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March 1974

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## A SAFE APPROACH TO NATURAL HOME RANGES, AS APPLIED TO THE SOLUTION OF EDGE EFFECT SUBJECTS, USING CAPTURE-RECAPTURE DATA IN VOLE POPULATIONS

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ABSTRACT: Capture-recapture work was performed in 1970 and 1971 with *Microtus montebelli* seeking to disclose the edge effect subjects. For the purpose, in principle, it is needful for us to approach the reality of home range in size and shape. As the result of these studies, it has been established that the method using observed range length and width is highly available for searching after natural ranges and that the natural range of the voles (*Microtus* and *Clethrionomys*) is ordinarily on the order of 0.05 for females and of 0.10 for males in acres and generally oblong in shape such as its eccentricity is about 0.80. Several tentative means have been thus far presented for determining the area of effect by sampling, but the process of Dice's assessment line has proved to be most useful in its sureness and simplicity; its empirical validity could be confirmed through mediation of Marten's notion (1972) and Wierzbowska's (1972).

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### INTRODUCTION

Through the last two decades my research of population ecology for small mammals has been focused on basic methodological problems in censusing by means of trapping. These are concerned with: (a) heterogeneous trappability among a population, especially its notable divergence between marked and unmarked animals in the process of capture-recapture; (b) incomplete exposition of a population to traps expected under the plan with too wide trap-spacing; and (c) seeking after natural home ranges in view of size and shape by way of solving the subjects of edge effect to establish the method of density calculation from estimated populations.

In this paper, I shall discuss the third of the above items chiefly on the basis of results of the latest two studies of edge effect (Tanaka, 1972; 1973) with populations of the vole (*Microtus montebelli*) carried out in grasslands within the enclosure of Sugadaira Biological Laboratory in the north of Nagano Prefecture. The overall review of all the items will be published later as one of the final contributions from JIBP-PT.

### O.R.L. AND O.R.W. AS SURE MEASURES OF HOME RANGE

By reference to the results of Stickel (1954) and on the ground of my important study on home range by means of Latin squares (Tanaka, 1961) and the other later studies, I had come to realize reasonability in employing "observed range length" (abbreviated to ORL) of Stickel as reliable measure for seeking after the truth of home range using capture-recapture data.

Afterward I have continued to use ORL in research of home range. By the two studies I have been confirmed in the view that besides ORL, "observed range width" (ORW), which is defined as maximum distance between capture loci measured in the direction perpendicular to ORL, should be used for pursuit of natural ranges on the supposition of its oblong shape lately emphasized by Mazurkiewicz (1971).

As contrasted with the processes for range pursuit by using ORL and ORW or by constructing range contours in diverse ways on the basis of observed capture loci, statistical approach to the subject on the assumption of random walk of animals within their home ranges has been attempted by many workers up to date. Among others, the means resting on bivariate normal distribution of points of occurrence around a single center of activity calculated over a home range has been prevalently adopted. But I (Tanaka, 1963) could not at all be in favor of its basic assumption for the single center of activity, to which Siniff and Jessen (1969), Wierzbowska (1972), and Murakami (1971) are plainly opposed at present.

Every student, except Mazurkiewicz (1971), applied the normal distribution to pooled capture data from different animals so as to be adjusted to circular ranges. It was objected by me (1963) to their methodology that: (1) superimposing of data from diverse animals leads us to entertain an unsubstantial range concept; (2) now there is every

possibility for a true range not to have generally the utmost probability of animal activity at its center; and (3) a true range has a fixed outer limit about which an abrupt decline in frequency rate of activity seems to occur.

Mazurkiewicz succeeded in approaching nearer the natural shape by attempting to calculate respective range sizes from each animal's capture data, whereas she appears to have missed approaching the natural size by conforming to the bivariate normal distribution around a single center of activity; the evidence for the remarks will be presented later on.

In the first study, the period and trapping plan of fieldwork common to two plots (A, B) were as in Table 1. Three series, equipped with diverse designs as shown in the Table, of the work was sequentially executed. The whole area of each plot was divided into the inner square (IS) and the external belt (EB) with the demarcating dashed lines as shown in Figure 1. Check of live traps was made twice daily, in the morning and in the evening, through all the series.

Table 1. The trapping plan in the first study.

Series	(1)	(2)	(3)
Date (August, 1970)	8 to 11th	12 to 15th	16 to 19th
Extent of Grid Laid Out	Inner Square and External Belt (100x100m)	Inner Square (60x60m)	Inner Square (60x60m)
Trap Spacing (d)	10m	10m	5m

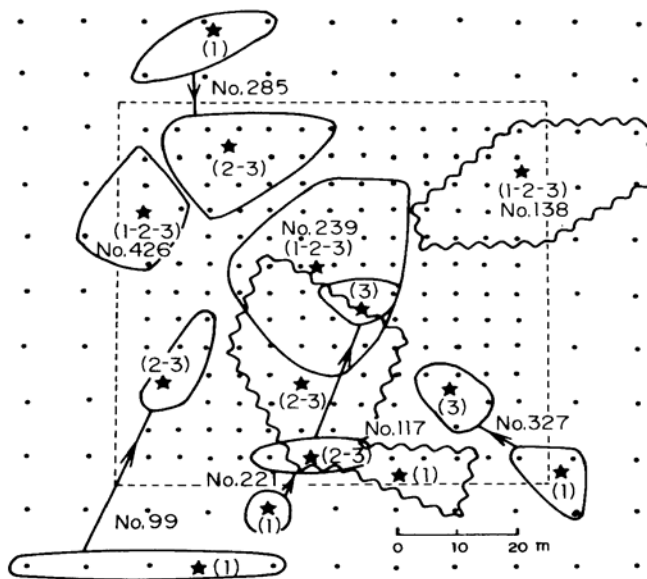


Figure 1. Map of outlines of settled and shifting home ranges for part of the males captured six times or more on Plot A in the first study: dots stand for trap stations, the inner square of the grid being demarcated with dashed lines from the external belt; pentagrams for geometric centers of activity to which series numbers within parentheses are attached respectively; typed figures for individual members.

A contour of trap-revealed range for each vole that was captured six times or more was constructed by circumscribing the entire set of capture loci (exclusive of occasional sallies) of the individual so as to form a convex polygon (Figure 1). But, in case it was postulated that a range shift occurred in a vole of them, separate range outlines assigned respectively to before and after the shift were afforded to the individual; these separate ranges were connected in such ways as shown for some specimens (Numbers 285, 99, 221, 327, 117 in Figure 1) by use of arrows or concave lines.

From the standpoint of location, conservation and shift of home range, the analysis of the outlines of settled or unsettled ranges through the three series of work for all the voles captured six times or more was attempted, with the result that diverse patterns in animal behavior pertaining to its home range were discerned. On the supposition that only the inner square of grid is the proper census area, the variations could be grouped into eight types.

Of these patterns, the following three (a,b,c) seem to have the greatest concern with the question of edge effect viewed from both their qualities and their frequency rates among the 183 examined specimens, nearly all of them being adult.

Type a: Complete ingress range-shift

Range was on EB in series (1) but on IS in both series (2) and (3); occasionally a further shift occurred in (2) and (3) (Numbers 285, 221, 99 in Figure 1).

Type b: Partial ingress range-shift

Range stretched to a large extent on EB but reached to one capture site of IS or it extended from the edge of IS to EB in series (1), while in the later series (2) and (3) or in (3) alone, it stretched more or less extensively within IS (Numbers 117, 327, in Figure 1)

Type c: Range conservativeness

Range was kept at nearly the same location over all the series; i.e., it extended on IS or from IS to EB in series (1), and every range (or its part) of the same vole located on IS in different series could actually or probably be, to a considerable degree, superimposed on each other (Numbers 426, 239, 138 in Figure 1).

The type c possessed the majority (52 percent), and both types a and b combined occurred at the rate of 28 percent. The prevalence of the stable range (type c) was approximately according to expectation, whereas it appears to me that the rate of the types of ingress range-shift were rather high contrary to our anticipation, for we have something like a common notion that a capture-recapture process causes, if any, no appreciable invasion by outside residents onto a census area.

Supposing the inner square to be a proper census plot, we are assured that all the voles of type c were sedentary animals at least for the census period of series (2) and (3). Home ranges of these residents are each localized in the proper census plot; some of them, however, extend over its edge line (outermost trap rows). According to the rule of Dice (1938), every individual whose range center is located inside the border line (I shall call "Dice's assessment line" henceforth, dashed line in Figure 2) of the additional boundary strip should be involved in the calculation of densities.

In this study, from the average range size the width of Dice's strip could be given at nine m which is about as wide as trap spacing in the external belt; hence the second inner trap row in the belt is regarded as nearly equivalent to Dice's assessment line of the census plot, i.e., the internal square of grid. Thus it turned out that only part of the voles with type a (complete ingress range-shift) had their range outside the assessment line and that the rest of the type and those of type b can be considered to have been ineffective or apparent immigrants. And the frequency rate of the effective immigrants, whose ranges removed from outside the assessment line to its inside, proved to be fortunately not so large (seven percent).

Here we ought to note that the ineffective and effective range shifts which took place at considerable rate are by no means ascribed to a peculiarity of the present trapping design, but that these shifts may arise also in usual capture-recapture processes fulfilled without setting the external belt of grid as in this study. As for the ineffective range shifts, these will be rather advantageous to sampling for census, because the animals are supposed to get better exposed to traps when they do the inward shifts than otherwise.

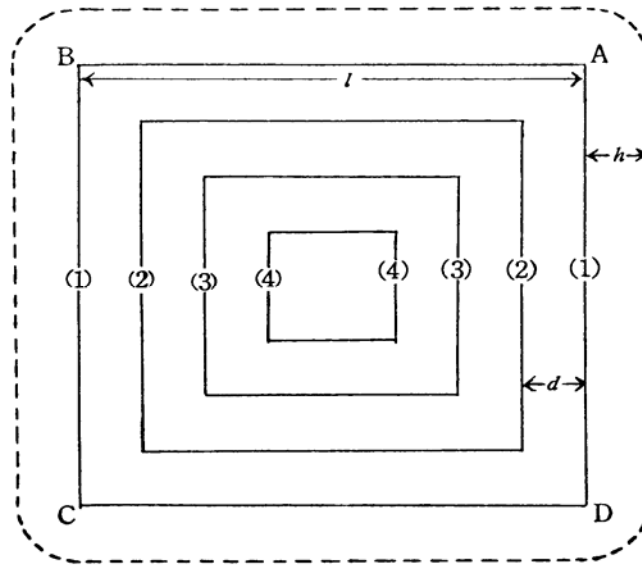


Figure 2. Illustrating a census quadrat ABCD (side length  $l$ ) marked with concentric trap-row squares (1), (2), (3) . . . , of which the grid of trap sites, spaced  $d$  apart, is composed, and the additional boundary strip,  $h$  in width, demarcated with the Dice's assessment line (dashed line).

How far their ranges were shifted by the voles of types a and b are measured from distances between the geometric centers of activity before and after a range shift and stretches of the post-shift range (Figure 1). Grossly speaking, the ranges of immigrants extend on the edge and adjacent trap rows, but yet to variable degrees some of them reach to the center of census plot. Accordingly, these immigrants would have caused rather larger catch per trap on the external trap rows than that at the central area if removal trapping had been worked; then, as one may call the result edge effect, such edge effect is seen gradually diminishing toward the center, so that it is almost unlikely that one should discover any sure intra-plot assessment lines (Hansson, 1969; Pelikan, 1969/70; Smith, et. al., 1969/70) demarcating a central area as is utterly free from the edge effect. I could substantiate infeasibility of such assessment lines from our own data (Tanaka and Kanamori, 1969).

It will be sound to understand that the individuals of type c have revealed their home ranges nearest to the reality in size and shape. Thus ORL and ORW were taken of these specimens (Table 2).

Table 2. Averages of ORL and ORW for the voles of type c in the first study.

Sex	Plot	No.*	Mean No. Of Capture		ORL (m)	ORW (m)
			Times			
Female	A	23	19.5	20.65±1.43	19.88±1.04	10.96±1.22
	B	25	15.0	19.16±1.52		8.76±0.985
Male	A	18	18.2	32.06±2.98	28.21±1.57	17.06±2.06
	B	29	17.9	25.83±1.63		15.00±1.32

\* Number of the observed voles of type c which were captured eight times or more.

Since there is no significant difference between different plots in any values of different sexes and measurements, both plot values were averaged respectively. Thus from the statistical comparison it proves to be disclosed: (1) that males are superior to females in both ORL and ORW; and (2) that ORL is approximately twice as long as ORW in either sex. The first item is of common knowledge, whereas the second is positively in support of the concept of elliptic range shape.

To start with, I attempted calculating oblong range sizes of three specimens (adult males) out of those in Table 2 using Mazurkiewicz's formulae, which are based on bivariate normal distribution, on the admission of an ellipse containing 95 percent captures and then the sizes calculated were compared with those as can easily be computed by the formula  $\pi ab$ , where 2a and 2b each denote lengths of long and short axes of an ellipse, putting 2a=ORL and 2b=ORW (Table 3, Figure 3).

Table 3. Range lengths and widths (m) worked out by two different means of three specimens out of those in Table 2.

Method	No. 138*	No. 239*	No. 54
Bivariate normal distribution (containing 95% of captures)	2a	54	56
	2b	28	46
ORL and ORW	2a=ORL	40	46
	2b=ORW	19	39

\* Their range contours are shown in Figure 1.

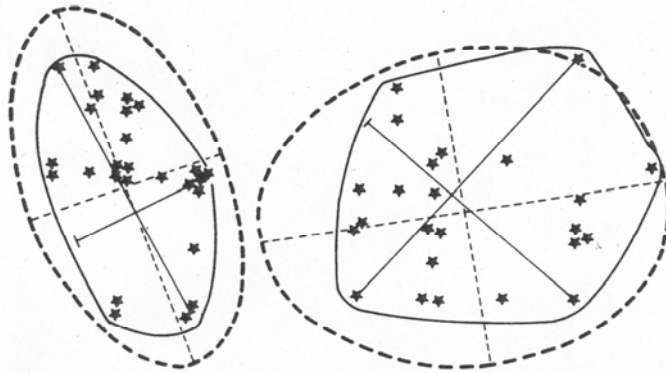


Figure 3. Solid curves represent home range outlines of two specimens, Number 54 (left) and Number 138 (right) in the first study, these enclosing a set of capture loci occurred in respective voles (number of captures is denoted with number of pentagrams at each trap station), and solid crossed lines are ORL and ORW; dashed elliptic outlines indicate ranges of the same voles, which are determined by Mazurkiewicz's formulae so as to contain 95 percent of captures.

From Table 3 and Figure 3, we may affirm that the elliptic ranges calculated on the basis of normal distribution around a center of activity are distinctly larger in area than those counted by the formula  $\pi ab$  using ORL and ORW as 2a and 2b respectively and that the latter reveal the truth much better than do the former in both size and shape.

The reliability of the ORL-ORW method to rate the true range size has been demonstrated from some findings with voles of *Microtus* which were deliberately brought about by the isotope method (Godfrey, 1954; Ambrose, 1969). As for the technique of tracing animals, the Ambrose's seems to be more advanced than the others in some respects. Ambrose could detect an animal at a distance of 6.7m, but Godfrey could do so at only 2.4~3.0m, from it, and while the former obtained as many finds as 100 or so for a single vole by three day tracing, the latter merely 17~50 finds by tracing for much longer period.

Their ways of assessing isotope-revealed range sizes from finds, however, were nearly the same; the range area was determined from the outline formed by connecting the peripheral location points with right line thereby constructing a convex polygon with the least possible number of sides passing through these outside finds, and range length and width, each just identical with ORL and ORW, were measured additionally. But Ambrose discriminated the adjusted range from the maximum range that was determined in the above way; the adjusted one, whose outline is composed of some concave lines, looks to be much more unnatural than the maximum, so that I would like to adopt the maximum range alone as natural range henceforth.

The matter full of suggestion to us among the contributions by Ambrose is the comparison, made by superimposition, of trap-revealed ranges induced by diverse means with the isotope-revealed ones. As a result, he remarked as follows:

The assumption that an animal will range over an area at least one half the distance to the next trap of a grid is not necessarily valid; thereby the exclusive or inclusive boundary strip method (Stickel, 1954) founded on the very assumption has proved to cause a gross overestimate of the actual range size in every case of his study, whereas the minimum area method (which is independent of the assumption and in direct relation to the ORL-ORW method) has proved to be most accurate.

The adjusted observed range length that was recommended as better than ORL by Stickel was also introduced on the same insubstantial assumption; it is the essential reason why I have adopted ORL as a sure measure for seeking after natural ranges.

Averages of home range area, range length and width afforded by Ambrose and Godfrey to their voles are shown in Table 4; additionally, by way of comparison, averages of ORL and ORW in Table 2 and mean range areas worked out from them by  $\pi ab$  are exhibited in Table 4.

Table 4. Calculations of the isotope-revealed ranges given by Ambrose and Godfrey to their several voles, *Microtus pennsylvanicus* and *M. agrestis*, accompanied with comparable values of the trap-revealed ranges of *M. montebelli* gained in the first study.

Author	Sex	n	Average Range Area (acres)	Average of Range Length (=ORL) (m)	Average of Range Width (=ORW) (m)	Eccentricity (c/a)
Ambrose (1969)	Female	3	0.04	21.7	12.5	0.758
	Male	5	0.09 } 0.08*	27.4 } 25.3	18.6 } 16.5	
Godfrey (1954)	Female	22	} 0.048	26.40±1.51	15=34±1.19	0.814
	Male	1				
Tanaka (1972)	Female	48	0.04	19.88±1.04	9.81±0.79	0.870
	Male	47	0.09	28.21±1.57	15.79±1.13	0.829

\*For maximum ranges in his paper.

The Table indicates that the calculations in the three studies are agreeable with each other to a surprising degree. The way of area count taken by the isotope-employers was formally different, but hardly so substantially, from mine. The agreement, which can by no means be due to fortuitous coincidence, is remarkable specifically in range area, but also it is grossly admitted in range shape in terms of ellipse viewed from their eccentricities ( $c/a$ ;  $c = \sqrt{a^2 - b^2}$ )

In the foregoing papers (Tanaka, 1961; 1962), it was claimed that the natural range size of the group of voles is, taken together, on the order of 25-30 m in length (ORL) at ordinary density levels; therefore, the present results in Table 4 are approximately in support of the claim.

On the ground of the above findings and discussions, we may truthfully say that the natural home range of the voles of *Microtus* and *Clethrionomys* is ordinarily on the order of 0.05 for females and of 0.10 for males in acres and that it is of elliptic shape such as its eccentricity is about 0.80. The statement has been further confirmed in the second study of edge effect (Tanaka, in press).

In the study, its design and process were nearly identical within the first except that only the inner squares (60x60 m) of both plots, which I regarded as the proper census area, were used by keeping the trap spacing at five m through the study period of ten days.

By way of approaching natural home ranges of the vole population using the capture-recapture data gathered in the work, 24 specimens (18 females, six males) have been selected out on the following rigid terms; they are those (a) that were captured ten times or more and survived within the plots for seven days or longer, i.e., precisely speaking, the interval between the first and the last capture of each vole was seven days or longer, and further (b) that satisfy such condition that 80 percent or more of a single-vole's capture loci are distributed on the trap rows exclusive of the edge row.

The range outlines, constructed in the same way as previously for the select specimens, were considered to reveal almost entirely their natural home ranges in terms of size and shape and to be comparable to those of type c in the preceding study. In practice, the averages of ORL and ORW (Table 5) denote rather larger values than, but no significant difference from, those (Tables 2 and 4) of type c, respectively.

Table 5. Averages of ORL (2a), ORW (2b) and range area ( $\pi ab$ ) for the select 24 specimens in the second study.

Sex	n	ORL (m)	ORW (m)	Range Area (acres)	Eccentricity (c/a)
Female	18	20.33±1.20	12.57±0.76	0.05	0.79
Male	6	32.04±1.24	17.42±1.33	0.11	0.84

#### WIERZBOWSKA'S FORMULA TO ESTIMATE RANGE SIZE

The mathematical methods of estimating range size, whether the range is assumed to be a circle or an ellipse, in accordance with bivariate normal distribution around a single center of activity have proved to be inappropriate, as discussed previously.

Alternatively, however, several means of assessing range size on the supposition of uniform probability of occurrence or random visit to every point by an animal over its home range are presented by Wierzbowska (1972) (it was for the first time published in 1966) and by Morisita and Murakami (1968). Among these methods, Wierzbowska's seems to be very useful because it is very simple only if his tables are available to us.

As for the method of Wierzbowska, it is in effect recommended to estimate range size of an animal from solving the ensuing equation so as to reach the value or  $r$ , that is range size measured in terms of number of all the trap stations involved in its home range:

$$E(X_{k,r}) = r[1 - (\frac{r-1}{r})^k]$$

where variable  $X_{k,r}$  represents number of different stations visited by the animal in  $k$  successive captures. The estimated range size in terms of acreage may be calculated as  $S = rd^2$ ,  $d$  being trap spacing in the grid. It is stated that averages of the realized values ( $X_k$ ) for  $X_{k,r}$ , gathered from individuals whose ranges are located in interior of a quadrat, are available for practical range estimating.

We should note that the estimated range size expressed as  $r$ -values may lead to an indefinite result according as how unit squares ( $d^2$ ) of the grid are arranged. Anyhow, the fundamental condition of the method is characterized by the random distribution of animal's occurrence at every point within range.

Nevertheless, the assumption of random walk over a home range appears to be unrealistic at least viewed from the distribution maps of abundant finds obtained with isotope by Ambrose (1969), for which Murakami (1971) could prove an overdispersed pattern by following the index  $I_5$  of Morisita (1959) working out at 1.82 on an average. The same will be true of the distributional pattern in fixes by telemetry for hares, foxes or raccoons (Siniff and Jessen, 1969).



I also investigated using  $I_{\delta}$  the distributional pattern of trappability over all the trap stations within each range contour of the select 24 voles, with the result that the random type could not be rejected at five percent significance level for every vole except only two having plainly overdispersed pattern ( $I_{\delta}=1.99, 3.43$ ).

The results look to be incompatible with what was remarked above. Putting the subsequent interpretation on the results, however, the inconsistency appears to be solved to some degree.

The intra-range capture distribution of the vole may change from the random to the overdispersed pattern with increase of number of captures per trap station. In other words, the random distribution is revealed at only such capture densities as treated there, and the overdispersed would be realized at such high densities that are shown in finds or fixes gathered with isotope or by telemetry.

For that reason, I attempted estimating the mean range size of the select specimens using Wierzbowska's formula; as the result, the most trustworthy estimate ( $r^*$ ) for the range size measured in terms of station number was given as follows:

$$r^*=11.4 \text{ for females} \quad r^*=19.5 \text{ for males}$$

Then I proceeded to compare these with the oblong range sizes counted from the values of ORL and ORW in Table 5. Seeing that the range size expressed as  $r$ -values may be largely affected by how the unit squares are arranged, in order to test if both estimates induced by the different two means lead to agreement, we should try arranging as many unit squares as  $r^*$ -values so as to form an ellipse (Figure 4).

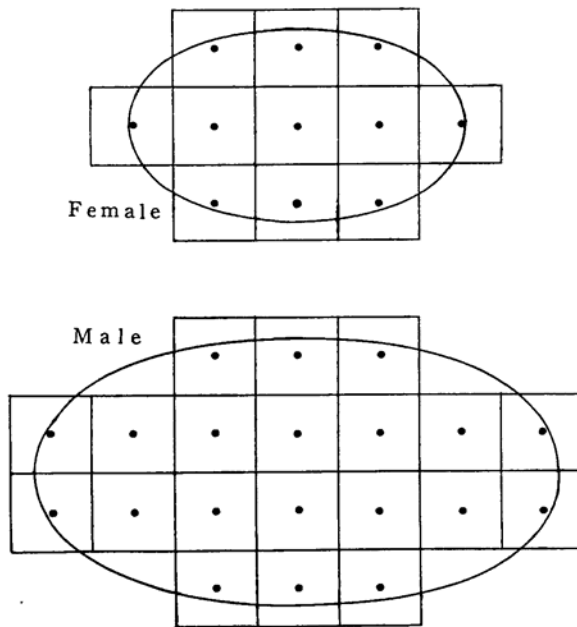


Figure 4. Showing elliptic range outlines, constructed by the formula  $\pi ab$  from respective averages of ORL (2a) and ORW (2b) of the select 24 specimens in the second study, circumscribing the set of centers (dots) of unit squares that are arranged so as to shape something like an ellipse; note that the unit square is  $d^2=25$  sq. m in area.

If, in accordance with the above values of  $r^*$ , the eleven unit squares for females and the twenty for males are arranged respectively in the manner as diagrammed in Figure 4, then a figure, which is surely symmetric in two directions and shaped something like an ellipse, can be constructed in either sex. Besides, there occurs a surprising coincidence, also in both sexes, such that the elliptic range outline, which is drawn from the scale of  $\pi ab$  based on respective means of ORD (2a) and ORW (2b) of the select 24 voles, covers with considerable accordance the set of centers of unit squares.

So good a coincidence of the observational method, accumulating successive realized capture loci, with the theoretical method in results for both sexes can convince us that: (a) the latter's basic assumption of intra-range random distribution of captures holds true; and that (b) it never brings forth any discordances for natural range to be oblong rather than circular in shape.

#### A THEORETICAL APPROACH TO EDGE EFFECT

For a trapping quadrat ABCD along with his assessment line diagrammed in Figure 2, Dice's notion to calculate the density ( $D$ ) is as follows:

$$D = \hat{N} / (l^2 + 4hl + \pi h^2) \Leftrightarrow \hat{N} / (l + 2h)^2 \text{ when } l \gg h$$

Where  $\hat{N}$  is the population estimated by sampling from the quadrat and  $h = 1/2 \sqrt{H}$  letting  $H$  be a mean area of home range. The theory is built up on the supposition that the animals, whose centers of home range are distributed within the width  $h$ , may be contained in the sample.

If a circular range is assumed, using radius instead of  $1/2 \sqrt{H}$  is more reasonable, as Hansson (1969) did so. At present, however, the elliptic range prevallying obtains; thereby the correct width ( $h$ ) should be  $\sqrt{ab}$ , because  $E(r^2) = ab$  and then  $E(r) = \sqrt{ab}$  when  $r$  is defined as radius vector of an elliptic range, whose long and short axes are  $2a(ORL)$  and  $2b(ORW)$  respectively.

It looks to be widely conceived that such edge effect as perceived from disproportionately larger catch per trap in the external belt of grid than in the inner square may be induced by the residents whose range centers are located over the Dice's strip as well as by the effective immigrants previously discussed. But it is needful to test whether or not the edge effect will indeed arise even under the condition that is quite free from disturbance of the immigrants. The test was attempted from the theoretical point of view in the first study.

Let each animal of a population of size  $N$  have a circular home range with mean radius  $h (= 1/2 ORL)$  and each center of range be distributed at random over the whole area, enclosed with the Dice's assessment line (Figure 2). Then, viewed from location of range centers, let  $N$  be divided into  $N_E$ , distributed on the belt that is circumscribed with the dashed line and the trap row (2), and  $N_I$ , situated inside the trap row (2), and it is proved that  $N = (l + 2h)^2 \delta$  and  $N_E = 4(l - d + h)(d + h)\delta$ ,  $\delta$  standing for population density. If, for brevity's sake, the realistic special case of  $d = h$  is considered, then  $N = (l + 2h)^2 \delta$ ,  $N_E = 8lh\delta$  and  $N_I = (l - 2h)^2 \delta$ .

On the supposition that the catchability for each animal in a given period is proportional to area of the portion of respective home ranges that is located within the quadrat ABCD, the calculations for respective total catches and catches per trap ( $C_E^*$ ,  $C_I^*$ ) from the  $N_E$  and  $N_I$  groups can be introduced. And the ratio  $\rho$  of  $C_E^*$  to  $C_I^*$  that is used for check of the edge effect is given as:

$$\rho = (l - h)^3 / l(l - 2h)^2$$

In general, the ratio is over unity, but it approximates unity when  $l \gg h$ ; for instance, if  $l = 10h$  or  $100h$ ,  $\rho = 1.14$  or  $1.01$ . Therefore, by reference to the fact that  $C_E^*$  is the maximum estimate but  $C_I^*$  is the minimum, it is very likely that the actual ratio will be near unity.

Since the theoretical verification has not yet been fulfilled by way of generalization, however, this conclusion must be tentative. Then we might say that there can be no edge effect such as discussed above unless any effective immigration do occur onto a sampling plot.

VALIDITY OF DICE'S ASSESSMENT LINE

Dice's assessment line for density determination will have been introduced on the ground of the supposition for the uniform distribution of an animal's occurrence on any diameter of its assumed circular home range, hence the mean of its locality, expressed in terms of abscissa, leading to radius  $r(=1/2 \text{ ORL})$  that is regarded as width ( $h$ ) of the additional boundary strip (Figure 2). The theory is valid for the case where the random distribution in number of captures per station within range is approved. But, for the elliptic range,  $h=\sqrt{ab}$  should be adopted as stated before.

The density per acre ( $D$ ) could be calculated after Dice's rule from the total population ( $\hat{N} = 123$ ) estimated in the second study by dealing with female and male groups separately. First,  $\hat{N}$  was divided into 74.2 for females and 48.8 for males after the actual sex ratio in all the captured animals, and then using the values in Table 5 we have the following:

(females)  $\hat{N}=74.2$ ,  $a=10.17$  m,  $b=6.29$  m and  $h=\sqrt{ab}=8.0$  m hence  $D=26.2$

(males)  $\hat{N}=48.8$ ,  $a=16.02$  m,  $b=8.71$  m and  $h=\sqrt{ab}=11.8$  m, hence  $D=14.4$

Thus the total density per acre proves to be 40.6.

Now, on purpose to prove the validity of Dice's process, one needs to try approaching the density in a way quite different from the assessment line method and the like.

Apart from the difficult problem as to how to make the number of tracks correspond to that of animals, the article of Marten (1972) which has applied tracks on smoked paper to censusing of small rodents is very instructive to us. Conforming to his new methodology, a population density can be directly from the samples gathered on a quadrat, without settling any assessment lines, on the basis of mouse-equivalents in terms of number of tracks. The notion, however, must be available for actual censusing under the strict condition that his so-called mouse-equivalent is represented by a definite extent corresponding to home range size of an animal.

The  $r$ -value of Wierzbowska's is suitably a measure of range size, in terms of number of stations, which is completely equivalent to range area. Accordingly I tried enforcing the idea of Marten by means of observed  $r$ -values (Table 6) from nearly all the members of the population, which are considered to have been marked judging from the census result, in the second study.

Table 6. Sums of observed values of  $r$  in Wierzbowska's formula for three subsamples, the combined sample consisting of nearly all the marked captures, in the second study.

Subsamples*	Female			Male				
	Subsample	Size	$\sum r$	$\bar{r}$	Subsample	Size	$\sum r$	$\bar{r}$
I		18	197.5	11.0	6		115.0	19.2
II		29	224.0		21		227.0	
III		16	71.5		13		69.5	
Combined		63	493.0		40		411.0	

\*See text for explanation of the subsamples.

The subsamples in Table 6 are each conditioned by the following items: Subsample I, the select specimens which are considered to have revealed almost entirely their natural home ranges so that the mean  $\bar{r}$  may indicate the vole-equivalent of range size with reason; note that  $\bar{r}$  is nearly the same with  $r^*$  in either sex.

Subsample II, the same with I, except that the part greater than 20 percent of each vole's capture loci are distributed on the edge trap rows.

Subsample III, the specimens were all captures three to nine times at stations more or less involved in the edge rows.

Provided that  $\bar{r}$  of subsample I is used as "vole-equivalent", the  $r$ -value observed in each vole of Subsamples II and III must be a fraction of the equivalent. Consequently, after the methodology of Marten, the population density per acre ( $D$ ) is simply calculated as the number of vole-equivalents on the quadrat areas (both plots) from  $\sum r$  for the

combined sample divided by  $\bar{r}$  as below:

$\hat{n} = 493.0/11.0 = 44.8$  for females and  $\hat{n} = 411.5/19.2 = 21.4$  for males, totaling to 66.2, hence  $D = 37.2$

Thus we may well say that this is fairly coincident with that (40.6) reached by Dice's method in the light of some reduction (13 voles unqualified for  $r$ -count were ruled out from all the captured animals) in sample size used for Marten's method.

The coincidence reflects that Marten's method as well as Dice's has proved to be trustworthy through the mediation of Wierzbowska's.

Most recently Smith et. al., (1971) and Kaufman et. al., (1970) presented a new, elaborate process for assessing the area of effect around a grid or along a trap line; it rests on linear regressions of cumulative catches against distances from a given origin. The method seems to be not only lacking in practical validity with its needful assumptions but also has a notable drawback in that it is too consumptive of time and labor.

#### ACKNOWLEDGEMENTS

Heartly thanks are due to Mr. M. Kanamori of Sugadaira Biological Laboratory, Tokyo Kyoiku University, for his energetic cooperation with me in fulfillment of the field work for the two studies. These were supported by the grant from the expenditure of Education Department of Japan.

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