

The distribution of *Microtus pennsylvanicus* within grassland habitat

P. R. GRANT AND RALPH D. MORRIS

Biology Department, McGill University, Montreal, Que.

and

Biosciences Department, Brock University, St. Catharines, Ontario

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A 4-year live-trapping study in southern Quebec demonstrated that *Microtus pennsylvanicus* was distributed randomly in three half acres of enclosed grassland habitat. It was not possible to establish, by correlation analysis, a strong association between number of captures at each position and environmental (mainly plant species) variables. The random distributions are attributed more to the operation of population factors than to the operation of habitat factors in these areas. A simple model is presented which shows how, at different densities, animal distribution varies in relation to the distribution of habitat structure. Specifically, it predicts that (a) as animal density increases the distribution tends toward uniformity, and (b) at a given density, animal distribution in a patchy habitat is more aggregated than in a uniform habitat.

The model is tested with data from the Quebec enclosures and from an enclosure in Saskatchewan which contained 1.4 ac of grassland. First it is established that the grassland is spatially more varied (patchy), in terms of plant species composition and presumed structure, in the Saskatchewan enclosure than in any of the three Quebec enclosures. In conformance with predictions of the model, *Microtus* distribution was aggregated in the Saskatchewan grassland. Also in conformance with the model the distributions became less aggregated as density increased, in both Saskatchewan and Quebec enclosures, but at a given density the animals were more aggregated in the patchy Saskatchewan grassland than in the uniform Quebec grassland.

Introduction

Blair (1940) suggested that the requirements to be met by an animal establishing a home range are adequate food and adequate shelter. Not only where an animal goes but the size of its home range (Linduska 1942) is dependent upon the disposition and abundance of these essentials.

The meadow vole, *Microtus pennsylvanicus*, tends to be found within grassland habitat most abundantly in areas where shelter is provided by dense vegetation. Eadie (1953) found that bait was taken by animals of this species most frequently in dense vegetation. The role of the vegetation in providing shelter or protective cover was confirmed by Mossman (1955), who demonstrated a significant negative correlation between abundance of animals and degree of light penetration. The association between distribution of animals and 'thickness' of the vegetation has also been noted by Blair (1948), LoBue and Darnell (1959), and Getz (1970) for this species, as it has for another grassland species, *Sigmodon hispidus*, by Goertz (1964).

However, many species of plants in the grassland habitat which provide cover for *Microtus pennsylvanicus* also provide food for it, the food preferences among the plant species being known, at least for two areas (Thompson 1965; Zimmerman 1965). Therefore it is not sufficient

to consider the correlation between animal occurrence and vegetation thickness as being indicative of a response of the animals to the need for protection from visual predators. Batzli (1968) has made the point clearly. He found *M. californicus* more in association with an estimate of the percentage coverage of wild oats (*Avena* sp.), upon which the animals most frequently feed, than with the percentage coverage of *Festuca* and *Lolium* species, which grow in more dense stands than *Avena*. It is probable therefore that the distribution of *M. pennsylvanicus* is determined as much by the need for food as for shelter, providing a sufficiently high humidity prevails in the vegetation (Getz 1961a).

During enclosure experiments on interspecific competition, information on the distribution of *M. pennsylvanicus* within the grassland habitat was obtained in 4 successive years (Grant 1969, 1971a, 1971b). It is the purpose of this article to discuss information relevant to the question of what factors determine *Microtus* distribution within the grassland habitat. This will lead to the formulation of a model which relates animal distribution to vegetation characteristics at different animal densities. The model will be tested with *Microtus* distribution data from an enclosure in Saskatchewan.

Methods

The data were obtained by live-trapping with Longworth traps for up to 4 months each year in three enclosures in southern Quebec (for the Saskatchewan data, see later). Each enclosure contained a half acre of grassland and an adjacent half acre of woodland. Little successional change occurred in the grassland areas in the 4 years. A regularly spaced trapping grid of 25 traps was operated two to four times a week in each grassland half acre (see Grant 1969, 1971a, 1971b, for further details). The distribution of captures for the total study period in each year was assessed by means of Morisita's index of dispersion, I_d , to determine departures from randomness. The significance of departures from random (1.00) is assessed by comparing a calculated variance (F_0) with the value of F listed in tables for the appropriate degrees of freedom (see Southwood 1966, for details).

It is assumed here that the distribution of captures represents the distribution of intensities of use of different parts of the habitat by the animals. It is further assumed that a fixed grid of traps is as sensitive to the pattern of distribution of activity as is a changed and random array of traps. This assumption was not examined in the experiments because it would have involved more destruction of the grassland habitat by trampling than was considered tolerable. It may seem a weak assumption, but it is supported by the results of a study of *Apodemus sylvaticus* by Tanton (1969), who found that better estimations of population size were obtained from a fixed trapping grid than from a changed and random array of traps.

Results of Quebec Studies

The results from the three areas used in 4 years are shown in Table 1. The densities did not reach 50% of the known maximum (Grant 1971a), and no overgrazing was evident, in any of these periods. The calculated indexes exhibit departures from unity in both directions, towards overdispersion (less than one) and aggregation (greater than one), but in no instance are

these departures significant ($P > 0.05$). Thus although the distribution of activity may have been non-random within a short time interval, such as 24 h, in the 1- to 4-month study periods it was random. It is worth noting that Lidicker and Anderson (1962) found the distribution of runways of the related species *M. californicus* to be random, with a tendency towards clumping in the best habitat. It is likely that the same holds true for *M. pennsylvanicus* in Wisconsin (Getz 1970).

The random distributions indicate that either there is no appreciable response of the population to variations in the suitability of the habitat, or else there is a response but the habitat features are themselves spatially distributed in a random pattern. Correlation analysis helps us to distinguish between these alternatives.

The number of captures at each trapping position in each enclosure in each year was regressed on more than 10 environmental variables, including several food plant species (abundance of *Phleum pratense*, *Medicago sativa*, etc.) in a multiple linear regression analysis. Results from 1966 have been reported in detail elsewhere (Grant 1969), where it was shown that few of the environmental variables were significantly correlated with number of captures, and their contributions to variations in number of captures were small. This trend was confirmed in analysis of 1967-1969 data. The largest combined contribution, or coefficient of determination (Steel and Torrie 1960), in any one area in any year was only 57.20%, and the largest contribution of a single variable was 36.44%. There was a lack of consistency from year to year in

TABLE 1

The spatial distribution of *Microtus pennsylvanicus* captures within grassland habitat, as revealed by trapping with a regular grid of 25 Longworth traps in each of three 0.5-ac areas. Random distributions are indicated when the Morisita index of dispersion (I_d) is 1.00, departures from which are tested for significance by a variance ratio method (see text)

Year	Dates	Enclosure	I_d	Distribution	Known trappable population
1966	6 July - 31 Oct.	I	1.19	Random	< 8
	6 July - 31 Oct.	II	1.12	Random	6-27
	6 July - 31 Oct.	III	1.01	Random	4-23
1967	10 July - 19 Sept.	II	0.91	Random	7-19
1968	5 June - 25 June	I	1.31	Random	7
	26 June - 10 Sept.	III	0.96	Random	3-8
1969	14 May - 6 Aug.	II	1.00	Random	5-18

NOTE: Other species (*Blarina brevicauda*, *Sorex cinereus*, *Clethrionomys gapperi*, and *Peromyscus maniculatus*) were either generally rare or absent in the grassland.

those environmental variables which were correlated with the number of captures in an enclosure. Furthermore, there were no significant correlations between the distribution of captures in the same enclosure in successive years.

It is possible that the methods used were inadequate for the purpose of detecting an appreciable response of the population to variations in the habitat. Either the trap spacing was too large to allow captures to reflect activity, or the measurement of the environmental variables was too imprecise or unrepresentative; both may be correct.

However, the density and height of the vegetation are quite uniform in all three grassland areas (Fig. 2). Therefore it is possible that under such conditions variations in habitat features are of little importance to the animals, in which case the pattern of distribution may be determined principally by population factors. These would include the attraction and repulsion of animals during the breeding season, the individual variations in home range according to the age, size, sex, social status, and density of the animals (Brant 1962; Koshkina 1965; Stickel 1968; Yerger 1953; etc.), and the frequent changes in home range and population composition as animals die and others are recruited. These factors might interact in a sufficiently complex way to give a random pattern of distribution of activity, and captures.

Hypothesis 1

The hypothesis, in a general form, states that the spatial distribution of animal activity in a relatively uniform environment (structurally) is determined more by population factors than by habitat structure. Consistent with the hypothesis is the fact that in the experiments animals died and others were recruited, and, associated with these events, the trap-revealed home ranges of individuals were observed to change.

It follows from the hypothesis that the spatial distribution of animal activity in a patchy environment (i.e. one whose habitat structure varies from place to place), such as much deciduous woodland habitat, is determined more by structural features of the habitat (extrinsic) than by population (intrinsic) factors. Strong associations between animal and vegetation density have been noticed frequently in woodland habitat (Ashby 1967; Evans 1942; Fairley 1967;

Gunderson 1959; Kikkawa 1964; Morris 1955; Radda 1968). Furthermore Rosenzweig and Winakur (1969) have shown that variation in the abundance of certain mammal species is related to variation in aspects of plant structure but not plant species composition, in a varied desert environment. In the present experiments, *Clethrionomys gapperi* captures in the woodland areas of two enclosures were significantly aggregated (Grant 1969). Likewise, in subsequent and successive years *Peromyscus maniculatus* captures were significantly aggregated in three woodland areas, and never randomly distributed (unpublished data). According to the hypothesis, the distribution of captures of these two woodland species should be more strongly correlated with habitat structure than are the distributions of captures of *M. pennsylvanicus* in the structurally uniform grassland. Unfortunately this cannot be ascertained because the captures of *P. maniculatus*, unlike those of *M. pennsylvanicus*, were significantly influenced by the tripping weights of the traps (Grant 1970). Further, as captures of *C. gapperi* in the woodland of enclosure I were also significantly influenced by the tripping weights of the traps in 1970 (unpublished data), it is possible that the bias may have affected the *C. gapperi* distribution results in an earlier year (Grant 1969) when the tripping weights of the traps were not known. As trap bias might be sufficient to account for the aggregated nature of the distributions of woodland captures, the hypothesis is neither strongly supported nor denied by the captures of woodland animals in the enclosures. It is worth noting, however, that aggregated distributions of captures of woodland species have been demonstrated with a different trap type (Andrzejewski and Glogowska 1962; Trojan and Wojciechowska 1964).

Hypothesis 2

Variations in animal density will modify the relationship between animal and plant distributions. There is much evidence to suggest that at low density only the most suitable habitat is occupied, but that as density increases animals recently recruited are induced, by aggressive interactions with the residents, to leave the most suitable and enter less suitable habitat (Christian 1970; Collias 1944; Haeck 1969; Svärdson 1949; etc.). Thus Bendell (1959, 1961) found that

Peromyscus leucopus introduced to an island became somewhat evenly distributed over the island as the density increased, even though vegetation types and rocks were patchily distributed. Reciprocally, during the decline in numbers of *Lepus americanus*, animals moved out of an apparently unsuitable habitat (sparse vegetation) and entered more suitable habitat (Keith 1966). Therefore it is suggested, as a second hypothesis, that the association between animal distribution and the distribution of habitat structural features tends to weaken as animal density increases. This is partly anticipated, as it applied specifically to *M. pennsylvanicus*, by the work of Getz (1961b), who considered that territorial behavior significantly influences the local distribution of this species only at high density.

A Model of Animal Distribution

The two hypotheses can be integrated into a simple model, illustrated in Fig. 1. It is not intended to be precise; indeed the exact form of the lines may be incorrect, but it is offered as a first step in the understanding of the interaction of factors which affect the distribution of a species within a habitat (however defined). Strictly speaking the model applies to reproductively active animals only, although it could easily be modified to allow for contemporaneous reproductively inactive animals ('clumped' in early independent life), or all animals at a non-reproductive season. As was pointed out, the operation of population factors may be so com-

plex that in a uniform habitat a random, rather than a uniform (overdispersed), pattern of distribution of activity, and captures, is generated. If this is the rule rather than the exception it would be more realistic to show the lines in the model converging on a point higher up on the ordinate, corresponding to a random distribution. However, it is sufficient for our purposes to ignore this complication and show a tendency to approach a completely uniform distribution.

The usefulness of the model may be determined by making predictions about how other variables not incorporated in it, such as microclimate, and competitor and predator species, might affect the basic relationships expressed and then by testing these predictions with field data. For example, it is reasonable to expect predators who rely principally on vision, such as hawks and owls, to enhance the patchiness of animal distribution by cropping those prey in the patches of habitat with the least cover (cf. Southern and Lowe 1968). In contrast, predators who rely principally on olfaction, such as mustelids, might have little effect upon the distribution of the prey other than that produced by a lowering of prey density. From this it can be predicted that the difference in effects of the two types of predation is greatest in the most patchy habitats, and greatest at low and moderate prey densities. In passing, we note also that low density and an aggregated distribution of a prey species leaves space for other prey species with different characteristics to exploit, and therefore we anticipate that high prey species diversity is promoted by patchy habitat and relatively abundant 'visual' predators.

We have taken an alternative approach. In the absence of information on other factors not incorporated in the model, we have tested the validity of the model by comparing distributions of *M. pennsylvanicus* in grassland habitats of contrasting characteristics. The grasslands in the Quebec enclosures are relatively uniform in structure. The grassland in the Saskatchewan enclosure, however, appears to be distinctly less uniform in structure (Fig. 2). Therefore we attempt two tasks: first, to show that the grasslands do differ in spatial variation of structural characteristics and, second, to show that the distributions of *M. pennsylvanicus* differ in the manner predicted by the model.

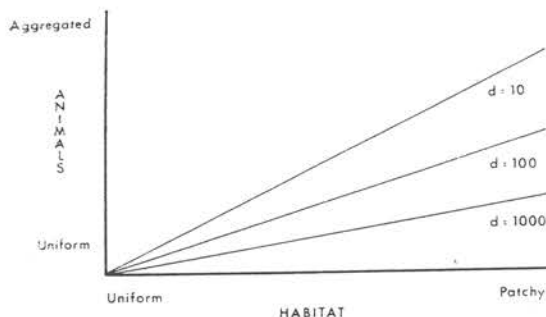


FIG. 1. A model of the distribution of animals in relation to the distribution of habitat structure at three different animal densities (d) sufficiently high that all parts of the area can be visited by animals.

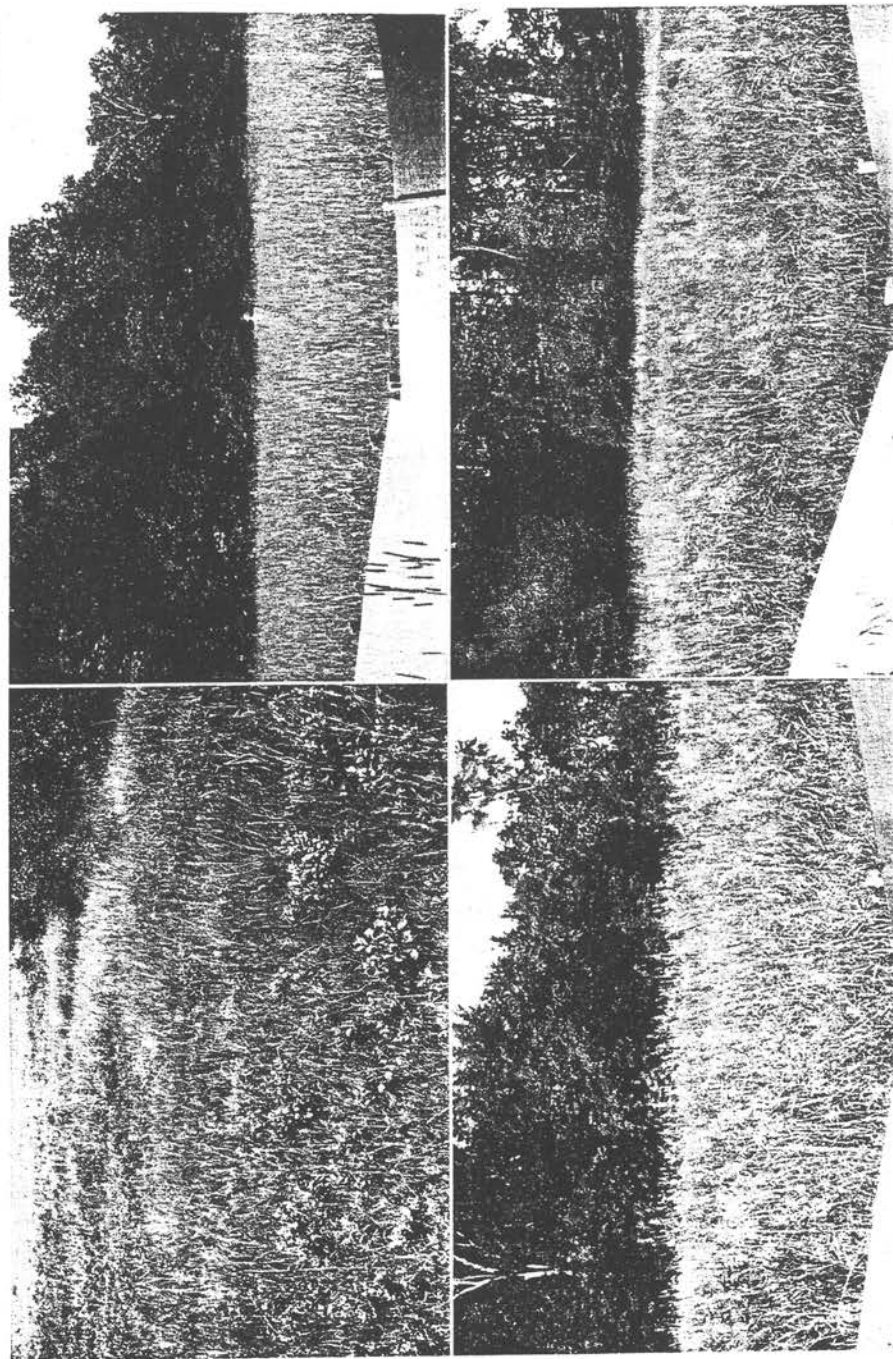


FIG. 2. The grassland in the enclosures. A = Saskatchewan enclosure (5 August 1970); B = Quebec enclosure I (20 July 1967); C = Quebec enclosure II (4 September 1967); D = Quebec enclosure III (4 September 1967). Scale is indicated in B by an assistant (P. J. Wells) 2 m tall. In C and D the maximum height of the tallest grass, *Bromus inermis*, is greater than 2 m. In contrast, the small shrubs in the foreground of A, mainly *Symphoricarpos occidentalis*, are no more than 0.5 m high.

Differences in Vegetation between the Quebec and Saskatchewan Grasslands

It is extremely difficult to measure the spatial arrangement of vegetation with different structural characteristics in a habitat so continuous and densely populated by plants as is grassland. It is easier to measure the spatial arrangement of plant species, either singly or in combination. Since species composition and structure are to some extent correlated, a measure of one provides information on both. Therefore we have chosen to measure species composition and percentage cover in sample plots, and by so doing hope to measure structural characteristics indirectly.

In each grassland a grid of quadrats each 10 meters square was established. A sampling area of 2 meters square in each quadrat was chosen by a random number method. Each plant species in the sampling area was recorded, and an estimate made, to the nearest 5%, of its percentage cover.

The data collected in the Quebec enclosures in 1966 by one of us (P. R. G.) have already been published (Grant 1969). In Saskatchewan, the data were collected by both of us, working together, in 1970 (see Appendix). The only species common to the two grassland regions are *Bromus inermis*, *Solidago canadensis*, and *Poa palustris*.

The required comparison of grasslands is one which is based upon a measure of the variation of all plant species, considered together, among sample plots. This, in turn, involves a measure of the overall similarity, or difference, between sample plots. There are several indexes of similarity in current use by plant ecologists (see Greig-Smith 1964) which might be used for this purpose. We have chosen one that was developed for the analysis of animal data in another context (Grant and Mackay 1969, 1970). It is called

a coefficient of ecological similarity, and is similar to the well-known Jaccard coefficient. It is versatile in that it can be applied to the comparison of two species in several habitats or, as here, to two sample plots containing several species. It is given by the formula

$$E_s = 100 \cdot \Sigma Y / \Sigma X.$$

Each species is treated separately. If present in both plots, the lesser figure of percentage coverage in one plot is entered into the numerator as a Y , and the greater figure from the other plot is entered into the denominator as an X . To be considered, a species must be represented by at least 5% coverage in at least one plot. If a species is not present in one plot, or is present with a coverage of less than 5% in one plot, but present with a coverage of 5% or more in the other, only the latter is entered, in the denominator, since $Y = 0$. When a species is equally represented in the two plots, say with 20% coverage, 20 is entered into both numerator and denominator. All the Y 's are summed, as are all the X 's, and the quotient multiplied by 100 to convert it to a percentage value. In the present calculations this final step is omitted as unnecessary. Therefore it is $E_s/100$ that is calculated. Identity of plots yields a value of 1.0, and pairs of plots of decreasing similarity yield values which approach zero.

The procedure is to make all possible comparisons of pairs of plots within an enclosure to obtain a matrix of coefficients. From the coefficients a mean and variance are calculated. The mean gives a measure of between-plot diversity. A high average coefficient of ecological similarity indicates homogeneity; plots generally resemble each other in composition. A low average coefficient indicates a large amount of spatial heterogeneity; plots generally differ from each other in plant species composition.

TABLE 2

Means and variances of the coefficients of ecological similarity ($E_s/100$) for all possible pairs of samples of vegetation

Area and enclosure	N	Range	\bar{x}	$S_{\bar{x}}$	S^2
Quebec I	300	0.04-0.73	0.28	0.0071	0.0153
Quebec II	300	0.11-0.86	0.48	0.0093	0.0296
Quebec III	300	0.00-0.90	0.32	0.0121	0.0438
Saskatchewan	2628	0.00-0.95	0.23	0.0031	0.0261

Means and variances are listed in Table 2. Statistical evaluation of differences between means must be made by computing t' rather than t , because variances are unequal (except Quebec II and Saskatchewan variances, which are not significantly different at the 5% level). The tests reveal that all means differ significantly from each other, except those of Quebec I and III ($P > 0.1$). More importantly the Saskatchewan mean is significantly lower than any of the Quebec means ($P < 0.01$). In other words, pairs of vegetation sample plots are more dissimilar, on the average, in the Saskatchewan enclosure than in the Quebec enclosures. Essentially the same result is obtained if, instead of using all coefficients in the calculations, we use a sample of them taken at random, or else we use neighboring pairs of samples.

We conclude that in plant species composition the Saskatchewan grassland is spatially more varied than any of the Quebec grasslands. We infer from this that vegetation structure, with which plant species composition is at least partly correlated, is also more varied in space in the Saskatchewan grassland. This confirms a judgment based upon appearance only.

Differences in Animal Distribution between the Quebec and Saskatchewan Grasslands

The animal distributions in the Quebec enclosures were random (Table 1). Since the model deals with reproductively active animals only, distributions were recalculated for just these animals and are random in every instance.

In contrast, in the Saskatchewan enclosure the distribution of either all animals ($I_8 = 1.21$, $P < 0.001$) or just reproductively active animals ($I_8 = 1.24$, $P < 0.01$) is aggregated. The data used for these determinations are taken from the period June 11 to August 10, 1968, when the number of total animals known to be present was about equal to or less than the number of traps. This restriction is desirable because as the number of animals increases, and exceeds the number of traps, the distribution of captures becomes a less reliable indicator of the distribution of activity. At high animal density, relative to number of traps, there is little difference in probability of capture by traps placed in relatively often used and relatively rarely used terrain; the probability is high in both cases.

Thus the difference between Quebec and Saskatchewan distributions conforms to the expectations of the model. There were differences in trapping details which might have contributed to this result, but we consider them to be of little importance. Thus Sherman traps were used in Saskatchewan whereas Longworth traps were used in Quebec; and the trap density was lower in Saskatchewan than in Quebec. However, Sherman and Longworth traps capture *M. pennsylvanicus* with about equal efficiency (Morris 1968). Further, it is probably more difficult to detect aggregations with a low trap density than a high one, yet an aggregated distribution was revealed in the area (Saskatchewan) with the low trap density. Therefore, it is likely that the magnitude of the difference between Quebec and Saskatchewan distributions is, if anything, underestimated.

Another method of comparison is possible, and this makes use of information theory. As generally used in ecology, the information theory statistic H of Brillouin (1956) is used as a measure of the uncertainty involved in predicting the species to which any individual in a community belongs. It can therefore be taken as an index of species diversity in that community (see e.g. Lloyd *et al.* 1968). The formula is

$$H = (1/N) \log (N! / n_1! n_2! \dots n_s!),$$

where N is total number of individuals, and n_1 to n_s are the numbers of individuals in the 1 to s species. The formula can be applied to the present data to ascertain the uncertainty of predicting the trap in which a capture was made. Uncertainty is maximized when all traps have the same number of captures (i.e. the distribution of captures is overdispersed); here $H_{\max} = \log t$, where t = number of traps. The ratio of H/H_{\max} represents the extent to which a distribution approaches uniformity, 1.0 at maximum. The smaller the ratio the more 'uneven' is the distribution of captures.

The ratios of H/H_{\max} have been calculated for the distributions in the Quebec ($t = 25$) and Saskatchewan ($t = 29$) enclosures. Wholly in accordance with the earlier results, the Saskatchewan ratio of 0.8386 is smaller than the Quebec ratios, which lie in the range 0.8669 to 0.9461 (1968 enclosure I data omitted for reasons of small sample size of captures).

In other words, by this measure the distribution of captures is shown to be most uneven in the Saskatchewan grassland. This confirms the result obtained from the analysis in which the Morisita index was used.

Differences in Animal Distribution with Density in the Quebec and Saskatchewan Grasslands

According to the model, as animal density increases the distribution changes from aggregated to random to uniform. At the same density, the distribution of animals is further advanced along this progression in a uniform habitat than in a patchy habitat. The model can be recast to show the latter more clearly by substituting density for the habitat axis in Fig. 1. This is done in Fig. 3. It suggests a means of making a further test of the model. The prediction is made that, at the

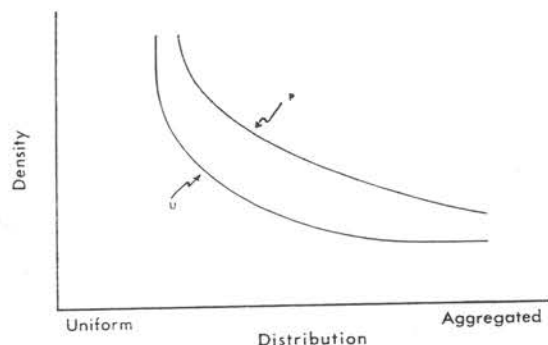


FIG. 3. The expected relationship between distribution of animals and density in two contrasting habitats. U = uniform; P = patchy.

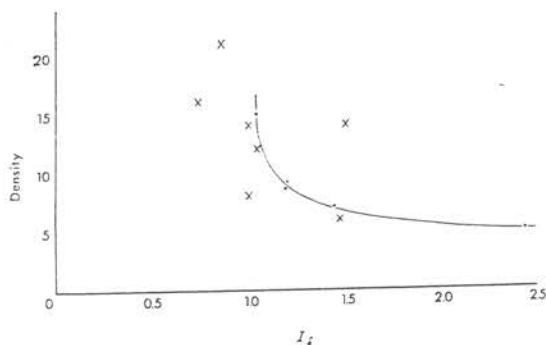


FIG. 4. The distribution of *M. pennsylvanicus* in relation to density (numbers per acre) in the Saskatchewan enclosure (●) and in Quebec enclosure III (×). The Saskatchewan points are connected by a line, fitted by eye. A large value of $I\delta$ indicates aggregation, a low value indicates uniform distribution, and an intermediate value (~ 1) indicates randomness.

same animal density, Quebec points should lie consistently to the left of Saskatchewan points.

To see if this is correct animal distributions at different densities in the Quebec and Saskatchewan enclosures are required. But the measurement of animal distribution presents a problem because Morisita's index, the Δ index of Lefkovich (1966), the coefficient of dispersion, and other commonly used indexes are designed for testing rather than for measurement purposes (see also Lloyd 1967). The parameter k of the negative binomial can be used as a measure of clumping, but suffers the disadvantage of being often dependent upon the size of the mean. The ratio H/H_{\max} is also unsatisfactory because it takes no account of the traps without captures which, at the lowest animal density, constitute more than 50% of the traps present. Also H generally increases as the number of traps with captures increases. Morisita's index seems the least objectionable because it is relatively independent of sample size and size of mean, and therefore will be used.

The Quebec data, which span the greatest range of densities of reproductively active animals, are from enclosure III in 1966 and 1968. They are grouped biweekly so that the number of trap-nights (4-6) and sum of captures (17-41) approximate the corresponding numbers from the well-defined trapping periods in the Saskatchewan study (5-6; 20-36). Seven data points are available from the Quebec area and five from the Saskatchewan area, four in 1968 and one in 1969. These are plotted in Fig. 4.

Comparison of Figs. 3 and 4 shows that the basic expectation is realized. As density increases in each area the distribution tends towards uniformity. Furthermore at a given density the Quebec distribution is less aggregated than the Saskatchewan distribution. One of the Quebec data points clearly violates this latter statement. Perhaps the explanation for this exceptional point is to be found in the behavior of young (non-reproductive) animals. An unusually large number of young animals entered the trappable population at that time; they may have had an appreciable restricting influence upon the number of traps available to capture breeding animals. Nevertheless, except for this point, all Quebec points are to the left of the Saskatchewan points, in agreement with the prediction.

Conclusion

The model is supported by the data at hand. It applies to animals which exhibit 'patch-selection' within a habitat, which space themselves out over suitable habitat and which respond to conditions of high density by avoidance. These characteristics are possessed by non-colonial animals in a variety of taxa, not just *Microtus pennsylvanicus*; therefore the model is likely to be widely applicable. The principal difficulty of carrying investigations of spatial distribution of small rodents further is that distribution is only inferred from trapping results because the animals can be rarely observed. As traps interrupt the flow of activity of the animals, are static, and may capture certain animals preferentially, they are generally unsatisfactory for the purpose. Other methods of study, such as those using smoked paper (e.g. Sheppe 1966), dropping boards (e.g. Emlen *et al.* 1957), radioactive tracers as labels (e.g. Godfrey 1954), etc., have different drawbacks. Ideally, a telemetric device is needed for simultaneously recording the positions of all members of a population. Equipping each animal with a radio transmitter which broadcasts signals of different characteristics is one solution, providing the transmitter is small enough not to affect its carrier's activity yet large enough to transmit a signal which can be received at a convenient distance. To our knowledge, these characteristics have not been combined in a transmitter suitable for work with *M. pennsylvanicus*. It is to be hoped that this will be remedied soon.

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Appendix

Listed below are the plants in the 1.4-ac grassland in the Saskatchewan enclosure. Numbers refer to the cumulative percentage coverage in 73 sampling areas 2 meters square. Two crosses indicate a cumulative percentage coverage of less than 5%. One cross indicates presence in the grassland but not in any of the sampling areas. Grasses and sedges (*Carex*) are listed first.

<i>Bromus inermis</i>	2110	<i>Rosa arkansana</i>	1750
<i>Bromus catharticus</i>		<i>Symphoricarpos occidentalis</i>	920
<i>Poa pratensis</i>	1665	<i>Artemisia frigida</i>	745
<i>Poa palustris</i>		<i>Artemisia absinthium</i>	
<i>Agropyron dasystachyum</i>	740	<i>Aster</i> sp.	480
<i>Agropyron trachycaulum</i>	420	<i>Vicia</i> sp.	400
<i>Stipa spartea</i>	365	<i>Thermopsis rhombifolia</i>	185
<i>Stipa comata</i>		<i>Galium boreale</i>	130
<i>Calamagrostis montanensis</i>	250	<i>Plantago (purshii?)</i>	105
<i>Agropyron cristatum</i>	125	<i>Solidago canadensis</i>	35
<i>Koeleria cristata</i>	60	<i>Achillea millefolium</i>	15
<i>Festuca scabrella</i>	15	<i>Populus tremuloides</i>	15
<i>Bouteloua gracilis</i>	5	<i>Scabra</i> sp.	15
<i>Agrostis hiemalis</i>	+	<i>Gaura coccinea</i>	5

<i>Avena</i> sp.	++	<i>Liatris punctata</i>	5
<i>Hordeum jubatum</i>	++	<i>Lepidium</i> sp.	5
<i>Carex pennsylvanicus</i>	105	<i>Psoralea argophylla</i>	5
<i>Rudbeckia</i> sp.		5	
<i>Arenaria lithofolium</i>	++		
<i>Campanula</i> sp.	++		
<i>Tragopogon</i> sp.	++		
Unidentified yellow legume	++		
<i>Prunus virginiana</i>	+		
<i>Spiraea alba</i>	+		
<i>Urtica procera</i>	+		
<i>Cirsium arvense</i>	+		
<i>Sonchus arvensis</i>	+		
<i>Elaeagnus commutata</i>	+		
<i>Agropyron smithii</i>	+		