

## Correct calculation of Dirichlet polygon areas

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In a planar field with many stationary objects, a mosaic of polygons can be drawn or tessellated whose network of boundaries are the set of points that are equally close to two or more nearby objects. Each polygon region, called a Dirichlet cell, contains all points that are closer to an object than to any other objects in the field (Green & Sibson 1978). The Dirichlet cell, first proposed in 1850, has been useful in many scientific disciplines and thus is known under a variety of names including Voronoi, 1909, Thiessen, 1911, Wigner-Seitz, 1933, cell model, 1953, and S-mosaic, 1977 (Rogers 1964; Mead 1971; Rhynsburger 1973; Upton & Fingleton 1985; David 1988). More recently, a Dirichlet tessellation algorithm was developed to define colonization territories of bark beetles (Coleoptera: Scolytidae) under the bark of host trees (Byers 1992). In addition, simulations of point patterns at increasing spatial uniformity resulted in a decrease in the variation of Dirichlet cell areas. Based on this relationship, a method was formulated that estimated a minimum allowed distance (MAD) of spacing between the attack holes of individual bark beetles. The results suggested that several species of bark beetle can reduce competition by not boring in areas closer than their species-specific distance from neighbouring attack sites.

Unfortunately, the program for drawing Dirichlet tessellations (Byers 1992) does not calculate the polygon areas correctly. The program draws the polygons and calculates average nearest neighbour distances appropriately. However, calculations of the area of a Dirichlet cell are undervalued by about 10–30%. The calculation of the Dirichlet area (always a convex polygon) is done by finding the cell's centre  $x_c, y_c$  (average of  $x, y$  coordinate values) and then sorting the vertices of the polygon by angle. The cell area is then the summed area of all triangles occurring between the centre and two successive vertices ( $x_i, y_i$  and  $x_{i+1}, y_{i+1}$ ). The last pair of successive vertices must cause closure (i.e. include the first vertex). Unfortunately, this was not done in the original program so that the area of the 'last' triangle was not added to the sum. The iterative formula for calculation of the area (Byers 1992):

$$A = \sum_{i=1}^k |0.5[x_c(y_i - y_{i+1}) + x_i(y_{i+1} - y_c) + x_{i+1}(y_c - y_i)]|$$

is correct if  $k$  is number of vertices and  $x_{k+1}, y_{k+1}$  are equal to  $x_1, y_1$ .

The relationship between the percentage of maximum point spacing and the CV (coefficient of variation) of cell areas (Fig. 2 in Byers 1992) was largely unaffected by the error since the partial sums of triangular areas varied approximately proportional to the real areas. Thus, the MAD (minimum allowed distance) calculations based on this relationship also were negligibly affected. Simulations according to the previous methods but using the corrected cell areas gave a curve similar to that reported earlier. The revised cubic equation is:

$$Y = 0.0000739X^3 - 0.01301X^2 + 0.043734X + 51.9243$$

with  $r^2 = 0.999$ . The new version of the program uses this equation to calculate the MAD for a population of objects.

Fortunately, the biological conclusions in Byers (1992) are still valid because a reanalysis of the spatial attack data gave a MAD for *Dendroctonus brevicomis* of 1.9 cm (0.2–6 cm, 95% CI, CV = 44.76%) that is close to the 2.0 cm reported earlier (Fig. 4, CV = 48.04). The revised MAD for *Tomicus piniperda* of 4.1 cm (3.9–4.2 cm, CI; CV = 23.71%) is near to the previous 4.3 cm (Fig. 5, CV = 24.46%). In *Pityogenes chalcographus*, the revised MAD of 1.6 cm (1.5–1.7, CI; CV = 27.51%) is identical to the former value (Fig. 6a, CV = 30.28%); while for the random distribution no MAD could be detected (0–0.52 cm, CI; CV = 54.44%) as before (Fig. 6b, CV = 58.76%). The species-specific values for the MADs are not expected to vary with density under endemic population levels (Byers 1984, 1992). However, at low densities and sample size the MAD can be difficult to reliably evaluate.

The revised calculations show that the average colonization territory of a bark beetle family group is actually larger than reported. The revised areas of  $42.07 \pm 6.24 \text{ cm}^2$  ( $\pm 95\%$  CL) for *D. brevicomis* (Fig. 4) is almost the same as  $42.13 \pm 2.95 \text{ cm}^2$  for *T. piniperda* (Fig. 5). This similarity could occur if the two population samples had reached a limiting attack density as a result of similar MADs (as reported above) causing later arriving individuals to leave for lack of free territory. Ultimately, monogamous mating pairs of both species may utilize comparable areas

of the bark because they are closely related species (Hylesininae, Tribe Tomicini), are alike in size (5 mm long, 10 mg fresh weight), and feed on the phloem of similar host trees (Ponderosa and Scots pines, respectively). The colonization territory of *P. chalcographus* (Scolytinae) is smaller at  $8.5 \pm 0.5 \text{ cm}^2$  probably due to the beetle's smaller resource requirements (its size is only 2 mm long, 1 mg weight), although several females may occupy the area with a single male. The same density for a random distribution of points (from Fig. 6b) gave an average cell area of  $8.35 \pm 0.93 \text{ cm}^2$ .

The undervalued cell areas were not discovered sooner because one usually tessellates within an inner border to avoid 'edge effects'. Thus, the total area of the polygons is variable and difficult to verify. However, the program can be used to place 50 points in an area of 100 units on a side, without any inner border, causing the polygons to fill the arena. The average cell area reported with the revised method and these parameters is, as expected, equal to  $100^2/50$  or 200 units.

The corrected version of the Dirichlet program is available by sending a formatted 3.5' or 5' IBM disk to the author. The software also can be downloaded

from the Internet (<http://alysum.stud.slu.se:8001/~johnb/software.html>).

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