Measuring aggregation of parasites at different host population levels

T. BOULINIER[1]*†, A. R. IVES[2] *and* E. DANCHIN[1]

[1] *Laboratoire d'Ecologie, C.N.R.S. – URA 258, Université Pierre et Marie Curie, 7 Quai St Bernard, 75252 Paris, France*
[2] *Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, USA*

(*Received 26 July 1995; revised 6 October 1995; accepted 4 January 1996*)

SUMMARY

Parasites are generally found aggregated among hosts. In this paper we propose a method for measuring aggregation at different scales in the host population. We use the method to characterize the pattern of aggregation of the tick *Ixodes uriae* on chicks of its seabird host, the Kittiwake *Rissa tridactyla*. We found evidence of aggregation at the among-nest scale, but not among chicks within nests. This shows that the processes leading to aggregation occur at a higher scale than the nest. The methods we develop provide a way to compare parasite aggregation at different scales in a quantitative fashion and can be applied in a large number of epidemiological studies.

Key words: aggregation, ectoparasite, heterogeneity, host–parasite interactions, *Ixodes uriae*, sampling, *Rissa tridactyla*.

INTRODUCTION

Parasites are generally found aggregated among hosts (e.g. endoparasites: Anderson & Gordon, 1982; Gregory, Montgomery & Montgomery 1992; Guyatt *et al.* 1994; ectoparasites: Randolph, 1975), and it is commonly believed that aggregation is an important feature of the population biology of these organisms. Parasite aggregation creates variability among hosts in the effects of parasites, so the net effect of parasitism on the population of hosts often depends not just on mean parasite burdens, but also on the variability of burdens. From an individual parasite's point of view, aggregation creates variability in the number of other parasites occurring in the same host. If parasites experience density dependence in reproduction or mortality, either due to direct interactions or interactions mediated through the host, then aggregation may change the parasite population growth rate. As shown theoretically, these features of parasite aggregation may have important consequences for the population dynamics of host–parasite interactions (Anderson & May, 1978; Medley, 1992).

Processes that lead to aggregated parasite distributions can be broadly divided into 2 categories: those that produce variability among hosts in exposure to parasites, and those that create variability either in host acceptability to the parasites or in host immune responses. Distinguishing between these types of processes is important for the understanding of host–parasite interactions and population dynamics (Medley, 1992). Although laboratory studies have provided insight into this problem, especially on the role of host immunity and genetics (e.g. Wasson *et al.* 1986; Gregory, Keymer & Clarke, 1990), field studies are necessary to disentangle the causes of parasite aggregation in natural populations (Munger, Karasov & Chang, 1989). However, field studies on the causes of parasite aggregation are often complicated by the myriad of confounding factors that affect host exposure rates and susceptibility to parasites.

For many host–parasite associations, a useful first step towards understanding the mechanisms of parasite aggregation can be made by determining the spatial structure of aggregation. For example, the system we examine in this article consists of a colonial bird species and parasitic ticks that attack the chicks. Aggregation of parasites among chicks within a colony could be produced by variability in parasite burdens among chicks in the same nest, variability in burdens among chicks from different nests, or a combination of these. Distinguishing between these sources of variability in parasite burdens could rule out some potential causes of parasite aggregation and implicate others.

The goal of this article is to derive a statistical procedure for measuring the pattern of parasite aggregation among hosts at 2 hierarchical scales. Two technical difficulties are solved by our procedure. First, the number of chicks per nest, and the

---

* Corresponding author: National Biological Service, Patuxent Environmental Science Center, 11510 American Holly Drive, Laurel, Maryland 20708, USA.
† Present address: National Biological Service, Patuxent Environmental Science Center, Laurel, Maryland 20708, USA.

number of ticks per chick, are often 3 or less. Other measures of aggregation, such as the variance-to-mean ratio, are biased for small sample sizes, giving estimates that are too low (Gregory & Woolhouse, 1993). Second, when comparing aggregation at different scales, it is necessary to use a measure that does not itself depend on the scale. For example, the variance-to-mean ratio depends on the mean for a wide range of mechanisms that produce aggregation (Taylor, Woiwod & Perry, 1978). The measure we derive, denoted J, is based on the viewpoint of a randomly chosen tick from the population. At the scale of parasite aggregation among chicks, J is the expected increase in the number of other ticks on the same chick relative to the case in which ticks are randomly distributed among chicks. At the scale of aggregation among nests, J is the expected increase in the number of other ticks in the same nest relative to that expected of a random distribution of ticks among nests. Thus, by basing the measure of aggregation on the perceived density of ticks from the viewpoint of a randomly chosen tick, it is possible to compare directly the degree of aggregation at different scales.

To illustrate the application of our measure of aggregation, we analyse the distribution of the tick *Ixodes uriae* on chicks of its host, the Kittiwake *Rissa tridactyla*. This example illustrates how field studies of the processes leading to parasite aggregation could benefit by determining the scale at which aggregation occurs.

MATERIALS AND METHODS

Study populations and collected data

The tick *I. uriae* parasitizes several seabird species and has a life-cycle lasting several years, depending on its host phenology and local climate (Eveleigh & Threlfall, 1974; Steele *et al.* 1990; Danchin, 1992). The tick has been shown to be a vector for several disease agents (arboviruses, Chastel 1988; the Lyme disease agent, *Borrelia burgdorferi*, Olsén *et al.* 1993), and it is thought to play a role in the population dynamics of kittiwakes (Boulinier & Danchin, 1996). The tick spends most of its life within the substrate of the seabird nesting areas, taking one long blood meal on its host per developmental stage. We determined the number of ticks feeding on chicks by thorough examination, consisting of visual inspection while palpating the skin (Danchin, 1992). This method reveals mainly nymphs and adults, as they are more conspicuous, but larvae sometimes produce local inflammations which makes them obvious even on highly feathered parts of the chick body. We checked the reliability of this method by measuring a sample of chicks twice at an interval of more than 1 week and found a highly significant repeatability (Boulinier, Sorci, Monnat & Danchin, unpublished observations).

Brood size in kittiwakes varies from 1 to 3, and usually a large proportion of the nests contain 2 chicks. Incubation lasts for 27 days, and nest duties are shared by both parents. Nests are situated on vertical cliffs, and chicks are reared in the nest for a minimum period of 35 days. Examination of all the chicks present on a breeding cliff provides data to test whether ticks are aggregated within and among nests within a host breeding cliff.

In 1987 and 1988, we conducted a large-scale horizontal survey of 700 nests in 22 colonies of British kittiwakes (details available in Boulinier & Danchin, 1996). Chicks were reached using artificial cliff-climbing devices or a hooked pole and all chicks were examined within the sampled region of a colony. As part of a long-term study of Kittiwake biology, we recorded comparable data in 1993 on the Cap Sizun Reserve, Brittany, France. On this study site the level of parasite infestation on more than 5000 Kittiwake chicks has been recorded since 1982, and the data on the spatio-temporal dynamics of the local tick population among Kittiwakes will be presented elsewhere (Boulinier, Monnat & Danchin, unpublished observations). Each host sample corresponds to the birds examined on a given breeding cliff in a given year. To detect parasite aggregation at the within and among nests levels, we considered only those samples in which a large number of chicks and nests had been examined (arbitrarily taken as samples with a minimum number of 60 chicks and 35 nests examined).

Measuring aggregation within and among nests

We present 2 methods for partitioning the aggregation of ticks among chicks occurring within nests from the aggregation occurring among nests. The first tests whether the observed distribution of ticks among chicks differs from that expected under the null hypothesis that ticks are distributed among chicks in a random fashion at both the within-nest and the among-nest scales.

Suppose there is a total of n chicks and N nests in a sample, with each nest j containing n_j chicks. Let x_{ij} denote the number of ticks found on chick i in nest j, and let X_m denote the mean number of ticks/chick pooled from all nests. The global variance of the number of ticks/chick, V, is

$$V = 1/n \sum_{j=1}^{N} \sum_{i=1}^{n_j} (x_{ij} - X_m)^2.$$

The global variance in the number of ticks/chick can be partitioned as

$$\begin{aligned} V &= 1/n \sum_{j=1}^{N} \sum_{i=1}^{n_j} (x_{ij} - X_j)^2 + 1/N \sum_{j=1}^{N} n_j (X_j - X_m)^2 \\ &= V_{wn} + V_{an}, \end{aligned}$$

where X_j is the mean number of ticks/chick in nest j, and V_{wn} and V_{an} represent the variances in the number of ticks/chick within and among nests, respectively.

The departure of V_{an} from that of a random distribution can be tested using a chi-square approximation. If ticks were distributed among chicks from different nests according to a Poisson distribution,

$$\sum_{j=1}^{N} (X_j - X_m)^2 / X_m$$

is approximately a chi-square distribution with N-1 degrees of freedom. If X_m has a value below 5, a Yates' correction should be used when testing for significant departures from random. This approximation follows from the fact that the variance-to-mean ratio for a Poisson distribution equals unity.

Testing the departure of V_{wn} from random is slightly more complex. The null hypothesis for the distribution of ticks among chicks among nests is that the number of ticks among nests is Poisson distributed, while the number of ticks on chicks in the same nest is binomially distributed. A binomial distribution is used because for a given nest, the Poisson distribution assigns the specific number of ticks. If these are distributed at random among chicks in the nest, the resulting distribution is binomial. Because within-nest aggregation can only be measured for nests with more than 1 chick and at least 1 tick, the analysis is restricted to only these nests. Let N_p denote the number of nests with at least 2 chicks and 1 tick, and let n_p denote the number of chicks in these nests. If ticks were distributed among chicks within the same nest according to a binomial distribution, with each tick having the same probability of being on any of the chicks,

$$\sum_{j=1}^{N_p} \sum_{i=1}^{n_j} (x_{ij} - X_j)^2 / (X_j(1 - 1/n_j))$$

is approximately a chi-square distribution with n_p-N_p degrees of freedom. In cases when X_j take values below 5, Yates' correction should be applied. This approximation follows from the fact that the variance-to-mean ratio for a binomial distribution for the number of ticks/chick in the same nest equals $1 - 1/n_j$.

The limitation of the analysis presented above is that it does not reveal the relative strengths of within and among nest parasite aggregation, only statistically significant departures from random. Both statistical tests are based on variance-to-mean ratios, which will likely change with mean densities (Taylor, Woiwod & Perry, 1978). Therefore, variance-to-mean ratios are difficult to compare at the within- and among-nest scales. An alternative method for measuring aggregation is the measure $\mathcal{J}$, which gives the relative increase in crowding of individuals among patches caused by aggregation (Ives, 1988, 1990). This measure is related to Lloyd's index of mean crowding (Lloyd, 1967, Pielou, 1977).

Define $\mathcal{J}_j$ as the aggregation of ticks among the chicks within nest j. For a randomly chosen tick in nest j, the expected number of other ticks on the same chick is

$$E(\text{aggregated}) = 1/n_j \sum_{i=1}^{n_j} x_{ij}(x_{ij} - 1)/X_j.$$

If the total number of ticks in a nest is known, then a random distribution of ticks among chicks is given by a binomial distribution. In this case,

$$E(\text{binomial}) = X_j - 1 + ((n_j - 1)/n_j)^2.$$

$\mathcal{J}_j$ gives the increase in the expected number of other ticks found on a chick for a randomly chosen tick:

$$\begin{aligned}\mathcal{J}_j &= \{E(\text{aggregated}) - E(\text{binomial})\}/E(\text{binomial}) \\ &= 1/n_j \sum_{i=1}^{n_j} x_{ij}(x_{ij} - 1)/\{X_j(X_j - 1 + ((n_j - 1)/n_j)^2)\} - 1.\end{aligned}$$

Thus, a value of $\mathcal{J}_j = 0{\cdot}75$ indicates a 75 % increase in the expected number of ticks on a chick than would be expected if ticks were distributed randomly among chicks in the same nest.

A similar measure can be calculated for the global level of aggregation, $\mathcal{J}$. Following from the previous argument

$$E(\text{aggregated}) = 1/n \sum_{j=1}^{N} \sum_{i=1}^{n_j} x_{ij}(x_{ij} - 1)/X_m.$$

When ticks are distributed among chicks according to a Poisson distribution,

$$E(\text{Poisson}) = X_m - 1/n.$$

Thus, the global measure of aggregation is

$$\begin{aligned}\mathcal{J} &= \{E(\text{aggregated}) - E(\text{Poisson})\}/E(\text{Poisson}) \\ &= 1/n \sum_{j=1}^{N} \sum_{i=1}^{n_j} x_{ij}(x_{ij} - 1)/\{X_m(X_m - 1/n)\} - 1.\end{aligned}$$

To give a measure of aggregation among nests, suppose the distribution of ticks among chicks in the same nest is binomial, so $\mathcal{J}_j = 0$ for all nests. In this case, the residual aggregation generated by differences among nests, $\mathcal{J}_k$, is

$$\begin{aligned}\mathcal{J}_k = 1/n \sum_{j=1}^{N} n_j\{X_j(X_j - 1 + ((n_j - 1)/n_j)^2)\} \\ \div \{X_m(X_m - 1/n)\} - 1.\end{aligned}$$

This expression is obtained from the definition of $\mathcal{J}$ by noting that in the absence of within-nest aggregation ($\mathcal{J}_j = 0$),

$$\sum_{i=1}^{n_j} x_{ij}(x_{ij} - 1) = n_j X_j(X_j - 1 + ((n_j - 1)/n_j)^2).$$

Finally, the global aggregation of ticks among chicks, $\mathcal{J}$, can be partitioned into within- and among-nest aggregation by the equality $J = J_k + EJ_j$, where EJ_j is the weighted average of within-nest aggregation,

$$EJ_j = 1/n \sum_{j=1}^{N} \{J_j n_j X_j (X_j - 1 + ((n_j - 1)/n_j)^2)\} \div \{X_m (X_m - 1/n)\}.$$

In summary, J measures the global aggregation of ticks among chicks, J_j measures aggregation within nest j, and J_k measures aggregation resulting from differences in the numbers of ticks/chick among nests. The difference between these measures, $J - J_k = EJ_j$ is the weighted average of the within-nest measure of aggregation, J_j, and provides a measure of the global within-nest aggregation for each colony. Computation of the different measures were carried out using the SAS software (SAS Institute, 1990). To test for the significant departure of the aggregation measures from values corresponding to a random distribution of the ticks within and among nests, confidence intervals under the null hypothesis of a random distribution of the ticks within and among nests were obtained. These confidence intervals were computed through Monte Carlo simulations. For each sample, 100 independent data sets were generated, and J, EJ_j and J_k were computed. Each data set was generated in 2 steps: first, a mean tick load/chick was generated randomly for each nest of the sample from a Poisson distribution with parameter X_m (the global mean of the sample); second, for each chick within each nest, the number of ticks was generated randomly from a binomial distribution using the mean tick load from the Poisson distribution. The measures obtained from these simulated data sets were sorted in ascending order for each sample, and the values of the confidence intervals were taken as the third smallest and 98th highest values obtained. An actual measure of J_k above the upper limit of the corresponding confidence interval means that ticks were aggregated among nests. An actual measure of EJ_j above the upper limit of the corresponding confidence interval means that ticks were aggregated within nests.

RESULTS

Ticks were found in all the sampled colonies, and a high proportion of the nests contained chicks with ticks (prevalence ranging from 0·49 to 0·86). Individual tick burdens/chick varied between 0 and 82. In all 7 colonies, there were high and statistically significant levels of among-nest parasite aggregation (Table 1). For 2 of the 7 sampled colonies, parasites were aggregated among chicks within nests, while within-nest aggregation was not found in the remaining 5 (Table 1). Moreover, in all colonies the estimates of J_k greatly exceeded EJ_j, showing clearly that among-nest aggregation was much stronger than within-nest aggregation (Table 1). In particular, for 3 colonies the among-nest aggregation J_k explained 99% of the total aggregation among chicks.

The level of among nest aggregation varied among colonies, but there was no evidence of a correlation with the colony mean number of ticks/chick ($n = 7$, $r^2 = 0{\cdot}002$, $P > 0{\cdot}50$). The highest among-nest aggregation was recorded for the colony with the lowest mean number of ticks/chick.

Levels of significance from the chi-square test and the tests based on the measures J_k and EJ_j were the same for all colonies except colony 'D', where the chi-square test indicated statistically significant within-nest aggregation while the confidence interval for EJ_j did not; this may be due to the small number of nests in the sample. The 2 colonies with within-nest aggregation (as determined by the chi-square test) were those with the highest mean number of ticks/chick. In these 2 colonies, the greater part of the total aggregation J resulted from among-nest aggregation, J_k (Table 1). Thus, for all colonies together, both methods show large amounts of among-nest aggregation but little evidence for within-nest aggregation.

DISCUSSION

We found evidence of a strong aggregation of *I. uriae* on chicks among nests within a colony, but not among chicks within the same nest. Thus, the important aggregative processes are operating at the among-nest scale, and research into the causes of aggregation should be focused at this scale.

Several factors may produce among-nest parasite aggregation. The spatio-temporal dynamics of tick infestation is likely to explain a large part of the among-nest aggregation. On the isle of May, the prevalence of infestation in Kittiwake colonies has been shown to be positively correlated to colony age (Danchin, 1992). Moreover, on Cap Sizun, tick prevalence increased dramatically over the course of our 11-year study from the initially low prevalence in the young colony. This highlights the importance of the local spread of ticks within colonies through time (Boulinier, Monnat & Danchin, unpublished observations). Spatial autocorrelations carried out within a cliff showed that ticks had a patchy distribution among nests, with infestation of nests close together being positively correlated (Boulinier, Monnat & Danchin, unpublished observations). Therefore, the aggregation of ticks among nests may reflect the spread of ticks from focal concentrations during the processes of colony infestation. We found no evidence of a correlation between among-nest aggregation and mean nestling parasite load, but it would be important to look at this relationship for the same cliff through time. A decrease of the among-nest aggregation would be expected in par-

Table 1. Aggregation of *Ixodes uriae* among Kittiwake *Rissa tridactyla* chicks at the within- and among-nest scales in different colonies

(J and J_k measure, respectively, the total and among nest aggregation of ticks. $EJ_i = (J - J_k)$ measures the weighted average of the within-nest aggregation of the ticks among chicks. Chi-square dispersion tests of among-nest aggregation (χ^2_{an}) and within-nest aggregation (χ^2_{wn}) of parasites are given. (n = total number of chicks/sample; N = total number of nests/sample; n_p = total number of chicks of nests with at least 2 chicks and with at least 1 parasitized; N_p = total number of nests with at least 2 chicks and with at least 1 parasitized; X_m = mean number of ticks/chick (global mean); P = prevalence (proportion of nests with at least 1 parasitized chick); (c.i.) = Confidence intervals at 96 % under the null hypothesis of no within- nor among-nest aggregation.))

							J measures				Chi-square values†			
Colony sample	n	N	n_p	N_p	X_m	P	J	J_k (c.i.)	EJ_j (c.i.)	J_k/J	χ^2_{an}	(D.F.$_{an}$)	χ^2_{wn}	(D.F.$_{wn}$)
'21'	67	37	28	14	0·90	0·49	9·49	9·34 (−0·44,1·41)	0·14 (−0·27,1·07)	0·99	541·79***	(36)	7·77 N.S.	(14)
'31'	81	49	50	24	1·74	0·80	1·34	1·06 (−0·28,0·83)	0·28 (−0·25,0·49)	0·79	121·41***	(48)	24·82 N.S.	(26)
'33'	198	126	127	62	1·88	0·86	0·47	0·38 (−0·08,0·28)	0·09 (−0·20,0·37)	0·82	134·42***	(125)	43·66 N.S.	(63)
'46'	87	50	49	24	2·20	0·66	2·28	2·11 (−0·29,0·59)	0·18 (−0·15,0·43)	0·92	197·90***	(49)	32·07 N.S.	(25)
'D'	71	52	20	10	5·96	0·61	4·44	4·39 (−0·23,0·30)	0·04 (−0·07,0·17)	0·99	1756·30***	(51)	25·54**	(10)
'E'	71	54	21	10	2·42	0·48	4·58	4·25 (−0·30,0·42)	0·33 (−0·15,0·22)	0·93	567·57***	(53)	27·88**	(11)
'P'	62	54	10	5	1·45	0·54	2·78	2·78 (−0·25,0·40)	0·00 (−0·11,0·23)	1·00	466·70***	(53)	1·33 N.S.	(5)

† Chi-squares were computed with Yates correction. D.F.$_{an}$ = degrees of freedom for the chi-square among nests ($= N-1$). D.F.$_{wn}$ = degrees of freedom for the chi-square within nests ($= n_p - N_p$).

** Significantly aggregated ($P < 0·01$).

*** Significantly aggregated ($P < 0·001$).

N.S. Not significantly aggregated ($P > 0·05$).

allel to a local increase in the parasite population if the local spread of parasites explains a large part of the pattern of aggregation observed.

Spatial heterogeneity in the cliff substrate may also result in the aggregation of ticks among nests. Temperature and humidity are known to affect tick survival between feeding bouts on chicks (Needham & Teel, 1991), and the infestation rate of ticks in a particular nest may depend on the local microclimate. Moreover, variability in the cliff substrate might provide varying quality of refuges from predation for the ticks (Duffy, 1983). Thus, studies can be performed to correlate characteristics of the cliff substrate with infestation rates within nests.

Population heterogeneity in host susceptibility and parasite infectivity may also partly explain differences of mean parasite loads among nests. Aggregation of ticks among nests may indeed result from the similarities of the chicks within the same nests. The prevalence of tick infection is lower on younger (below 5 days) and older (above 25 days) chicks (Boulinier & Danchin, 1996). Because chicks in the same nest tend to be of similar age, this could explain some of the variability in infection rates among nests, notably the one due to the different lengths of exposure to the ticks or to the delay of mounting an effective response. Also, chicks within the same nests are siblings and therefore may show a similar inherited susceptibility. Parent–offspring regressions carried out on the long-term Cap Sizun data set suggest an heritable susceptibility to the tick *I. uriae* in the Kittiwake population (Boulinier, Sorci, Monnat & Danchin, unpublished observations). In some cases, dissimilarities of the chicks of the same nest may result in within-nest aggregation.

Determining the spatial scale of aggregation has narrowed the search for processes creating tick aggregation among Kittiwake chicks. In many epidemiological studies, the scale of aggregation is never investigated. Sometimes, data from different samples are even pooled together, and aggregation is measured thereafter (e.g. see Grafen & Woolhouse (1993) for a discussion of the consequences of data pooling of variables following negative binomial distributions). The methods we have presented here provide an easy and understandable way of measuring aggregation across different scales, and for some epidemiological studies our methods may aid in identifying the processes producing parasite aggregation. This has direct implications for the understanding of parasite transmission in natural populations.

We would like to thank J. C. Coulson, R. D. Gregory, C. Guiguen, M. Hochberg, Y. Michalakis, J. Y. Monnat, R. Nordheim, and G. Sorci for their help at different stages of this work. Moreover, two anonymous referees made useful comments on a previous version of the manuscript. We thank the S.E.P.N.B. (Société d'Etude et de Protection de la Nature en Bretagne) for allowing us to work on the Cap Sizun Reserve. Field work was financed in Great Britain by The Royal Society and the French Embassy in London, and in France by the S.R.E.T.I.E, Ministère de l'Environnement. T.B. was in receipt of a Fellowship from the Ministère de la Recherche et de la Technologie.

REFERENCES

ANDERSON, R. M. & GORDON, D. M. (1982). Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. *Parasitology* **85**, 373–98.

ANDERSON, R. M. & MAY, R. M. (1978). Regulation and stability of host–parasite population interactions. I. Regulatory processes. *Journal of Animal Ecology* **47**, 219–47.

BOULINIER, T. & DANCHIN, E. (1996). Population trends in Kittiwake *Rissa tridactyla* colonies in relation to tick infestation. *Ibis* (in the Press).

CHASTEL, C. (1988). Tick-borne virus infections of marine birds. In *Advances in Disease Vector Research* Vol. 5 (ed. Harris, K. F.), pp. 25–60. New York: Springer-Verlag.

DANCHIN, E. (1992). The incidence of tick parasite *Ixodes uriae* in Kittiwake *Rissa tridactyla* colonies in relation to the age of the colony, and a mechanism of infecting new colonies. *Ibis* **134**, 134–41.

DUFFY, D. C. (1983). The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* **64**, 110–19.

EVELEIGH, E. S. & THRELFALL, W. (1974). The biology of *Ixodes* (*Ceratixodes*) *uriae* White, 1952 in Newfoundland. *Acarologia* **16**, 621–35.

GRAFEN, A. & WOOLHOUSE, M. E. J. (1993). Does the Negative Binomial Distribution add up? *Parasitology Today* **9**, 475–7.

GREGORY, R. D., KEYMER, A. E. & CLARKE, J. R. (1990). Genetics, sex and exposure: the ecology of *Heligmosomoides polygyrus* (Nematoda) in the wood mouse. *Journal of Animal Ecology* **59**, 363–78.

GREGORY, R. D. & MONTGOMERY, S. S. J. & MONTGOMERY, W. I. (1992). Population biology of *Heligmosomoides polygyrus* (Nematoda) in the wood mouse. *Journal of Animal Ecology* **61**, 749–57.

GREGORY, R. D. & WOOLHOUSE, M. E. J. (1993). Quantification of parasite aggregation: a simulation study. *Acta Tropica* **54**, 131–9.

GUYATT, H. L., SMITH, T., GRYSEELS, B., LENGELER, C., MSHINDA, H., SIZIYA, S., SALANAVE, B., MOHOME, N., MAKWALA, J., NGIMBI, K. P. & TANNER, M. (1994). Aggregation in schistosomiasis: comparison of the relationships between prevalence and intensity in different endemic areas. *Parasitology* **109**, 44–55.

IVES, A. R. (1988). Aggregation and coexistence of competitors. *Annales Zoologici Fennici* **25**, 75–88.

IVES, A. R. (1990). Aggregation and coexistence in a carrion fly community. *Ecological Monographs* **61**, 75–94.

LLOYD, M. (1967). Mean crowding. *Journal of Animal Ecology* **36**, 1–30.

MEDLEY, G. F. (1992). Which comes first in host–parasite systems: density dependence or parasite distribution. *Parasitology Today* **8**, 321–2.

MUNGER, J. C., KARASOV, W. H. & CHANG, D. (1989). Host genetics as a cause of overdispersion of parasites among hosts: how general a phenomenon. *Journal of Parasitology* **75**, 707–10.

NEEDHAM, G. R. & TEEL, P. D. (1991). Off-host physiological ecology of ixodid ticks. *Annual Review of Entomology* **36**, 659–81.

OLSEN, B., JAENSON, T. G., NOPPA, L., BUNIKIS, J. & BERGSTRÖM, S. (1993). A Lyme borreliosis cycle in seabirds and *Ixodes uriae* ticks. *Nature, London* **362**, 340–2.

PIELOU, E. C. (1977). *Mathematical Ecology*. New York: John Wiley & Sons.

RANDOLPH, S. E. (1975). Patterns of distribution of the tick *Ixodes trianguliceps* Birula on its hosts. *Journal of Animal Ecology* **44**, 451–74.

SAS INSTITUTE INC. (1990). *SAS User's manual*. Cary, NC, USA.

STEELE, M., DAVIES, C. R., JONES, L. D., NUTTALL, P. A. & RIDEOUT, K. (1990). Life history of the seabird tick *Ixodes (Ceratixodes) uriae* at St Abb's Head, Scotland. *Acarologia* **31**, 125–30.

TAYLOR, L. R., WOIWOD, I. P. & PERRY, J. N. (1978). The density-dependence of spatial behavior and the rarity of randomness. *Journal of Animal Ecology* **47**, 383–406.

WASSON, D. L., DICK, T. A., ARNASSON, N., STRICKLAND, D. & GRUNDMANN, A. W. (1986). Host genetics: a key factor in regulating the distribution of parasites in natural host populations. *Journal of Parasitology* **72**, 334–7.