HEXAGONAL PACKING OF ROYAL TERN NESTS

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ABSTRACT.—Observed nest density as well as nearest-neighbor internest distances in a colony of Royal Terns on the southeastern U.S. coast demonstrate that the species has achieved an exceedingly close approach to maximal or hexagonal packing of its nests, probably the first firm demonstration of this effect in any aspect of a vertebrate social system. Various formulas for calculating both deviations from randomness and approaches toward hexagonality are discussed, using data in the form of nearest-neighbor distances, or in the form of nest density per unit area. The biological significance of Royal Terns' hexagonal nest packing is related to the species' high degree of sociality and low levels of aggression, and while observed predation on them at nesting time seems limited to egg-stealing (heaviest on the colony periphery), it is likely that the high nest density demonstrated here did evolve originally in response to just this sort of peripheral predation, synergistically magnified by the species' colony site choice of tiny shoals and sand bars with drastically reduced spaces for nesting.—*North Atlantic Regional Office, National Park Service, 150 Causeway Street, Boston, Massachusetts 02114, and Manomet Bird Observatory, Manomet, Massachusetts 02345.*
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DURING investigations of extreme ecological and behavioral adaptations shown by the breeding cycles of Royal Terns (*Sterna m. maxima*) in coastal Virginia and North Carolina, we became aware that, in addition to having a single egg clutch, Royal Terns pack their nests very closely together, with an average internest distance of only 0.370 m and nest densities on the order of 7.5/m^2 (Buckley and Buckley 1970, 1972a, 1972b, 1974, 1976). In the course of measuring internest distances, we noticed a high incidence of individual nests surrounded by and sharing a feces-covered, slightly raised nest rim with six other immediately adjacent nests (Fig. 1). A timely paper (Grant 1968) describing "polyhedral" territories in an arctic shorebird (*Calidris melanotos*) called our attention to the significance of our observation, although it soon became apparent that the mathematical description of so-called hexagonal packing is far more complex than Grant (1968) indicated.

In addition to demonstrating the occurrence of hexagonal packing of nests of one species of seabird and the probably responsible selective factors, it is our purpose here to point out some mathematical techniques (and their limitations) used in the detection of varying degrees of randomness and orderliness in the packing of natural objects. Spatial distribution patterns have rarely been investigated and probably never conclusively demonstrated in vertebrates (Thompson 1952, Grant 1968, Barlow 1974), perhaps because the pertinent literature is scattered among such disparate disciplines as botany, geology, communications theory, statistics, entomology, and animal behavior, and because certain crucial theoretical facts have not been incorporated into prior analyses.

THEORETICAL CONSIDERATIONS

D'Arcy Thompson's classic book (1952) devoted extensive space to the natural packing of round or malleable objects, especially maximal or hexagonal packing, and notwithstanding recent, highly significant theoretical advances, we found this to be an imperative starting place. Despite his otherwise creditable condensation of Thompson's (1961) book, Bonner removed virtually all discussion of hexagonal packing from his version, so the original is to be preferred.

Before considering hexagonal packing of objects, one must know what obtains at

Fig. 1. Closely packed nests in a functional Royal Tern colony illustrating shared, feces-covered nest rims and distribution pattern.

the other extreme, namely, a random distribution of objects—best examined by considering a series of polygons generated by a Poisson-point process that allows polygons to grow outward from the center points until meeting other polygons on all sides, stopping growth. The resulting figures, called Voronoi polygons, have several interesting properties, most important being an average number of six sides (that is they are generally hexagonal), and although the modal class size is also six, pentagons are almost equally frequent, at least in randomly generated, computer-drawn sets (Coxeter 1969, Hamilton 1971, Crain 1972). Despite intensive investigation by workers in a variety of fields, little is known about the mathematical and statistical properties of Voronoi polygons. For example (1) the theoretical probabilities of oc-

TABLE 1

FORMULAS ALLOWING CALCULATION OF EXPECTED VALUES UNDER CONDITIONS OF RANDOM DISTRIBUTION OR OF HEXAGONAL PACKING

	Density	Nearest-neighbor distances
Random distribution	$r = \sqrt{\frac{0.2500}{m}}$ [1] (Southwood 1966)	$m = \frac{1}{4\bar{r}^2}$ [2] (Southwood 1966)
Hexagonal packing	$r = \sqrt{\frac{2}{m\sqrt{3}}}$ [3] (Southwood 1966)	$m = \frac{2}{\bar{r}^2\sqrt{3}}$ [4] (J. M. Cullen pers. comm.)

[where $\bar{r}$ = individual nearest-neighbor distances (tern data: 0.370 = $\bar{r}$) and m = density/unit area (tern data: 7.5/m^2 = m)]

	Expected results	Observed data
Density method		
Equation [1]	0.183 m	0.370 m
Equation [3]	0.392 m	
Nearest-neighbor method		
Equation [2]	1.83 birds/m^2	7.50 birds/m^2
Equation [4]	8.44 birds/m^2	

currence of the various-sided polygons are unknown; (2) the theoretical probability distributions of perimeter lengths, polygonal areas, and distances from one polygon center to another are also unknown, as is, obviously, the average length of a single side in any class of polygons; (3) theoretical variances for all such quantities, except total area, are unknown, but so is the theoretical variance about the known mean number of sides (six) of *n* randomly generated polygons. So even though much is still unknown about them and even though hexagonal packing is the result of an unimpeded tendency toward maximal density of round or malleable objects—whether steel shot, crystals, bird nests, or beehive cells—one might legitimately ask: Is it sufficient proof of hexagonal packing merely to demonstrate, as Grant (1968) and Barlow (1974) did, that six was the mean number of sides of some naturally occurring polygon series? The answer is no. Let us examine the problem in the light of our own data.

DATA AND ANALYSIS

Considering living organisms here, two major conditions are possible relative to their distribution in planar space: they can be randomly or nonrandomly distributed vis-à-vis one another. Further, nonrandomness can be subdivided into, at extremes, clustering (clumping and aggregating are equivalent terms) and perfectly even spacing but at maximal density—hexagonal packing. Tests for deviations from the random condition have been developed by dendrologists and entomologists in particular, and are summarized in two ecological field methods textbooks (Greig-Smith 1964, Southwood 1966), and a particularly important extension (Campbell and Clark 1971). Discussions in these works deal more with the interactions between point sources such as trees and insects, but by extension impinge directly on Voronoi polygons and the concept of hexagonal packing, as each point source can be considered extending outward until it meets adjacent units, forming polygons.

TABLE 2

FIELD COUNTS OF DISTANCES OF NEAREST-NEIGHBOR NESTS TO SUBJECT (CENTRAL) NESTS[1]

No. adjacent/ shared-wall nests	Nearest-neighbor distances (m) from each subject nest	No. nests in class	Mean nearest-neighbor distance (m)
4	0.395, 0.410, 0.380, 0.420, 0.360	5	0.393
5	0.380, 0.395, 0.380, 0.380, 0.370, 0.380, 0.315, 0.340, 0.375, 0.390, 0.350, 0.340	12	0.366
6	0.385, 0.400, 0.380, 0.365, 0.330, 0.390, 0.310, 0.410, 0.345, 0.340, 0.380, 0.355, 0.335, 0.315, 0.355, 0.360, 0.375, 0.345	18	0.360
7	0.360, 0.350, 0.440	3	0.383
8	0.410, 0.420	2	0.415
$\bar{X} = 5.7 \pm 0.3$[2]	0.370 ± 0.009[2]	$\Sigma = 40$	

[1] Data are grouped according to the number of nests sharing a common wall with the subject nest. See text for additional discussion.

[2] 95% confidence interval.

Two methods most traditionally used for investigating departures from randomness usually measure either density per unit area or some distance between points. That measurement of the distance to the single neighbor nearest the subject allows greatest objectivity seems generally agreed, and most statistics have made use of those data. Table 1 indicates formulae that allow calculation of the expected values of either density or mean nearest-neighbor distance under two conditions: (1) randomness and (2) regularity at maximal density (i.e. hexagonal packing). Royal Tern internest data inserted into these formulae were derived from measurements summarized in Table 2; nest densities were obtained by placing square meter grids so that they included the greatest number of nests in 50 sample plots, each of which was located well away from the edge of the single colony tested (Buckley and Buckley 1972a); internest distances were measured from 40 randomly chosen, nonperipheral central (or subject) nests. The observed values, whether for internest distances or for density, are exceedingly close to those predicted under conditions of hexagonal packing. Thus Thompson's test of Royal Tern data for significant deviation from density values predicted under random conditions (Campbell and Clark 1971) yielded $\chi^2 = 260.3$, 80 df, $P < 0.005$. But what of tests for significant deviations from density values obtaining under conditions of hexagonal packing? At first sight, the question seems reasonable, until one realizes that the hexagonal packing described in the formulae of Table 1 is perfect hexagonal packing, as in beehive cells: this would be obvious on inspection, and tests or counts of any sort would be superfluous. We know from our field observations that the colony contained small patches of hexagonally packed nests. This plus the close approximation of observed to expected values confirms that, while the condition has not been fully attained, such might only be due to occasional clusters of beach grasses (*Ammophila* and *Uniola*) and pieces of wrack, or to minor topographical irregularities: the colony site is almost never absolutely flat, and is often atop dredge islands. (Campbell and Clark (1971) discuss several other tests that can be done on these and similar data, tests not only sensitive

TABLE 3

FREQUENCY COUNTS AND RELATIVE PERCENTAGES OF n-SIDED POLYGONS GENERATED RANDOMLY, AND FROM EXAMINATION OF ROYAL TERN NESTS

	Random Voronoi polygons		Royal Tern nests	
Number of sides	Observed frequency	% frequency	Observed frequency	Expected frequency[1]
4 or less	1340	12.1	4.0	4.8
5	2846	25.9	13.0	10.4
6	3172	28.8	18.0	11.5
7	2266	20.6	3.0	8.3
8 or more	1376	12.5	2.0	5.0
	11000	100.0	40.0	40.0

[1] Based on Voronoi polygons.

to deviations from randomness but in addition to whether the nonrandom trend is toward aggregation or toward hexagonal packing.)

If the data as originally obtained are of a third sort—in the form of different polygon frequency counts (in our case the polygons being the nests whose centers were used as end points for internest distance measurements), the lack of information about predicted, theoretical parameters of Voronoi polygons limits analysis to some degree. Crain (1972) generated 11,000 Voronoi polygons (so far, out of a projected 100,000), and while he has not yet been able to derive formulae for the prediction of most parameters, some of his empirically derived data can be used as standards for comparison to our data. Table 3 gives frequency counts for the number of sides in his polygons and their percentages; below are similar data with a more modest n (= 40) taken by us in one Royal Tern colony. Considering his frequencies to be reasonable approximations of the expected random condition (cf. similar random frequencies with an $n = 376$ (Hamilton 1971)) one may do a G goodness-of-fit test (Sokol and Rohlf 1969) on our observed class frequency distribution, with the null hypothesis being no difference between random (expected) and observed frequency distributions. For these two sets of data, this yielded a significant difference (G = 10.754; 4 df; $P < 0.05$).

Fig. 2 graphs the class percentages of the two sets of data, emphasizing the difference. While there may indeed be a common modal class of six-sided figures, the spread of values in the real situation is far less than in the computer-generated, random one. Indeed, this indicates that once the theoretical variance of the number of sides is known, a simple F-test of variance would answer the question more easily than goodness-of-fit tests of frequency distribution, although this robust test properly requires a normal distribution of numbers of sides.

Another important difference between randomly generated Voronoi polygons and regular hexagons, apparently not commented on by previous authors, is side length: it is constant in regular hexagons but varies enormously in Voronoi polygons (Fig. 3). A similar F-test could be made if the variance of Voronoi polygon side length were known. We should add that we did not measure side length of our tern nest rims, but field impressions indicated no approximation whatever to Voronoi sides (compare Figs. 1 and 3).

A fourth technique that both we and W. D. Hamilton (pers. comm.) independently deduced would involve measuring distances from one subject nest center to the centers of all other nests in the colony. In a situation of perfect hexagonal packing

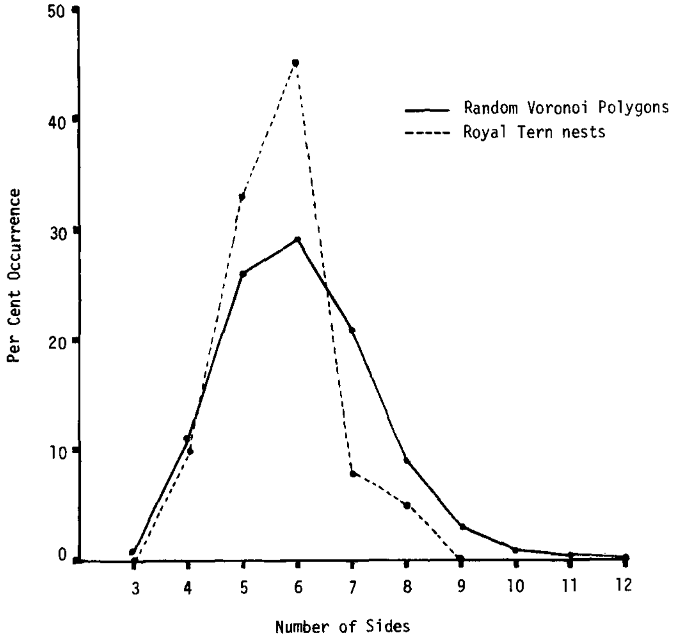

Fig. 2. Frequency distribution polygons for number of sides of randomly generated Voronoi polygons (from Crain 1972) and of Royal Tern nests.

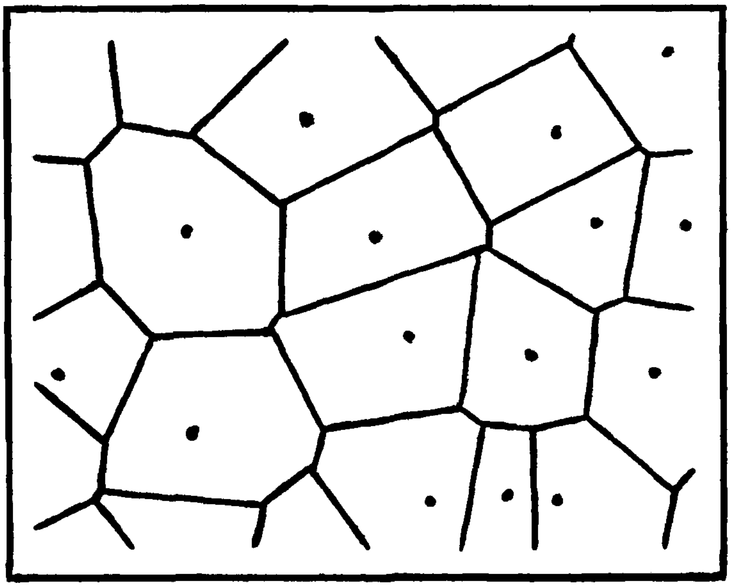

Fig. 3. Typical realization of randomly generated Voronoi polygons (from Crain 1972).

Fig. 4. Nest density and proximity of incubating adults in typical Royal Tern colony.

this testing would hardly be necessary, but for heuristic purposes, it would yield the following series of measurements: the first six distances (*d*) would be all the same—to the six nests immediately surrounding the subject nest (1st order nests); then would come a run of 12 measurements varying between $2d$ and 2 (cos $30° \cdot d$), representing the next set of nests surrounding the first six (2nd order nests); followed by a third series of 18 measurements varying between $3d$ and 3 (cos $30° \cdot d$); each higher order *n* increasing by six nests and each set of grouped measurements increasing in the manner indicated. One might compare observed measurements to these expected measurements for some degree of previously chosen, acceptable departure from the maximal condition of full hexagonal packing, but we have not pursued the techniques here because theoretical values for too many parameters of Voronoi polygons are still unknown.

CONCLUSION

Despite patches of irregularity, Royal Terns seem to have generally achieved almost perfect hexagonal packing of their nests and indeed have done so in very small parts of the colony. The nest scoops whose planar distribution is examined here constitute their only defended areas or territories, maintained by the incubating or brooding adults reaching out and lunging at their neighbors.

One might wonder if there is any relationship between (a) the distance from a subject nest to its nearest neighbor and (b) the number of neighbors around the subject nest. The spread of distance values and their means (Table 2) suggest little relationship of this sort, confirmed by subjecting the data to product-moment correlation analysis: $r = 0.03$, $r^2 = 0.0009$, not significantly different from zero. Thus the relationship between distance to nearest neighbor and number of neighbors is totally random. If all birds had essentially the same levels of aggression or tolerance of neighbors, one would predict total hexagonal packing as in a beehive. If there were several clear-cut classes of aggressive birds (morphs), one would predict, for example, that all five-neighbor nests would have the largest (and uniform) nearest-neighbor distance; a smaller value, also uniform, would obtain for all six-neighbor nests; and so forth. These are clearly not occurring, and one must conclude that individual differences in aggression/tolerence are responsible for the variation, and—in conjunction with minor topographical irregularities—for the failure of the colony to achieve total, uniform hexagonal packing.

Thus, given present aggressive levels and normal topographic variation, nesting Royal Terns seem to be packed together as densely as they can be. Only by reducing their aggression—already minimal compared to the other normally mercurial tern species—could they reduce their internest distances, and then by very little inasmuch as they are already practically touching one another (Fig. 4). Thus nest density is but another manifestation of the extreme gregariousness of the species, also evident in their dense creches, strong parent-young bonds, and winter-ground roosting and feeding behavior (Buckley and Buckley 1976).

It is likely that such a high nesting density evolved as a consequence of two major selective pressures: (1) the species' habit of locating its colonies on quadruped-free, bare sand islands near, at, or in the middle of inlets, which often forces them to tiny sandbars and shoals with only minimal areas above mean high water suitable for nest sites; and (2) extreme egg predation, especially by Laughing Gulls (*Larus atricilla*), on the periphery of the colony (Buckley and Buckley 1972a). Both these forces should lead to increasingly denser colonies, the density eventually peaking when the incubating birds cannot physically come much closer to each other. We feel this point has probably been reached in the Royal Terns' evolution. Hamilton (1971) presents an elegant discussion of the general problems faced by animals occurring in open spaces, and the reader is referred there for further information.

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