WESTERN BIRDS

Volume 39, Number 2, 2008

NEST SPACING IN ELEGANT TERNS: HEXAGONAL PACKING REVISITED

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ABSTRACT: Within an important breeding colony in southern California, Elegant Terns (*Thalasseus elegans*) nest in one to several tightly packed clusters. Inter-nest distances within these clusters average 31.2 cm. This value is less than that reported for the larger-bodied Royal Tern (*T. maximus*) and Great Crested Tern (*T. bergii*). For Elegant Terns, the modal number of adjacent nests was six (range 5–7). This type of nest arrangement has been previously described as hexagonal packing and now appears to be typical of all *Thalasseus* terns for which data are available.

Many seabirds nest in large, often traditional, colonies (Coulson 2002, Schreiber and Burger 2002). The ontogeny of annual colony formation has been reviewed by Kharitonov and Siegel-Causey (1988), and the evolutionary processes which have led to coloniality have been considered by a number of authors (Lack 1968, Fischer and Lockley 1974, Wittenburger and Hunt 1985, Siegel-Causey and Kharitonov 1990, Coulson 2002).

Seabird colonies may be rather loosely organized aggregations of breeding pairs of one to several species at a single site. At the other extreme, they may be dense, tightly packed, largely monospecific clusters where distances between nests are minimal. A graphic example of the latter is the dense clustering of nests recorded for several species of crested terns (Buckley and Buckley 1972, 2002, Hulsman 1977, Veen 1977, Symens and Evans 1993, Burness et al. 1999, Shealer 1999) currently included in the genus *Thalasseus* (Bridge et al. 2005, AOU 2006).

In their detailed analysis of the nest spacing of the Royal Tern (*Thalasseus maximus*) Buckley and Buckley (1977) determined that densities had been nearly maximized. In most cases individual nests were surrounded by, and in direct contact with, six neighboring nests as predicted by the theory of Voronoi polygons and represented hexagonal packing (Buckley and Buckley 1977, 2002).

The data for other species of crested terns are, however, somewhat disparate in that some authors have reported only nest densities (nests/m^2;

Hulsman 1977, Suter 1986, Symens and Evans 1993, Meininger et al. 1994), nest area (m^2; K. Hulsman in Cramp 1985), or inter-nest distances (nest rim to nest rim [Shealer pers. comm.] or nest center to nest center [Stirling et al. 1970, K. Hulsman in Cramp 1985, this study]). We report here data on nest spacing in an additional crested tern, the Elegant Tern (*T. elegans*).

We made three predictions: (1) since the distance between nests seems dictated by the distance a bird can stretch its neck and lunge at a neighbor (Buckley and Buckley 1972), these distances should be smaller in the smaller crested terns, including the Elegant, with shorter bills and greater in the larger species such as the Royal and Great Crested (*T. bergii*); (2) the modal number of bordering nests should be 6, as predicted by hexagonal packing; and (3) since hexagonal packing maximizes density, there should be no significant difference in inter-nest distances between peripheral nests and nests located more centrally within the colony.

METHODS

We measured distances between nests of Elegant Terns in 1996 and 2001 at the Bolsa Chica State Ecological Reserve in coastal southern California, where the species has nested since 1987 (Collins et al. 1991, Collins 2006a). In both years, Elegant Tern nests were in one to several separate tightly packed clusters (Figure 1) on a 1.7-ha man-made sand island also used by Caspian Terns (*Hydroprogne caspia*; Collins 2006b), Royal Terns, Forster's Terns (*Sterna forsteri*), and Black Skimmers (*Rynchops niger*).

Figure 1. Cluster of nesting Elegant Terns on North Island, Bolsa Chica State Ecological Reserve, Orange County, California, 1996.

Photo by C. T. Collins

The few Royal Tern nests were generally mixed among those of the Elegant Terns, providing us the opportunity to measure distances between nests of two Elegant Terns, between an Elegant and a Royal Tern, and between two Royal Terns. We used a metric tape measure and recorded the results to the nearest 1.0 cm. We repeated these measurements in 2001 to look for year-to-year differences. We categorized the measurements as from peripheral nests (<1 m from edge of nest cluster) or central nests (>2 m from edge of nest cluster); all measurements were of different pairs of eggs chosen at random. In addition, we analyzed ten focal nests by choosing a nest at random and measuring the distance to each of the six adjoining nests. All measurements were made from the center of the egg in one nest to the center of the egg in the neighboring nest. We determined the number of adjoining nests for a sample of 138 randomly chosen nests representing both peripheral and central areas in both small (< 300 nests) and large (>500 nests) clusters of nests. We used Mann–Whitney tests in all comparisons of inter-nest distances.

RESULTS

In 1996, the mean distance between nests in randomly chosen pairs of peripheral Elegant Tern nests (30.8 cm ± 4.3 cm standard deviation, n = 38) did not differ signifcantly from that of central nests (31.4 ± 4.4 cm, n = 16) (W = 1025.5, p = 0.7). Neither did it differ from the mean distance in a sample (30.7 ± 2.6 cm, n = 39) measured in 2001 in which peripheral and central nests were pooled (W = 2519.5, p = 0.9). Similarly, the mean distances of the six adjacent nests from each of the ten focal nests were not different from each other and the distances between randomly chosen nests; the pooled value for all recorded inter-nest distances of Elegant Terns was 31.2 ± 4.1 cm, n = 153, range 22–42). The mean distance between Elegant Tern nests and those of neighboring Royal Terns (6 measured in 1996, 6 in 2001) was 33.9 ±3.3 cm, n = 12, range 30–40). The distance between two Royal Tern nests (2 measured in 1996, 5 in 2001) at Bolsa Chica was 36.6 ± 3.2 cm, n = 7).

For the Elegant Tern, the modal number of neighboring nests for any given nest (n = 138) was 6 (95 nests) and ranged from 5 (23 nests) to 7 (20 nests). In the comparison between large and small clusters of nests there was no difference in the number of neighboring nests. Neither was there a difference in this number between nests peripheral or central in a cluster. We excluded nests on the outer edge of clusters as they lacked neighbors on all sides.

DISCUSSION

The mean inter-nest distance of 31.2 cm for Elegant Terns in our study is smaller than the 37 cm previously reported for Royal Terns (Buckley and Buckley 1977) and the 36.6 cm for Royal Terns we found at Bolsa Chica. These results support our first prediction based on differences in body size (Burness et al. 1999, Buckley and Buckley 2002). That the mean distance between an Elegant Tern nest and an adjoining Royal Tern nest was intermediate between those for nests of conspecific pairs of Elegant or Royal Tern nests also supports this prediction. Despite this apparent trend, regression analyses of three measures of size (culmen length, wing length, and body weight) in several species of crested terns against reported inter-nest distances failed to show any significant relationships ($R^2 = 15.8–28.2$, $p = 0.09–0.23$, A. del Nevo pers. comm.). This may be due to the small sample of data available and some possible variation in the way the data were collected. The extremely low inter-nest distances previously reported for the Sandwich Tern (*T. sandvicensis*) (24.8 ± 12.6 cm; Shealer 1999) were actually measurements made from nest rim to nest rim (D. Shealer pers. comm.) rather than from the centers of the nests, the method we used at Bolsa Chica.

We found support for our second prediction in the modal number of adjacent nests (6; Figure 2), indicating that Elegant Terns provide an additional example of the hexagonal packing previously reported for Royal Terns (Buckley and Buckley 1977). The observed lack of difference in inter-nest distance between peripheral and central nests indicates that this hexagonal packing is minimizing these distances, supporting our third prediction.

Although our study of Elegant Terns revealed no apparent difference in inter-nest distance in clusters of differing size or from year to year, this constancy does not seem to prevail in other crested terns. In the Lesser Crested Tern (*T. bengalensis*) nest densities, and hence inter-nest distances, vary considerably with nests sometimes being rather loosely spaced and other times tightly packed (Hulsman 1977, P. Symens pers. comm.). L. Nicholson (pers. comm.) found much larger inter-nest distances (51.6 ± 16.4 cm, $n = 58$) in a mixed colony of Lesser Crested and Great Crested Terns (*T. bergii*) on Abutilon Island, Australia; 27% of these distances were ≥60 cm. Elsewhere, densities of

Figure 2. Nests and eggs of Elegant Terns on North Island, Bolsa Chica State Ecological Reserve, Orange County, California, 1993.

Photo by C. T. Collins

Lesser Crested Terns appear significantly higher in areas where nesting space is limited than in areas with more extensive open areas available for nesting. They also seem to be greater in larger colonies (>10,000 pairs) than in smaller colonies (<200–300 pairs; P. Symens pers. comm.). In the Netherlands, Veen (1977) found most Sandwich Tern nests to be tightly packed with 54.7% of the inter-nest distances falling in the 31–40-cm range but some being more loosely spaced, with some up to 80–100 cm and 9.7% being ≥60 cm.

The tight clustering of nests is widely thought to be, in part, an antipredator behavior, mutual defense decreasing losses of eggs and chicks to predators, particularly gulls. As noted by Hulsman (1977), Great Crested Terns in the center of nesting clusters help defend the eggs of neighbors from Silver Gulls (*Larus novaehollandiae*). On the periphery, the "gulls were unhampered by terns when dealing with an unattended nest because nests were far apart" (Hulsman 1977). In Sandwich Terns, hatching success is higher in older birds, which also tend to be early breeders with nests in the more densely packed central portions of the colony (Veen 1977).

If predators, particularly gulls, exert strong influence on nest spacing we might expect hexagonal packing (inter-nest distances of 30–40 cm, as we measured) to be characteristic where predation is most intense and more loosely placed nests (inter-nest distances >50 cm) to be more typical where predation is reduced or minimal. This expectation is not met in all cases. Even where gull predation is intense nests may be widely spaced (Hulsman 1977, Veen 1977, L. Nicholson pers comm.). On the other hand, in most years at Bolsa Chica Elegant Terns face only a minimal threat of predation from gulls (pers. obs.) but still have uniformly tightly packed nests. This behavior may be an evolved response to the more intense predation pressure the species typically faces from Heermann's Gull (*L. heermanni*) at its principal nesting colony at Isla Rasa in the Gulf of California, Mexico (Burness et al. 1999, Velarde et al. 2005). On the island of Aruba Cayenne Terns (*T. sandvicensis eurygnatha*) have uniformly tightly packed nests and also face intense predation pressure from Laughing Gulls (*L. atricilla*), which are quick to grab an undefended egg (A. del Nevo pers. comm.).

The risk of predation could also influence the spacing of nests within clusters. Terns nesting on the periphery of nesting clusters are seemingly at the highest risk (Fischer and Lockley 1974, Hulsman 1977, Veen 1977) and might be expected to "crowd in," decreasing inter-nest distances. As noted earlier, our data did not support this hypothesis. The opposite seems true for Great Crested Terns in Australia, among which inter-nest distances tend to be less for central nests (31.4 ±4.9 cm, n = 59) than for edge nests (32.5 ± 5.0 cm, n = 43), although these differences are small and apparently not statistically significant (Stirling et al. 1970). The risk of predation and its effect on nest spacing may vary with the type of predator and prey species. In a more loosely packed colony of Least Terns (*Sternula antillarum*) predation by Black-crowned Night Herons (*Nycticorax nycticorax*) was most intense in the central area, while predation by American Crows (*Corvus brachyrhynchos*) was restricted to the periphery (Brunton 1997). In mixed colonies of Cayenne and Royal Terns, Kelp Gulls (*L. dominicanus)* were more successful in preying on the eggs of the smaller-bodied Cayenne Terns, whereas the larger-bodied Royal Terns could defend their eggs more efficiently (Yorio and Quintana 1997).

Additional studies are needed to clarify the selective pressures influencing inter-nest distances in crested terns and other colonial seabirds. Of particular value will be observations of banded birds whose age and past breeding experience are known and can be related to behavioral decisions made with respect to the degree of nest dispersion and hexagonal packing.

ACKNOWLEDGMENTS

Permission to conduct studies at Bolsa Chica State Ecological Reserve was granted by the California Department of Fish and Game. We are indebted to the several biologists working on other crested terns who have shared unpublished information: A. del Nevo, P. Symens, L. Nicholson, D. Shealer, and K. Hulsman. A. del Nevo and K. Molina provided invaluable statistical analyses. Comments from K. Molina, S. Emslie, and an anonymous reviewer improved earlier drafts of this paper.

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Accepted 22 February 2008