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Empirical Analysis of the Andrzejewski and Wierzbowska Model for Estimating the Migratory Fraction of Small Mammal Populations

[With 3 Figs]

Andrzejewski & Wierzbowska (1961) formulate a model for estimating the amount of dispersal in small mammal populations from the results of live trapping studies. Application of the data from live trapping studies of *Microtus* populations to this model indicate that the assumptions made in the model are not always valid. Comparison of the results based on the model to those obtained from the analysis of the dispersal of *Microtus* into vacant habitat indicated sufficient disagreement to question the use of the model for the analysis of dispersal in small mammal populations.

I. INTRODUCTION

Dispersal is recognized as being an important aspect of population dynamics; however, it is a difficult factor to quantify. Evans (1942) suggested that small mammal populations might be composed of a sedentary component and a moving component. With this in mind, Andrzejewski & Wierzbowska (1961) proposed a method by which the resident and migratory fractions of a population might be distinguished. The basis of this model is that animals which are trapped for the first time consist of (1) future residents which will be recaptured on the study area (2) potential residents which will die before the next trapping period, and (3) migratory animals which are moving through the study area. The assumption is made that the survival rate of animals

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on the study area is constant and that the distribution of the length of stay of individuals can be described by an exponential distribution. The existence of a migratory fraction among that group of animals which are captured only once will result in a greater loss between the first and second trappings than would be predicted from the disappearance of animals between subsequent trappings (Fig. 1). Thus the extent
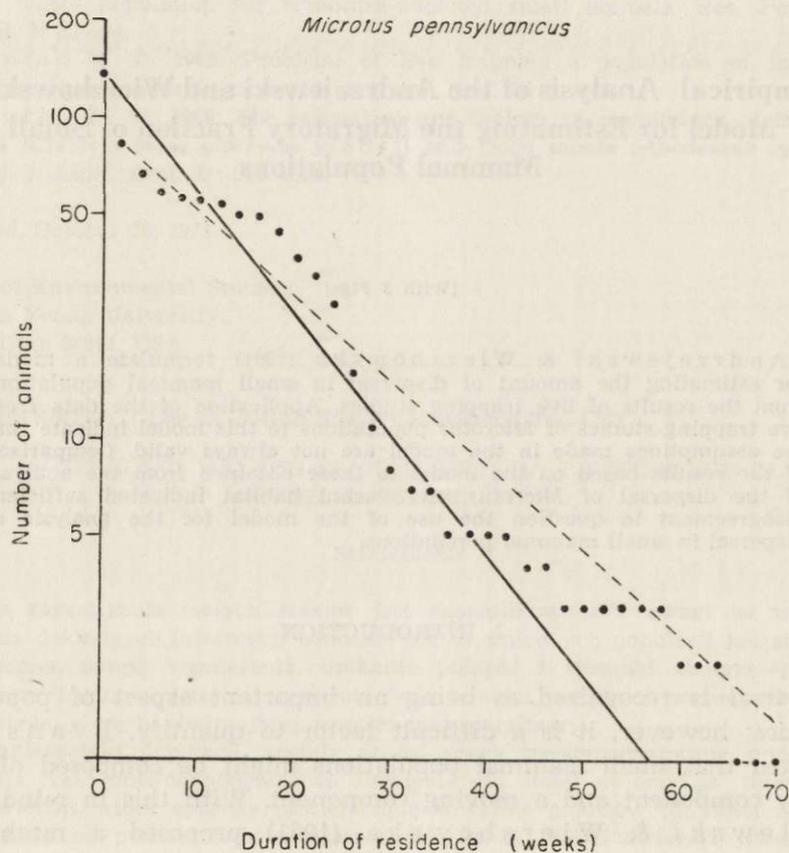

Fig. 1. Survivorship curve for *Microtus pennsylvanicus* males first captured weighing 25 grams of less during the phase of population increase. The solid line is the expected exponential rate of loss from the population calculated including the category of animals which were caught only once. The dashed line is the exponential rate of loss excluding the category of animals caught only once. The data are significantly different from both exponentials primarily because survival is better than predicted from weeks 16 to 24.

of migratory movements in the population can be analyzed by comparing the amount of loss observed between the first and second trappings to that calculated by extrapolation of the exponential curve describing the loss of animals over subsequent trappings.

Holgate (1964 and 1966) investigated the use of trapping data for estimating the migratory fraction of small mammal populations and concluded that the fact that some individuals miss being trapped at each census could account for the deviation from the expected amount of loss between the first and second capture periods. However, Holgate's analysis is biased by the fact that the probability of evading capture by an individual in the population he studied was approximately 84% (Holgate, 1966 p. 930). Since this work of Holgate, the Andrzejewski and Wierzbowska model has been generally discredited (Tanton, 1965). However, we have found the trappability of *Microtus* populations to be much higher (probability of avoiding capture for *M. ochrogaster* = 8% and for *M. pennsylvanicus* = 28%; Myers & Krebs, 1971a). Therefore, we do not feel that Holgate's argument is valid for all populations.

Because it could be very useful to have a method of extracting a dispersal component from live trapping data, the applicability of the Andrzejewski and Wierzbowska Model deserves further consideration. In this study we test the results obtained by applying the Andrzejewski and Wierzbowska Model to the data from a live-trapping study of vole populations to those in which dispersal was monitored by the movement of animals into a vacant habitat (Myers & Krebs, 1971b). We are also able to test some of the assumptions of the model by analyzing the data from enclosed populations which would have no dispersal.

II. MATERIALS AND METHODS

Eight populations of *Microtus ochrogaster* (Wagner, 1842) and *M. pennsylvanicus* (Ord, 1815) in southern Indiana were trapped for periods of 2 to 5 years (Krebs, Keller & Tamarin, 1969; Gaines, 1970; and Myers & Krebs, 1971b). Trapping was done every two weeks throughout the year on approximately 0.8 ha plots with trapping station 7.6 m apart. Techniques and the study area have been further described elsewhere (Krebs *et al.*, 1969). Three populations of *M. ochrogaster* and one of *M. pennsylvanicus* were in fenced areas and therefore dispersal into or from these populations was prevented.

From June 1968 to April 1970 all voles were removed every two weeks from two experimental areas in the vicinity of the other populations. Voles moving into the removal areas were considered to be dispersing animals. Individuals in both experimental and control populations were characterized as to weight, sex, breeding condition and genotype for two electrophoretic polymorphisms, the serum protein transferrin and the enzyme leucine aminopeptidase. The results of these experiments have been reported elsewhere (Myers & Krebs, 1971b) but were used in this study for comparison to those derived from the Andrzejewski and Wierzbowska Model.

The formulation for the model is given in Andrzejewski & Wierzbowska (1961). Analysis was carried out on a CDC 3600 computer and the data were categorized so that comparisons could be made between males and females, animals

weighing more than 25 g at first capture, and among different stages of population growth (increase, peak, and decline for *Microtus pennsylvanicus*; increase and decline for *M. ochrogaster*). In addition, the data for the various genotypes of the transferrin and leucine aminopeptidase polymorphisms were analyzed to investigate the possibility of different tendencies for dispersal among these groups.

III. RESULTS

The first assumption of the Andrzejewski and Wierzbowska Model is that the rate of disappearance of small mammals from a population will be exponential if there is no dispersal. To test this we analyzed data for enclosed populations of *Microtus ochrogaster* and *M. pennsylva-*
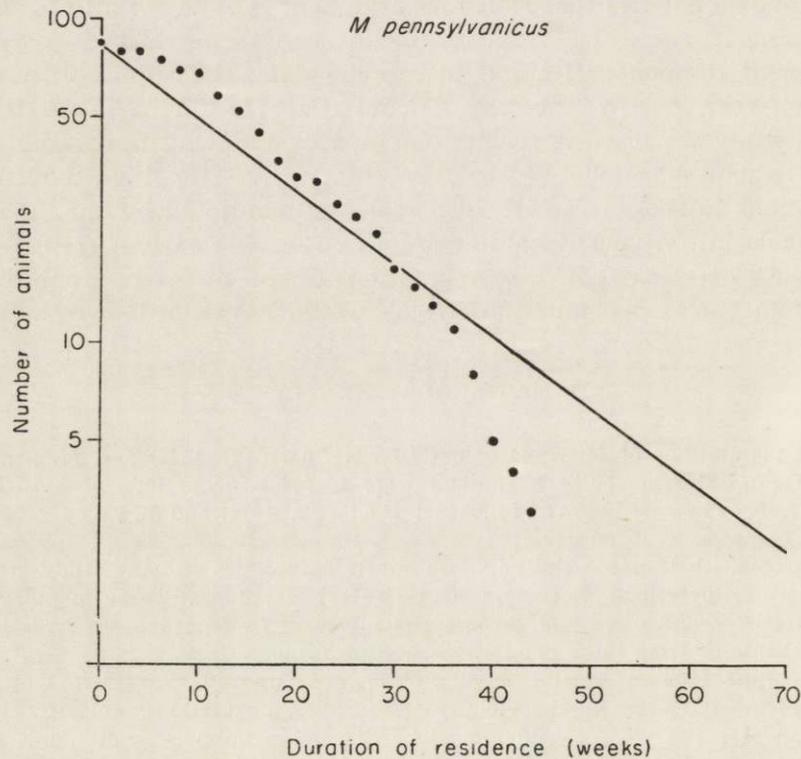

Fig. 2. Survivorship curve for *Microtus pennsylvanicus* females in an enclosed population. The data do not fit the expected exponential because survival is better than predicted during the first 25 weeks after first capture.

nicus. Neither the male *M. ochrogaster* nor the female *M. pennsylvanicus* fit the expected distribution (Fig. 2). In both cases survival is better than predicted by the exponential over the first 20 weeks after first capture, and then falls off more rapidly than expected. Therefore, if dispersal

is prevented, the exponential distribution does not always adequately describe the loss of small mammals from a population over time.

The second assumption of the Andrzejewski and Wierzbowska Model is that if the category of animals which are captured only once is included in the analysis, the distribution will be statistically different from the exponential but that if this category is eliminated, the rate of loss will be adequately described by the exponential. Thus in each set of data (two species, two sexes, two weight categories, and three phases
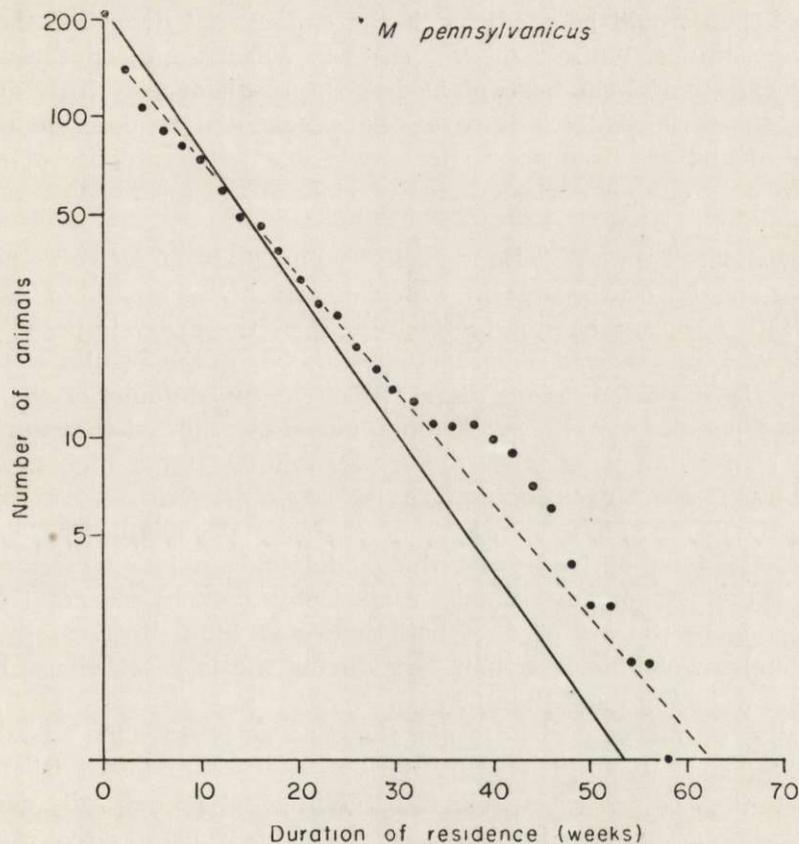

Fig. 3. Survivorship curve for *Microtus pennsylvanicus* males first caught weighing less than 25 grams in the peak phase of population fluctuation. The data are not significantly different from either the exponential calculated including the category of animals caught only once (solid line) or that excluding this category (dashed line).

of population for *M. pennsylvanicus* and two phases for *M. ochrogaster)* the observed distribution of loss should be statistically different from the predicted if the category of animals caught only once is included and not statistically different if this category is eliminated. In seven

of the 20 sets of data which were analyzed, the addition of the category
of animals which were caught only once did not cause the distribution
to vary significantly from the predicted exponential (Fig. 3). On the
other hand, both male and female *M. pennsylvanicus* first caught
weighing less than 25 g during the phase of population increase had
disappearance rates which deviated significantly from the exponential
even when the category of animals which were caught only once was
excluded (Fig. 1). In both cases this deviation was due to a greater
proportion of the animals living from 16 to 24 weeks after their first
capture than would be predicted if the exponential described their rate
of disappearance. While the seven cases in which the disappearance rate
fit the exponential can be explained as the result of very little dispersal
during those times, the failure of the exponential to describe the rate
of loss of animals from populations even when the category of animals
trapped only once is excluded clearly violates the assumptions made by
Andrzejewski and Wierzbowska.

We compared the predictions made by our study of *Microtus pennsyl-
vanicus* and *M. ochrogaster* in which dispersal was measured as move-
ment into a vacant habitat to the results of the analysis based on the
model. While there was some agreement between the results of the two
studies, there was sufficient disagreement to cause doubt of the results
derived from the model. For example, our study showed that during the
period of population increase, dispersal accounted for a high proportion
of the loss from control populations (M y e r s & K r e b s, 1971b) while
during the decline phase very little of the loss was explained by dispersal.
Dispersal indices derived from the model and an index calculated by
dividing the category of animals trapped only once by the total number
of animals in the set of data both indicated high dispersal by males
and females weighing less than 25 g during the increase phase, but not
by those weighing more than 25 grams.

Finally, estimates derived from the Andrzejewski and Wierzbowska
Model are strongly influenced by the size of the sample. Division of the
data into finer categories such as transferrin genotype naturally decreased
the number of animals in the categories. This generally decreased the
dispersal index calculated from the model and made any comparison
among groups of different sample sizes difficult.

IV. CONCLUSION

We have been defeated in our attempt to extract meaningful informa-
tion on dispersal from live-trapping data by use of the Andrzejewski
and Wierzbowska Model and must recommend more arduous methods

of obtaining this information. One technique is to remove animals continuously from an area of suitable habitat. This technique may be biased by the fact that it requires that the dispersing animal is trapped and therefore might overlook animals which would avoid traps during their dispersal. The use of drift fences and pit traps is perhaps the most successful way of catching all dispersing animals but this technique will also be biased by the fact that it will catch some animals whose home ranges include the area of the fence and some animals who are wandering around and not really dispersing. It is possible that a dispersal index derived from dividing the category of animals caught only once by the total number of animals will be shown by future work to be useful. This index will not be influenced by the distribution of the lifespan data, as is the Andrzejewski-Wierzbowska Model, and still takes into account the fact that if animals are dispersing there should be a large proportion of animals which are caught only once. For example comparison of Figures 1 and 2 shows that loss during the first 8 weeks after capture is greater in open populations than in enclosed populations. However, in both cases the distribution of the observed data is not exponential. A dispersal index based on the comparison of the amount of loss between the first and second trappings would reveal this difference without being complicated by other distributional differences. Confidence cannot be placed in such an index however until it is verified by experimental studies of dispersal in small mammals.

REFERENCES

1. Andrzejewski R. & Wierzbowska T., 1961: An attempt at assessing the duration of residence of small rodents in a defined forest area and the rate of interchange between individuals. Acta theriol., 5: 153—172.

2. Gaines M. S., 1970: Genetic changes in fluctuating vole populations. Ph. D. Thesis. Indiana University, Bloomington, Indiana. 1—95.

3. Holgate P., 1964: Modified geometric distribution arising in trapping studies. Acta theriol., 9: 353—356.

4. Holgate P., 1966: Contributions to the mathematics of animal trapping. Biometrics, 22: 925—935.

5. Krebs C. J., Keller B. L. & Tamarin R. H., 1969: *Microtus* population biology: Demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology, 50: 587—607.

6. M y e r s J. H. & K r e b s C. J., 1971 a: Sex ratios in open and enclosed vole populations: Demographic implications. Am. Natur., *105*: 325—344.

7. M y e r s J. H. & K r e b s C. J., 1971b: Genetic, behavioral and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecol. Monogr., *41:* 53—78.

8. T a n t o n M. T., 1965: Problems of live-trapping and population estimation for the wood mouse *Apodemus sylvaticus* L. J. Anim. Ecol., *34:* 1—22.

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EMPIRYCZNA ANALIZA MODELU ANDRZEJEWSKIEGO I WIERZBOWSKIEJ
DLA OCENY MIGRACYJNEJ CZĘŚCI POPULACJI DROBNYCH SSAKÓW

Streszczenie

A n d r z e j e w s k i i W i e r z b o w s k a (1961) opisali model oceny wielkości migracji w populacjach drobnych ssaków na podstawie ich połowów żywołówkami. Zastosowanie do tego modelu danych z analogicznych odłowów norników rodzaju *Microtus* wskazuje, że założenia autorów modelu nie zawsze są prawdziwe. Porównanie wyników opartych na modelu oraz otrzymanych z analizy rozprzestrzeniania się *Microtus* na niezasiedlone siedliska ukazuje dostateczną niezgodność użycia modelu do analizy migracyjności w populacjach drobnych ssaków.