

A POPULATION MODEL FOR FLEAS OF THE GRAY-TAILED VOLE, *MICROTUS CANICAUDUS* MILLER¹

Richard G. Robbins², G. David Faulkenberry³

ABSTRACT: Negative binomial probability distributions are successfully fit to observed frequency distributions of fleas on the gray-tailed vole, *Microtus canicaudus* Miller, in western Oregon. The host flea population is thus shown to be contagiously dispersed.

This is the second in a projected series of papers on the population dynamics of the fleas that parasitize the gray-tailed vole, *Microtus canicaudus* Miller, a field mouse that occurs in grassy, uncultivated areas between the Cascade and Coast Ranges of western Oregon and Washington. Earlier (Faulkenberry and Robbins, 1980), the odds ratio was used to measure the degree of association between different flea species on this vole. However, ecologists also recognize the predictive value intrinsic to a mathematical description or model of the dispersion of organisms in space, and in medical entomology such spatial relationships between hosts and their parasites are often expressed by the negative binomial (or Pascal) distribution (Bliss, 1953; Crofton, 1971a, b). The negative binomial is a theoretical frequency distribution or probability distribution that may be fit to frequency distributions observed in nature. Thus, Fisher (1941) successfully fit the negative binomial to Milne's (1943) frequency distributions for the tick *Ixodes ricinus* (Linnaeus) on sheep in England, thereby mathematically describing the dispersion of the parasite population on a particular host. More recently, Easton (1973) and Easton and Goulding (1974) fit the negative binomial to data for *Ixodes angustus* Neumann and larval trombiculid mites (chiggers) on various hosts in western Oregon. Yet, with the possible exception of Williams' (1964) work on J.L. Harrison's data for *Xenopsylla astia* Rothschild and *X. cheopis* (Rothschild) on the murine rat *Bandicota bengalensis* (Gray) in Rangoon, Burma, the present paper is the first published record wherein the negative binomial is successfully fit to data for fleas.

¹Received August 26, 1981

²Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560

³Department of Statistics, Oregon State University, Corvallis, OR 97331

Application of the Negative Binomial Distribution

Specifically, the negative binomial can arise (1) as a result of a series of exposures to parasites in which each exposure is random and the chances of acquiring parasites differ at each exposure, (2) as a result of nonrandom dispersion of parasites, (3) as a result of differences between individual hosts that affect the chances of acquiring parasites, and (4) as a result of a change with time in the chances of being parasitized (Crofton, 1971a). The negative binomial is described by two parameters, the mean and the exponent k , and is fit to contagious (over-dispersed or clumped) populations in which the variance always exceeds the mean. With combinatorial notation, the distribution takes the form:

$$p(x) = \begin{bmatrix} k + x - 1 \\ k - 1 \end{bmatrix} (1-\theta)^x \theta^k \quad x = 0, 1, 2, \dots$$

where the mean is $k\theta/(1-\theta)$ and the variance is $k\theta/(1-\theta)^2$. When the dispersion parameter k is small, the degree of clumping is great and the variance is much larger than the mean, but as k increases the distribution approaches a Poisson series in which the variance equals the mean.

Among the many methods of estimating k from sample data are the following three given by Southwood (1978):

$$(1) \quad k = \frac{\bar{x}^2}{s^2 - \bar{x}}$$

$$(2) \quad \log \left[\frac{N}{n_0} \right] = k \log \left[1 + \frac{\bar{x}}{k} \right]$$

$$(3) \quad N \ln \left[1 + \frac{\bar{x}}{k} \right] = \sum \left[\frac{A_x}{k + x} \right]$$

where	$\bar{x}$	=	mean number of parasites per sample (host)
	s^2	=	variance
	N	=	total number of samples
	n_0	=	number of samples bearing no parasites
	$\ln$	=	Napierian logs
	A_x	=	the sum of all frequencies of sampling units bearing more than x parasites

Unless the mean is quite low, formula (1) is not reliable when $k \leq 3$, that is, when populations show a moderate degree of clumping. For this reason, formula (1) is usually used only to describe low density populations.

Formula (2) is applicable to most populations with very small means but to large ones only when there is extensive clumping. Generally, about one-third of the hosts must be free of parasites if the mean is below ten, and as the mean increases greater numbers of hosts must fall into the zero class. Formula (3) is considered a better estimator than either (1) or (2) but is also subject to bias when the mean is very small and k very large.

Once values of k have been obtained, the negative binomial population model can be fit in three ways to the observed frequency distribution. First θ is estimated by $k/(k + \bar{x})$, then expected frequencies are calculated by:

$$P_x = \frac{\gamma(k+x)}{x! \gamma(k)} \cdot \left(\frac{\bar{x}}{\bar{x} + k} \right)^x \cdot \left(\frac{k}{k + \bar{x}} \right)^k$$

where P_x is the probability of a host bearing x parasites and the values $x!$ and $\gamma(k)$ are obtained from tables of factorials and of log gamma functions respectively (Southwood, 1978). Expected and observed frequency distributions are compared by a chi-square which has three fewer degrees of freedom than the number of comparisons that are made. Chi-square comparisons are considered strongest when expected frequencies are at least 1.

Results and Discussion

Table 1 compares the k , chi-square, and degree of freedom values for negative binomial distributions fit to observed frequency distributions of *Atyphloceras multidentatus* (C. Fox), *Catallagia charlottensis* (Baker), and fleas collectively on 377 comparable voles taken from ecologically similar sites to the north, south, and west of Corvallis, Oregon (for an account of sampling techniques and a list of all flea species obtained during this study, see Faulkenberry and Robbins, 1980, or Robbins, 1976). Because formulas (2) and (3) for the calculation of k must be made to balance by the method of iteration, all models were generated by computer. In order to obtain the best possible fit, each of the three observed frequency distributions was assigned two values of G , the expected frequency below which all classes were pooled. Of course, in the case at hand, pooling was only possible when G was set at 1 because all classes had expected frequencies greater than 0. In addition, each distribution was subjected once to truncation by removal of the zero class, which is by far the largest class in every case. In Table 1 the best chi-square value in each category is underscored.

It is clear that the fleas of the gray-tailed vole are very contagiously dispersed. All three formulas for k led to the best fit an equal number of times and only once was the difference between expected and observed

frequencies significant at $P < 0.05$. On the other hand, the fit of the negative binomial to the frequencies for zero and one flea per host was seldom close — an indication of top-heaviness in these classes. Consequently, the best distributions were almost always truncated.

Table 1. Comparison of k , chi-square, and degree of freedom values for all negative binomial distributions.

	G = 1; not truncated			G = 0; truncated			G = 0; not truncated		
<i>Atyphloceras multidentatus</i>	k_1	=	0.41384	k_1	=	1.50700	k_1	=	0.41384
	X^2	=	2.1868355	X^2	=	<u>1.5863500</u>	X^2	=	2.8879404
	df	=	3	df	=	7	df	=	8
	k_2	=	0.35500	k_2	=	2.08000	k_2	=	0.35500
	X^2	=	<u>1.8917037</u>	X^2	=	1.9245513	X^2	=	<u>2.5099838</u>
	df	=	3	df	=	7	df	=	8
	k_3	=	0.36202	k_3	=	1.74250	k_3	=	0.36202
	X^2	=	1.9010235	X^2	=	1.6964298	X^2	=	2.5288784
	df	=	3	df	=	7	df	=	8
<i>Catallagia charlottensis</i>	k_1	=	0.36196	k_1	=	0.46719	k_1	=	0.36196
	X^2	=	12.3286353	X^2	=	6.4885838	X^2	=	12.5538454
	df	=	6	df	=	7	df	=	8
	k_2	=	0.45250	k_2	=	0.40000	k_2	=	0.45250
	X^2	=	12.3763963	X^2	=	<u>6.0815673</u>	X^2	=	12.7556870
	df	=	6	df	=	7	df	=	8
	k_3	=	0.42405	k_3	=	0.40788	k_3	=	0.42405
	X^2	=	<u>11.8824064</u>	X^2	=	6.0885154	X^2	=	<u>12.1912021</u>
	df	=	6	df	=	7	df	=	8
All species	k_1	=	0.50407	k_1	=	0.52748	k_1	=	0.50407
	X^2	=	14.7781608	X^2	=	<u>15.6730234</u>	X^2	=	<u>20.7273663</u>
	df	=	10	df	=	17	df	=	18
	k_2	=	0.67375	k_2	=	0.70375	k_2	=	0.67375
	X^2	=	12.0033085	X^2	=	21.4046443	X^2	=	32.1796904*
	df	=	9	df	=	17	df	=	18
	k_3	=	0.62230	k_3	=	0.62526	k_3	=	0.62230
	X^2	=	<u>11.6262368</u>	X^2	=	17.2498995	X^2	=	25.7152032
	df	=	9	df	=	17	df	=	18

*Significant at $P < 0.05$.

ACKNOWLEDGMENTS

This paper, like its predecessor, can truly be called a team endeavor, for its completion would not have been possible without the assistance of workers from several disciplines. We are especially grateful to Professor Gerald W. Krantz, Department of Entomology, Oregon State University, Corvallis, for providing the facilities to conduct this research. Sincere thanks are also due Dr. Emmett R. Easton, Plant Science Department, Agricultural Experiment Station, South Dakota State University, Brookings, and Dr. Wayne N. Mathis, Chairman, Department of Entomology, Smithsonian Institution, Washington, D.C., for their constructive reviews of the manuscript. Special appreciation is extended to Mr. Richard F. Hoyer, of Corvallis, who collected the voles used in this study. Dick is a first-class field naturalist with whom it was an honor to cooperate. Our thanks also to Dr. Edward J. Grafius, Department of Entomology, Michigan State University, East Lansing, for his patient instruction in the use of the OS-3 computer. Dr. Vernon J. Tipton and his colleagues at the Center for Health and Environmental Studies, Brigham Young University, Provo, Utah, kindly determined a synoptic series of the flea species discussed herein.

LITERATURE CITED

- Bliss, C.I. 1953. Fitting the negative binomial distribution to biological data. *Biometrics* 9:176-196.
- Crofton, H.D. 1971a. A quantitative approach to parasitism. *Parasitology* 62:179-193.
- _____. 1971b. A model of host-parasite relationships. *Parasitology* 63:343-364.
- Easton, E.R. 1973. A study of ticks (Acarina: Ixodidae) and chiggers (Trombiculidae) from two areas in western Oregon. Ph.D. thesis, Oregon State Univ., Corvallis. 77 numbered pp.
- _____, and R.L. Goulding. 1974. Ectoparasites in two diverse habitats in western Oregon. I. *Ixodes* (Acarina: Ixodidae). *Journal of Medical Entomology* 11(4):413-418.
- Faulkenberry, G.D., and R.G. Robbins. 1980. Statistical measures of interspecific association between the fleas of the gray-tailed vole, *Microtus canicaudus* Miller. *Entomological News* 91(4):93-101.
- Fisher, R.A. 1941. The negative binomial distribution. *Annals of Eugenics* 11(2):182-187.
- Milne, A. 1943. The comparison of sheep-tick populations (*Ixodes ricinus* L. [sic]). *Annals of Applied Biology* 30(3):240-250.
- Robbins, R.G. 1976. A quantitative survey of the fleas associated with the gray-tailed vole, *Microtus canicaudus* Miller. Master's thesis, Oregon State Univ., Corvallis. 102 numbered pp.
- Southwood, T.R.E. 1978. Ecological methods. New York, John Wiley & Sons; London, Chapman and Hall. xxiv + 524 pp.
- Williams, C.B. 1964. Patterns in the balance of nature and related problems in quantitative ecology. Academic Press, New York and London. viii + 324 pp.



Robbins, R G and Faulkenberry, G. David. 1982. "A Population model For Fleas Of The Gray tailed Vole, *Microtus canicaudus* Miller." *Entomological news* 93, 70–74.

View This Item Online: <https://www.biodiversitylibrary.org/item/20655>

Permalink: <https://www.biodiversitylibrary.org/partpdf/26604>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Smithsonian

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: American Entomological Society

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.