1$, $p = .3224$).

Defensive Attacks

The chi-square test showed that, when we consider interactions of each gull species individually, defensive attacks performed by each tern species on Yellow-footed Gulls did not differ, while Heermann's Gulls received a significantly higher number of defensive attacks from Elegant Terns ($\chi^2 = 10.94$, $df = 1$, $p = .0009$).

When these types of interactions were evaluated in a single contingency table, we found a significant interaction between gull and tern species. Royal Terns were found to attack Yellow-footed Gulls significantly more and Heermann's Gulls significantly less than expected, while Elegant Terns were found to attack Yellow-footed Gulls less and Heermann's Gulls more than expected ($\chi^2 = 11.31$, $df = 1$, $p = .0008$). This interaction is, again, mostly due to the preferential predation pattern of the Heermann's Gulls.

If the relative proportions of both gull species in the observation area are taken into account, a higher number of defensive attacks were performed on Yellow-footed Gulls than on Heermann's Gulls by both Royal as well as Elegant Terns than expected from their relative abundances ($\chi^2 = 123.60$, $df = 1$, $p < .0001$).

DISCUSSION

Our results show that, although there were some 130,000 Heermann's Gull pairs nesting on Isla Rasa and, at the most, 13 Yellow-footed Gull pairs (a ratio of about 10,000:1), the proportion of these two gull species in the tern nesting area was 10:1, showing that only a very small proportion of the Heermann's Gull population was engaging in tern egg predation compared with Yellow-footed Gulls. These individuals were mostly from other nesting sites (islands other than Isla Rasa) and have been using the tern colony as a feeding source. Heermann's Gulls on Isla Rasa feed mainly on small pelagic fish (Velarde et al., 2013; Velarde, Ezcurra, & Anderson, 2015), and we have never found a regurgitation that contains traces of tern eggs. This indicates that tern eggs have made up only a minute amount of their diet. Furthermore, due to the territorial behavior of both gulls, there seems to be a limit to the number that can be present at the periphery of the tern colonies. If more Heermann's Gulls were present by the tern nesting area, their higher density would likely result in intraspecific interference, possibly leading to lower predation success. Interference, in the form of territorial behavior, has been shown to occur among foraging individuals of the same species, to a point at which this effect reduces foraging efficiency (Sih, 1982; Velarde, 1992).

Elegant Terns seem to have an advantage when nesting among Heermann's Gulls. We have observed that the former tend to seek

nesting sites close to the latter. Nesting Heermann's Gulls exhibit territorial behavior towards both their conspecifics and the Yellow-footed Gulls that approach their territory. This behavior keeps the numbers of predatory gulls down to virtually zero at the edge of the tern colony that is next to the nesting Heermann's Gulls. By contrast, at the edges of the Elegant Tern colony that are not fringed by territorial Heermann's Gulls, there is relatively free access by both gull species for tern egg predation. A very similar phenomenon was reported by Yorio and Quintana (1997) in their study in Patagonia of Royal and Cayenne Terns *T. acuflavidus eurygnathus* nesting in the midst of Kelp Gulls *L. dominicanus*, which also prey on these terns' eggs. Nesting Heermann's Gulls do not engage in tern egg predation within their own colony and instead concentrate on their own breeding activities.

Our results also show that, considering raw numbers, significantly more egg predation attempts and actual egg predations were carried out by Heermann's Gulls on Elegant Terns than on Royal Terns. This interaction pair is formed by the lightest of the four possible gull-tern species combinations (see Table 1 for mass of each species). It is likely more difficult for a Heermann's Gull to displace a Royal Tern (with almost the same mass) from its egg than it is to displace an Elegant Tern (with about half the mass of a Heermann's Gull). This is evident from the fact that Heermann's Gulls carried out over four times as many predation attempts on Elegant Tern eggs as on Royal Tern eggs. The same argument holds with actual egg predations. Besides these relative body mass considerations, the eggs of the Royal Tern (also of larger mass than those of the Elegant Tern) offer the Yellow-footed Gull greater energy content, thus perhaps constituting a more sought-after meal by this larger gull, even when Royal Terns are larger and more aggressive. Royal Terns are more dangerous to the predator in the defense of their eggs than Elegant Terns.

Furthermore, we found that when we accounted for the relative number of individuals of each gull species, egg predation by Yellow-footed Gulls was significantly higher than that by Heermann's Gulls, indicating that, although high in terms of absolute numbers, Heermann's Gull individual predation on terns' eggs, and in this case even on Elegant Tern eggs, was insignificant compared to that of individual Yellow-footed Gulls. This may again be the result of the gulls' interference with their conspecifics and with the other gull species. Generally, when both Yellow-footed and Heermann's Gulls were near the terns' nesting areas, they behaved in a territorial fashion towards their conspecifics and towards each other, threatening other individuals that invaded their individual space in this feeding area through either threat vocalizations or displays. Yellow-footed Gulls responded to conspecifics at larger distances, thus resulting in larger individual feeding areas, a behavior that may reduce the numbers of both gull species and thus increase control of their predation in these areas. This limit to the number of gulls preying on eggs of nesting terns is another observation reported by Yorio and Quintana (1997) in their study of gull-tern predation. Interestingly, Yorio and Quintana observed much higher predation by Kelp Gulls on Cayenne Tern eggs, indicating that this smaller tern was much more vulnerable to these large gulls than the larger Royal Tern. In our case, since Heermann's Gulls were reducing the number of potentially depredating Yellow-footed Gulls, the presence of the former may well result in a reduction of Yellow-footed Gull predation on the smaller and more vulnerable Elegant Tern.

In addition, the higher aggressiveness of the Royal Tern towards the Yellow-footed Gull is clear, as almost three times as many defensive attacks were carried out on the latter as on the Heermann's Gull, while the Elegant Tern performed almost twice as many attacks on the Heermann's Gull as on the Yellow-footed Gull. This situation was possibly due to two factors: (1) the Elegant Terns suffered numerically more egg predation attempts from the Heermann's Gull, but (2) also important are the same relative body mass considerations mentioned above—the Elegant Tern is disadvantaged against the Yellow-footed Gull, which is about four times as heavy. This tendency of the larger tern to engage in more attacks against a large gull predator compared with the smaller tern was another similar observation by Yorio and Quintana (1997). Interestingly, we see no significant difference between the egg predation success of either gull species on either tern species. This may be a key factor determining the balance of the interactions among these four species in this nesting area.

Isla Rasa offers nesting seabirds several particularly advantageous conditions: (1) the island is situated in an area of high marine productivity, with large populations of small pelagic fish seeking the colder, more productive waters of the Midriff Islands region at a time when all seabird species are breeding in the area (Sokolov, 1974); (2) there are no land predators; and (3) there are very few aerial predators (Velarde, 1992, 1993). These factors have been observed elsewhere also—i.e., the importance of food abundance (Krebs, 1973; Lack, 1968; Ward & Zahavi, 1973) and avoidance of predation on adults, eggs, or chicks (Altman, 1956; Crook, 1964; Hamilton, 1971; Velarde, 1992). If predators become more numerous or if prey abundance decreases, predation success will also decrease, particularly if predators exhibit some type of interference or competition among themselves (Velarde, 1992, and references therein).

The Isla Rasa array of nesting seabird species has been reported since the first historical scientific records of this island, from approximately the last quarter of the 19th century (Boswall & Barrett, 1978, and references therein). It, therefore, appears to be quite stable, although traditional information from the Comcaac people (also known as Seri) teaches us that this island was once an important nesting site for the Brown Pelican *Pelecanus occidentalis californicus*. Indeed, the name of the island given by the Comcaac is Tosni Iti Ihíquet, which means "where pelicans have their offspring" (Moser & Marlett, 2010). Thus, the present array of nesting seabird species was different before European disturbance of the area (see also Bowen et al., 2015). The latter authors revealed that Federico Craveri and team, extracting guano on the island during eight consecutive days in 1856, disturbed the nesting pelicans, causing them to abandon their colony. Later, repeated guano mining activities on the island prevented the re-establishment of the pelican colony, due to both the human presence as well as the considerable alteration of the island's substrate and topography during guano mining activities.

CONCLUSIONS

Nesting in large, high-density colonies is of crucial importance for both Elegant and Royal Terns, who suffer egg predation from two gull species at Isla Rasa. In this study, egg predation was observed to be concentrated exclusively to the periphery of the terns' nesting colonies, in areas that are open and not adjacent to the Heermann's Gull nesting area. The more aggressive nature of the Royal Tern provides direct protection to the Elegant Tern when they are nesting in mixed colonies. From the point of view of the Elegant Terns,

they experienced both predation attempts and actual egg predations from Heermann's and Yellow-footed Gulls, while the Royal Terns experienced significantly more attempts and actual predations from the latter. The presence of the Heermann's Gulls at the edges of the terns' nesting colonies also offered some protection in the form of intra- and interspecific interference competition (due to their territorial behavior) both towards the Yellow-footed Gulls and among themselves.

The case of this combination of four seabird species in Isla Rasa is interesting, since it seems to be an example of how the presence of one predator (the Heermann's Gull) influences the behavior of another (the Yellow-footed Gull). Also, it seems that the presence of each of the terns reduces the chances of predation on the other. If only the Royal Terns were present on the island, all the predation would be concentrated on them, possibly greatly affecting their nesting population. If only the Elegant Terns were nesting on the island, predation on them might also be too high, particularly from the Yellow-footed Gull, which directs its predation preferentially towards Royal Tern eggs when the latter are present. Therefore, through different phenomena, the presence of the bigger and more aggressive Royal Terns also helps protect the nesting Elegant Terns.

Isla Rasa, with its large valleys, provides excellent conditions for the high nesting density of both tern species, as well as for the establishment of the large Heermann's Gull nesting population. For example, Isla Partida Norte has a large nesting population of Yellow-footed Gulls, estimated to be ~400 nests. It seems that this island—although only 7 km from Isla Rasa and, therefore, surrounded by the same productive waters and forage fish and also devoid of land predators—is not suitable for the nesting of either these tern species or Heermann's Gulls. Therefore, our observations indicate that island physical characteristics and interactions among species likely determine the presence of some seabirds in large nesting populations on some islands in preference to other islands where they do not nest. This sort of knowledge about seabird species interactions and their habitat requirements is necessary for devising basic management practices and regulations (regarding factors such as human access to the islands and control of feral species) to support the conservation of the rich biodiversity of the area.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

EV: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review & editing. EE: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, validation, writing—original draft, writing—review & editing.

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