BREEDING ECOLOGY OF THE ROYAL TERN (*THALASSEUS MAXIMUS*) AT ISLA EL RANCHO, MEXICO: COLONY SIZE AND NEST LOCATION AFFECT PREDATION

Ulises T. Angulo-Gastélum[1], José Alfredo Castillo-Guerrero[1,2], & Eric Mellink[1]

[1]Centro de Investigación Científica y de Educación Superior de Ensenada, Km 107 Carretera Tijuana-Ensenada, Código Postal 22860, Apdo. Postal 360, Ensenada, B.C., México.
E-mail: emellink@cicese.mx

[2]Instituto de Ciencias del Mar y Limnología, Unidad Académica Mazatlán (UNAM), Av. Joel Montes Camarena S/N, Apdo. Postal 811, C.P. 82040, Mazatlán, Sinaloa, México.
E-mail: acastillo@ola.icmyl.unam.mx

Resumen. – Ecología reproductiva del Charrán real (*Thalasseus maximus*) en la isla El Rancho, México: El tamaño de la colonia y la ubicación del nido afectan a la depredación. – Estudiamos la biología de anidación del Charrán real (*Thalasseus maximus*) en una colonia grande (c. 1500 nidos) y una chica (c. 300 nidos), de la isla El Rancho, Sinaloa, durante la temporada reproductiva 2007. Medimos el volumen de huevo, densidad de anidación y distancia al borde de la colonia, e investigamos su relación con el éxito reproductivo. También evaluamos la depredación de huevos por parte de la Gaviota de Heermann (*Larus heermanni*). El tamaño de la colonia, densidad de anidación, zona de la colonia, depredación y posiblemente la escasez de alimento, afectaron el éxito reproductivo del Charrán real. La densidad de anidación fue mayor en zonas centrales (9.57 nidos/m² ± 0.28) que en las periféricas (8.20 nidos/m² ± 0.34) y mayor en la colonia grande (9.24 nidos/m² ± 0.21) que en la chica (6.66 nidos/m² ± 0.66). Hubo mayor éxito de eclosión en la colonia grande (82.5%) que en la colonia chica (50%), y en zonas centrales que en las zonas periféricas. La cantidad de Gaviotas de Heermann merodeando fue similar entre colonias, pero depredaron más huevos en la colonia chica (0.54 huevos/h ± 0.11) que en la grande (0.25 huevos/h ± 0.06), y solo en la periferia de las colonias. Esto resalta la importancia del tamaño de la colonia y de la ubicación del nido como protección contra depredadores en el Charrán real. Al igual que en otras especies de charranes, la depredación fue la causa principal de fallo reproductivo, lo cual sugiere que para este grupo la depredación es una fuerza selectiva que contribuye al mantenimiento de la colonialidad y puede regular el tamaño mínimo de colonia.

Abstract. – We studied the nesting biology of the Royal Tern (*Thalasseus maximus*) in a large (c. 1500 nests) and a small colony (c. 300 nests), at Isla El Rancho, Sinaloa, Mexico, during the 2007 breeding season. We measured egg volume, nest density, and distance to the edge of the colony, and investigated their effects on hatching and fledging success. We evaluated also egg predation by the Heermann's Gull (*Larus heermanni*). Colony size, nesting density, location within the colony, predation by gulls, and a possible food shortage affected breeding success. Nesting density was higher in the centre of colonies (9.57 nests/m² ± 0.28) than at the periphery (8.20 ± 0.34), and higher in the large colony (9.24 ± 0.21) than in the small one (6.66 ± 0.66). Hatching success was higher in the large colony (82.5%) than in the small one (50%), and in central areas than at the periphery. Both colonies attracted similar numbers of Heermann's Gulls, but these predated eggs at a higher rate in the small (0.54 eggs/h ± 0.11) than in the large colony (0.25 eggs/h ± 0.06), and focused predation attempts at the periphery. This highlights the importance of colony size and nest location in protecting against predation in Royal Terns. Similar to other tern

studies, egg predation was the main cause of reproductive failure, suggesting that in Royal Terns this is a major selective pressure that contributes to the maintenance of coloniality and regulates minimum colony size. *Accepted 23 February 2011.*

INTRODUCTION

About 96% of all seabirds are colonial, making this a characteristic attribute of them (Coulson 2002). Coloniality has been considered an evolutionary response to predation (Lack 1968, Gotmark & Anderson 1984), or resulting from the concentration of high quality breeding habitat (Lack 1968, Wittenberger & Hunt 1985), the search for mates, or extrapair copulations (Danchin & Wagner 1997, Danchin *et al.* 1998, Wagner *et al.* 2010, Doligez *et al.* 2003). Although different mechanisms to explain the origin and maintenance of coloniality have been proposed, the conditions under which it was selected in seabirds and the factors that have maintained it have not been clarified (Coulson 2002, Sachs *et al.* 2007, Varela *et al.* 2007).

Colonies are variable in size and distribution, a fact that may reflect intraspecific competition for food near the colony (Lewis *et al.* 2001, Forero *et al.* 2002). Prey consumption around the colony can create a "halo" of food shortage that forces the birds to make longer foraging trips, with higher energy expenditure, and this can regulate the upper limit of colony size (Ballance *et al.* 2009). Large colonies have also dense-dependent costs, reflected in lower breeding success, body condition of chicks, or chick growth rates than at smaller colonies (Lewis *et al.* 2001, Forero *et al.* 2002). There might be also other factors regulating colony size.

It has been suggested that breeding in congregations increases predation risks by providing a predictable supply of food for predators, and, hence, coloniality may not have its origin in a reduction of predation risks (see Varela *et al.* 2007). However, in colonies of some species predation could be a selective force influencing the maintenance of coloniality, and/or contribute to regulate the size of the colony. For example, colonies might provide anti-predator services derived from the effect of predation dilution, group vigilance, and communal defense, in which colony size and breeding synchrony are important to optimize the anti-predator behavior and to reduce individual costs (see Hernández-Matías *et al.* 2003, Varela *et al.* 2007, and references therein). However, not all parts of a colony are equally protected and susceptibility to predation depends on nest placement within the colony. Nest in the centre of a colony have a better breeding output, partly due to reduced exposure to predation (Tenaza 1971, Becker 1995, Yorio & Quintana 1997). The centre of a colony is sometimes occupied by experienced pairs, which are also in better body condition than those nesting at the periphery where generally young, inexperienced pairs nest (Coulson 1968).

Royal terns (*Thalasseus maximus*) are colonial, widely distributed seabirds (Buckley & Buckley 2002). The population in western Mexico has been estimated at about 13,000 pairs nesting at 11 sites, from the northern Gulf of California and the west coast of the Baja California Peninsula, south to Laguna Cuyutlán, Colima (Mellink *et al.* 2007). The majority of pairs, however, nest at a single site, Isla Rasa (8000–10,000 pairs), followed by Isla El Rancho (~2000 pairs) and Laguna Ojo de Liebre (1845 pairs: Mellink *et al.* 2007). Our study was focused on two colonies of Royal Terns at Isla El Rancho, south-central Gulf of California, Mexico. Both colonies

were established in a distance of about 2 km from each other. As they shared feeding areas and environmental factors, food availability and such factors could be excluded as direct drivers of colony size. We characterized the breeding ecology of Royal Tern and egg predation by gulls at both colonies, focusing on three hypotheses related with colonialism and predation. We aimed to test whether breeding (1) in larger colonies, (2) at central places or (3) aggregately confered protection against predation and improved breeding success and potentially regulated colony size.

METHODS

Study area. The Gulf of California is a marginal sea of the Pacific Ocean. Very dynamic and highly productive, it has a weak upwelling along its western edge during the summer, and strong along its eastern edge during winter and spring (Álvarez-Borrego 2002). At the south-central margin of the Gulf of California, the coast of Sinaloa is characterized by a series of large coastal lagoons, among them the Bahía Santa María-La Reforma at whose northern mouth lies Isla El Rancho (25°10'N, 108°23'W; Fig. 1), the site of this study. Isla El Rancho (Fig. 1), approximately 120 ha, is a sandy islet with coastal sand dune vegetation in some central parts, and marsh vegetation at the edges (González-Medina *et al.* 2009). In 2007 this island supported four colonies of Royal Terns on flats devoid of vegetation, but two of them were small and ephemeral, and the terns abandoned them some days after their onset. We studied the largest colony and the small one that was not abandoned. The large colony, located in the southwestern section of the island, was 10–15 m from the high tide mark, about 1 m above maximum tide level, and contained approximately 1600 nests. The small colony, located in the northeastern section of the island, was 1700 m away from the large one and 150 m

away from the high tide mark, and had approximately 300 nests (Fig. 1).

Breeding success, colony size, and predation rate. From January to March 2007, we made two visits per month to the island to monitor, through behavior, the onset of colony formation. After the larger colony formed between late March and early April, we stayed on the island continuously until 11 June, except for 9–15 April and 16–21 May. We estimated total number of nests at both colonies at the time of incubation (early April) from vantage points 30 m away. Counts were made by two independent observers on two consecutive days (results include minimum and maximum counts).

We defined the periphery of the colony as its outer 1-m band, and the zone of the colony more than 1 m from the edge was considered the centre. Nest density was calculated by means of 1 m² plots placed at the intersections of 2x2 m grids throughout both colonies (large colony n = 41, small colony n = 10). These plots covered roughly 40% of each colony area. Approximately seven days after the colonies were established, we randomly selected 75 nests (33 in the centre and 42 at the periphery) in the large colony and 30 nests (15 and 15, respectively) in the small colony and marked them with numbered flags.

We measured the width and length of eggs in these nests with calipers (± 0.1 mm), and marked them with waterproof ink. We obtained each egg's volume (sensu Worth 1940) and determined hatching success of each nest by daily monitoring. Hatchlings were marked with color numbered adjustable cable ties, and survival at fledging age (approximately 30 days, Buckley & Buckley 2002) was determined by semiweekly recaptures at crèches.

To estimate gull predation, two observers recorded the number of predated eggs per hour during 69.5 h (observations made during
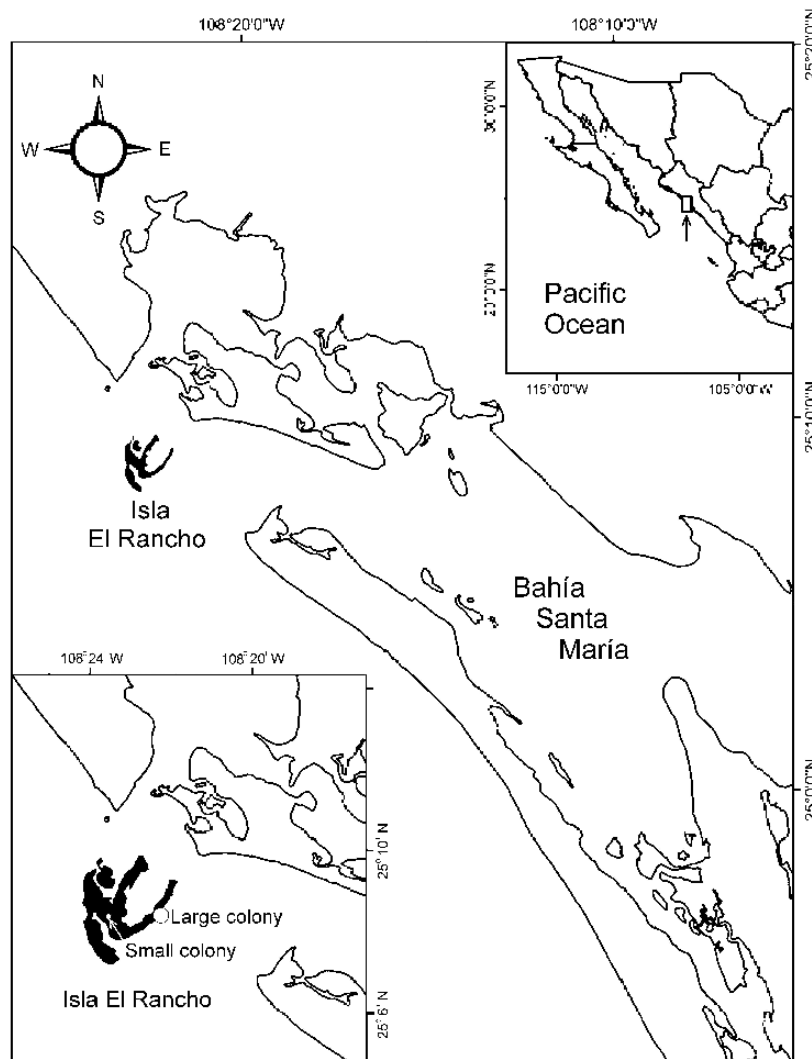
FIG. 1. Isla El Rancho, Sinaloa, Mexico, including the location of a large and a small colony of Royal Terns (*Thalasseus maximus*) studied during the 2007 breeding season.

19 days, duration of shifts of observation = 2 h) between April 5 and May 11, which included all phases of the incubation period. To this end, we observed the colony (simultaneously the periphery and the centre), with binoculars from a fixed vantage point 30-m from the colony in the morning (06:30–11:00 h MST), at mid-day (11:00–15:30 h), and in the afternoon (15:30–20:00 h). Our vantage points allowed for the observation of the entire colony. We are certain that no predation by gulls occurred in the centre of the colony during our observations as nest density is so high that walking of gulls between the

nests is impossible. Also, if gulls had approached from the air, the terns calling and raising would have allowed us to detect them. In each observation period, we recorded the number of gulls searching for or trying to predate eggs. At most nests monitored we could determine the causes of egg failure from the remains.

Statistical analysis. We used a 2-way ANOVA to determine whether there was an effect of colony (large/small) or colony zone (centre/periphery) on nest density and on egg volume. To determine the factors that affected breeding success we used a general linear model with logit link (due to the binomial nature of the response variable). Colony and colony zone were included as fixed factors, and egg volume was included as covariate. To analyze the predation rate of eggs by gulls we used an ANCOVA, with colony and time of day as independent variables and number of gulls as covariate. We did not include colony zone in this model since predation occurred exclusively at the periphery. All analyses were carried out with the Statistica ver. 7 (StatSoft, Inc. 2005. STATISTICA [data analysis software system], version 7.1.; www.statsoft.com). All values presented are mean ± SE, and the significance level was set to $P = 0.05$.

We generated separate capture-history matrices for 66 chicks. Encounter histories were constructed for individual terns from live encounter data where 0 = not detected and 1 = captured on the study area. In analyses of the apparent survival of chicks, the first record in the encounter history was the day that the tern was banded as hatchling. We used Jolly-Seber mark-recapture methods using program MARK to calculate daily probabilities of apparent survival (Φ) and encounter (p). We included age, colony zone, and recapture time-dependence in models of apparent survival. Colony size was neglected because there was low hatching success at the

small colony and just one chick was ever recaptured.

To compensate for over-dispersion, we estimated the variance inflation factor (ĉ) by performing 1000 parametric bootstrap simulations on the model using the median ĉ test in MARK (White & Burnham 1999). The estimated ĉ (0.98) was used for adjusting AICc values during model selection. Then, we proceeded with model testing by fitting reduced models with fewer parameters. All models were constructed with design matrices and the logit-link function. Starting with our global model, we applied constraints to the probabilities in the following order: encounter rates (p), apparent survival of birds (Φ). Model fit was assessed with quasi-Akaike's Information Criterion (QAIC*c*).

To account for uncertainty in model selection, we calculated an average value for Φ by averaging over the most parsimonious models (ΔAIC = 2.5) in the model set with common elements in the parameter structure, weighted by normalized AIC model weights.

RESULTS

Breeding chronology. The 2007 breeding season lasted about 4 months, from courtship in early March to the last fledglings leaving the colony in June (Fig. 2). There was a high synchrony in egg laying and hatching within the colonies with a maximum range of 26 days between the earliest eggs/chicks and the latest. At its largest size, the large colony had between 1400 and 1600 nests. In early April, Royal Terns began to form the small colony, which grew to about 300 nests, which hatched in mid-May. Two other small colonies formed at different times. The formation of small satellite colonies at Isla El Rancho was documented also on other years (UTA and JACG, unpubl. data).

Most nests contained a single egg, and only five of the monitored nests contained
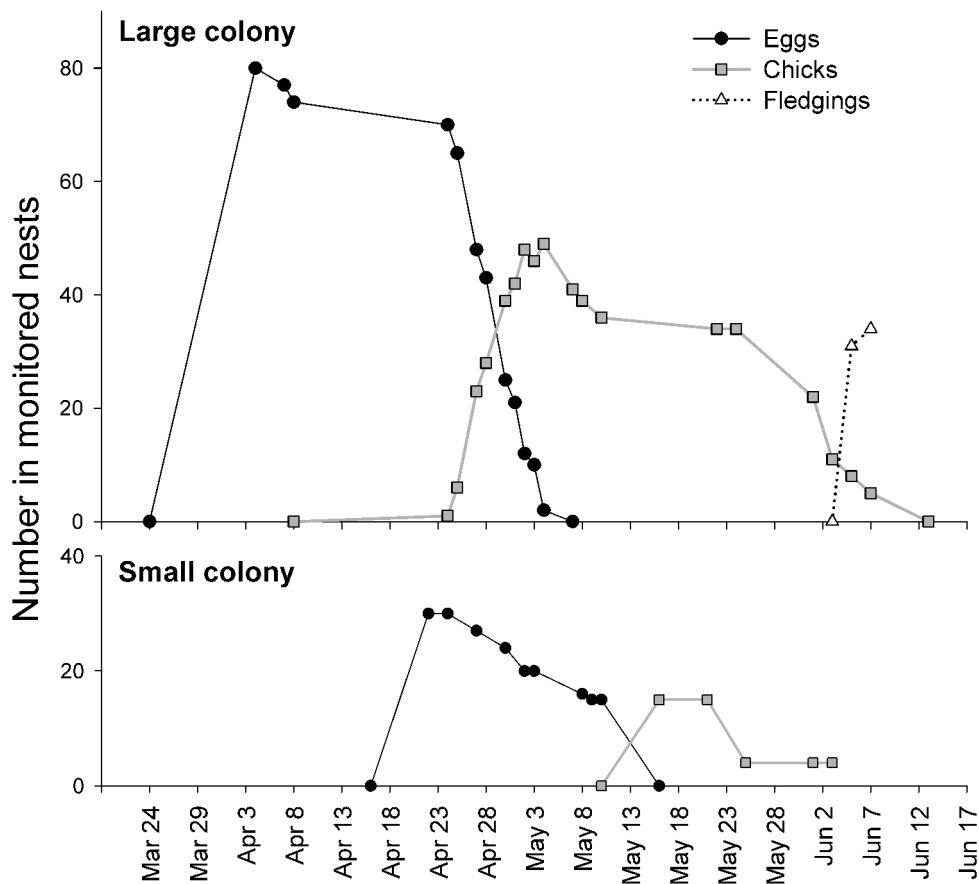
FIG. 2. Breeding chronology of Royal Terns (*Thalasseus maximus*) at Isla El Rancho, Sinaloa, Mexico, 2007.

two eggs. The incubation period was 29.28 ± 0.42 days (N = 7). Chicks remained between three and five days at the nest (3.61 ± 0.08, N = 49), and then moved to crèches at the beach. Up to seven crèches developed in this colony, and they slowly moved away from the colony until they were 1400 m from it. At three weeks of age, chicks were relatively independent and were able to defend themselves to some degree from kleptoparasitizing gulls that tried to steal food from them. The first fledglings were sighted in the fifth week after hatching began, and by the first week of June, at 30–32 days of age, most chicks had fledged (Fig. 2). Of 66 chicks banded, at the large colony, 34 (51.51%) became fledglings.

The model with the lowest AICc for the survival of hatchlings included age effects and time dependent encounter rate (p), while the colony zone of the chicks was not included (Fig. 3). Apparent survival in the first two age intervals (< 10 days) after capture was ≈0.93 (95% CI: ≈0.90–0.96), whereas survival for birds during subsequent capture periods was ≈ 0.99 (95% CI: ≈0.97–1.0, Fig. 3).
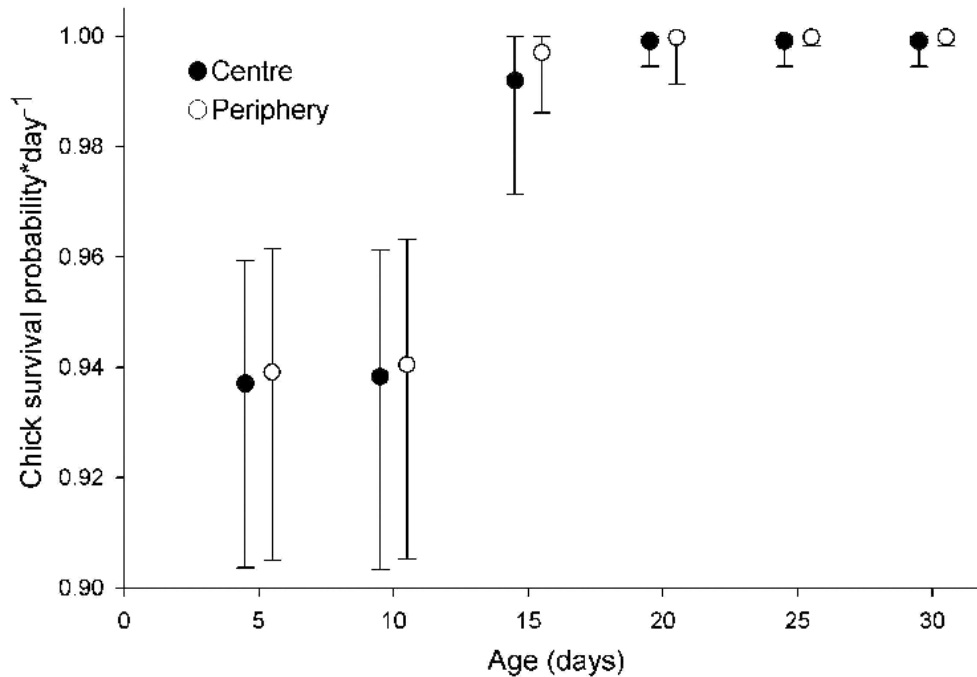
FIG. 3. Royal Tern (*Thalasseus maximus*) chick survival probability at Isla El Rancho, Sinaloa, Mexico, during the 2007 breeding season.

Effects of colony size and colony zone. Nest density was higher in the centre of the colonies (9.57 nests/m² ± 0.28) than at the periphery (8.20 nests/m² ± 0.34; $F_{1, 46}$ = 17.148, P = 0.0001), and greater in the large colony (9.24 ± 0.21) than in the small colony (6.66 ± 0.66; $F_{1, 4}$ = 27.872, P = 0.0001; Fig. 4). Egg volume was larger in the large colony ($F_{1, 100}$ = 11.1; P = 0.001), but not different among areas within the colony ($F_{1, 100}$ = 2.4; P = 0.12).

Heermann's Gulls were common around both colonies during incubation (13.08 ± 2.05, n = 35, Fig. 4) and tried to steal eggs from the terns frequently. Egg predation was lower at the larger colony ($F_{1, 32}$= 5.48, P = 0.02), where 10 eggs were lost due to predation in 36 hours of observation (0.25 eggs/h ± 0.06) than at the small colony, where 18 eggs were lost in 33.5 hours observation (0.54 eggs/h ± 0.11, Fig. 4). The gulls stole eggs only from nests at the periphery of the colonies, and predation rate was higher in the mornings than at mid-day or in the afternoon ($F_{2, 28}$ = 21.75, P < 0.001).

In the large colony, 66 out of 80 eggs hatched from 75 nests, 12 eggs were lost due to predation, and 2 were infertile. Of 30 eggs monitored at the small colony, 15 hatched and 15 were lost due to predation. Hatching success was significantly higher at the larger than at the smaller colony (*Wald* = 8.480, P = 0.003), and at the centre of the colonies than at the periphery (*Wald* = 17.022, P < 0.001; Table 1), with an interaction between variables (*Wald* = 3.744, P = 0.052): Success at the periphery was proportionally much lower at the smaller colony (Table 1). At the large colony, colony zone did not have an effect on fledging success (*Wald* = 0.161, P = 0.69). Egg volume did not have any effect on
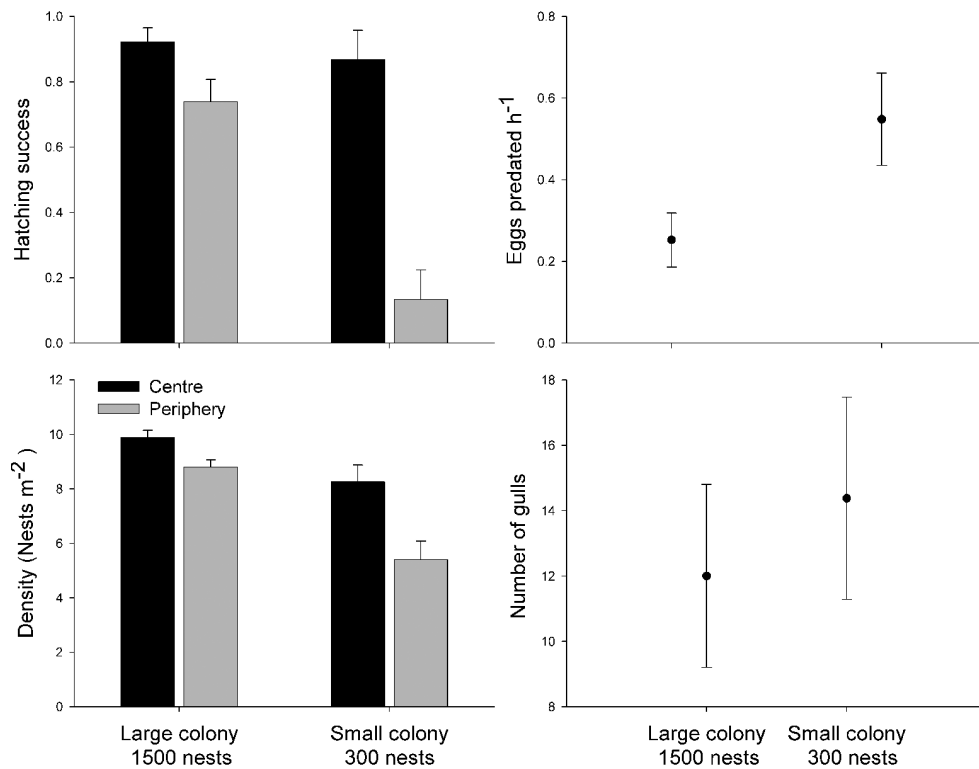
137

FIG. 4. Hatching success, nest density, predation rate, and number of gulls (mean ± SE) at colonies of the Royal Tern (*Thalasseus maximus*), in relation to colony size (large or small) and colony zone (centre or periphery) at Isla El Rancho, Sinaloa, Mexico, 2007.

hatching success in either colony (*Wald* = 1.519, P = 0.21), nor on fledging success (at the large colony; *Wald* = 0.348, P = 0.55).

DISCUSSION

Arrival of Royal Terns and onset of egg laying at Isla El Rancho was earlier in the year than that observed at colonies of the Atlantic coast of North America (Buckley & Buckley 1972, Blus *et al.* 1979). This is concordant with other species of Laridae that exhibit a latitudinal gradient, with earlier breeding seasons at lower latitudes (Montevecchi *et al.* 1979). Overall nest characteristics and breeding chronology were similar to those at other sites, including those on the Atlantic coast of North and South America (Buckley & Buckley 1972, Blus *et al.* 1979, Quintana & Yorio 1997).

In comparison with other colonies (Buckley & Buckley 2002), the low fledging success at El Rancho (51.5%) was caused by high mortality of chicks during the first ten days of life (= 91% of total mortality). Chicks at a Patagonian (Argentina) colony had a 90% survival at day 10 (Quintana & Yorio 1997), but the Patagonian chicks did not abandon their nests to form crèches until they were 20 days old. Despite leaving their nests as early as at El Rancho, chicks at other north Atlantic colonies have similarly high survival rates

TABLE 1. Hatching success in different zones (centre and periphery) of two colonies (large and small) of the Royal Tern (*Thalasseus maximus*) at Isla El Rancho, Sinaloa, Mexico 2007. * defined as the number of chicks reaching fledging age (25–30 days), percent relative to the number of eggs hatched.

	Zone	
	Centre	Periphery
Large colony		
Nest monitored	33	42
Eggs layed	38	42
Eggs hatched	35 (92.1%)	31 (73.8%)
Chicks fledging*	17 (48.6)	17 (54.8)
Small colony		
Nest monitored	15	15
Eggs layed	15	15
Eggs hatched	13 (86.6%)	2 (13.3%)
Chicks fledging*	2 (15.4%)	0 (0%)

(Buckley & Buckley 2002). Given that we studied the El Rancho colony in a single year, it is not possible to deduce whether such low fledging success is regular or anomalous. However, the 2007 breeding season was under the influence of a mild El Niño Southern Oscillation event (ENSO) (NOAA 2007), and breeding success of other seabirds in the region was low (González-Medina *et al.* 2009, Castillo 2009).

Predation by several species of gulls on eggs, chicks, and, in some cases, adults can limit seabird populations (Birkhead 1977, Massaro *et al.* 2001, O'Connell & Beck 2003). In Patagonia, Royal Terns lost significant numbers of eggs due to predation by gulls (Quintana & Yorio 1997). At El Rancho colonies, Heermann's Gulls preyed upon Royal Tern's eggs when the parents moved a little from the nest, and also tried to force the adults to rise from the nest to steal eggs. On two occasions, we observed a Heermann's Gull actually pushing an incubating adult Royal Tern to displace it from the nest, albeit

unsuccessfully. Like in the Patagonian colony (Quintana & Yorio 1997), at El Rancho all eggs lost due to predation where from nests at the periphery.

On Isla El Rancho, like at other colonies in homogeneous habitats with little protection, the distribution of nests followed a centre-periphery model, with higher nest density and higher breeding success in the centre. Nesting in the centre of the colony was clearly advantageous at both El Rancho colonies. Given that the major cause of breeding failure was egg depredation, nesting surrounded by con-specific birds in zones densely packed with nests offered protection, derived possibly from increased vigilance, group defense, and a higher efficiency to deter predators (Hamilton 1971, See Hernández-Matías *et al.* 2003, Varela *et al.* 2007, and references therein). In colonies with low nesting densities, open spaces between nests allow the gulls to approach nesting terns without being attacked by nesting neighbors, leading to high egg and chick predation (Birkhead 1977). Thus, the quality of nesting habitat is largely a function of the presence of nesting conspecific pairs (Velando & Freire 2001).

At both El Rancho colonies the number of gulls prowling was similar, but they had a higher predation success at the smaller colony. Larger colonies tend to have lower predation rates (Birkhead 1977) due to two non-exclusive causes. First, there is a sheer effect of numbers: with more eggs in the colony, less individual predation is probable. Secondly, a larger group may defend itself better against predators (Birkhead 1977, Gotmark & Anderson 1984, Becker 1995, Oro 1996, Hernández-Matías & Ruiz 2003). Although some studies have separated the effects of colony size from colony density (see Oro 1996), in most cases these two factors are correlated (Tenaza 1971, Gotmark & Anderson 1984, Barbosa *et al.* 1997). Nesting in denser colonies may also provide better protection due to

increased vigilance and defense (Massaro *et al.* 2001), and lower nest accessibility by gulls. At El Rancho, being a member of the larger colony was clearly advantageous to reduce egg predation but we could not discriminate whether this resulted from the effect of colony size, nest density, or a combination of both.

The fact that eggs were smaller in the smaller colony might reflect a disproportionate number of younger females nesting there (Croxal *et al.* 1992), females with lower body condition which were unable to devote as much energy to egg production (Lifjeld *et al.* 2005), or pairs that had failed their first breeding attempt in the larger colony and had less resources to devote to a second nesting attempt (Parsons 1976, Urrutia & Drummond 1990). Given that the smaller colony was formed later in the breeding season (after nests began to fail in the large colony), any of these three non-exclusive scenarios could explain smaller eggs in the smaller colony.

Although the role of predation as a driver of coloniality in birds is still debated and some evidences indicate that the causes of the latter are not related with the reduction of predation risks (Varela *et al.* 2007), in some mid-size terns (Royal, Cayenne, Roseate, and Common) predation can be the main cause of breeding failure (Yorio & Quintana 1997, Whittam & Leonard 1999, Hernández-Matías & Ruiz 2003). Thus, predation seems to be a selective force favoring the nesting in large and dense colonies. Independently of the origin of coloniality in birds, predation can influence its maintenance, especially in mid-size species that use open habitats with no physical protection.

On the other hand, it has been argued that colony size is regulated by intra-specific competition among nesters and the availability of food near the colony (Lewis *et al.* 2001, Forero *et al.* 2002). The maximum size of a colony seems to be related with high ener-getic demands required by increasingly longer foraging trips to feeding sites with better fish availability (Ballance *et al.* 2009). The Royal Tern colony at Isla El Rancho has grown during recent years and density-dependent costs seem still less important than predation. In species vulnerable to predators, predation could regulate the lower size limit of a colony.

Royal Tern pairs nesting at centre and in the larger colony at El Rancho clearly had a higher breeding success than those at small colony and peripheral sites, then predation was exacerbated at the periphery of small colony. Therefore it is surprising that Royal Terns at this site would prefer to nest in a new, small colony rather than to gather in a larger one, albeit to the periphery. We hypothesize that benefits derive from being synchronous with neighbor pairs, allowing for uniform defense activities. If late nesters laid eggs in the large colony, they would be incubating while the majority of pairs were tending to chicks in crèches at the beach, which would leave them less protected in a low-density, spread-out colony, than at a smaller, but densely-packed one. Given this scenario, forming a new, albeit small, colony seems a better choice even if probability of success is lower.

In conclusion, breeding success was positively affected by colony size and central nest location, due to lower egg predation by Heermann's Gulls. Most chick mortality occurred in the first days after hatching, which may have been related to food scarcity near the colony under modest El Niño conditions during the study period. Our results support the idea that colonial nesting in Royal Terns offers protection against predation and could contribute to maintain coloniality and regulate minimum colony size. Late nesters appear to form smaller new colonies rather than remaining in the large colony, possibly to maintain breeding synchrony with their

neighbors, and its consequent higher nest density.

ACKNOWLEDGMENTS

REFERENCES

Álvarez-Borrego, S. 2002. Physical oceanography. Pp. 41–59 *in* Case, T. J., M. L. Cody, & E. Ezcurra (eds). A new island biogeography of the Sea of Cortez. Oxford Univ., New York, New York, USA.

Ballance, L. T., D. G. Ainley, G. Ballard, & K. Barton. 2009. An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin *Pygoscelis adeliae*. J. Avian Biol. 40: 279–288.

Barbosa, A., J. Moreno, J. Potti, & S. Merino. 1997. Breeding group size, nest position and breeding success in the chinstrap penguin. Polar Biol. 18: 410–414.

Becker, P. H. 1995. Effects of coloniality on gull predation on Common Tern *Sterna hirundo* chicks. Colon. Waterbirds 18: 11–22.

Birkhead, T. R. 1977. The effect of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). J. Anim. Ecol. 46: 751–764.

Blus, L. J., R. M. Prouty, & B. S. Neely. 1979. Relation of environmental factors to breeding status of Royal and Sandwich terns in South Carolina, USA. Biol. Conserv. 16: 301–320.

Buckley P. A., & F. G. Buckley. 1972. The breeding ecology of Royal Terns *Sterna* (*Thalasseus*) *maxima maxima*. Ibis 114:344–359.

Buckley P. A., & F. G. Buckley. 2002. Royal Tern. *In* Poole, A., & F. Gill (eds). The birds of North America, No. 200. The birds of North America,

Inc., Philadelphia, Pennsylvania, USA.

Castillo, J. A. 2009. Variación intercolonial en la reproducción del bobo de patas azules (*Sula nebouxii*) en el Golfo de California: probando las hipótesis sobre el dimorfismo de talla en la familia Sulidae. Ph.D. thesis. Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, México.

Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217: 478–479.

Coulson, J. C. 2002. Colonial breeding in seabirds. Pp. 87–114 *in* Shreiber, E. A., & J. Burger (eds). Biology of marine birds. CRC Press, Boca Raton, Florida, USA.

Croxal, J. P., P. Rothery, & A. Crisp. 1992. The effect of maternal age and experience on eggsize and hatching success in Wandering Albatrosses *Diomedea exulans*. Ibis 134: 219–228.

Danchin, E., & R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. Trends Ecol. Evol. 12: 342–347.

Danchin, E., T. Boulinier, & M. Massot. 1998. Conespecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79: 2415–2428.

Doligez, B., C. Cadet, E. Danchin, & T. Boulinier. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. Anim. Behav. 66: 973–988.

Forero, M. G., J. L. Tella, K. A. Hobson, M. Bertellotti, & G. Blanco. 2002. Conspecific food competition explains variability in colony size: a test in Magellan Penguins. Ecology 83: 3466–3475.

González-Medina, E., J. A. Castillo-Guerrero, & E. Mellink. 2009. Relación entre las características de los huevos y del sitio de anidación, con el éxito reproductivo de la Gaviota reidora (*Leucophaeus atricilla*) en la isla El Rancho, Sinaloa durante la temporada 2007. Ornitol. Neotrop. 20: 553–564.

Gotmark, F., & M. Anderson. 1984. Colonial breeding reduces nest predation in the Common Gull (*Larus canus*). Anim. Behav. 32: 485–492.

Hamilton, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31: 295–311.

Hernández-Matías, A., L. Jover, & X. Ruiz. 2003. Predation on Common Tern eggs in relation to sub-colony size, nest aggregation and breeding synchrony. Waterbirds 26: 280–289.

Hernández-Matías, A., & X. Ruiz. 2003. Predation on common tern eggs by the Yellow-legged Gull at the Ebro Delta. Sci. Mar. 67 (Suppl. 2): 95–101.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, UK.

Lewis, S., T. N. Sherratt, K. C. Hamer, & S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature 412: 816–819.

Lifjeld, J.T., A. Johnsen, & T. Petitguyot. 2005. Egg-size variation in the Bluethroat (*Luscinia s. svecica*): constraints and adaptation. J. Ornithol. 146: 249–256.

Massaro, M., J. W. Chardine, & I. L. Jones. 2001. Relationships between Black-legged Kittiwake nest-site characteristics and susceptibility to predation by large gulls. Condor 103: 793–801.

Mellink, E., E. Palacios, & E. Amador. 2007. Colonies of four species of terns and the Black Skimmer in Western México. Waterbirds 30: 358–366.

Montevecchi, W. A., M. Impekoven, A. Segre-Terkel, & C. G. Beer. 1979. The seasonal timing and dispersion of egg laying among Laughing Gulls *Larus atricilla*. Ibis 121: 337–344.

O'Connell, T. J., & R. A. Beck. 2003. Gull predation limits nesting success of terns and skimmers on the Virginia barrier islands. J. Field Ornithol. 74: 66–73.

Oro, D. 1996. Colonial seabird in dense and small sub-colonies: an advantage against aerial predation. Condor 98: 848–850.

Parsons, J. 1976. Factors determining the number and size of egg laid by the Herring Gull. Condor 78: 481–492.

Porter, J. M. 1990. Patterns of recruitment to the breeding group in the Kittiwake *Rissa tridactyla*. Anim. Behav. 40: 350–360.

Quintana, F., & P. Yorio. 1997. Breeding biology of Royal and Cayenne terns at a mixed-species colony in Patagonia. Wilson Bull. 109: 650–662.

Tenaza, R. 1971. Behavior and nesting success relative to nest location in Adélie penguins (*Pygoscelis adeliae*). Condor 73: 81–92.

Urrutia, L. P., & H. Drummond. 1990. Brood reduction and parental infanticide in Heermann's Gull. Auk 107: 772–794.

Velando, A., & J. Freire. How general is the central-periphery distribution among seabird colonies? Nest spatial pattern in the European Shag. Condor 103: 544–554.

Varela, S. A. M., E. Danchin, & R. H. Wagner. 2007. Does predation select for or against avian coloniality? A comparative analysis. J. Evol. Biol. 20: 1490–1503.

Wagner, R. W., E. Danchin, T. Boulinier, & F. Helfenstein. 2000. Colonies as byproducts of commodity selection. Behav. Ecol. 11: 572–573.

Whittam, R. M., & M. Leonard. 1999. Predation and breeding success in roseate terns (*Sterna dougallii*). Can. J. Zool. 77: 851–856.

Wittenberger, J. F., & G. L. J. Hunt. 1985. The adaptive significance of coloniality in birds. Pp. 1–78 *in* Farner, D. S., J. R. King, & K. C. Parkes (eds). Avian biology. Academic Press, New York, New York, USA.

Yorio, P., & F. Quintana. 1997. Predation by Kelp Gulls *Larus dominicanus* at a mixed-species colony of Royal and Cayenne Terns *Sterna maxima* and *S. eurygnatha* in Patagonia. Ibis 139: 536–541.