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"Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review"

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Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review

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SUMMARY

In this paper we review the published literature on patterns of abundance and aggregation of macroparasites in wildlife host populations. We base this survey on quantitative analyses of mean burden and a number of measures of the degree of aggregation of parasite burdens between hosts. All major parasite and vertebrate host taxa were represented in the database. Mean parasite burden was found to be log-normally distributed, indicating that all parasite burdens are regulated to some degree. In addition, all but one of the parasitic infections were aggregated with respect to their hosts, and the relationship between log mean parasite burden and log variance was found to be very strong ($R^2 = 0{\cdot}87$). That is, for a given mean parasite burden there are constraints on the degree of variation in individual host burdens. The aggregated nature of the parasitic infections is also apparent from other measures of the degree of aggregation: prevalence – mean relationships, and the negative binomial parameter, k. Using a relatively new technique for parasitological infection data – tree-based models, as well as traditional linear models – a number of the parasitic infections was found to be associated with systematically lower or higher parasite burdens. Possible biological explanations for these and other patterns are proposed.

Key words: macroparasites, aggregation, negative binomial, distribution, worm burden, population dynamics.

INTRODUCTION

Aggregation is very widespread in ecological populations (Taylor, 1961; Taylor & Taylor, 1977; Taylor, Woiwod & Perry, 1978; Anderson *et al.* 1982). Aggregation is characterized by the estimated *variance to mean ratio* (hereafter denoted by $s^2/\bar{x}$). A variance equal to the mean would indicate a completely random (Poisson) distribution. If the estimated $s^2/\bar{x}$ is significantly greater than unity, the distribution is *aggregated*, i.e. individuals tend to be clumped in sampling units.

The importance of aggregation to the dynamics of animal populations in general has been the focus of much theoretical work. For example, in insect populations, spatial aggregation has been shown to enhance density-dependent processes, provide potential refuges for prey, and allow apparently competing species to co-exist in the same habitat (Skellam, 1951; Hassell, Comins & May, 1991).

The distribution of macroparasites between hosts is also characteristically aggregated (e.g. Crofton, 1958; Crofton, 1971*a*, *b*; Pennycuick, 1971; Anderson & May, 1978, 1979*a*; Anderson & Gordon, 1982; Dietz, 1982; Dobson, 1985; Grenfell, Smith & Anderson, 1987; Pacala & Dobson, 1988; Guyatt & Bundy, 1991; Bundy & Medley, 1992). This aggregation is frequently represented by the negative binomial distribution, where an inverse measure of aggregation, k, together with the mean, is used to describe the distribution of parasites between hosts (e.g. Bregev, 1973*a*; Boxshall, 1974; Kennedy, 1984; Anderson & May, 1991). However, to date there have been no systematic comparative analyses of the observed distribution patterns in natural infections of wildlife, despite a large literature.

This aggregation of parasites leads to an increase in the effective density that each parasite experiences. Anderson & Gordon (1982) and Grenfell *et al.* (1995), this volume, present reviews of some of the processes likely to generate aggregated distributions in hosts. In a homogeneous host population infected randomly by parasites, theory points to a Poisson distribution of parasites (Pacala & Dobson, 1988). The widely observed aggregation in parasite burden arises from *heterogeneities* in host populations or in infection pressure. These heterogeneities are generated by changes in the climate over time or space; genetic differences between hosts in terms of parasite induced host mortality (Anderson & May, 1979*b*); heterogeneity in infection levels, because of host behaviourial or physiological (age, sex) differences, or even variation in the number of infectious stages encountered per infection event. In general the smaller the difference between hosts for the above (and other) factors the less the degree of aggregation. However, the dynamic effects of aggregation depend on its interaction with density-dependent processes (Anderson & Gordon, 1982; Medley, 1992). In particular, a highly aggregated distribution 'concentrates' the effect of density-dependent limitation on parasitism, leading to a potentially stabilising influence (Anderson & May, 1978; May & Anderson, 1978; Grenfell, 1988; Grenfell, 1992; Grenfell & Dobson, 1995).

Here we report a comparative study, that attempts

to disentangle the effects of changes in mean burden from changes in heterogeneity around this mean. In particular, we have considered how abundance and aggregation vary between very diverse groups of wildlife host-parasite systems. The aim is to establish whether: (a) there are general underlying trends in observed patterns of abundance and aggregation and (b) question whether specific taxonomic or ecological groups appear to differ from these underlying trends? The former set of results can give us information about whether there are constraints on parasite abundance and aggregation, and the latter can perhaps give indications as to what these constraints might be. With such comparative analyses we can only ever detect associations between biological factors and worm burdens. However, these analyses may provide pointers for more specific experimental and theoretical work.

In the next section we introduce the analytical methods used in this paper, as well as providing a brief discussion of the characterization of parasite data. We then describe the database used in the analyses. The results section is divided into two parts: (i) general patterns of mean burden and aggregation; (ii) examination of specific host-parasite infections. All the results are then brought together in the discussion.

METHODS

Characterization of parasite data

The fundamental description of parasite burden data is the (inherently) discrete *frequency distribution* of parasite counts between hosts. The statistical distribution which has provided an excellent empirical fit to the aggregated data for macroparasites, is the negative binomial distribution. It provides the basis of a large part of published theoretical work on the interaction between parasites and hosts (e.g. Crofton, 1971*a*; Pennycuick, 1971; Anderson, & May, 1978; May & Anderson, 1978; Anderson & Gordon, 1982; Keymer, 1982*a*; Bundy *et al.* 1985; Scott, 1987; Pacala & Dobson, 1988; Grenfell *et al.* 1990; Smith & Grenfell, 1994).

The negative binomial is characterized by two parameters: the mean and k, an inverse measure of the degree of aggregation (Bliss & Fisher, 1953). Fig. 1 provides a graphical illustration of the excellent nature of this fit to many parasite distributions. In all four cases illustrated, the estimated negative binomial frequency distribution does not significantly differ from the observed parasite frequency distribution (analyses of deviance, $P > 0{\cdot}1$); whereas the estimated Poisson frequency distribution always differs significantly ($P < 0{\cdot}001$).

While moment estimates of k can be used to give an indication of the degree of aggregation in parasite burdens when the mean parasite burden is relatively large (> 1) (Shaw, Grenfell & Dobson, unpublished), we really require the complete observed frequency distributions for accurate maximum likelihood estimation. In the main, such distributions are not provided in the published literature. Therefore, three simple summary measures of distribution structure are used to make broad comparisons between parasite data: the arithmetic mean burden, $\bar{x}$ (the basic measure of macroparasite intensity (Anderson & May, 1991; Bundy & Medley, 1992)); the sample variance, s^2 (the dispersion of parasites between hosts) and the prevalence of infection, p. The latter is the easiest obtainable measure of the level of parasitism (for example, by scoring the presence of parasite eggs in host faeces). However, it gives much less information than the mean about the intensity of parasitism, and is especially sensitive to false negatives (Williams, 1963).

Statistical analysis of parasite burdens

Mean parasite burden. The calculated mean parasite burdens in the database are from very diverse systems, and the associated data values encompass several orders of magnitude. In addition, the distribution of mean values are highly skewed: overall average 79·5, 25% quartile 0·57, and 75% quartile 10·3. That is the overall average is greater than the 75% quartile. Therefore mean parasite burden was $\log_{10}$ transformed (hereafter log) which normalised the data. Standard unbalanced analysis of variance and covariance was used to examine patterns of log mean parasite burden, weighted by host sample size. Any significant variation in log mean burden between hosts was examined using a simple yet powerful method – category deletion analysis (Chambers & Hastie, 1992): particular groups of infections are excluded, and the analysis re-run. If there is no longer significant variation in log mean parasite burden, the data for the species excluded from the analysis are then said to be associated with significant variation in mean burden.

Prevalence-mean analysis. The relationship between prevalence of infection and mean parasite burden has been used to estimate the degree of aggregation in particular helminth infections of humans (Anderson & May, 1985*a*, Guyatt *et al.* 1990). The technique involves using the zero probability term of the negative binomial distribution:

$$p = (1 + \bar{x}/k)^{-k}.$$

This equation is then fitted to the observed prevalence-mean data using a standard binomial maximum likelihood technique proposed by Guyatt *et al.* (1990). The aim of this set of analyses was to extend the work of Anderson & May 1985*a* and Guyatt *et al.* (1990) to consider parasite infections in animal populations.

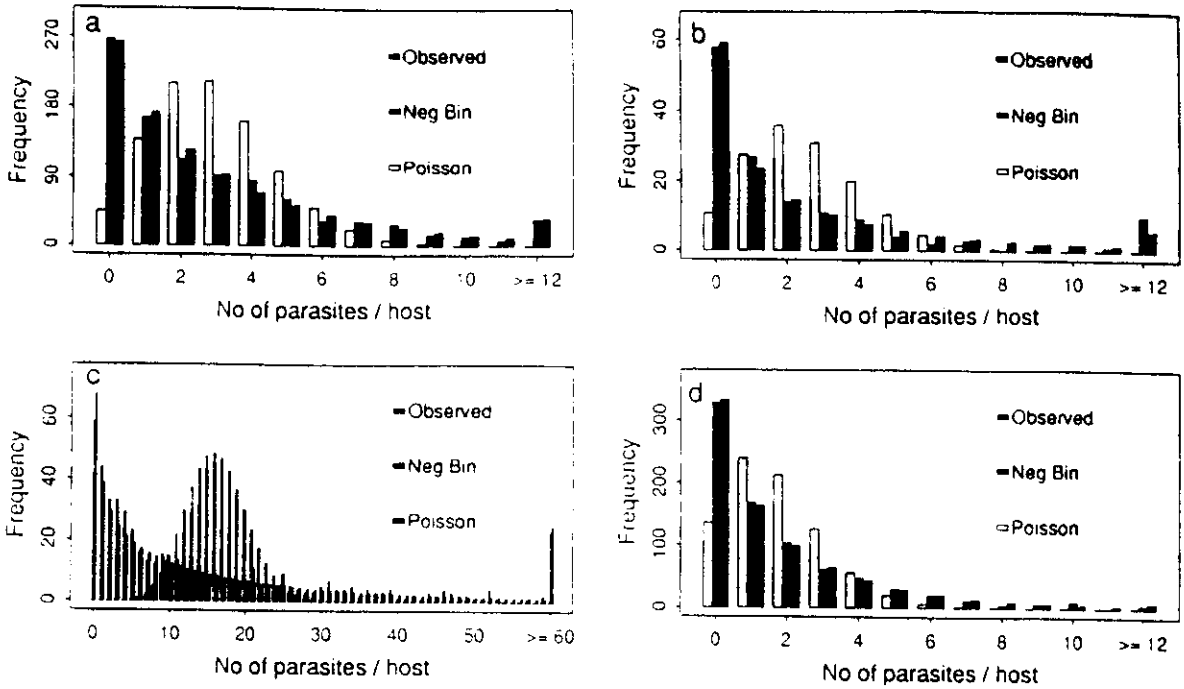

Fig. 1. Observed parasite frequency distributions in a number of different hosts, compared with expected distributions based on Poisson and negative binomial fits, estimated by maximum likelihood techniques. (a) Gastropod, *Valvata piscinalis*, infected by *Echinoparyphium recurvatum* (Digenea: Echinostomatidae, (Evans *et al.* 1981)); Poisson goodness of fit to observed frequency distribution: $\chi^2 = 1896{\cdot}4$, D.F. = 8, $P < 0{\cdot}001$; Negative binomial fit: $\chi^2 = 23{\cdot}26$, D.F. = 16, $P < 0{\cdot}107$. (b) Gnat, *Culicoides crepuscularis*, infected by *Chandlerella quiscali* (Nematoda: Filarridae (Schmid & Robinson, 1972)); Poisson fit: $\chi^2 = 270{\cdot}7$, D.F. = 6, $P < 0{\cdot}001$; Negative binomial fit: $\chi^2 = 7{\cdot}35$, D.F. = 8, $P < 0{\cdot}5$. (c) Sheep, *Ovis domestica*, infected by *Ixodes ricinus* (Arthropoda: Ixodida (Milne, 1943)); Poisson fit: $\chi^2 = 1597{\cdot}2$, D.F. = 18, $P < 0{\cdot}001$; Negative binomial fit: $\chi^2 = 40{\cdot}76$, D.F. = 41, $P < 0{\cdot}481$. (d) Crayfish, *Orconectes rusticus*, infected by *Paragonimus kellicotti* (Digenea: Paragonimadae (Stromberg *et al.* 1978)); Poisson fit: $\chi^2 = 722{\cdot}5$, D.F. = 6, $P < 0{\cdot}001$; Negative binomial fit: $\chi^2 = 11{\cdot}5$, D.F. = 11, $P < 0{\cdot}402$.

Variance/mean analysis. Taylor and others (Taylor, 1961; Southwood, 1966; Pielou, 1969; Elliot, 1977; Taylor & Taylor, 1977; Taylor *et al.* 1978; Taylor & Woiwod, 1980; Anderson *et al.* 1982) have provided considerable ecological data supporting the notion that the relationship between the variance and mean of an organism's ecological distribution is related by a power law:

$$s^2 = 10^a \bar{x}^b.$$

The result is an expected linear relationship between $\log_{10}$ variance and $\log_{10}$ mean (hereafter $\log s^2$ and $\log \bar{x}$) – i.e. $\log s^2 = a + b \log \bar{x}$. In this paper, we present this relationship for the infections in the database. We also extend this idea to examine variability in the degree of aggregation between particular infections. The basic idea is the same as for mean parasite burden – the change in significance in linear models of covariance, associated with the exclusion of particular infections. However, in this case we have two types of result: (i) particular infections can be associated with consistent differences in the degree of aggregation over a range of mean; (ii) the degree of aggregation significantly changes as mean parasite burden increases.

There are other qualitative analytical methods which could be used to describe aggregation in animals (Lloyd, 1967; Pólya, 1931; Neyman, 1939; Preston, 1948; Thomas, 1949; Bailey, 1959; Cassie, 1962; Williams, 1964), however these are of limited use in host-parasite dynamics for two main reasons. First, many of the proposed distributions are too complex or multi-modal, which restricts their application and makes biological relevance and interpretation very difficult (Crofton, 1971*a*). Secondly, in some distributions, notably Williams logarithmic series (1964) no account of uninfected individuals is included in the distribution. This exclusion of uninfected hosts is a major biological problem when apply a distribution to data for parasites and their hosts: in many host-parasite systems uninfected hosts represent one of the main sources of information on the distribution of parasites, because this group of hosts are the easiest to count (Crofton, 1971*a*).

Tree-based statistical models. This paper uses a relatively new technique to analyse some of the observed patterns in mean parasite burden: tree-based statistical models (Sonquist & Morgan, 1964; Breiman *et al.* 1984; Clark & Pregibon, 1992). They provide a graphical alternative to the linear regression models described above. As with linear models, tree-based models involve a dependent

variable (in this case log mean parasite burden) and a series of independent factors. At a particular level of analysis, we make a binary division of the data, between groups of categories, which produces the best fit to the data. In practice, this involves an interactive maximum likelihood procedure which attempts to maximize the deviance resulting from a multinomial distribution, to determine which binary partition is 'most likely' given the data (Fisher, 1958; Ciampi *et al.* 1987; Clark & Pregibon, 1992) around this problem.

This approach is readily extendable to many factors and the result is a tree which gives an optimal hierarchy of the different factors. The great advantage of tree-based models is that it does not matter in which order the factors are put into the model. Once the first binary division has been determined, the tree algorithm then determines which partition is the next most important. Tree-based models do not explicitly allow for interactions between factors. However, by recursive partitioning down through the various levels, they do allow a graphical illustration of the interaction structure of the data, in terms of the various independent factors. The result is a tree which gives an optimal hierarchy of the different factors.

THE DATABASE

In order to investigate the general patterns in parasite load and aggregation, data were collected from a large variety of published host-parasite systems in the wild. Indirect measures of worm burden – such as faecal egg counts or circulating antigen levels – were not included in the database. This is because the relationship between such measures and the actual worm burden present in the host are very complex and compound each other. Host-parasite systems were included when at least $\bar{x}$, μ, s^2, and an estimate of k, the degree of aggregation of parasites in hosts, had been given. Where the full parasite frequency distribution was published, this too was included. The minimum host sample size was set to 30 in order to reduce the effects of sampling error, a potential problem when trying to estimate the degree of aggregation (Anderson & Gordon, 1982).

It is very unlikely that compiling such a database will result in equal representation of the full diversity of host-parasite systems. That is, we have to operate with an unbalanced database, where not all types of interaction are represented equally. This lack of balance will in turn determine which analyses can be performed and the conclusions that should be drawn from them. In an attempt to reduce the potential problem of imbalance, a small number of host-parasite systems were excluded from the final database. If a particular type of host-parasite system (e.g. monogenean infections, or infection of invertebrate hosts) was represented by five or less data points, these systems were excluded. In consequence, the database does not represent the full range of parasitic infections, it is rather a representation of host-parasite systems that are relatively frequently published. However, this collection (Appendix A) does represent the largest comparative data-set on wildlife parasite distributions presented to date. As an illustration of its diversity, Fig. 2 presents a taxonomic tree showing which parasite groups are represented in the database. The figure also includes the relative frequency of the parasite genera in the database, i.e. most of the published literature on macroparasite infections involve platyhelminth and nematode infections.

Ecological and physiological processes involved in infections

In addition to the statistical parameters, a number of ecological and physiological characteristics of host or parasite species have been included in the database (Appendix A). Potentially there are a large number of possible host and parasite factors that might be important in influencing patterns of abundance and aggregation and therefore should be included in the database. In the analyses presented here we have attempted to keep these categories as broad as possible. This is because we are interested in looking at the general patterns of abundance and aggregation as opposed to very specific examination of individual systems. These factors are summarized in Table 1. A simple coding system is adopted. [For example, in Infection process *T:prey* refers to those infections where *Transmission* is via the consumption of infected *prey*, and so on]. The different factors included in the analysis are briefly outlined below:

Parasite type – Ectoparasite burdens will be limited by the surface area of the host's exterior available to infection (hair, gills); whereas endoparasite burdens will be constrained (ultimately) by the 'internal' volume they inhabit (gut, muscle, liver *etc.*). Differences in ectoparasite burdens may result from differential exposure to changes in the external environment. Endoparasites, on the other hand, may experience heterogenous host immune responses (because of genetic, nutritional or immunocompetence differences).

Parasite taxonomic class – Parasites have been classified into various taxonomical groups. All members of a particular group share certain unique characteristics. If these identifying features are involved in infections, then systematic differences in abundance and aggregation between parasite groups might be expected.

Host type – In this paper we have coarsely divided host type into the major vertebrate genera, though

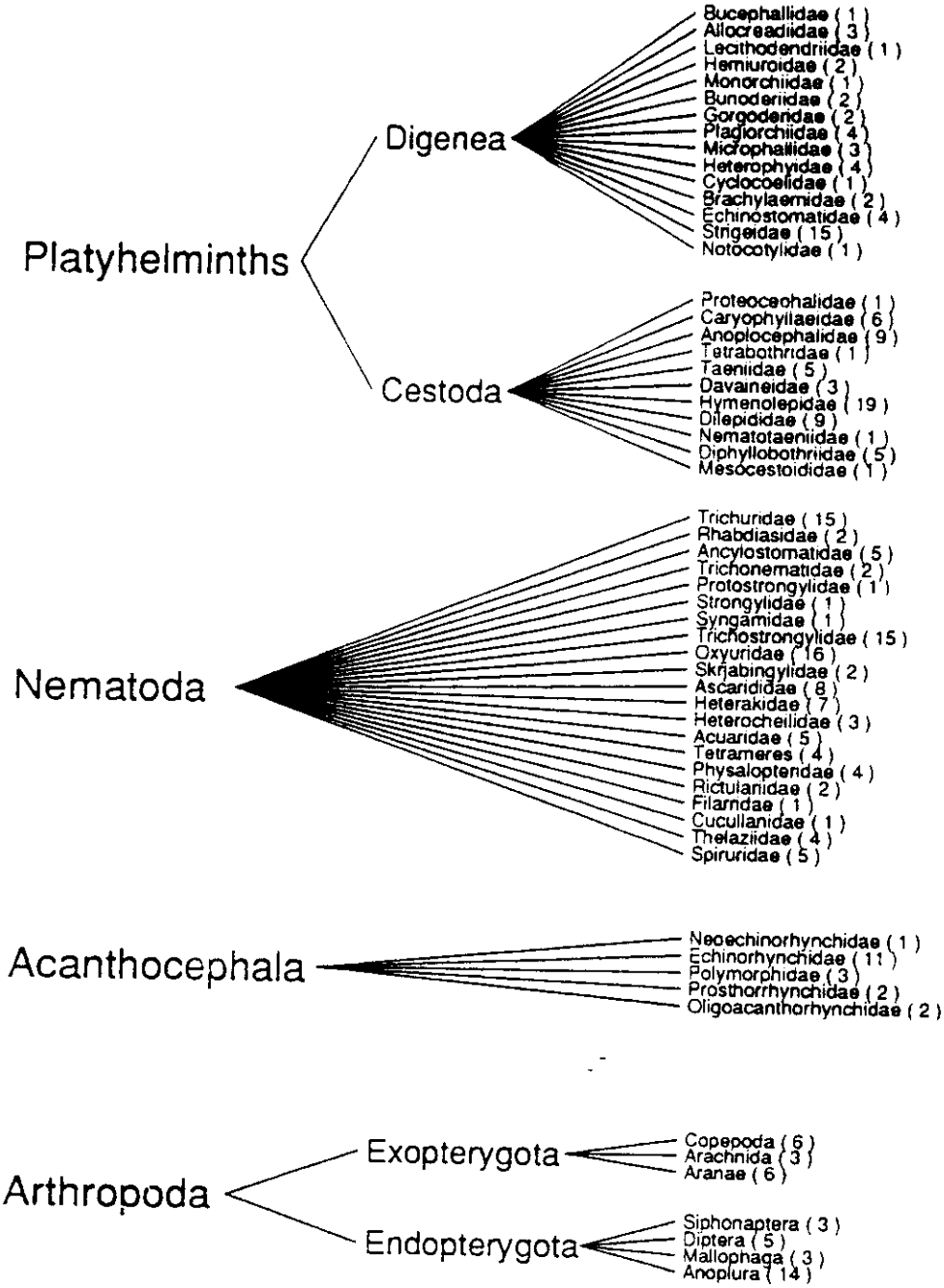

Fig. 2. Taxonomic tree of the parasite infections in the database. The numbers in brackets, at the end of each node denote how many of that parasite group are present in the database.

more subtle divisions could be used. The type of host infected might be expected to result in differences in worm burden – perhaps through the influence of greater immunity (mammals) or types of diet.

Number of hosts in the life cycle – The transmission processes involved in any one infection will depend on the number of hosts in the life cycle. A life cycle involving more than one host is likely to involve more than one type of infection process, in order that parasites can infect the different host types. Such complexity is likely to result in different patterns of burdens, than those infections only involving one host. Therefore, we might expect that abundance and aggregation will depend on the complexity of any one parasite system.

Definitive/intermediate hosts – For the purposes of this paper we have defined *definitive* hosts as those hosts where egg production occurs, and *intermediate* hosts as the other hosts in the life cycle. Because of the relatively few 1st intermediate hosts that were found in the literature review, only second intermediate hosts are included in the database.

Host habitat – The host habitat will determine the type of host present, and therefore may alter which

Table 1. Summary of host-parasite independent variables in the database. The numbers indicate the number of systems in the database of each category

Parasite type	
PT: endoparasite	223
PT: ectoparasite	40

Number of hosts in life cycle	
Hsts: 1	109
Hsts: 2	99
Hsts: 3	55

Infection process	
T: active.larvae	26
T: active.adult	34
T: passive	61
T: prey	142

Parasite taxonomic class	
P: Digenea	44
P: Cestoda	57
P: Nematoda	104
P: Acanthocephala	18
P: Exopterygota	15
P: Endopterygota	25

Definitive vs. second intermediate	
definitive = Def: y	246
second intermediate = Def: n	17

Host migratory behaviour	
migratory = Mig: y	65
non migratory = Mig: n	198

Host type	
H: fish	46
H: fish	15
H: fish	80
H: fish	122

Host habitat	
Hab: marine	31
Hab: fresh	73
Hab: terr	159

parasites are present, and at what levels. In particular habitat may have a crucial effect on the spatial distribution of the infective stages. Thus infections involving infective stages released into a flowing stream from freshwater snails may result in very different burdens and patterns of aggregation, from those involving infective stages present in the bodies of terrestrial beetles.

Transmission process – (i) An active parasite larval stage actively seeks out and infects the host; (ii) Active adult; (iii) The host passively consumes infectious parasite stages present on vegetation during normal feeding; (iv) The host consumes a prey item which contains an infectious parasitic stage.

Host migratory behaviour – hosts undergoing seasonal migration away from a particular habitat may have lower burdens, from those that do not migrate. This has been demonstrated with an association between host migration distance and lower burdens in warble fly infections of reindeer (Folstad *et al.* 1991). All hosts in the database, were therefore classified as either migratory or not.

There are other possible categories that could be included in the database. For example, the size of a parasite, the number of eggs produced and the effect of crowding due to conspecifics as well as other parasite species could all be important in determining parasite burdens. However, precise information of this sort is not usually readily available and there are problems relating to, for example, the reduction in parasite size and egg production due to host immunity (Michel, 1963), or arrestment of parasitic stages – occupying space but not producing eggs.

Another potentially important factor not included here is some measure of host volume/surface area. Parasite burdens are ultimately constrained by the volume/surface area of the host (or the volume/surface area of the particular site of infection, e.g. the liver for *Fasciola hepatica*). However, it was not possible to estimate the volume or surface area of all the hosts in the database and therefore initial analyses used a more approximate measure – host weight. The assumption is that host weight is related to both volume and surface area and provides an index of the amount of 'space' available for infection. There was a significant positive relationship between log mean parasite burden and log host weight ($P < 0{\cdot}001$, $R^2 = 0{\cdot}07$)). However, this relationship was very variable; for a given host weight observed mean parasite burdens varied over several orders of magnitude. This result either indicated that host volume, as represented by host weight, is not important in

determining burdens, or (more likely) we need a better measure of host tissue available to the parasite as a potential site of infection. Therefore, no further analyses on host weight was performed.

RESULTS

Overall comparative patterns

Mean parasite burden. Fig. 3 presents a histogram of the log mean parasite burdens observed for the entire database. The equivalent frequency distribution of a fitted log normal distribution, with the same average and standard deviation as the observed log mean parasite burden, is included on the graph. There is no significant difference between the two distributions (χ^2 value = 20·003, D.F. = 18, $P < 0{\cdot}33$). That is, mean parasite burden can be assumed to be distributed log normally. This result reflects a general feature of species abundance data: free-living organisms tend to be log normally distributed in their habitats (May, 1975). Log normal distributions are generated by the conjunction of a variety of independent factors acting on species. In terms of host-parasite systems, these factors are likely to be: transmission rates of parasites between hosts; mortality rates of the different parasitic stages; influence of climate and temperature of parasite life cycles; parasite egg production rates; and the severity of density dependence in hosts (Keymer, 1982*a*). Different parasite species have evolved a number of mechanisms to facilitate this transmission to a wide variety of hosts in many diverse habitats.

Despite this heterogeneity between systems, there appears to be a general constraint on the levels of mean abundance: 90% of infections have mean abundances between 0·1 and 100. Clearly there is a minimum abundance level below which parasite species cannot persist over time, i.e. a transmission threshold (Anderson, 1980; Keymer, 1982*a*). In a given infection there also is a maximum abundance level which reflects the maximum transmission rates possible. The fact that less than 5% of the observed mean burdens are greater than 100 worms implies that large burdens are only associated with a few specific host-parasite interactions. In the next section these, and those systems with relatively low burdens, will be considered in detail. Such infections should represent the limits of abundance levels possible in hosts.

Sampling effort may make a major contribution to the tails of the observed log normal distribution. At one extreme very few systems will have been examined where mean burdens are less than one worm in 1000 hosts. At the other, the counting of several thousand parasites per host is very time intensive. That is, the data presented here do not represent the actual distribution of mean parasite burdens, rather the majority of systems. Nee, Harvey & May (1991) highlighted this problem in other animal abundance data, which showed an apparently truncated log normal distribution – rare species were apparently under-represented. However, in the log parasite abundance data presented here there is a very good fit to a log normal distribution. Therefore, in this database, possible biases in estimation of parasite burdens do not appear to be significantly altering the overall observed pattern.

Prevalence of infection and mean parasite burden. The overall relationship between prevalence of infection and log mean parasite burden is presented in Fig. 4. The relationship, essentially a rapid rise with burden to a high asymptotic prevalence, is in general agreement with published work on human infections (e.g. Guyatt *et al.* 1990; Guyatt & Bundy, 1991; Booth & Bundy, 1992; Medley *et al.* 1993*a*, *b*). However, whilst low prevalence is associated with low mean burdens, as burdens increase prevalence can vary markedly. For example, at a mean burden of 10 parasites per host, the prevalence ranges between 10% and 100%. As described in the methods, the relationship between mean parasite burden and prevalence can potentially be used as an estimate of the degree of aggregation. Unfortunately, the large variability in mean burden shown in Fig. 4, and the large range in sample sizes (which greatly influence any maximum likelihood estimation) make estimating the degree of aggregation from prevalence of little quantitative use and therefore no further analysis of mean parasite burden and prevalence is presented.

Dispersion pattern of parasites between hosts. As described in a previous section, the ratio of variance in worm burden to the mean parasite burden can be used to indicate the dispersion pattern of parasites between hosts. From the 269 host-parasite systems in the database all but one have $s^2/\bar{x}$ significantly greater than unity, indicating significant aggregation compared to a Poisson distribution. This result provides very strong support for the notion that parasites are in general aggregated in their hosts. The only exception is an infection of a 2nd intermediate host the Perch, *Perca fluviatilis*, infected by the cestode *Triaenophorus nodulosus* (Chubb, 1964), where the $s^2/\bar{x} = 1{\cdot}053$. Possible reasons for this discrepancy include the amalgamation of different age classes or seasonal changes in infection by the consumption of infected invertebrates.

The variance/mean relationship for parasite burden. Fig. 5 presents a plot of $\log s^2$ against $\log \bar{x}$ for the database, and shows a tight linear relationship. The estimated slope of the relationship ($b = 1{\cdot}55 \pm 0{\cdot}037$ S.D.) is significantly greater than one, again indicating that parasites are aggregated in their hosts (Taylor, 1961). This value is also in broad agreement with the

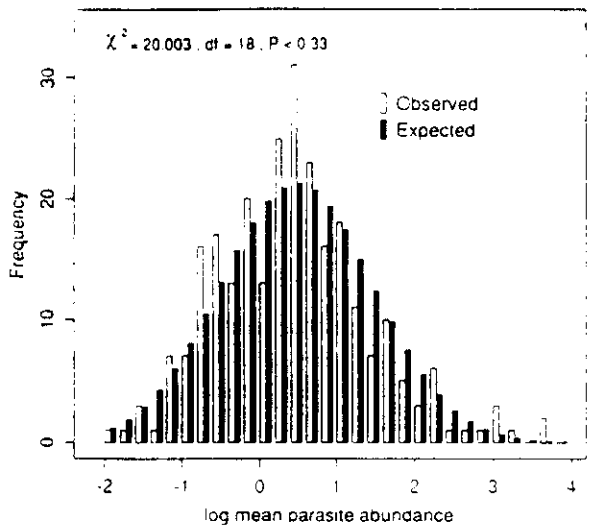

Fig. 3. Frequency distribution of the observed log mean parasite burden data, □. Also included is a fitted log normal distribution, ■, with the same average and standard deviation as the observed mean parasite burden data. The χ^2 value, df and p-value associated with the difference between the two distributions are also presented.

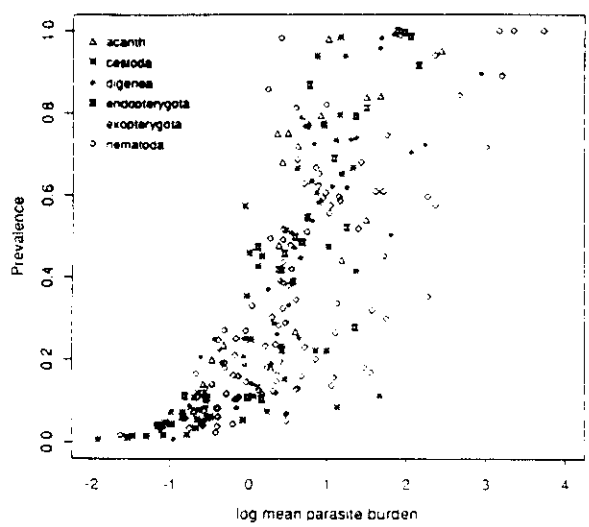

Fig. 4. Prevalence versus log mean parasite burden; data points are sub-divided according to parasite taxonomic class.

results of Taylor *et al.* (1978) who examined 156 animal populations in different habitats and estimated that b was 1·45 (S.D. ±0·39). The tightness of the relationship in Fig. 5 ($R^2 = 0{\cdot}87$) is surprising however. This suggests that parasites may be constrained in the degree of variation observed for any given mean burden. From an evolutionary context this suggests that there may be a trade-off between parasites becoming too aggregated in their hosts (loss of an infected hosts results in too many parasites being lost), or becoming too random (decreased mating chances) in their distribution (Pennycuick, 1971; Anderson & Gordon, 1982).

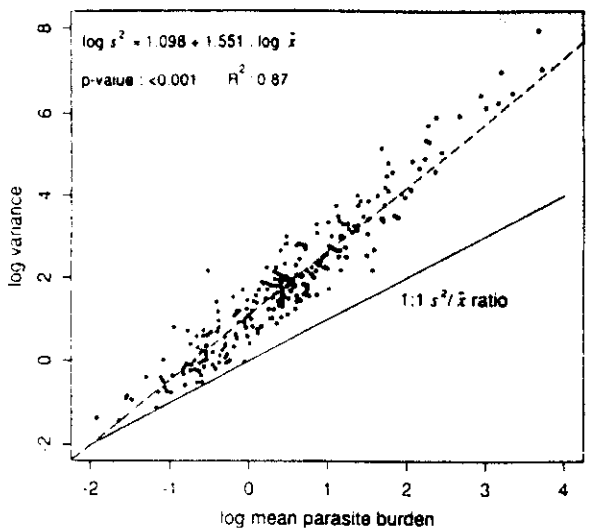

Fig. 5. Log variance against log mean parasite burden for the whole database. Also included is a regression line that would represent a 1:1 $s^2/\bar{x}$ ratio; the regression (dotted line) of log variance against log mean data, with equation; and the p-value and R^2 associated with the fit.

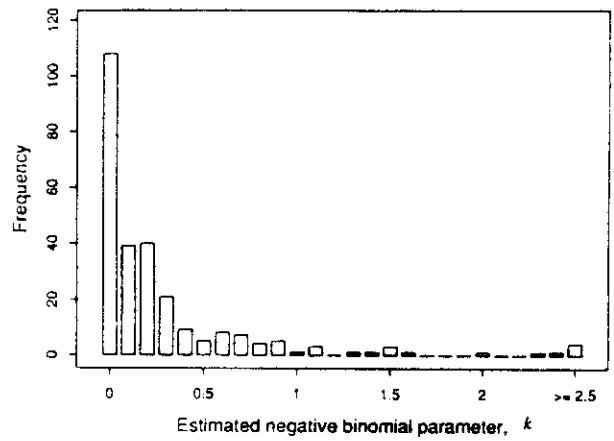

Fig. 6. Histogram of all the estimates of the negative binomial paraketer, k.

The *a priori* expectation was a series of relationships with perhaps similar slopes, but different intercepts (see Taylor *et al.* 1978; Anderson *et al.* 1982). In other words, the change in the amount of variation as mean parasite burden increases would be similar; but the estimated variation for given mean parasite burdens would differ between groups. The implication of this result is that, regardless of the infection, mean parasite burden is the main determinant of the variance in burden between hosts. However, 13% of the spread in parasite burden variance is unexplained by mean parasite burden. In a later section we consider whether any of the biological factors presented in Table 1 are associated with this variation in the relationship.

Estimates of the negative binomial parameter, k. Fig. 6 presents a histogram of the negative binomial

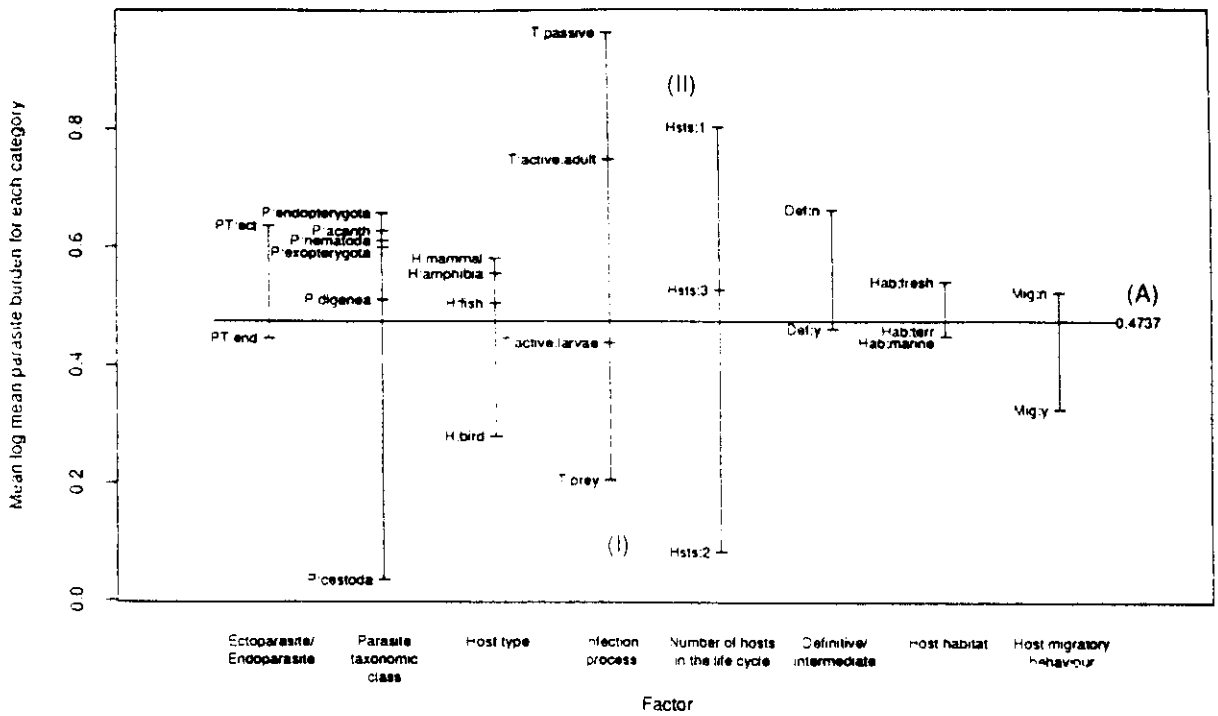

Fig. 7. Summary diagram of the log mean parasite burden data, partitioned by the ecological and parasitological factors in the database. Each factor is divided into its respective categories (*e.g.* in the case of host migratory behaviour, Mig:y and Mig:n) and an average log mean parasite burden for that category is calculated. Each category is then placed on the diagram at the associated average log mean parasite burden. (A) – average log mean parasite burden for all the host-parasite systems. (I–II) areas referred to in the text.

parameter, k, estimated for all the host-parasite infections in the database. Where possible, maximum likelihood estimation was used, otherwise the standard moment estimates were calculated. From Fig. 6, the vast majority of k values are less than one – once again indicating highly aggregated parasite populations. This is in agreement with Fig. 5 and equivalent reviews on human-parasite infections (Anderson, 1978; Anderson & May, 1978; Guyatt *et al.* 1990; Bundy & Medley, 1992; Maizels *et al.* 1993). The negative binomial distribution is in fact dependent on two parameters – k and $\bar{x}$. This means that a given k can be associated with different means, and *vice versa* (Pennycuick, 1971). Therefore direct comparisons of k values are equivocal unless considered in terms of the mean and prevalence of the respective host-parasite system (Grafen & Woolhouse, 1993; Pennycuick, 1971; Scott, 1987). Fig. 4 has already demonstrated that the relationship between mean parasite burden and prevalence is inexact. Consequently, no further analysis of between any associations between particular groups of infection and estimate of k is presented.

Patterns of abundance and aggregation associated with specific host-parasite systems

Figs. 3 & 5 demonstrated that mean parasite burdens were log normally distributed and that there was a tight relationship between log mean parasite burden and log variance. Both these results suggest constraining influences on burdens. In this section we will consider whether specific host-parasite systems are associated with significant differences in abundance and aggregation. We do this by considering those infections that are on the extremes, in terms of abundance and aggregation, which may provide clues as to the possible determinants of worm burdens.

Patterns in log mean parasite burden. Fig. 7 presents the average log mean parasite burden for each of the respective categories from Table 1. The average log mean parasite burden for *all* host-parasite systems is shown as a horizontal line (A). We can use it as an indication of which categories are associated with lower or higher mean burdens. Those categories with the widest difference in average log mean burden are likely to be associated with significant differences in mean burden. From Fig. 7 these categories are infection processes, the number of hosts in the life cycle, and parasite taxonomic class.

Fig. 7 also provides some indication of the interactions between categories. For example, the relatively low average log mean parasite burden observed for cestode infections is for the most part responsible for the observed difference between the average log mean parasite burdens of ectoparasites and endoparasites. In particular, cestode infections, predator–prey mediated infection processes and 2-host systems all have low average log mean parasite burdens (Fig. 7(I)). These three groups of systems

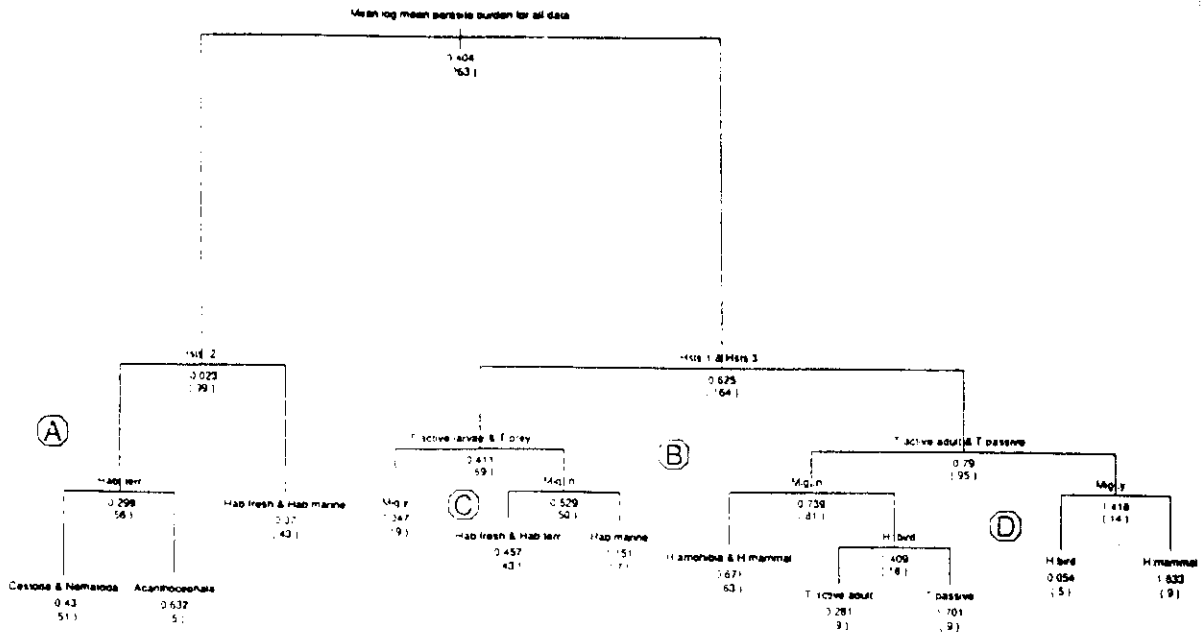

Fig. 8. Tree model output from log mean parasite burden data. Numbers at the end of each binary division are the average log mean parasite burden for that group. A–D = regions referred to in the text.

are not independent of each other: in our database all the predator–prey mediated infection processes are associated with life cycles with 2 hosts, and 88% of these are cestode infections. Another group of host-parasite systems to emerge from Fig. 7 are those infections with relatively high average burdens (Fig. 7(II)). These systems involve only 1 host in the life cycle. Transmission into the host is either via the passive consumption of infectious larvae residing on vegetation, or active searching of hosts by adult parasites.

From detailed analysis of mean parasite burden and the host and parasite factors shown in Table 1, two groups in particular are associated with significant differences in mean parasite burden: (1) *Hymenolepis* and other tapeworm infections ($n = 17$) have systematically lower mean burdens (James & Llewellyn, 1967; Threlfall, 1968; Hodasi, 1969; Vincent, 1972; Mead-Briggs & Vaughan, 1973; Mead-Briggs & Page, 1975; Grundmann, Warnock & Wassom, 1976; Yanez & Canaris, 1988). (2) Trichostrongylid ($n = 11$) and *Hypoderma* infections ($n = 4$) have systematically higher mean burdens (Mykytowycz, 1964; Breyev & Minar, 1976; Helle, 1980; Bye, 1987; Halvorsen & Nilssen, 1987; Folstad *et al.* 1991; Hudson, Dobson & Newborn, 1992).

The majority of the other host-parasite systems were not associated with systematic differences in log mean parasite burden. This lack of significance can be interpreted in a number of ways: either the host and parasite factors chosen are not explicit enough, or the wrong factors were chosen; or the majority of parasitic infections are constrained in terms of burden. Given the large diversity of host-parasite systems in the database, we would suggest the latter.

Tree-based model of log mean parasite burden. Fig. 7 provided a summary of some of the broad patterns of log mean parasite burden in the database. One problem with the database is that not all combinations of categories are present and those that are, are not represented to the same degree. This unbalanced 'design' means that it is unclear which linear model of log mean parasite burden against the various host and parasite factors should be fitted. A tree-based statistical model is one possible solution (Sonquist & Morgan, 1964; Breiman *et al.* 1984; Clark & Pregibon, 1992).

Fig. 8 is the output from the first four levels of a tree-based model of log mean parasite burden against all the ecological and parasitological independent variables i.e.

log(mean parasite burden)
= parasite taxonomic class + host type
+ infection process
+ definitive *vs.* intermediate host
+ number of hosts in the life cycle
+ host habitat
+ host migratory behaviour.

The tree illustrates all the major patterns in mean parasite burden detected in the previous sections: thus tapeworms are associated with significantly lower log mean parasite burdens (Fig. 8(A)); infections where transmission is either via passive consumption of larvae or by actively searching adult parasites are associated with significantly higher mean parasite burdens (Fig. 8(D)).

The tree also reveals information that was not readily apparent from the linear models. In particular, the partition after infection process is host migratory behaviour (Region B). However, the

expectation that there would be an association between lower mean parasite burdens and hosts undergoing seasonal migration only holds for Region C. In fact, it appears that those migratory hosts in Region D experience much higher burdens than those non-migratory hosts. The answer to this potential contradiction lies in the fact that this group of migratory hosts includes some of the relatively heavy burdens of trichostrongylid infections. If the trichostrongylid infections in the database are split according to whether hosts migrate or not, then the average burdens are 153 and 684 respectively. That is, there *is* an association between host migration and lower mean burdens. The tree also reveals that as we descend further down, host habitat and host type also appear to have associations with mean burden. In other words, most of the factors included in Table 1 do seem to influence observed parasite burdens, but some are more subtle in their effect than others.

All the information presented in Fig. 8 could be found by traditional linear modelling techniques. For example, there is a significant association between host migratory behaviour and mean burden in those 1- and 3-host systems where transmission is via active larvae or by predator-prey mediated processes ($P < 0{\cdot}013$) (i.e. Region C). However, it is unlikely that such clear graphical patterns would readily emerge from a complex series of linear models of all the possible combinations in the database. Furthermore, binary divisions occur as a result of the maximum likelihood algorithm, making subjectivity in the choice of models less likely. We would suggest that such tree-based analyses can be used to help come to grips with other large, potentially unwieldy epidemiological databases.

Patterns in aggregation. We now examine patterns of aggregation in specific host-parasite infections. From the analysis of the variance to mean relationship already presented, we can conclude that mean parasite burden is by far the most important determinant of estimated variation in parasite abundance (Fig. 5). However, 13% of the variation in log variance cannot be explained by log mean parasite burden. Therefore the associations between host-parasite factors and the relative degree of aggregation also needs to be explored. These analyses produced two types of patterns: first, specific groups of host-parasite systems were associated with consistently higher or lower degree of aggregation over a relevant range of mean burdens (1); or second, the degree of aggregation changed with increasing mean burden (2).

(1) Trichostrongylid, oxyurid and those infections where the definitive hosts are infected by consuming infected invertebrate intermediate hosts are associated with relatively high degrees of aggregation when compared to the rest of the database. A number of small groups of other parasites are associated with consistently higher or lower degrees of aggregation: some digenean infections involving invertebrate intermediate hosts have unusually higher levels of aggregation; in contrast, dipteran *Hypoderma* infections of cattle and reindeer, and some acanthocephalan infections of fish have unusually lower levels of aggregation.

(2) There are two small groups of host-parasite infections where the degree of aggregation significantly decreases as mean burden increases: *Hymenolepis* and other tapeworms: and a general group of infections of mammalian hosts where the life cycle is facilitated by the consumption of infected invertebrate intermediate hosts.

DISCUSSION AND CONCLUSIONS

This paper has presented analyses of the patterns of abundance and aggregation of macroparasites in wildlife hosts. The simplest result can be readily stated: the observed empirical data suggest that most parasitic helminths and ectoparasites are aggregated in their distribution in their natural host populations (Crofton, 1971*a*; Anderson & May, 1978; Anderson & Gordon, 1982; Dobson, 1985; Grenfell *et al.* 1987; Bundy & Medley, 1992). In many ways this result complements the aggregated distributions observed by Taylor *et al.* (1978) in their exhaustive studies of free-living populations. The variation in the level of aggregation at any mean density that is observed in our study is less than that observed by Taylor (Taylor, 1961; Taylor & Taylor, 1977; Taylor *et al.* 1978; Taylor & Woiwod, 1980); this probably reflects the ease with which we can define individual host organisms as natural sampling units of habitat for parasites, i.e. hosts are the quadrats for sampling parasites.

The observed relationship between variance and mean parasite burden raises an interesting point: there seem to be evolutionary constraints on the degree of aggregation. If parasites are not benign inhabitants of hosts; host mortality rates (and with it the loss of parasites) may be influenced by the presence of parasites (Anderson & May, 1979*a*). As parasites become more pathogenic then mean worm burdens will decline – as will the observed degree of aggregation – essentially because hosts in the tail of the distribution will die at a much faster rate than those with low to intermediate burdens. However, selection for high levels of parasite-induced mortality (virulence) is likely to lead to situations of reduced mating opportunities, which may lower egg production below a level where the parasites selected for this increased virulence would be unable to maintain itself in the population (Pennycuick, 1971; Anderson & Gordon, 1982). The interaction between parasite fecundity and aggregation, leads to the selection for

intermediate levels of pathogenicity and intermediate levels of aggregation (in microparasites this is equivalent to the trade-off between transmission and virulence (Dobson & Merenlender, 1991)).

Patterns of abundance and aggregation

Our analyses, whilst relatively broad, have turned up some important general patterns. In particular, the process that determines how the parasite enters the host is clearly important in determining both the level of aggregation and mean parasite burden.

Parasites that enter hosts passively (are ingested with food) tend to exhibit higher levels of aggregation and mean burden. These parasites are mainly trichostrongylids involving single host life cycles. Larvae can survive over a year on vegetation (Rees, 1950; Smith, Grenfell & Anderson, 1986; Waller & Thomas, 1978), and adults produce large numbers of eggs. The net result is likely to be large worm burdens. Not all hosts experience such burdens, therefore, the estimated variance will be relatively high, resulting in a high degree of aggregation. However, the vast majority of work on trichostrongylids involves the management of relatively large host populations at artificially high densities, which may exaggerate the intensity of infections that observed in natural populations.

Dipteran infections of relatively large hosts also display relatively high mean burdens. These *Hypoderma* infections involve active searching by winged and very mobile females flies, with up to a thousand *Hypoderma* larvae found on hosts (Breyev, 1973*b*; Folstad *et al.* 1989), which indicates a very efficient transmission process, thereby increasing potential burdens. In contrast with the trichostrongylids, *Hypoderma* infections show relatively low degrees of aggregation, possibly because of the efficient transmission process.

At the other extreme, hosts that become infected by eating infected invertebrate prey tend to show low burdens. These infections predominantly involve cestodes and acanthocephalans, with high and seasonal invertebrate mortality rates (Keymer, 1982*a*); seasonal larval developmental rates in invertebrates (Heyneman, 1958); very low transmission rates between hosts (Jarroll, 1980; Keymer & Anderson, 1979; Anderson & May, 1978); and relatively large parasites compared to hosts – the latter indicating strong density dependence. There may also be differences in feeding behaviour between different predators in the same population. This group of infections also shows a decline in estimated aggregation as mean burden increases. A possible explanation is a maximum burden per host: an increase in mean burden relates to a greater proportion to the sampled host population with the maximum parasite burden, thereby decreasing the difference between host burdens.

All of our results presented above suggest that future attempts to unravel exactly what factors produce the observed patterns of abundance and aggregation could profit from more experimental studies. In particular, we would still like to know more about the spatial distribution of parasite infective stages in the environment affects patterns of aggregation observed in the final host. The only examples so far are a number of papers on the spatial distribution of infectious stages of human infections, e.g. Hominick, Dean & Schad (1987) on hookworm, Woolhouse & Chandiwana (1989) & Udonsi (1990) on schistosomes. However, these are on human pathogens, where the relationship between host and parasite may be different from wildlife hosts. The pioneering laboratory experiments of Keymer & Anderson (1979), could certainly be extended and undertaken over a range of field conditions.

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APPENDIX A: Database of all the host-parasite systems that form the basis of the comparative analyses

	Host	N	k	x	$^{95}_{0}$ inf	s^2/x	log $\bar{x}$	log s^2	log wt						
PT: endoparasite															
Phylum: Platyhelminths															
Class: Digenea															
Bucephalidae															
Bucephalus varicus	Fish	52	0·701	4·942	0·769	8·02	0·6939	1·5981	1·0414	H:fish	T:prey	Hsts:3	Def:y	Hab:marine	Mig:n	Rees, 1970
Allocreadiidae															
Sphaerostoma bramae	Roach	200	0·203	1·776	0·37	9·75	0·2494	1·2384	0	H:fish	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Evans, 1977
Crepidostomum farionis	Trout	905	0·156	0·46	0·193	3·949	−0·3372	0·2592	0·699	H:fish	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Thomas, 1964
Crepidostomum metoecus	Trout	905	0·322	19·86	0·736	62·68	1·298	3·0951	0·699	H:fish	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Thomas, 1964
Lecithodendriidae															
Pleurogenes spp.	Toad	316	0·042	1·228	0·133	30·238	0·0892	1·5698	−1·3979	H:amphibian	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Li & Hsu, 1951
Heimuroidae															
Genolinea laticauda	Sculpin	526	0·069	4·354	0·521	63·54	0·6389	2·4419	0·301	H:fish	T:prey	Hsts:3	Def:y	Hab:marine	Mig:n	Burreson & Olsen, 1974
Tubulovesicula lindbergi	Sculpin	526	0·271	3·446	0·508	13·726	0·5373	1·6749	0·301	H:fish	T:prey	Hsts:3	Def:y	Hab:marine	Mig:n	Burreson & Olsen, 1974
Monorchiidae															
Lymphylodora kubanicum	Roach	153	0·254	11·281	0·621	45·352	1·0523	2·7089	0	H:fish	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Evans, 1978
Bunoderidae															
Bunodera luciopercae	Perch	215	0·224	3·716	0·474	17·679	0·5724	1·8199	0·301	H:fish	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Skorping, 1981
Bunodera luciopercae	Perch	181	0·311	23·464	0·74	76·563	1·3704	3·2544	0·301	H:fish	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Wootton, 1973b
Gorgoderidae															
Gorgoderina vitelliloba	Frog	2413	0·029	2·2	0·117	77·783	0·3424	2·2333	1·6021	H:amphibian	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Lees, 1962
Phyllodistomum simile	Trout	905	0·085	0·91	0·188	11·706	−0·041	1·0274	0·699	H:fish	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Thomas, 1964
Plagiorchiidae															
Dolichosaccus rastellus	Frog	2413	0·014	3	0·072	218·134	0·4771	2·8158	−1·6021	H:amphibian	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Lees, 1962
Haematoloechus coloradensis	Frog	104	0·476	6·625	0·724	14·903	0·8212	1·9945	−1	H:amphibian	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Dronen, 1978
Haplometra cylindracea	Frog	2413	0·047	5·2	0·542	111·242	0·716	2·7623	−1·6021	H:amphibian	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Lees, 1962
Plagiorchis vitellatus	Phalarope	100	0·127	2·3	0·26	19·132	0·3617	1·6435	−1·301	H:bird	T:prey	Hsts:	Def:y3	Hab:terr	Mig:y	Yanes & Canaris, 1988
Microphallidae															
Gymnophallus deliciosus	Gull	96	0·184	4·479	0·448	25·378	0·6512	2·0556	−0·1549	H:bird	T:prey	Hsts:3	Def:y	Hab:marine	Mig:n	Ellis & Williams, 1973
Microphallus claviformis	Gull	146	0·013	2·897	0·068	223·56	0·4619	2·8113	−0·6021	H:bird	T:prey	Hsts:3	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Maritrema apodemicum	Mouse	96	0·026	9·594	0·146	365·54	0·982	3·5449	−2·699	H:mammal	T:prey	Hsts:3	Def:y	Hab:terr	Mig:n	Lewis, 1966
Heterophyidae															
Apophallus donicus	Cat	500	0·002	0·112	0·008	57·513	−0·9508	0·809	0·4771	H:mammal	T:prey	Hsts:3	Def:y	Hab:terr	Mig:n	Vamparys & Thienport, 1973
Cryptocotyle lingua	Gull	96	0·046	2·333	0·167	51·269	0·3679	2·0778	−0·1549	H:bird	T:prey	Hsts:3	Def:y	Hab:marine	Mig:n	Ellis & Williams, 1973
Cryptocotyle lingua	Gull	146	0·037	0·651	0·103	18·519	−0·1864	1·0812	−0·6021	H:bird	T:prey	Hsts:3	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Cryptocotyle lingua	Fish	642	0·282	864·56	0·896	3067·733	2·9368	6·4236	0·301	H:fish	T:active larvae	Hsts:3	Def:n	Hab:marine	Mig:n	Sekhar & Threlfall, 1970
Cyclocoelidae															
Cyclocelum mutabile	Snipe	268	0·059	1·94	0·19	33·442	0·2878	1·8121	−1	H:bird	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:y	Threlfall, 1968
Brachylaemidae															
Brachylaemus fuscatus	Starling	122	0·102	0·87	0·205	9·562	−0·0605	0·9201	−1·3979	H:bird	T:prey	Hsts:3	Def:y	Hab:terr	Mig:y	James & Llewellyn, 1967
Brachylaemus fuscatus	Redwing	171	0·122	3·25	0·333	27·641	0·5119	1·9534	−1·0969	H:bird	T:prey	Hsts:3	Def:y	Hab:terr	Mig:n	James & Llewellyn, 1967
Echinostomatidae															
Curtuteria australis	Oystercatcher	97	0·11	63·498	0·504	576·699	1·8028	4·5637	−0·301	H:bird	T:prey	Hsts:3	Def:y	Hab:marine	Mig:y	Allison, 1979
Himasthla leptosoma	Gull	146	0·032	1·507	0·116	48·162	0·1781	1·8608	−0·6021	H:bird	T:prey	Hsts:3	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Echinochasmus perfoliatura	Dog	101	0·189	114·861	0·703	608·73	2·0602	4·8446	1·2553	H:mammal	T:prey	Hsts:3	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Echinostoma revolutum	Snipe	268	0·087	0·235	0·108	3·71	−0·6289	−0·0596	−1	H:bird	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:y	Threlfall, 1968
Strigeidae															
Cotylurus erraticus	Rainbow Trout	125	0·223	0·427	0·224	3·114	−0·3696	0·1237	0·3031	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:y	Wootton, 1973a
Cotylurus erraticus	Rainbow Trout	89	0·217	17·944	0·618	82·496	1·2539	3·1704	0·9031	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:y	Wootton, 1973a
Tylodelphys clavata	Rainbow Trout	89	0·223	6·252	0·539	27·865	0·796	2·2411	0·9031	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:y	Wootton, 1974
Tylodelphys clavata	Trout	56	0·078	0·179	0·089	3·283	−0·7471	0·2309	0·699	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:n	Wootton, 1974
Tylodelphys clavata	Perch	181	1·059	48·56	0·983	47·847	1·6863	3·3661	0·301	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:n	Wootton, 1974
Tylodelphys clavata	Fish	165	0·958	16·808	0·939	18·551	1·2255	2·4939	−0·5229	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:n	Wootton, 1974
Tylodelphys podicipia	Perch	181	0·559	0·374	0·249	1·669	−0·4271	−0·2047	0·301	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:n	Kennedy, 1981
Tylodelphys podicipia	Perch	421	1	0·25	0·207	1·25	−0·6021	−0·5051	0·301	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:n	Wootton, 1974
Diplostomum spathecum	Trout	56	0·146	0·9	0·25	7·158	−0·0458	0·809	0·699	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:y	Wootton, 1974
Diplostomum spathecum	Rainbow Trout	89	0·774	45·792	0·958	60·187	1·6608	3·4403	0·9031	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:n	Wootton, 1974
Diplostomum spathecum	Perch	181	0·846	4·503	0·79	6·319	0·6535	1·4542	0·301	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:n	Wootton, 1974

APPENDIX A: (*cont.*)

	Host	N	k	$\bar{x}$	% inf	$s^2/\bar{x}$	log $\bar{x}$	log s^2	log wt						
Diplostomum gasterostei	Stickleback	1863	0·151	9·4	0·561	63·085	0·9731	2·7731	−2·699	H:fish	T:active larvae	Hsts:3	Def:n	Hab:fresh	Mig:n	Pennycuick, 1971
Alaria marianae	Coyote	177	0·13	171·5	0·723	1315·36	2·2343	5·3533	1·301	H:mammal	T:prey	Hsts:1	Def:y	Hab:terr	Mig:n	Pence & Windberg, 1984
Zamarchis allentoshi	Coyote	177	0·032	0·7	0·085	22·757	−0·1549	1·2022	1·301	H:mammal	T:prey	Hsts:1	Def:y	Hab:terr	Mig:n	Pence & Windberg, 1984
Athesmia heterolecithodes	Coyote	177	0·082	1·1	0·141	14·48	0·0414	1·2022	1·301	H:mammal	T:prey	Hsts:1	Def:y	Hab:terr	Mig:n	Pence & Windberg, 1984
Notocotylidae																
Notocotylus attenuatus	Phalarope	100	0·083	0·09	0·08	2·086	1·0458	−0·7264	1·301	H:bird	T:prey	Hsts:1	Def:y	Hab:terr	Mig:y	Yanez & Canaris, 1988
Class: Cestoda																
Proteocephalidae																
Proteocephalus filicollis	Stickleback	1450	0·243	0·471	0·229	2·938	−0·327	0·1411	−2·699	H:fish	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Hopkins, 1959
Caryophyllaeidae																
Caryophyllaeus laticeps	Dace	335	0·038	2·84	0·152	75·346	0·4533	2·3304	−0·3979	H:fish	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Kennedy, 1969
Distaichometra bufonis	Toad	477	0·902	5·45	0·768	7·045	0·7364	1·5843	−1·3979	H:amphibian	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Hardin & Janovy, 1988
Bothriocephalus varius	Newt	249	0·084	2·93	0·514	35·948	0·4669	2·0225	−1·301	H:amphibian	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Jarroll, 1970
Triaenophorus nodulosus	Perch	497	16·564	0·879	0·575	1·053	0·056	−0·0336	0·301	H:fresh	T:prey	Hsts:3	Def:n	Hab:fresh	Mig:n	Chubb, 1963
Triaenophorus nodulosus	Pike	104	0·495	9·017	0·769	19·335	0·9551	2·2414	0·699	H:fish	T:prey	Hsts:3	Def:y	Hab:fresh	Mig:n	Chubb, 1964
Digramma interrupta	Carp	102	0·155	0·23	0·118	2·451	−0·6383	−0·2489	0·301	H:fish	T:prey	Hsts:3	Def:n	Hab:fresh	Mig:n	Breyev, 1973a
Anoplocephalidae																
Andrya cuniculi	Rabbit	968	0·024	0·33	0·063	14·588	−0·4815	0·6825	0	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Mead-Briggs & Vaughan, 1973
Cittotaenia pectinata	Rabbit	154	0·027	0·222	0·058	9·275	−0·6536	0·3137	0·4771	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Mead-Briggs & Page, 1975
Cittotaenia pectinata	Rabbit	968	0·115	2·08	0·287	19·016	0·316	1·5951	0	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Mead-Briggs & Page, 1975
Cittotaenia denticulata	Rabbit	278	0·007	0·083	0·018	12·562	−1·0809	0·0181	0	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Mead-Briggs & Vaughan, 1973
Cittotaenia praecognis	Gopher	200	0·014	0·84	0·055	61	−0·0757	1·7096	1	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Catenotaenia peromysci	Deer mouse	1094	0·028	0·082	0·038	3·971	−1·0862	0·4873	−1·6021	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Catenotaenia peromysci	Deer mouse	572	0·008	0·028	0·012	4·5	−1·5528	−0·8996	1·6021	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Cysticercus fasciolaris	RAt	358	0·664	1·02	0·461	2·536	0·0086	0·4127	−0·8239	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Schizorchis ochotonae	Pikas	115	0·387	1·443	0·452	4·729	0·1593	0·834	1	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Tetrabothriidae																
Tetrabothrius cylindraceus	Gull	96	0·311	0·956	0·354	4·072	−0·0195	0·5903	−0·1549	H:bird	T:prey	Hsts:2	Def:y	Hab:marine	Mig:n	Ellis & Williams, 1973
Taeniidae																
Hydatigera taeniaeformis	Cat	500	0·376	1·284	0·428	4·431	0·1086	0·7531	0·4771	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Vamparija & Thienport, 1973
Taenia pisiformis	Coyote	177	0·25	7·2	0·605	29·745	0·8573	2·3307	1·301	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Pence & Windberg, 1984
Taenia pisiformis	Dog	125	0·045	0·24	0·08	6·296	−0·6198	0·1793	1·2553	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Vamparija & Thienport, 1973
Taenia macrocystis	Coyote	177	0·001	0·3	0·107	477·9	−0·5229	2·1565	1·301	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Pence & Windberg, 1984
Taenia multiceps	Coyote	177	0·026	7·1	0·22	271·483	0·8513	3·285	1·301	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Pence & Windberg, 1984
Davaineidae																
Raillietina cesticillus	Fowl	108	0·005	0·167	0·019	31·85	−0·7773	0·7258	0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:y	Hodasi, 1969
Raillietina echinobothrida	Fowl	108	0·607	13·519	0·085	23·285	1·1309	2·498	0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Hodasi, 1969
Raillietina tetragona	Fowl	108	0·254	7·685	0·583	31·201	0·8856	2·3798	0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Hodasi, 1969
Hymenolepidae																
Aploparaksis cirrosa	Gull	146	0·017	1·692	0·075	101·224	0·2284	2·2337	−0·6021	H:bird	T:prey	Hsts:2	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Aploparaksis diagonis	Phalarope	100	0·043	0·25	0·05	6·867	−0·6021	0·2347	−1·301	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	Yanez & Canaris, 1988
Diorchis brevis	Coot	152	0·256	20·934	0·667	82·773	1·3209	3·2387	−0·0969	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:y	Pojmanska, 1982
Diorchis inflata	Coot	152	0·459	14·424	0·796	30·989	1·153	2·6442	−0·0969	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:y	Pojmanska, 1982
Diorchis ransomi	Coot	152	0·258	15·106	0·652	59·55	1·1791	2·954	−0·0969	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:y	Pojmanska, 1982
Halpluparaksis filum	Snipe	268	0·494	4·007	0·664	9·111	0·6028	1·5624	−1	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:y	Threlfall, 1968
Hymenolepis carioca	Fowl	108	0·099	23·241	0·417	236·718	1·3663	3·7405	0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Hodasi, 1969
Hymenolepis cantamana	Fowl	108	0·015	46·056	0·111	3149·185	1·6633	5·1615	0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Hodasi, 1969
Hymenolepis capellae	Fowl	284	0·051	0·086	0·049	2·699	−1·0655	−0·6343	−1	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:y	Threlfall, 1968
Hymenolepis citelli	Rodent	109	0·064	0·147	0·073	3·297	−0·8327	−0·3146	−0·9208	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Hymenolepis citelli	Rodent	151	0·033	0·106	0·046	4·212	−0·9747	−0·3502	−0·1549	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Hymenolepis citelli	Deer mouse	1094	0·007	0·05	0·015	8·143	−1·301	−0·3902	−1·6021	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Hymenolepis citelli	Rodent	572	0·018	0·077	0·03	5·278	−1·1135	−0·391	−1·6021	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Hymenolepis farciminosa	Starling	64	1·656	7·22	0·938	5·359	0·8585	1·5876	−1·0969	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Hymenolepis horrida	Gopher	200	0·06	0·285	0·1	5·73	−0·5452	0·213	−4	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Vincent, 1972
Hymenolepis octacanthoides	Gull	146	0·046	9·959	0·219	217·681	0·9982	3·336	−0·6021	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Hymenolepis serpentulus	Starling	122	0·013	0·033	0·016	3·493	−1·4815	−0·9383	−1·3979	H:bird	T:prey	Hsts:2	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Hymenolepis serpentulus	Redwing	171	0·004	0·012	0·006	3·698	−1·9208	−1·3528	−1·0969	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	Vincent, 1972
Hymenolepis brachycephala	Phalarope	100	0·092	2·59	0·23	29·027	0·4133	1·8761	−1·301	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	James & Llewellyn, 1967
Dilepididae																
Anomotaenia micracantha	Gull	146	0·129	1·068	0·247	9·465	0·0286	1·0047	−0·6021	H:bird	T:prey	Hsts:2	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Anomotaenia gallinagilis	Phalarope	100	0·052	1·15	0·11	23·252	0·0607	1·4272	−1·301	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	Yanez & Canaris, 1988

APPENDIX A: (*cont.*)

	Host	N	k	ε	$\%_0$ inf	$s^2/\bar{x}$	log $\bar{x}$	log r^2	log wt						
Anomotaenia clavigera	Phalarope	100	0·07	1·27	0·13	19·074	0·1038	1·3842	−1·301	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	Yanez & Canaris, 1988
Amobotaenia fuhrmanni	Snipe	268	0·023	0·299	0·059	13·944	−0·5243	0·6201	−1	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:y	Threlfall, 1968
Dilepis undula	Starling	122	0·104	0·205	0·107	2·975	−0·6882	−0·2148	−1·3979	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	James & Llewellyn, 1967
Dilepis undula	Redwing	171	0·007	0·029	0·012	4·929	−1·5376	−0·8448	−1·0969	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Vincent, 1972
Dipylidium canicum	Cat	500	0·013	0·216	0·036	18·042	−0·665	0·5907	0·4771	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Dipylidium caninum	Dog	101	0·34	6·178	0·634	19·171	0·7908	2·0735	1·2553	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Vamparija & Thienport, 1973
Luteriporus skrjabini	Gull	146	0·371	12·692	0·733	35·236	1·1035	2·6505	0·6021	H:bird	T:prey	Hsts:2	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Nematotaeniidae																
Baeriette baeri	Toad	252	0·285	0·528	0·258	2·858	−0·2774	0·1787	−3	H:fish	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Li & Hsu, 1951
Diphyllobothriidae																
Diphyllobothrium ditremum	Arctic Charr	602	0·236	8·71	0·774	37·873	0·94	2·5183	0·6021	H:fish	T:prey	Hsts:3	Def:n	Hab:fresh	Mig:n	Halvorsen & Anderson, 1984
Diphyllobothrium ditremum	Arctic Charr	108	1·465	67·95	0·992	47·37	1·8322	3·5077	0·6021	H:fish	T:prey	Hsts:3	Def:n	Hab:fresh	Mig:n	Henricson, 1977
Diphyllobothrium dendriticum	Arctic Charr	108	1·573	14·49	0·965	10·212	1·1611	2·1702	0·6021	H:fish	T:prey	Hsts:3	Def:n	Hab:fresh	Mig:n	Henricson, 1977
Schistocephalus solidus	Gull	146	0·147	0·103	0·075	1·697	−0·9872	0·7575	0·6021	H:bird	T:prey	Hsts:3	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Schistocephalus solidus	Stickleback	1863	0·476	4·4	0·883	10·25	0·6435	1·6542	−2·699	H:fish	T:prey	Hsts:3	Def:n	Hab:fresh	Mig:n	Pennycuick, 1971*a*
Mesocestoididae																
Mesocestoides lineatus	Coyote	177	0·188	10·3	0·475	55·678	1·0128	2·7585	1·301	H:mammal	T:prey	Hsts:3	Def:y	Hab:terr	Mig:n	Pence & Windberg, 1984
Phylum: Nematoda																
Trichuridae																
Capillaria aerophila	Cat	500	0·071	0·648	0·162	3·288	−0·1884	0·3285	0·4771	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Vamparija & Thienport, 1973
Capillaria anatis	Fowl	289	0·037	0·697	0·104	20·021	−0·1568	1·1447	0·301	H:bird	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Wakelin, 1964
Capillaria caudinflata	Redwing	171	0·035	0·021	0·018	1·661	−1·6383	−1·4179	1·3979	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	James & Llewellyn, 1967
Capillaria caudinflata	Starling	122	0·018	0·262	0·049	15·186	−0·5817	0·5997	−1·0969	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	James & Llewellyn, 1967
Capillaria caudinflata	Fowl	289	0·035	4·67	0·159	132·88	0·6693	2·7928	0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Wakelin, 1964
Capillaria contoria	Gull	146	0·293	2·678	0·493	10·129	0·4278	1·4334	−0·6021	H:bird	T:passive	Hsts:1	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Capillaria obsignata	Fowl	289	0·095	53·34	0·453	560·31	1·7271	4·4755	0·301	H:bird	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Wakelin, 1964
Capillaria ovopunctata	Starling	64	0·021	0·411	0·063	21·925	−0·3862	0·9548	−1·0969	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	Vincent, 1972
Trichuris suis	Boar	216	0·1	2·934	0·289	30·281	0·4675	1·9486	2·1761	H:mammal	T:passive	Hsts:1	Def:n	Hab:terr	Mig:n	Jacobs & Dunn, 1969
Trichuris trichura	Human	709	0·057	0·185	0·079	4·246	−0·7328	−0·1048	1·8451	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Trichuris citella	Rodent	151	0·071	0·748	0·159	11·535	−0·1261	0·9359	−0·1549	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Trichuris fossor	Gopher	169	0·029	0·414	0·083	15·276	−0·383	0·301	−0·9208	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Trichuris fossor	Gopher	200	0·224	1·115	0·33	5·978	0·0473	0·8238	−1	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Trichuris diplodomis	Kangaroo rat	84	0·221	5·476	0·512	25·778	0·7385	2·1497	−1·0969	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Trichuris diplodomis	Kangaroo rat	308	0·054	2·516	0·196	45·14	0·4007	2·0553	−1·301	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Rhabdiasidae																
Rhabdias bufonis	Frog	2413	0·214	4·6	0·487	22·443	0·6628	2·0138	−1·6021	H:amphibian	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Lees, 1962
Rhabdias spp.	Toad	316	0·714	5·18	0·779	8·255	0·7143	1·631	−1·0969	H:amphibian	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Li & Hsu, 1951
Ancylostomatidae																
Ancylostoma caninum	Coyote	177	0·624	82·7	0·989	133·574	1·9175	4·0432	1·301	H:mammal	T:active larvae	Hsts:1	Def:y	Hab:terr	Mig:n	Pence & Windberg, 1984
Ancylostoma caninum	Dog	202	0·243	3·356	0·48	14·811	0·5258	1·6964	1·2553	H:mammal	T:active larvae	Hsts:1	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Ancylostoma duodenale	Human	888	0·053	0·941	0·144	18·753	−0·0264	1·2467	1·8451	H:mammal	T:active larvae	Hsts:1	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Ancylostoma tubaeformae	Cat	500	0·174	2·7	0·386	16·527	0·4314	1·6496	0·4771	H:mammal	T:active larvae	Hsts:1	Def:y	Hab:terr	Mig:n	Vamparija & Thienport, 1973
Uncinaria stenocephala	Dog	125	0·006	0·384	0·024	67·595	−0·4157	1·4142	1·2553	H:mammal	T:active larvae	Hsts:1	Def:y	Hab:terr	Mig:n	Vamparija & Thienport, 1973
Trichonematidae																
Oesophagostomum dentatum	Boar	70	0·254	1580	0·891	6229·15	3·1987	6·9931	2·1761	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Jacobs & Llewellyn, 1969
Oesophagostomum quadrispinulatum	Boar	70	0·246	461·668	0·844	1877·699	2·6643	5·938	2·1761	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Jacobs & Llewellyn, 1969
Protostrongylidae																
Aelurostrongylus abstrusus	Cat	500	0·014	0·18	0·036	13·933	−0·7447	0·3993	0·4771	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Vamparija & Thienport, 1973
Strongylidae																
Ransomus rodentorum	Gopher	200	0·122	0·68	0·21	6·313	−0·1675	0·6327	−1	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Syngamidae																
Cyathostoma lari	Gull	146	0·14	0·5	0·192	4·566	−0·301	0·3585	−0·6021	H:bird	T:passive	Hsts:1	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Trichostrongylidae																
Oswaldocruzia filiformis	Frog	2413	0·373	4·9	0·628	14·127	0·6902	1·8402	−1·6021	H:amphibian	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Lees, 1962
Oswaldocruzia pipiens	Toad	162	0·298	7·63	0·623	26·604	0·8825	2·3075	−1·0969	H:amphibian	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Li & Hsu, 1951
Nematodirus spathiger	Sheep	300	0·068	231·54	0·576	3406	2·3646	5·8969	1·7404	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Mykytowycz, 1964
Ostertagi spp.	Sheep	100	0·051	56·1	0·3	1101	1·749	4·7908	1·7404	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Mykytowycz, 1964
Ostertagi gruhneri	Reindeer	71	2·482	5233·6	1	2109·769	3·7188	7·043	1·7404	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Mykytowycz, 1964
Ostertagi gruhneri	Reindeer	72	1·187	1445·1	1	1218·69	3·1599	6·2458	1·8129	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Bye, 1987
Trichostrongylus spp.	Sheep	303	0·065	182·97	0·597	2815·923	2·2624	5·712	1·7404	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:y	Bye *et al.* 1987
																Mykytowycz, 1964

APPENDIX A: (*cont.*)

	Host	N	k	$\bar{x}$	P_a inf	$s^2/\bar{x}$	log $\bar{x}$	log s^2	log wt							
Trichostrongylus axei	Reindeer	33	2·974	80·4	0·48	11·222	1·4829	2·5329	1·8129	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:y	Bye, 1987
Trichostrongylus tenuis	Red Grouse	744	1·6	2200	1	1376	3·3424	6·481	−0·1549	H:bird	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Hudson *et al.* 1992
Heligmosomum mixtum	Vole	317	0·748	4·08	0·686	6·457	0·6107	1·4207	−1·699	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Haukisalmi *et al.* 1988
Teladorsagia circumcincta	Reindeer	74	0·174	189·01	0·352	1087·04	2·2765	5·3127	1·8129	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Bye, 1987
Teladorsagia davtiani	Reindeer	45	11·431	35·94	0·169	4·144	1·5556	2·173	1·8129	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:y	Bye, 1987
Marshallagia marshalli	Reindeer	71	0·747	1003	0·716	1343·42	3·0013	6·1295	1·7404	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Bye *et al.* 1987
Skrjabinagia arctica	Reindeer	71	1·324	224·6	0·941	170·663	2·3514	4·5835	1·7404	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:y	Bye, 1987
Skrjabinagia arctica	Reindeer	53	3·244	37·49	0·32	12·56	1·5739	2·6729	1·8129	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:y	Bye *et al.* 1987
Oxyuridae																
Aplectana acuminata	Frog	2413	0·058	5·2	0·229	91·147	0·716	2·6757	−1·6021	H:amphibian	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Lees, 1962
Aspicularis tetraptera	Mouse	134	0·253	56·709	0·746	225·146	1·7537	4·1061	−0·8239	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Behnke, 1975
Aspicularis tetraptera	Mouse	57	0·056	13·1	0·263	234·446	1·1173	3·4873	−0·8239	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Behnke, 1975
Aspicularis tetraptera	Mouse	45	0·028	12·4	0·156	447·204	1·0934	3·7439	−0·8239	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Cosmocerca ornata	Frog	2413	1·116	3·9	0·813	4·495	0·5911	1·2438	−1·6021	H:amphibian	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Lees, 1962
Enterobius vermicularis	Human	1244	0·285	11·587	0·135	41·688	1·064	2·684	1·8451	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Syphacia obvelata	Mouse	150	0·241	27·093	0·68	113·42	1·4329	3·4875	0·8239	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Syphacia peromysci	Mouse	1094	0·027	3·967	0·127	147·926	0·5985	2·7685	1·6021	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Syphacia peromysci	Mouse	572	0·031	2·04	0·122	66·595	0·3096	2·3331	1·6021	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Syphacia stylli	Rodent	151	0·164	50·755	0·609	310·482	1·7055	4·1975	−0·1549	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Syphacia eutamu	Rodent	102	0·08	2·196	0·235	28·45	0·3416	1·7957	−1·301	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Labiostoma coloradensis	Pika	115	0·107	0·287	0·13	3·682	0·5421	0·024	−1	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Cephalaris coloradensis	Pika	115	0·393	1·852	0·496	5·712	0·2676	1·0244	−1	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Exgenaris spp.	Pika	115	0·099	0·348	0·139	4·515	0·4584	0·1962	−1	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Heteroxynema cucullatum	Rodent	102	0·129	2	0·304	16·504	0·301	1·5186	−1·301	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Citellina trivalvata	Rodent	109	0·216	14·083	0·596	66·199	1·1487	2·9695	−0·9208	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Skrjabingylidae																
Skrjabingylus nasicola	Weasel	614	0·605	9·676	0·82	16·98	0·9857	2·2156	−0·9031	H:mammal	T:prey	Hsts:3	Def:y	Hab:terr	Mig:n	Lewis, 1978
Skrjabingylus nasicola	Weasel	614	0·653	5·544	0·77	9·487	0·7438	1·721	−1·2218	H:mammal	T:prey	Hsts:3	Def:y	Hab:terr	Mig:n	Lewis, 1978
Ascarididae																
Ascaris laevis	Gopher	200	0·037	0·16	0·06	5·324	−0·7959	−0·0696	1	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Grundmann *et al.* 1976
Ascaris lumbricoides	Human	1184	0·155	3·243	0·38	21·842	0·5093	1·8486	1·8451	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Ascaris suum	Boar	70	0·079	0·286	0·114	4·615	−0·5436	0·1205	2·1761	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Jacobs & Llewellyn, 1969
Toxascaris leonina	Coyote	177	0·068	2·4	0·282	36·138	0·3802	1·9382	1·301	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Pence & Windberg, 1984
Toxascaris leonina	Dog	125	0·027	4·224	0·128	156·902	0·6257	2·8214	1·2553	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Vamparsys & Thienport, 1973
Toxascaris canis	Dog	125	0·089	1·624	0·232	19·1	0·2106	1·4916	1·2553	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Vamparsys & Thienport, 1973
Toxascaris cati	Cat	500	0·329	7·82	0·652	24·782	0·8932	2·2873	0·4771	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Vamparsys & Thienport, 1973
Toxascaris mackerrasae	Rat	585	0·127	0·503	0·179	4·961	−0·2984	0·3971	−1·0969	H:mammal	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	Warren, 1970
Heterakidae																
Heteraxis brevispiculum	Fowl	108	0·251	8·75	0·593	35·889	0·942	2·497	0·301	H:bird	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Hodasi, 1969
Heteraxis gallinarum	Fowl	289	0·171	40·92	0·609	239·78	1·6119	3·9917	0·301	H:bird	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Wakelin, 1964
Heteraxis gallinae	Fowl	183	0·206	10·516	0·557	52·143	1·0227	2·7399	0·301	H:bird	T:passive	Hsts:1	Def:y	Hab:fresh	Mig:n	Li & Hsu, 1951
Heteraxis spumosa	Rat	165	0·255	9·594	0·606	38·623	0·982	2·5688	−1·0969	H:mammal	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Ascardia galli	Fowl	289	0·079	13·64	0·336	172·581	1·1348	3·318	0·301	H:bird	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Wakelin, 1964
Ascardia galli	Fowl	201	0·207	14·527	0·587	71·18	1·1622	3·0145	0·301	H:bird	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Li & Hsu, 1951
Ascardia galli	Fowl	108	0·166	0·926	0·269	6·578	−0·0334	0·7847	0·301	H:bird	T:passive	Hsts:1	Def:y	Hab:terr	Mig:n	Hodasi, 1969
Heterocheilidae																
Porrocaecum ensicaudatum	Starling	122	0·364	0·5	0·27	2·373	−0·301	0·0743	−1·0969	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:n	James & Llewellyn, 1967
Porrocaecum ensicaudatum	Redwing	171	0·375	0·421	0·246	2·121	−0·3757	0·0492	−1·3979	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	James & Llewellyn, 1967
Porrocaecum spp.	Gull	146	0·315	0·527	0·116	2·675	−0·2782	0·1491	−0·6021	H:bird	T:prey	Hsts:2	Def:y	Hab:terr	Mig:y	Pemberton, 1963
Acuaridae																
Cheilospirura hamulosa	Fowl	108	0·182	0·704	0·25	4·874	−0·1524	0·5355	0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Hodasi, 1969
Cheilospirura hamulosa	Fowl	254	0·182	3·488	0·421	20·166	0·5426	1·8472	0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Li & Hsu, 1951
Cosmocephalus obvelatus	Gull	96	0·409	2·669	0·438	7·525	0·4263	1·3029	−0·1549	H:bird	T:prey	Hsts:2	Def:y	Hab:marine	Mig:y	Pemberton, 1963
Cosmocephalus obvelatus	Gull	146	0·092	0·261	0·116	3·841	−0·5834	0·0011	−0·6021	H:bird	T:prey	Hsts:2	Def:y	Hab:marine	Mig:y	Ellis & Williams, 1973
Paracuaria tridentata	Gull	96	0·546	0·217	0·167	1·397	−0·6635	−0·5183	−0·1549	H:bird	T:prey	Hsts:2	Def:y	Hab:marine	Mig:n	Ellis & Williams, 1973
Tetrameres																
Tetra fissispina	Fowl	108	0·126	2·704	0·324	19·571	0·432	1·7236	0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Hodasi, 1969
Tetra fissispina	Pigeon	72	0·058	1·722	0·181	30·581	0·236	1·7215	−0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Williams, 1965
Tetra fissispina	Pigeon	68	0·039	2·235	0·147	58·08	0·3493	2·1133	−0·301	H:bird	T:prey	Hsts:2	Def:y	Hab:fresh	Mig:n	Williams, 1965

APPENDIX A: (*cont.*)

	Host	N	k	x	$\%_{n}$ inf	s^2/x	log x	log s^2	log wt						
Oslerus osleri	Coyote	177	0·086	24·9	0·52	291·161	1·3962	3·8603	1·301	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Pence & Windberg, 1984
Physalopteridae																
Physaloptera capensis	Spring hare	406	0·123	11	0·575	90·431	1·0414	2·9977	0·2553	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Butynski, 1982
Physaloptera capensis	Spring hare	154	0·041	1·7	0·858	42·463	0·2304	1·8585	0·2553	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Butynski, 1982
Physaloptera massino	Rodent	109	0·034	0·394	0·083	12·588	−0·4045	0·6955	−0·9208	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Grundmann *et al.* 1976
Physaloptera rara	Coyote	177	0·102	2·5	0·39	25·488	0·3979	1·8043	1·301	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Pence & Windberg, 1984
Rictulariidae																
Rictularia coloradensis	Mouse	572	0·564	0·068	0·044	1·121	−1·1675	−1·1179	−1·6021	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Grundmann *et al.* 1976
Rictularia coloradensis	Mouse	1094	0·041	0·152	0·061	4·707	−0·8182	−0·1454	−1·6021	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Grundmann *et al.* 1976
Filariidae																
Dirofilaria immitis	Dog	697	0·331	2·702	0·519	9·162	0·4317	1·3937	1·2553	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Li & Hsu, 1951
Cucullanidae																
Dacnitis buttae	Trout	905	0·365	7·05	0·667	20·315	0·8482	2·156	0·699	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: n	Thomas, 1964
Thelaziidae																
Spirocerca lupi	Coyote	171	0·014	2·5	0·983	181·248	0·3979	2·6562	1·301	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Pence & Windberg, 1984
Mustelus harpesporidium	Pika	115	0·044	7·191	0·2	164·432	0·8568	3·0728	1	H: mammal	T: active larvae	Hsts: 1	Def: y	Hab: terr	Mig: n	Grundmann *et al.* 1976
Nematospiroides dubius	Kangaroo rat	308	0·009	2·951	0·052	328·888	0·47	2·987	1·301	H: mammal	T: active larvae	Hsts: 1	Def: y	Hab: terr	Mig: n	Grundmann *et al.* 1976
Nematospiroides dubius	Gopher	200	0·011	0·405	0·01	37·818	0·3925	1·3852	1	H: mammal	T: active larvae	Hsts: 1	Def: y	Hab: terr	Mig: n	Grundmann *et al.* 1976
Spiruridae																
Protospirura numidica	Coyote	177	0·146	4	0·345	28·32	0·6021	2·0542	1·301	H: mammal	T: prey	Hsts: 3	Def: y	Hab: terr	Mig: y	Pence & Windberg, 1984
Protospirura numidica	Mouse	1094	0·038	0·755	0·108	20·868	−0·1221	1·1974	−1·6021	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Grundmann *et al.* 1976
Protospirura numidica	Mouse	572	0·014	0·267	0·042	20·071	−0·5735	0·7291	−1·6021	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Grundmann *et al.* 1976
Spiroxys japonica	Frog	688	0·036	1·339	0·124	38·185	0·1268	1·7087	−1·6021	H: amphibian	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: n	Li & Hsu, 1951
Spirura infundibuliformis	Rodent	109	0·012	0·633	0·045	53·75	−0·19896	1·5318	−0·9208	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Grundmann *et al.* 1976
Phylum: Acanthocephala																
Neoechinorhynchidae																
Neoechinorhynchus rutili	Trout	905	2·325	10·18	0·98	5·378	1·0077	1·7484	0·699	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: n	Thomas, 1964
Echinorhynchidae																
Echinorhynchus lageniformis	Flounder	116	0·079	3·931	0·267	50·682	0·5945	2·2994	0·301	H: fish	T: prey	Hsts: 2	Def: y	Hab: marine	Mig: y	Ekbaum, 1938
Echinorhynchus salmonis	Fish	446	0·969	3·102	0·751	4·199	0·4916	1·1148	0·301	H: fish	T: prey	Hsts: 2	Def: y	Hab: marine	Mig: y	Amin, 1981
Echinorhynchus clavula	Stickleback	1863	0·108	1·3	0·315	13	0·1139	1·2279	−2·699	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: n	Pennycuick, 1971a
Acanthocephalus lucii	Eel	295	0·378	31·43	0·839	84·058	1·4973	3·4219	0·6021	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: y	Kennedy & Moriaty, 1987
Acanthocephalus lucii	Perch	525	0·28	8·1	0·794	29·97	0·9085	2·3852	0·301	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: n	Lee, 1981
Acanthocephalus lucii	Perch	360	0·05	0·203	0·078	5·069	−0·6925	0·0124	0·301	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: n	Brattey, 1988
Acanthocephalus parksidei	Fish	300	0·27	0·347	0·2	2·285	−0·4597	−0·1008	0	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: n	Amin, 1975
Acanthocephalus parksidei	Fish	205	0·121	15·307	0·444	127·406	1·1849	3·2901	0	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: n	Amin, 1975
Acanthocephalus ranae	Frog	2413	0·056	1·9	0·181	34·742	0·2788	1·8196	−1·6021	H: amphibian	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: n	Lee, 1981
Acanthocephalus anguillae	Eel	209	0·161	0·268	0·14	2·67	−0·5719	−0·1454	0·6021	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: y	Kennedy, 1984
Acanthocephalus clavula	Eel	1622	0·076	0·491	0·234	7·423	−0·3089	0·5617	0·6021	H: fish	T: prey	Hsts: 2	Def: y	Hab: fresh	Mig: y	Kennedy, 1984
Polymorphidae																
Polymorphus botulus	Eider duck	54	0·829	47·1	0·842	57·79	1·673	3·4349	0·301	H: bird	T: prey	Hsts: 2	Def: y	Hab: marine	Mig: n	Liat & Pike, 1980
Polymorphus botulus	Eider duck	62	0·648	271·6	0·952	420·12	2·4339	5·0573	0·243	H: bird	T: prey	Hsts: 2	Def: y	Hab: marine	Mig: n	Liat & Pike, 1980
Corynosoma semerme	Mink	190	1·551	2·24	0·75	3·475	0·3502	0·8912	−0·0969	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Nuorteva, 1966
Prosthorhynchidae																
Prosthorhynchus cylindraceus	Redwing	171	0·297	2·39	0·48	9·051	0·3784	1·3351	−1·3979	H: bird	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: y	James & Llewellyn, 1967
Prosthorhynchus cylindraceus	Starling	122	0·774	2·598	0·68	4·354	0·4146	1·0535	−1·0969	H: bird	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: y	James & Llewellyn, 1967
Oligoacanthorhynchidae																
Moniliformis moniliformis	Rat	1787	0·647	4·13	0·72	7·38	0·616	1·484	−0·8239	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Crompton *et al.* 1984
Oncicola canis	Coyote	177	0·136	31·3	0·542	231·627	1·4955	0·8603	1·301	H: mammal	T: prey	Hsts: 2	Def: y	Hab: terr	Mig: n	Pence & Windberg, 1984
PT: ectoparasite																
Phylum: Arthropoda																
Class: Exopterygota																
Copepoda																
Acanthochondria depressa	Flounder	422	0·361	3·18	0·562	9·809	0·5024	1·4941	0·301	H: fish	T: active larvae	Hsts: 1	Def: y	Hab: marine	Mig: y	van der Broeck, 1979
Chondracanthopsis nodosus	Red fish	581	0·302	0·246	0·153	1·814	−0·6091	−0·3504	0·7782	H: fish	T: active larvae	Hsts: 1	Def: y	Hab: marine	Mig: y	Williams, 1963
Chondracanthopsis nodosus	Red fish	1395	0·69	0·51	0·318	1·739	−0·2924	−0·0521	0·7782	H: fish	T: active larvae	Hsts: 1	Def: y	Hab: marine	Mig: y	Williams, 1963

APPENDIX A: (*cont.*)

	Host	N	k	x'	% inf	s^2/x	log x	log s^2	log wt						
Lepeophtheirus pectoralis	Plaice	2271	0·457	1·99	0·351	5·359	0·2989	1·0279	0·301	H: fish	T: active larvae	Hsts: 1	Def: y	Hab: marine	Mig: y	Boxshall, 1974
Lepeophtheirus pectoralis	Flounder	422	0·282	2·066	0·45	8·326	0·3151	1·2356	0·301	H: fish	T: active larvae	Hsts: 1	Def: y	Hab: marine	Mig: y	van der Broeck, 1979
Lepeophtheirus lasi	Fish	293	0·774	0·573	0·348	1·741	−0·2418	−0·001	0·1761	H: fish	T: active larvae	Hsts: 1	Def: y	Hab: marine	Mig: n	Evans *et al.* 1983
Arachnida																
Ixtrophorus gibbus	Rabbit	64	0·259	4767·7	0·497	18374·75	3·6783	7·6783	0	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Williams, 1972
Trocmartia tosteri	Starling	119	0·049	2·1	0·168	44·121	0·3222	1·9669	−1·0969	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: y	Vincent, 1972
Ixodes ricinus	Sheep	491	0·511	16·34	0·88	32·99	1·2133	2·7316	1·7404	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Milne, 1943
Acarae																
Dermanyssus gallinae	Pigeon	72	0·042	0·291	0·083	7·972	0·5361	0·8655	0·5229	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Brown, 1971
Harpirhynchus spp	Pigeon	72	0·085	0·989	0·194	12·636	0·0048	1·0968	0·5229	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Brown, 1971
Neonyssus columbae	Pigeon	72	0·104	0·874	0·208	9·397	0·0585	0·9145	0·5229	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Brown, 1971
Neonyssus mellus	Pigeon	72	0·156	3·038	0·375	20·534	0·4826	1·7951	−0·5229	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Brown, 1971
Cheyletiella parasitivorax	Rabbit	64	0·341	165·67	0·827	486·934	2·2192	4·9067	0	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Williams, 1972
Haemodipsus ventricosus	Rabbit	44	0·435	50·34	0·89	116·81	1·7019	3·7694		H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Williams, 1972
Class: Endopterygota																
Siphonaptera																
Leptopsylla segnis	Rat	61	0·509	1·295	0·475	3·541	0·1123	0·6614	0·8239	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Mayfield, 1938
Nosopsyllus fasciatus	Rat	61	1·118	5·77	0·869	6·162	0·7612	1·5509	−0·8239	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Mayfield, 1938
Xenopsylla cheopis	Rat	61	0·243	2·803	0·459	12·538	0·4476	1·5459	−0·8239	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Brown, 1971
Diptera																
Pseudolynchia canariensis	Pigeon	72	0·223	0·155	0·111	1·695	−0·8097	0·5805	−0·5229	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Andrews, 1979
Hypoderma bovis	Cattle	7217	0·43	5·47	0·547	11·721	0·738	1·807	2·3979	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Breyev & Minar, 1976
Hypoderma tarandi	Reindeer	840	0·824	31·17	0·813	36·87	1·4937	3·0604	1·8129	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: y	Helle, 1980
Hypoderma tarandi	Reindeer	418	1	92·67	0·997	93·65	1·9669	3·9384	1·8129	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Folstad *et al.* 1991
Hypoderma tarandi	Reindeer	645	2·025	75·52	1	38·285	1·8781	3·4611	1·8129	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: y	Folstad *et al.* 1991
Mallophaga																
Campanulotes bidentatus	Pigeon	72	0·429	140·85	0·917	329·007	2·1488	4·666	−0·5229	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Brown, 1971
Columbicola columbae	Pigeon	72	0·884	110·2	0·986	124·777	2·0422	4·1383	−0·5229	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Brown, 1971
Hohrstiela lata	Pigeon	72	0·208	2·585	0·417	13·452	0·4125	1·5412	−0·5229	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Brown, 1971
Anoplura																
Brueelia nebulosa	Starling	119	0·04	0·28	0·08	7·964	−0·5528	0·3483	−1·0969	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: y	Vincent, 1972
Enderleinellus suturalis	Ground squirrel	139	0·154	3·604	0·389	24·357	0·5568	1·9434	−0·9208	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Ignoffo, 1959
Fahrenholzia pinnata	Kangaroo rat	154	0·212	4·734	0·487	23·343	0·6752	2·0434	−1·301	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Ignoffo, 1959
Hoplopleura acanthopus	Vole	231	0·319	12·074	0·689	38·825	1·0819	2·671	−1·5229	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Cook & Beer, 1955
Hoplopleura hesperomydis	Mouse	192	0·248	3·797	0·5	16·285	0·5794	1·7912	−1·6021	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Cook & Beer, 1955
Hoplopleura hesperomydis	Mouse	380	0·068	2·261	0·222	39·344	0·4185	2·0133	−1·6021	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Ignoffo, 1959
Menacanthus mutabilis	Starling	119	0·225	2·352	0·42	11·573	0·3714	1·4349	−1·969	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: y	Vincent, 1972
Menacanthus stramineus	Pigeon	72	0·046	0·071	0·042	2·547	−1·1487	−0·7427	−0·5229	H: bird	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Brown, 1971
Neohaematopinus citellinus	Ground squirrel	174	0·382	22·891	0·792	60·907	1·3597	3·1443	−0·9208	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Ignoffo, 1959
Pediculus humanus capitis	Human	392	0·033	0·959	0·107	29·747	−0·0182	1·4553	1·8451	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Buxton, 1938
Pediculus humanus capitis	Human	239	0·157	17·482	0·523	112·555	1·2426	3·294	1·8451	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Buxton, 1938
Pediculus humanus capitis	Human	177	0·053	22·833	0·277	428·538	1·3586	3·9906	1·8451	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Buxton, 1938
Pediculus humanus capitis	Human	406	0·027	1·45	0·103	54·28	0·1614	1·896	1·8451	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Buxton, 1938
Polyplax auricularis	Mouse	192	0·043	0·146	0·062	4·36	−0·8356	−0·1962	−1·6021	H: mammal	T: active adult	Hsts: 1	Def: y	Hab: terr	Mig: n	Ignoffo, 1959