ON THE PATTERN OF SPACE DIVISION BY TERRITORIES

Masami Hasegawa and Masaharu Tanemura

Summary

In this paper the tesselation of territories is discussed. When a mass of animals with territoriality is introduced at random simultaneously into a finite two-dimensional (2D) region, territories are gradually formed and finally settle to a steady state. A model calculation for this process is carried out, where a Voronoi polygon is assumed as a territory. Comparisons are made between the model calculation and Barlow's observation on an artificial population of mouthbreeder fish. Differences between 1D and 2D case are also discussed.

1. Introduction

Territorial behaviour is displayed by a wide variety of animals. A term "territory" is defined as an area occupied more or less exclusively by an animal or a group of animals by means of repulsion through overt defense or advertisement against an intruder of the same species (see Wilson [1]). The habitat of such a population is partitioned into territories, and the pattern of partition is affected by the nature of the environment, such as the disposition of trees or rocks. The geometrical pattern of territories in an ideal situation of uniform environment is an interesting problem of mathematical biology.

Grant [2] has mentioned that the tundra should provide such an ideal situation. Through the analysis of Holmes' data [3] on the territories of pectoral sandpipers (*Calidris melanotos*) which breed on the arctic tundra, he has found that at high densities territories are polygonal. Recently, Barlow [4] has observed remarkable polygonal territories formed by male mouthbreeder fish, *Tilapia mossambica*, kept in a large outdoor pool with an initially uniform sand bottom. A territorial male of *T. mossambica* excavates breeding pits by spitting sand away from the pit centre toward his neighbours. As the density of fish increases, reciprocal spitting results in sand parapets, which are conspicuous territorial boundaries, as is schematically shown in Fig. 1. The number of sides of the polygonal territory has a fluctuation around 6.
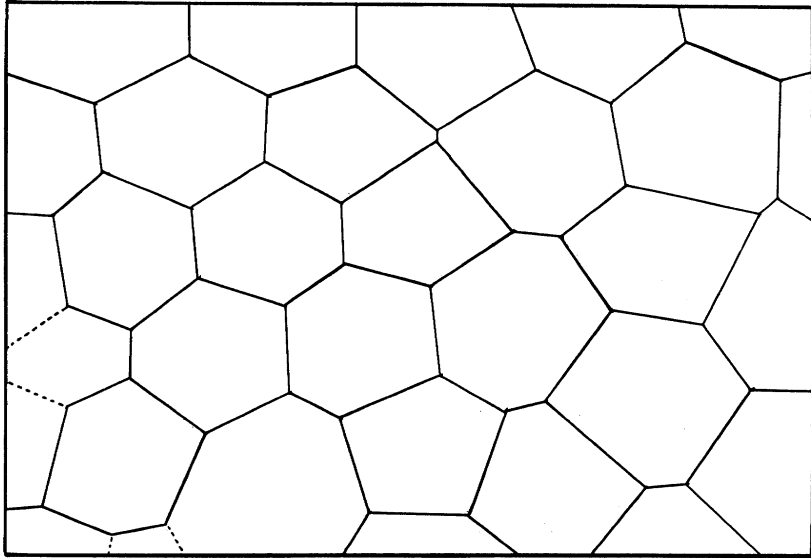
Fig. 1 Schematic diagram of polygonal territories formed by male mouthbreeder fish
(replicated from the photograph in Barlow's paper [4]).

In this paper, we intend to provide a simple behavioural model
which accounts the pattern of polygonal territories.

2. A behavioural model

A simple model of territorial behaviour has been previously pro-
posed by Maynard Smith [5], and we utilize his idea.

An owner of a territory defends the area with an aggressive be-
haviour against an intruder of the same species.   Unless the owner is
ill, he is usually undefeatable by the conspecific intruder at the centre
of his territory.   However, the aggressive tendency and the strength
of the owner decrease monotonically with the distance from the centre
of the territory.   Therefore, in 2-dimensional (2D) case, if all the indi-
viduals are identical in strength, the pressure between two neighbours
balances on the perpendicular bisector between the two centres, and
this line becomes the boundary between the territories (see Lorenz [6]).
In this way the habitat of the population is partitioned into polygons,
which are well known as Voronoi polygons.

Since the territories are two-dimensional in most cases, we restrict
ourselves to a planar model for the moment.   Suppose that a mass of
individuals are introduced simultaneously into a limited area.   Here,
the simultaneity is essential for the territories to be established through
mutual adjustment.   The model for successive introduction will be pre-
sented in a forthcoming paper.   We assume that in the couse of the

establishment of territories, each territory has a centre at any moment, in the sense that its owner exerts equal pressure on all sides of the centre. To each centre a Voronoi polygon is associated, which consists of all the points in the area that are nearer to that centre than to any other. The initial pattern of the arrangement of the centres is supposed to be completely at random. Generally the crowded regions and sparse regions are found here and there in this instant of time. The position of the centre of such a territory is transient and is not fixed in space.

Each individual should have a tendency to occupy his own territory in such a way that he is distant from his neighbours as far as possible. Then the centres are adjusted all together from the initial positions to preferable positions. This is followed by a new adjustment of the boundaries, and the process is continued iteratively until a stationary set of boundaries is achieved. Finally, the centres of the territories become fixed. This may mean nests are going to be built up there.

Maynard Smith has claimed that such a limiting configuration is hexagonal tessellation, the validity of which we want to see in the following. Let us specify our model. We call the territorial animals particles and regard them to be dimensionless. At the initial time step $(t=0)$, N particles are distributed in a square box of side length L. The coordinates of the ith particle at the time $t=n$ are denoted by $x_i^{(n)}$ $(i=1, 2, \cdots, N)$. The number density $\rho = N/L^2$ is supposed to be large enough, so that the stable territories are of polygonal shape, but not so large as something like the dense packing of hard discs. As an initial configuration $\{x_i^{(0)}\}$ we take completely uniform random points in the box. At time n $(n=0, 1, 2, \cdots)$, to each particle $x_i^{(n)}$ we assign a Voronoi region $\Pi_i^{(n)}$, namely, the set of all points x satisfyng

$$(1) \qquad |x - x_i^{(n)}| \leqq |x - x_j^{(n)}| , \qquad (j \neq i)$$

for any other particles $x_i^{(n)}$ than $x_j^{(n)}$ (Rogers [7]). Vertices of the polygon are denoted by $y_i^{(n)}(k)$, for $k=1, \cdots, p_i^{(n)}$, where $p_i^{(n)}$ is the number of its sides. When a configuration of particles is given, the Voronoi polygons $\Pi_i^{(n)}$ divide the space uniquely and we call it " Voronoi division " of space. Throughout our calculations a periodic boundary condition is used. We now define $\Pi_i^{(n)}$ as the " territory " of the ith particle at time n. The repulsive forces among them cause to change the positions of particles to more stable places. We can regard that a particle moves within the territory of the respective moment. Then we choose as the new coordinate at the next time $n+1$

$$(2) \qquad x_i^{(n+1)} = (1/p_i^{(n)}) \sum_{k=1}^{p_i^{(n)}} y_i^{(n)}(k) .$$

When a set of new coordinates of the particles is obtained, we carry out a Voronoi division of the space again, obtaining a new set of coordinates of vertices $\{y_i^{(n+1)}(k), \ k=1, \cdots, p_i^{(n+1)}\}$. The process is iteratively repeated until a stable configuration is obtained. Practically, the quantity $\Delta_{n+1} \equiv (1/N) \sum_{i=1}^{N} |x_i^{(n+1)} - x_i^{(n)}|^2$ may be a measure of the motion of the whole system, and the system can be considered to be actually in equilibrium when the quantity reaches a sufficiently small value. Then a stationary set of boundaries is obtained. In all the runs we performed, the value of Δ_n decreased monotonically after it reached $10^{-4}/\rho$. Hence, the process was stopped at time $m=m_s$ when $\Delta_m \leq 10^{-6}/\rho$ was first attained. A number of series of that process was carried out in the case of $N=200$ and $\rho=1.0$.

In the course of the simulation, we compute in each step geometrical quantities which are associated with Voronoi division, such as number of sides, area, side lengths, interior angles, etc., for each polygon. They are stored on magnetic tapes together with the data of the coordinates of particles and those of vertices ready for statistical analysis.

3. The results and discussions

In this section we present the results of our simulation, and compare them with some experiments and observations on territorial animals. In Fig. 2, two patterns of the Voronoi division of our model are illustrated. The small circle in each polygon represents the position of the particle. Fig. 2 A shows a pattern at an initial time step in which the points are distributed completely at random. The polygons show various types of shape and their areas extend over a wide range. Circles in polygons are often located close to edges, which implies a very unstable configuration for the animals. Fig. 2 B, on the other hand, is one of the final step patterns, which shows considerably uniformly sized polygons, and circles are situated almost at the centre of gravity of each polygon, exhibiting a stable configuration of territories. Now, Figs. 3, 4 and 5 are histograms of number of edges, of area and of interior angles of a polygon, respectively.

In each figure, histograms at the initial time and at the final time are compared. The tendency to the equalization is recognized for area and number of edges from the figures, but, contrary to Maynard Smith who assumed the territories eventually become equally sized regular hexagonals, our results seems to show that the area and the number of edges of polygonal territory asymptotically approach to some definite distributions with finite standard deviations. The same is true for the interior angles which are finally distributed around 120° with a standard deviation of about 12° (Fig. 5 B). These results were corroborated
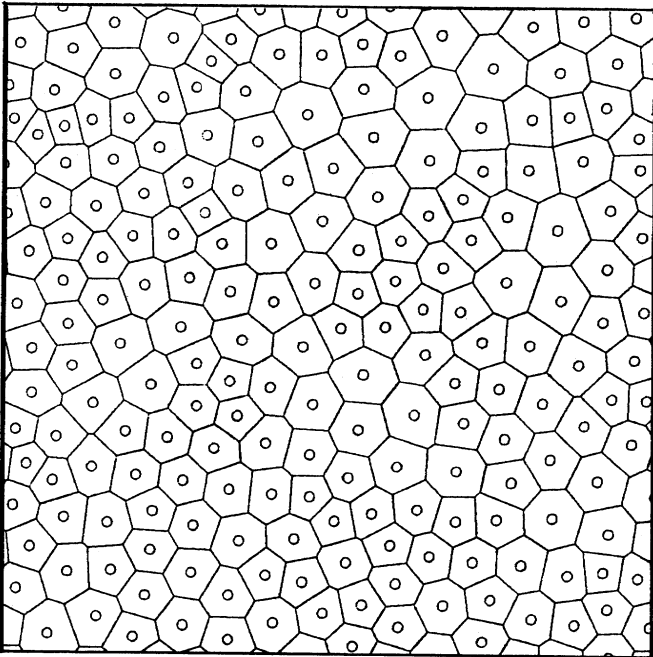
A. $t=0$
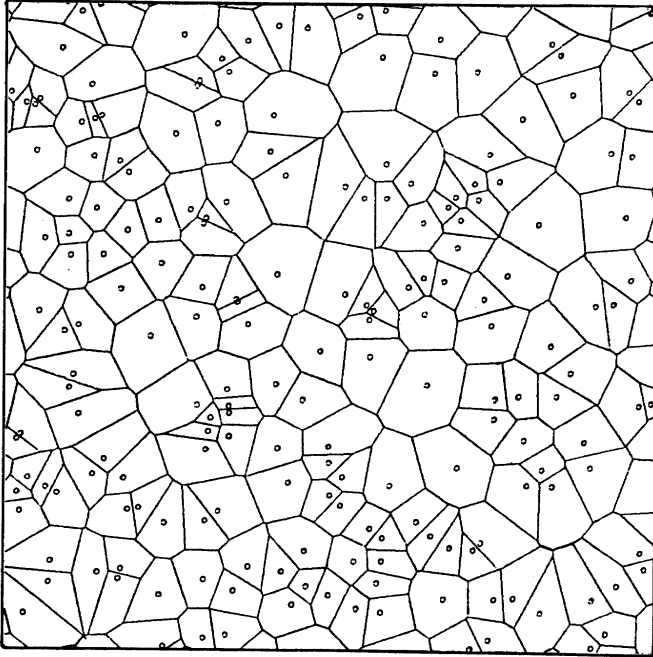
B. $t=m_s$

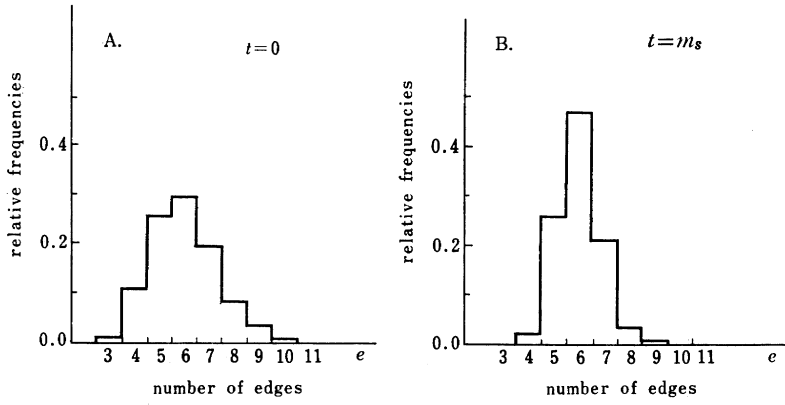Fig. 2 Patterns of Voronoi division obtained by model calculations.
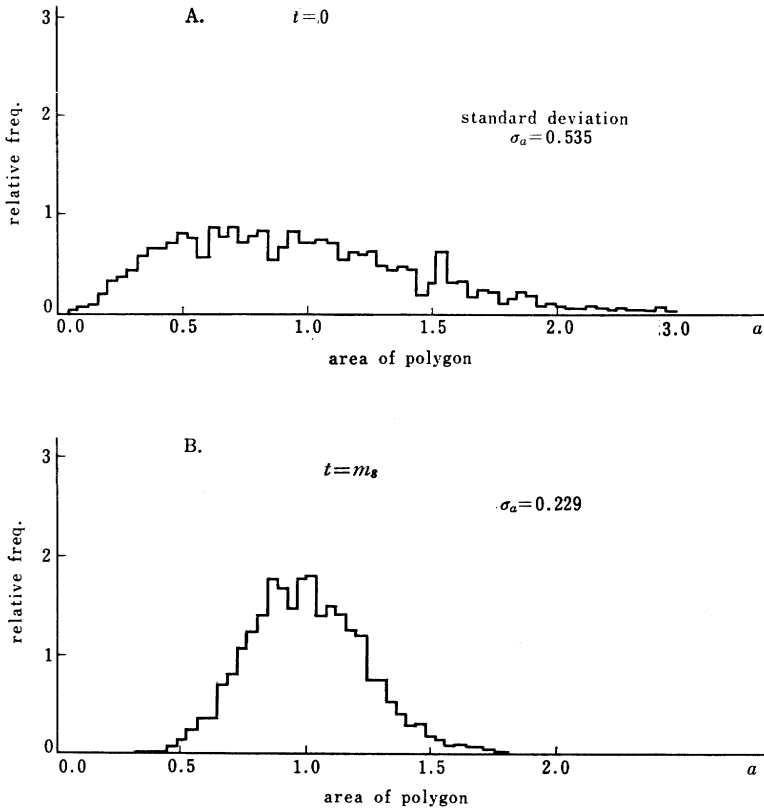
Fig. 3 Histograms of number of edges of polygons.

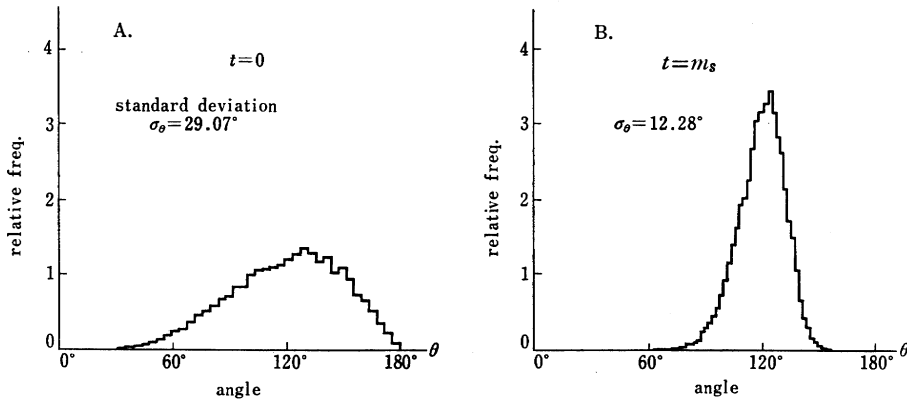Fig. 4 Histograms of area of polygons.

Fig. 5 Histograms of interior angle.

by another series of simulations for $N=500$, the process of which shows nearly the same behaviour and nearly the same distributions of geometrical quantities as in the case of $N=200$. Therefore, the system size dependence seems to be small.

Now we shall compare our results with the observations. Fig. 1 is a schematic drawing of territorial boundaries of males of *Tilapia mossambica* replicated from the photograph in Barlow's paper [4]. From the figure, the number of edges and the interior angles were counted. In Figs. 6 and 7, their distributions are illustrated. The corresponding data are summarized in Tables I and II together with the results of the model calculations. χ^2 test was done for the goodness of fit of the observation against our territorial model on the distributions of the above quantities. At the test of the interior angles we chose as the
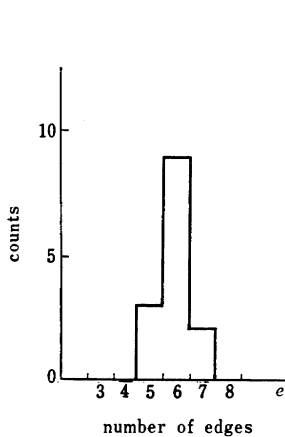

Fig. 6 Histograms of number of edges of territorial boundaries of *T. mossambica* obtained from Fig. 1.
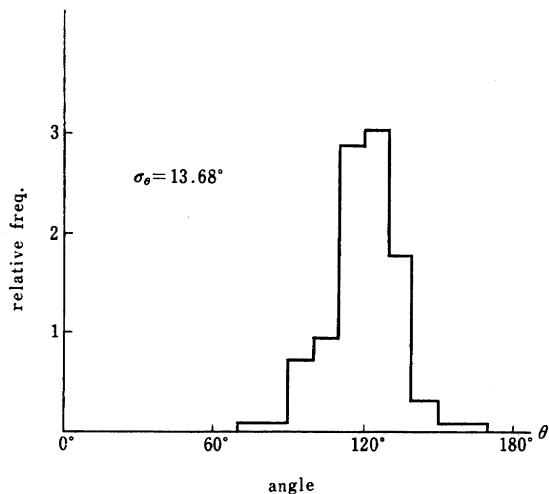
Fig. 7 Histograms of interior angles obtained from Fig. 1.

Table I Counts of number of edges of polygons

e	Males of $T.$ $mossambica$ obtained from Fig. 1	Model at time $t=m_s$ (10 series)*
3	0	0
4	0	44
5	3	515
6	9	934
7	2	422
8	0	74
9	0	11

* The values of m_s vary of course for each of the 10 series
 of run such as 62, 96, 69, 51, 66, 62, 69, 62, 74 and 60.
 But the variances of geometrical quantities among these
 times are very small.

Table II Counts of interior angles ($\Delta\theta=10°$)

$\theta°$	Males of $T.$ $mossambica$ obtained from Fig. 1	Model calculation at time $t=m_s$ (10 series)
50- 60	0	0
- 70	0	3
- 80	1	30
- 90	1	149
-100	9	567
-110	12	1688
-120	37	3194
-130	39	3805
-140	23	2167
-150	4	381
-160	1	16
-170	1	0
-180	0	0

class interval of histogram, $\Delta\theta=8°$ and $10°$ for respective tests, and for each interval two different locations were adopted, i.e., altogether four differents ways. Each test accepted (at 5% level) the null hypothesis that two distributions are identical. With respect to number of edges the test also accepted (at 5% level) the null hypothesis of identical distributions. However, a χ^2 test rejected, at 1% level, the null hypothesis that the observed angle distribution for *Calidris melanotos* is identical to that of our model. Presumably it is because the artificial population of *Tilapia mossambica* is different from the natural population of *Calidris melanotos* in the way of forming territories. With regard to the latter, we shall present a reasonable model in the forthcoming paper.

Next we show that, contrary to the computational results for 2D

case, in 1D space the equilibrium state is uniform, that is, Voronoi regions (Voronoi segments) are all identical and centres are spaced regularly. As in Section 2, we suppose $x_i^{(n)}$ is the coordinate of the ith particle at time n and $y_i^{(n)}(k)$, for $k=1, 2$, are those of edges of Voronoi segment. We consider particles arranged in the order of their number from left to right. Therefore, we can set $y_i^{(n)}(2)=y_{i+1}^{(n)}(1)\equiv y_{i+1}^{(n)}$, and the set of vertices are rewritten as $\{y_i^{(n)}\}$. The set $\{x_i^{(n+1)}\}$ at the next step is obtained similarly as in the 2D case by

$$(3) \qquad x_i^{(n+1)}=\frac{1}{2}(y_i^{(n)}+y_{i+1}^{(n)}) .$$

Then the set $\{y_i^{(n+1)}\}$ is obtained from $\{x_i^{(n+1)}\}$ through Voronoi division. In this way our iterative process for 1D case is specified. We now set $u_i^{(n)}\equiv x_i^{(n)}-x_{i-1}^{(n)}$ as the length of neighbouring pair between $i-1$ and i, and $v_i^{(n)}\equiv y_{i+1}^{(n)}-y_i^{(n)}$ as the length of Voronoi segment of particle i. There are relations between $\{u_i^{(n)}\}$ and $\{v_i^{(n)}\}$ such as

$$(4) \qquad v_i^{(n)}=\frac{1}{2}(u_{i+1}^{(n)}+u_i^{(n)}) , \qquad u_i^{(n+1)}=\frac{1}{2}(v_i^{(n)}+v_{i-1}^{(n)}) .$$

By means of the set $\{u_i^{(0)}\}$ for an initial time, $u_i^{(n+1)}$ and $v_i^{(n+1)}$ can be expressed as

$$(5) \qquad u_i^{(n+1)}=\frac{1}{2^{2n}}\sum_{l=0}^{2n} {}_{2n}C_l u_{i-n+l}^{(0)} , \qquad v_i^{(n+1)}=\frac{1}{2^{2n+1}}\sum_{l=1}^{2n+1} {}_{2n+1}C_l u_{i-n+l+1}^{(0)} .$$

The probability density functions for $u_i^{(n)}$ and $v_i^{(n)}$ are denoted by $f_n(u)$ and $g_n(v)$, respectively. As before, we choose a completely random point distribution for the initial set of coordinates $\{x_i^{(0)}\}$. In the case of an infinite straight line with a fixed number density λ, the series $\{x_i^{(0)}\}$ becomes a Poisson point process and p.d.f. of u becomes $f_0(u)=\lambda e^{-\lambda u}$ ($u\geq 0$). Now we set $\lambda=1$ for simplicity. From eq. (5), which are linear combinations of independent variables of identical distribution, $f_n(u)$ and $g_n(v)$ can be successively obtained. Expectations $\mathrm{E}(U^{(n)})$, $\mathrm{E}(V^{(n)})$ and variances $\mathrm{Var}(U^{(n)})$, $\mathrm{Var}(V^{(n)})$ are directly estimated from (5), as follows;

$$\mathrm{E}(U^{(n)})=\mathrm{E}(V^{(n)})=1 ,$$
$$(6) \qquad \mathrm{Var}(U^{(n)})=2^{-(4n-4)}(4n-4)!/[(2n-2)!]^2$$
$$\mathrm{Var}(V^{(n)})=2^{-(4n-2)}(4n-2)!/[(2n-1)!]^2 .$$

In the limit of $n\to\infty$, $\mathrm{Var}(V^{(n)})$ becomes

$$(7) \qquad \mathrm{Var}(V^{(n)})\sim(\pi(2n-1))^{-1/2}$$

by means of Stirling's formula, and tends to zero. Therefore, the

Voronoi segments tend to equality in our process.

A spacing pattern of starlings on an electric wire will be a good example of this situaion. Immediately after their arrival, the starlings distribute themselves at irregular intervals. In the mean time, the individuals in a crowed region begin to peck each other and then separate. Finally a regular distribution intervals is attained (Lorenz [8]).

Thus we can see a remarkable difference between 1D and 2D cases in the way of establishment of territories.

The idea of the territorial model can be also applied to other systems. Consider, for example, a system of molecules interacting with a short range repulsive potential. If the system is put into a limited region filled with a frictional medium, each molecule moves according to repulsive forces among molecules and finally settles to a steady position by frictional forces of the medium. The resulting pattern of molecules will be such that the total potential energy of the system is as small as possible. Therefore, each molecule will be arranged so as the distances between them are as great as possible. This situation may be the same as in the case of territorial animals.

Note added in proof

In Barlow's paper the number of sides of polygonal territories shows a distribution with a peak at 5 in the whole of his experimental pool. But in the limited region where we have considered, this distribution shows a peak at 6. Barlow informed us this discrepancy with a comment that the region had not been selected as a random sample. In our opinion, the density of individuals is so high that the space is divided by territories without any gap in the region we have considered, but this is not the case in the whole of the pool. And what we would like to consider was a model for the former case, and therefore we used the region of the photograph in his paper. Thanks are due to Prof. G. W. Barlow for his comment in the correspondence with us.

Acknowledgement

THE INSTITUTE OF STATISTICAL MATHEMATICS

References

[1] Wilson, E. O. (1975). *Sociobiology, The New Synthesis*, The Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.

[2] Grant, P. R. (1968). Polyhedral territories of animals, *Amer. Nat.*, **102**, 75-80.

[3] Holmes, R. T. (1966). Breeding ecology and annual cycle adaptations of the red-backed sandpiper (*Calidris alpina*) in northern Alaska, *Condor.*, **68**, 3-46.

[4] Barlow, G. W. (1974). Hexagonal territories, *Anim. Behav.*, **22**, 876-878.

[5] Maynard Smith, J. (1974). *Models in Ecology*, Cambridge Univ. Press, Cambridge.

[6] Lorenz, K. (1949). *Er Redete mit dem Vieh, den Voegeln und den Fischen*, Dr. G. Borotha-Schoeler Verlag, Wien.

[7] Rogers, C. A. (1964). *Packing and Covering*, Cambridge Univ. Press, Cambridge.

[8] Lorenz, K. (1963). *Das sogenannte Boese—Zur Naturgeschichte der Aggression*, Dr. G. Borotha-Schoeler Verlag, Wien.