

# Parasite Abundance, Body Size, Life Histories, and the Energetic Equivalence Rule

Per Arneberg,<sup>1,\*</sup> Arne Skorping,<sup>1,†</sup> and Andrew F. Read<sup>1,2,‡</sup>

1. Department of Ecology/Zoology, Institute of Biology, University of Tromsø, 9037 Tromsø, Norway;

2. Institute of Cell, Animal and Population Biology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, United Kingdom

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**ABSTRACT:** If common processes generate size-abundance relationships among all animals, then similar patterns should be observed across groups with different ecologies, such as parasites and free-living animals. We studied relationships among body size, life-history traits, and population intensity (density in infected hosts) among nematodes parasitizing mammals. Parasite size and intensity were negatively correlated independently of all other parasite and host factors considered and regardless of type of analyses (i.e., nonphylogenetic or phylogenetically based statistical analyses, and across or within communities). No other nematode life-history traits had independent effects on intensity. Slopes of size-intensity relationships were consistently shallow, around  $-0.20$  on log-log scale, and thus inconsistent with the energetic equivalence rule. Within communities, slopes converged toward this global value as size range increased. A summary of published values suggests similar convergence toward a global value around  $-0.75$  among free-living animals. Steeper slopes of size-abundance relationships among free-living animals could be related to fundamental differences in ecologies between parasites and free-living animals, although such generalizations require reexamination of size-abundance relationships among free-living animals with regard to confounding factors, in particular by use of phylogenetically based statistical methods. In any case, our analyses caution against simple generalizations about patterns of animal abundance.

**Keywords:** parasites, free-living animals, body size, abundance, ecological laws.

Identifying the determinants of species abundance is one of the central problems in ecology (Begon et al. 1996). So far, body size is the best single predictor of animal abundance, and with size varying from minute crustaceans to elephants, body size and abundance are strongly negatively correlated, with size accounting for about 90% of the variation in animal species abundance (Damuth 1987). Determining the precise form of this relationship is now emerging as one of the major issues in macroecological research, and a central question is whether it is generated by processes related to population energy usage (e.g., Damuth 1981, 1987; Peters and Wassenberg 1983; Lawton 1989; Marquet et al. 1990, 1995; Nee et al. 1991; Griffiths 1992; Blackburn et al. 1993; Currie 1993; Silva and Downing 1994, 1995).

Underlying this debate is the idea that similar processes may influence abundance in all kinds of animals, yet, so far, large-scale relationships between body size and abundance have been studied in free-living animals only (e.g., Griffiths 1992). The majority of animal species are parasites (free-living animals almost certainly harbor at least one host-specific parasite species; Price 1980), so that parasites form an important challenge to general theories of animal abundance. At least on the face of it, they occupy quite different niches from free-living animals. Such differences are exactly what ecological principle must cut across, making parasites ideal organisms to test general theories about the processes generating size-abundance relationships. Here we relate body size to abundance among parasites, by focusing on a particularly well-studied group, the nematodes parasitizing mammals.

## Size-Abundance Patterns

Body-size abundance relationships with slopes around  $-0.75$  on logarithmic axes have been taken as evidence that processes related to population energy usage are important in generating size-abundance patterns (Damuth 1981, 1987; Lawton 1989; Griffiths 1992; Blackburn et al. 1993; Currie 1993). This is based on the relationship be-

\*To whom correspondence should be addressed; E-mail: para@ibg.uit.no.

†E-mail: arnesk@ibg.uit.no.

‡E-mail: aread@holyrood.edinburgh.ac.uk.

tween body mass and metabolic rate, where the latter is assumed to reflect per capita energy usage. The relationship typically has a slope of 0.75 on log-log scales (Kleiber 1961), meaning that if abundance scales to mass with a slope of  $-0.75$ , total amount of energy used by a population would be independent of species body mass, a relationship termed the energetic equivalence rule (Damuth 1981; Nee et al. 1991). Damuth (1981, 1987), explained this pattern of energy usage as the result of biotic interactions and random environmental fluctuations acting over evolutionary time, whereas others have taken it to imply that animal abundance is limited by energy availability through processes in ecological time (Lawton 1989; Blackburn et al. 1993).

An alternative explanation to body size–abundance relationships concerns the correlations between body size and other life-history traits, in particular, those traits that theory suggests may affect population growth. For example, Blackburn et al. (1996) found that body size was not significantly associated with abundance of British birds once confounding factors had been controlled for, whereas a relationship was found with life-history parameters describing life span. Among mammalian nematodes, body size is significantly correlated with several life-history traits (Skorping et al. 1991), which may, in theory, be linked to population dynamics. Here, we consider traits that are related to generation time, fecundity, and life cycle, which are linked to components of basic models of parasite population dynamics (Anderson and May 1978, 1991; May and Anderson 1979). Another potentially important character of nematode species is the location within the mammalian body (e.g., inside or outside the gastrointestinal tract), which may be related to somatic growth and survival rates (Read and Skorping 1995). Is body size a better predictor of population density than these life-history traits, or is size only a surrogate variable reflecting the effects of various other life-history traits on nematode population density?

Relationships between body size and abundance found within single communities often differ from those found in global studies, with size-abundance relationships often being weaker and with flatter slopes in the former (e.g., Blackburn et al. 1993; for studies of local parasite communities, see Haukisalmi and Henttonen 1994; Rhode et al. 1994). Lawton (1989) argues that this may be because global relationships are artifacts, resulting from databases being built up by single-species studies rather than samples of entire communities. If rare species are hard to study, then they may be underrepresented in the literature, which in turn may produce a bias against rare species in the database and give spuriously strong and too steeply negative relationships between body size and abundance.

Currie (1993), on the other hand, suggests that relationships within single communities represent truncated subsamples of global relationships and that weak relationships stem from the smaller range of body size in single communities. If so, we should expect within-community relationships to converge toward global relationships in communities with large range in body size. Some evidence supports this: increasing body size range within communities may lead to stronger relationships between body size and abundance (Silva and Downing 1995; reanalysis of data in Blackburn et al. 1993: Spearman rank-order correlation between body size range and  $r^2$  of size-abundance correlations:  $n = 9$  communities,  $r_s = 0.8$ ,  $P = .009$ ). Similar patterns have been found in a wide range of other allometric studies (Smith 1984), underlining the need to pay attention to size range. Obviously, if within-community range in body size affects size-density relationships, then analyses should put more weight on communities with large differences in species body size.

We also examine size-abundance relationships among the most common species in each community. Lawton (1989), focusing on processes in ecological time, argues that only such species are likely to be energy limited, so that a slope around  $-0.75$  for energetic reasons is only expected among the most common species in each size group (Blackburn et al. 1992). Finally, space limitation may generate size-abundance relationships, if available physical space within hosts limits densities of large worms to lower levels than densities of more small-bodied worms (e.g., Nee et al. 1992). We consider this explanation by comparing the volume made up by the total number of parasite individuals in a population with host body mass.

### Methodological Issues

Here we express parasite population density as intensity, which measures densities in infected hosts only. This parallels ecological density (density over areas used by the species only), which is the measure typically used to assess the form of size-abundance relationships among free-living animals (e.g., Damuth 1987; Carrascal and Tellería 1991). Thus, using intensity should make slopes of size-density relationships comparable across parasites and free-living animals. Variation in host body size could of course be a problem, but not within single-parasite communities, which is here defined as parasites in single-host populations, where host size will be fairly constant relative to differences among host species. A second problem may arise if worm species in one end of the nematode body-size spectrum—say, large-bodied ones—tend to use larger portions of the host body than species toward the other end of the size range, because intensity

would overestimate density per unit exploitable host mass among the former. Although an interesting problem, it is currently not feasible to examine it because data on the exact locations used within mammalian host bodies are available for only a handful of nematode species (see Anderson 1992 and references therein).

It could be argued that uninfected hosts should also be included in a measure of parasite density, because this could include potentially colonizable parasite habitat. However, large segments of host populations may (often) be uncolonizable for mammalian nematodes (e.g., infection is restricted to particular age groups, nonimmune hosts, or hosts in particular geographic locations; Montgomery 1982; Bye 1987; Rubenstein and Hohmann 1989). Thus, measures involving uninfected hosts may also involve significant amounts of habitat never used by the species. Additionally, parasite abundance, which measures densities across both infected and uninfected hosts, is a less repeatable measure within nematode species than is intensity (Arneberg et al. 1997), which suggests that comparative studies of abundance will be less informative than of intensity.

Comparative studies focus on the variation found among rather than within species. In spite of often impressive intensity fluctuations within mammalian nematode species (e.g., Prestwood et al. 1970; Montgomery and Montgomery 1988), intensity differs significantly among parasite species. About 50% of the total variation in intensity is found among nematode species, which both justifies comparative studies of nematode intensity and implies that a full understanding of intensity variation is not to be achieved without involving explanations in terms of factors differing among species (Arneberg et al. 1997). Intensity also varies significantly among nematode species within single community types (host species; Arneberg et al. 1997), which opens the prospect that patterns from data compiled across communities may be found also in single communities.

Throughout, we use phylogenetically based statistical methods to deal with the statistical problems of lack of independence and lack of identical distributions presented by multispecies data (Felsenstein 1985; Harvey and Pagel 1991; Garland et al. 1992; Díaz-Uriarte and Garland 1996). Using such methods reduces the probability of both Type I and Type II error compared with using nonphylogenetic analyses (Garland et al. 1992; Díaz-Uriarte and Garland 1996) and may also control for the effects of confounding factors that are shared through descent (Harvey 1996). In particular, it is reasonable to assume that many factors that are correlated with phylogeny (e.g., physiological, behavioral) exert yet undemonstrated effects on abundance patterns, which suggests that a possible effect of using phylogenetically based sta-

tistical methods may be to control for the effects of confounding variables that cannot be dealt with using nonphylogenetic methods (Harvey 1996). In most studies of size-abundance relationships, however, nonphylogenetic analyses have been used (i.e., ordinary regression with species values as independent data points; Griffiths 1992; Harvey 1996), and for comparison we also present results from such analyses. Assessing the effects of habitat directly may also be important when studying relationships between population density and body size/life histories (e.g., Damuth 1981, 1987; Tellería and Carrascal 1994). The host is a major part of the parasite habitat, and traits of host species may be important determinants of parasite densities (Arneberg et al. 1997). In particular, host population density may affect parasite densities, with high densities of hosts generating dense parasite populations (P. Arneberg, A. Skorping, B. Grenfell, and A. F. Read, unpublished manuscript). Here, we employ data on host population densities and other traits of host species that theory suggests may affect parasite densities.

The benefits of using phylogenetic information in comparative analyses of host-parasite relationships would be amplified if it were possible to take host phylogeny into account as well. That approach would deal with the increased power in comparative studies of mammalian nematode intensities that is gained by basing statistical analyses on mammalian phylogeny compared with ignoring phylogeny (P. Arneberg, A. Skorping, B. Grenfell, and A. F. Read, unpublished manuscript). We have still not taken host phylogeny into account here, because statistical techniques that use information from two phylogenies jointly have not yet been developed, and doing so would be a major undertaking in its own right. Nevertheless, we see the development of such techniques as a major challenge for those interested in comparative analyses of biotic interactions. We note that to the extent that host phylogeny captures similarity between habitats experienced by parasites in related hosts, a similar tool to address varying degrees of similarity between habitats among free-living animals currently does not exist.

### Our Approach

We first test whether parasite body size affects intensity independently of other nematode life-history traits and whether any of the latter traits have independent effects. This is done with three different approaches: using nonphylogenetic analyses on a global data set compiled across a large number of communities, applying phylogenetically based statistical analyses on the same data, and using both nonphylogenetically and phylogenetically based statistical analyses within single nematode communities. Host variables are included in all analyses of the

global data set and will of course be held fairly constant within single communities. We then go on to assess the form of size-intensity relationships in communities where body size ranges over more than two orders of magnitude. Where size ranges over less than two to three orders of magnitude, size-abundance relationships are typically weak or absent within communities, and both positive and negative relationships are common (Cotgreave et al. 1993; Silva and Downing 1995). Finally, we explore whether there is a tendency for within-community relationships to converge toward a global relationship as body size range increases within communities.

## Methods

### *Nematode Population Density Data*

Data on parasite population intensity were gathered from the literature, and estimates were included if 30 or more host individuals had been sampled and if only adult parasites were included. Frequently, only a portion of the organ (e.g., gastrointestinal tract or heart) where a nematode species is found had been examined in these studies, but such subsampling does not introduce bias, as has been shown by comparisons between estimates produced by subsampling and complete examinations for single nematode species (Arneberg et al. 1997). Nematode species where no life-history data could be obtained were excluded, which left data on intensity for 146 nematode species. This included species from all nematode orders parasitizing mammals and represents examination of 11,507 host individuals from 36 mammalian species and recovery of more than 10 million individual nematodes. The number of population estimates per parasite species ranged from one to 17 (median = 2; lower-upper quartile = 1–3). Parasite species were frequently found in several host species, ranging from one to five host species per parasite (median = 1, 1–2). Within-community analyses were done on data from the 36 host populations with more than three nematode species. In these communities, median number of nematode species was four (3–7, maximum 14). Parasite species averages of intensity were calculated as geometric means, and analyses were performed on logarithmically transformed values. Raw data on intensity and nematode and host traits with references to sources are available from P.A. on request.

Analyses were performed also for abundance (average number of parasites across both infected and uninfected hosts). Slopes of size-abundance relationships were broadly similar to those obtained using intensity and are therefore not reported. Additionally, abundance was only related to characters that were also related to intensity, and as expected from the lower repeatability of abundance compared with intensity (see above), relationships

were weaker for abundance than for intensity. Another measure of parasite density that in theory may be relevant for species levels differences in density is prevalence (fraction of hosts infected) (Anderson and May 1978; May and Anderson 1978). Analyses were also performed for prevalence (again not reported), which is a less repeatable measure than abundance within nematode species (Arneberg et al. 1997). Consistent with the low repeatability, prevalence was not significantly associated with any of the parasite or host characters analyzed.

### *Nematode Life Histories*

Nematode body size was measured as female volume and was calculated from published measurements of length and maximum width as described by Skorping et al. (1991). This measure was available for more species than was average volume of males and females and may reasonably be used as a substitute for the latter: female volume and average of male and female volume correlates strongly with a nearly 1:1 relationship (regression on logarithmically transformed values with female volume as independent variable,  $n = 83$ ,  $r^2 = 0.99$ , slope = 0.99). Across the 92 nematode species for which data were available, female volume varied over more than six orders of magnitude.

The other nematode life-history traits analyzed were prepatency time (the minimum time from entry into the host to first observation of the production of egg or larvae), patency time (maximum recorded period of egg or larvae production by a female), fecundity (the average number of eggs produced by a female in 24 h), life cycle (with or without an intermediate host), adult location, and juvenile location (inside or outside the gastrointestinal tract). All continuous nematode life-history traits were logarithmically transformed.

### *Host Traits*

In addition to host population density, we considered the effects of host body mass, diet, fecundity, and age at maturity. Host body mass may be important if, for example, greater food intake results in greater worm intake or total energy and available space within hosts limits parasite population density. Host diet may also affect worm load if higher food intake of herbivores compared with carnivores leads to higher ingestion rates of parasites. On theoretical grounds, host birth and death rates have been identified as important factors for parasite population density (May and Anderson 1979; Dobson 1990). Age at maturity was used as an inverse measure of death rate as it is the mammalian life-history traits that best reflects interspecific variation in ecological life span (Read and

Harvey 1989). Birth rate was measured as annual fecundity following Read and Harvey (1989). Host diet was classified into primary (herbivores) and secondary (animal eaters) consumers following Damuth (1987). A small subset of the parasite species (29 of 146), were excluded from analyses of the effects of host diet, because diet either was not classifiable for all host species or varied between alternative host species.

Although host population density may be strongly correlated with nematode intensity, this relationship may go undetected if host body mass is not controlled for: nematode intensity is higher in mammals that have high population density for their body mass than in rarer hosts, but no relationship is seen when comparing, say, mice and bears directly (P. Arneberg, A. Skorping, B. Grenfell, and A. F. Read, unpublished manuscript). Thus, here we analyze host population density in two ways: as original values and as values relative to host body mass. To obtain relative values, we first regressed host population density on body mass across host species (log-transformed data,  $n = 25$  species,  $r = -0.76$ ,  $P < .0001$ , estimated density =  $4.24 - 0.88 \times \log_{10}$  body mass). Relative population density for a host species was then taken as the residual from this relationship.

All continuous host traits were logarithmically transformed before analyses. When a parasite species occurred in several host species, average values of host traits were calculated as geometric means.

#### Data Analyses

Phylogenetically based statistical analyses were done using a modification of Felsenstein's (1985) independent contrast method (Pagel 1992; Purvis and Rambaut 1995). Phylogenetic information was partly based on molecular data (superfamily Ascaridoidea; Nadler 1995). However, cladistic or molecular phylogenies are unavailable for most taxa of mammalian nematodes, so for the most part we have attempted to construct a consensus from morphological systematics. Phylogeny was inferred from the taxonomies in the *CIH Keys to the Nematode Parasites of Vertebrates* (Anderson et al. 1974–1983); additional resolution was derived from the phylogenetic hypotheses of Skrjabin (1949–1954, 1953–1971), Lichtenfels (1979), Butterworth and Beverly-Burton (1980), Moravec (1981, 1982), Anderson (1984, 1988), Barus and Libosvsky (1984), Durette-Desset (1985), Adamson (1986), and Moravec et al. (1987). Recent analyses of a molecular character suitable for resolving phylogenetic relationships at the level of orders among mammalian nematodes do not contradict this phylogeny (Chilton et al. 1997). Data on branch lengths are available for only a few taxa of mammalian nematodes, and they were thus assigned ar-

bitrary values. The phylogeny derived is given in the appendix.

The independent contrast method (Felsenstein 1985) takes the form of calculating a set of linear contrasts (or differences) between pairs of subtaxa (e.g., A and B) within higher taxa. In this context, a negative correlation between, say, parasite body size and population intensity means that if body size is higher in taxa A than in B, parasite intensity should be predictably lower in A than in B. To fit the criteria of equal variances in statistical analyses, the contrasts are weighted (or standardized) by the expected variance of character change, as estimated by the appropriate branch lengths. The adequacy of a set of branch lengths can be assessed by looking at the relationship between expected variance and the standardized contrasts: lack of significant relationship implies adequate standardization of contrasts (Garland et al. 1992; Díaz-Uriarte and Garland 1996). This was achieved here by (arbitrarily) setting all branch lengths equal to unity ( $P$  values for all correlations between standardized contrasts and their expected variances  $>.15$ ). Grafen (1989) provides another algorithm to obtain relative branch lengths when data on lengths are lacking, but this method has been shown to perform less well than setting all lengths to unity (Purvis et al. 1994) and generated heteroscedasticity in our data (correlation between expected variance and standardized contrasts in female nematode volume,  $n = 53$  contrasts,  $r = -0.33$ ,  $P = .02$ ). Contrasts were calculated using the statistical package CAIC (Purvis and Rambaut 1995). In CAIC, polytomies are treated as soft (i.e., represent unrecognized phylogeny) following Pagel (1992), meaning that one bifurcating node is reconstructed at each polytomy. Reconstruction is based on information from one of the characters under study, and for consistency the same character should be used in all analyses, preferably the trait that can be assumed to best reflect the underlying phylogeny (Pagel 1992). Here female nematode volume was used, as this variable is calculated from taxonomic characters (female maximum width and average length), is the continuous nematode life-history trait for which we have most data, and is measured with less error than other continuous traits of nematode life history (Skorping et al. 1991). An alternative way to deal with polytomies is to reconstruct a fully bifurcating tree using information from the variables under study (Purvis and Garland 1993), which would produce a higher number of contrasts than the method used in CAIC. The CAIC approach is probably more conservative.

With independent contrast analyses, associations were tested for by using regression through the origin (Harvey and Pagel 1991; Garland et al. 1992, 1993; Purvis and Rambaut 1995). Nonphylogenetic analyses were done us-

ing ordinary regression, and dichotomous traits were fitted as dummy variables. In regression it is assumed that there is no error variance in the independent variables. For nematode life-history traits, variation within species (or higher taxa) will be small compared with that across all mammalian nematodes. However, as nematodes were frequently sampled in different host species, can the same be said for host traits? The answer is yes. When a nematode species was found in different host species, the hosts tended to be similar. Among parasite species found in different mammalian species, 66%–86% of the variation in traits of their hosts was found among parasite species rather than among host species within nematode species (one-way ANOVA, host body mass,  $F = 17.1$ ,  $df = 38$ ,  $66$ ,  $P < .0001$ ,  $r_1 = 0.86$ ; host age at maturity,  $F = 8.1$ ,  $df = 38$ ,  $66$ ,  $P < .0001$ ,  $r_1 = 0.73$ ; host fecundity,  $F = 6.0$ ,  $df = 32$ ,  $52$ ,  $P < .0001$ ,  $r_1 = 0.66$ ; host population density,  $F = 8.1$ ,  $df = 31$ ,  $35$ ,  $P < .0001$ ,  $r_1 = 0.73$ ; the coefficient of intraclass correlation,  $r_1$ , estimates the proportion of variance that occurs among rather than within species; Sokal and Rohlf 1981). We did not control significance levels for multiple comparisons, because this significantly increases the probability of dismissing real patterns (Rothman 1990).

#### *Slope Estimation*

Slopes of relationships between nematode body size and population density were estimated in two ways, and real values probably lie between these two estimates. First we used ordinary least-square regression (OLS), which is frequently used for size-abundance relationships (e.g., Damuth 1993). With OLS it is assumed that there is no error variance in the independent variable. When violated, as is likely for biological data, estimated slopes will be too close to 0 (Rayner 1985; Riska 1991). This problem may be circumvented by using the structural relation (SR), which assumes a specific ratio ( $\lambda$ ) of the error variances in the independent and dependent variables (here error in size divided by error in intensity; Rayner 1985). Error variance has two components, that due to sampling error and that due to real biological differences among species, where the latter component is problematic to estimate because it requires an adequate model of biological variation (Riska 1991). However, as body size changes in evolutionary time and intensity takes values in ecological time, it is reasonable to assume that error variance in size will be largely made up by measurement error here. If we for the moment ignore intensity error variation due to real biological differences among species and base our calculation of  $\lambda$  on error variance that is due to sampling problems only, then we get an underestimate of  $\lambda$ . Because SR slopes converge toward OLS slopes as  $\lambda$  in-

creases (Rayner 1985), using this (under)estimate will give SR slopes that are too steep, meaning that real slopes of size-intensity relationships will lie somewhere between the estimated OLS and SR slopes. To estimate variance due to measurement error, we followed Pagel and Harvey (1989) in studying variation within species in mean values of size and density reported from different populations in the literature. For each species where two or more means were available, we calculated the variance in size (10 species) and in intensity (73 species). Then,  $\lambda$  was calculated as the average species variance in intensity divided by average species variance in size. This gave a value of 11.1, meaning that variance due to measurement error in intensity is approximately 11 times that in nematode body size.

Slopes among the most common species within a community were calculated using the method to estimate negative upper-bound slopes (NUBS) of plots of body size and population density (Blackburn et al. 1992). The highest population density estimate within a community is often found for an intermediate-sized species (Blackburn et al. 1992), and NUBS are calculated as the slope of the regression line through the most abundant species to the right of this peak abundance. The species are divided into size classes of equal range, and the most abundant species in each class is employed in the analysis. Analyses of NUBS were limited to the 11 communities with six or more species, because otherwise there might be too few species to get a meaningful estimate of maximum intensity in each size class. For the same reason, we used two size classes. An assumption of the NUBS method is that body size is uniformly distributed within communities (Blackburn et al. 1992). This assumption was violated here: there were more species in the lower than in the upper size group in nine of the 11 communities analyzed (binomial  $P = 0.066$ ). Thus, by chance alone, maximum density may be overestimated among the small-bodied species relative to larger ones. If so, the NUBS calculated here will be artificially steeply negative. Additionally, in one of 11 communities, maximum intensity was found for the largest species, which prohibits calculation of an upper-bound slope using the method of Blackburn et al. (1992), although the slope among the most common species clearly could be positive.

## **Results**

### *Nonphylogenetic Analyses of the Global Data Set*

Nematode body size and intensity were negatively correlated across all species: commoner nematodes are generally smaller than rarer species. However, commoner parasite species also have simpler life cycles, tend to be located in the gastrointestinal tract, and develop faster to

**Table 1:** Nonphylogenetic analyses of the relationship between parasite population intensity (mean number of parasites per infected host) and parasite life-history traits, host life-history traits, or host population density

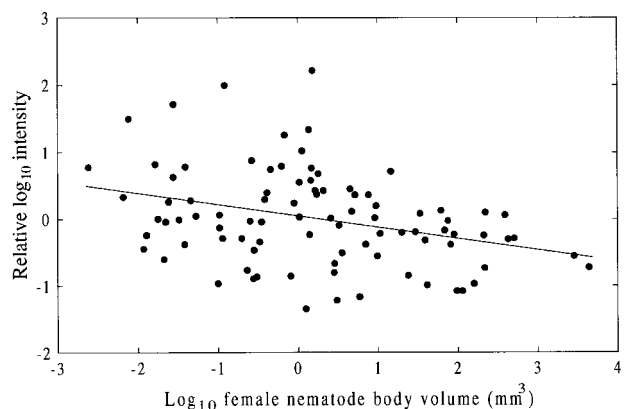
	n	r
Log female parasite body volume	92	-.23*
Log parasite prepatency period	67	-.30*
Log parasite patency period	36	-.09
Log parasite fecundity	16	-.32
Adult parasite location	146	.22*
Juvenile parasite location	25	.18
Parasite life cycle	86	.25*
Log host body mass	146	.23*
Log host population density	98	.12
Log relative host population density	98	.23*
Log host fecundity	145	-.10
Log host age at maturity	146	.08
Host diet	107	.15

Note: For the dichotomous variables, a positive correlation coefficient ( $r$ ) means a higher mean value of intensity in the gastrointestinal tract (adult or juvenile nematode location) among nematodes without an intermediate host (life cycle) or among nematodes in herbivores (host diet);  $n$  = number of species.

\*  $P < .05$ .

maturity once inside a host. Intensity was significantly correlated also with traits of host species: parasites living in larger host species or in relatively dense host populations have generally higher intensities than nematodes in more small-bodied or rarer mammals (table 1). Thus, we consider both host body mass and relative host density (density for a given host body mass), which have the potential to confound size-intensity relationships, as both variables were correlated also with nematode body size (host body mass,  $n = 92$ ,  $r = 0.41$ ,  $P < .0001$ ; relative host density,  $n = 63$ ,  $r = -0.25$ ,  $P = .057$ ).

When the effects of host body size were held constant by partial correlation, the relationship between parasite body size and intensity were strengthened, with size accounting for about 10% of the variation in intensity across species ( $n = 92$ , partial  $r = -0.33$ ,  $P < .005$ ; fig. 1). If the effects of both host and parasite body size were removed, then no other aspects of nematode life history were significantly associated with intensity (table 2), which implies that these traits were correlated with intensity because they are also correlated with parasite body size (Skorping et al. 1991; Read and Skorping 1995). On the other hand, if we removed the effects of other nematode life-history traits and host body mass, there were still significant associations between parasite body size and intensity (table 2). Thus, using nonphylo-



**Figure 1:** Relationship between  $\log_{10}$  parasite body size (female volume) and relative  $\log_{10}$  intensity across 92 mammalian nematode species as revealed by ordinary regression (i.e., nonphylogenetic analyses). Values of relative intensity are residuals from a regression between  $\log_{10}$  host body mass and  $\log_{10}$  intensity (mean number of parasites per infected host).

genetic analyses and with the effects of hosts size removed, small nematodes are commoner than large ones independent of effects of particular other traits of nematode life history.

However, nematode body size was not significantly correlated with intensity when the effects of relative host population density was controlled for ( $n = 63$ , partial

**Table 2:** Nonphylogenetic partial correlation analyses of the relationships between parasite population intensity (mean number of parasites per infected host) and parasite life-history traits when the effects of host body mass and parasite body size has been controlled for (center), or intensity and parasite body size when the effects of the parasite life-history trait in the first list and host body mass has been controlled for (right)

Parasite life-history trait (n)	Partial r for nematode life-history trait	Partial r for nematode body size
Log parasite prepatency period (56)	-.09	-.21
Log parasite patency period (31)	-.13	-.23
Log parasite fecundity (13)	-.08	-.13
Adult parasite location (92)	.15	-.31**
Juvenile parasite location (22)	.20	-.03
Parasite life cycle (69)	.20	-.26*

Note: Partial  $r$  = partial correlation coefficient (see table 1 for interpretation for dichotomous traits);  $n$  = number of species. For nematode life-history traits, all  $P$  values  $> .10$ .

\*  $P < .05$  for nematode body size (log female body volume).

\*\*  $P < .005$  for nematode body size (log female body volume).

**Table 3:** Independent contrast analyses of the relationships between parasite population intensity (mean number of parasites per infected host) and parasite life-history traits, host life-history traits, or host population density

	n	r
Log female parasite body volume	53	-.28*
Log parasite prepatency period	36	-.24
Log parasite patency period	22	.21
Log parasite fecundity	10	-.48
Adult parasite location	8	.41
Juvenile parasite location	4	.90
Parasite life cycle	6	.00
Log host body mass	53	.06
Log host population density	37	.04
Log relative host population density	37	.07
Log host fecundity	53	.12
Log host age at maturity	53	-.05
Host diet	10	-.08

Note: Here  $r$  = correlation coefficient (see table 1 for interpretation for dichotomous traits);  $n$  = number of phylogenetically independent contrasts.

\*  $P < .05$ .

$r = -0.20$ ,  $P = .11$ ). Similarly, if the effects of relative host density and nematode body size were removed by partial correlation, no other traits of nematode life history was significantly associated with intensity (all  $P$  values  $> .06$ ).

#### *Independent Contrast Analyses of the Global Data Set*

From independent contrast analyses, the picture was simpler than with nonphylogenetic analyses: intensity was significantly correlated only with nematode body size (table 3). Negative relationships between size and density did not tend to dominate at only higher levels in the phylogeny, as has been observed in birds (Nee et al. 1991; Cotgreave and Harvey 1994). Contrasts of nematode body size and intensity were significantly negatively correlated also after effects of taxonomic level (above or below median ranked taxa, subfamilies) was controlled for ( $n = 53$ , partial  $r = -0.30$ ,  $P = .03$ ), and there was no significant interaction between the effects of body size and taxonomic level ( $n = 53$ , partial  $r = -0.03$ ,  $P = .84$ ). For parasite juvenile and adult location and life cycle, there were few contrasts, which shows that these traits vary little between closely related nematode taxa. Host traits were not correlated with intensity (all  $P$  values  $> .35$ ), which demonstrates that also these traits vary lit-

tle and/or in no consistent direction among closely related nematode taxa.

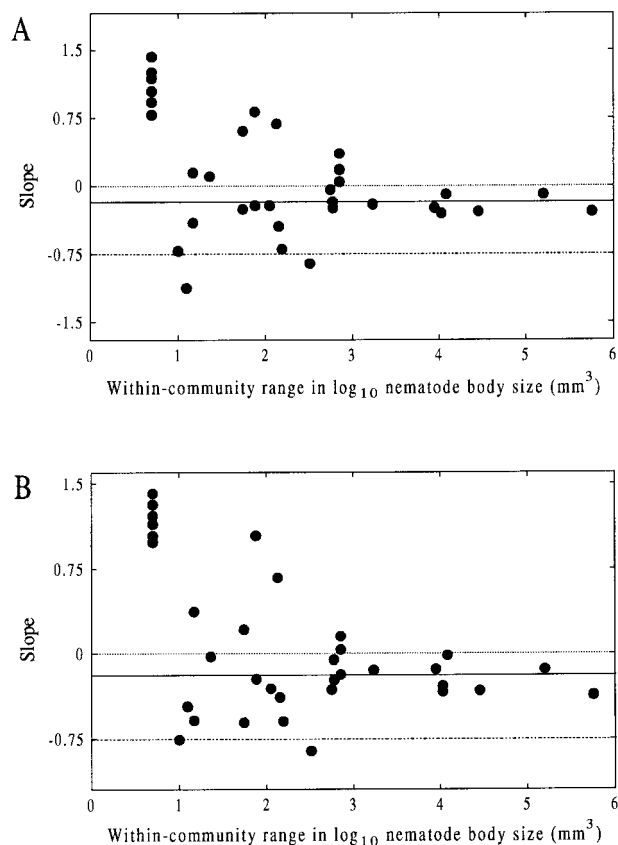
#### *Within-Community Analyses*

How much nematode body size varies within a parasite community affects associations between nematode body size and intensity. Relationships varied wildly among communities of evenly sized worms but were largely negative in communities with nematodes of more varying sizes; this pattern is seen both with nonphylogenetic analyses and independent contrast analyses (fig. 2A and B, respectively). With size ranging over less than two to three orders of magnitude, size-density relationships are typically variable (see the introduction). Here, there were significantly more communities with negative than with positive size-intensity relationships, once body size ranged over more than two orders of magnitude. Again, this is seen with both methods of analyses (16 vs. four communities, binomial  $P = .01$  with nonphylogenetic analyses; 17 vs. three communities, binomial  $P = .002$ , with independent contrast analyses).

Do we observe mainly negative relationships between nematode body size and intensity within communities because some host species had particular biological characters giving rise to negative relationships? If so, we might expect negative size-intensity correlations in only a few, well-sampled mammalian species. This was not observed. More negative than positive correlations were generally found also within single host species. Still looking at correlations calculated using independent contrast analyses, nine host species had an excess of communities with negative relationships, whereas positive correlations dominated in only two mammals (binomial  $P = .066$ ). Thus, once body size ranges over two orders of magnitude or more, parasite body size and intensity tend to be negatively correlated within nematode communities, and this size effect appears independently of host species and other characters shared by closely related nematode taxa.

To further see whether nematode body size has an independent effect on intensity within single communities, multiple regression separating effects of parasite size and other life-history traits were repeated within the five most species-rich communities. Nonphylogenetic analyses were used, because independent contrast analyses in all cases but one gave too few contrasts (i.e., seven or less) for multiple regression to be meaningful (showing that parasite phylogenies with better resolution are needed; see also Rhode 1996). Additionally, because data on life-history traits lacked for several species in these communities, only nine regression models could be fitted (five for adult habitat, two for life cycle, and two for pre-





**Figure 2:** Relationship between range in  $\log_{10}$  parasite body size (female volume) and ordinary least-square slope of the relationship between  $\log_{10}$  parasite body size and  $\log_{10}$  intensity (mean number of parasites per infected host) within nematode communities. Slopes have been estimated using (A) ordinary regression (i.e., nonphylogenetic analyses) and (B) phylogenetically independent contrast analyses (see the text). Data are shown for 36 parasite communities. The dotted line denotes a slope of 0 (i.e., no relationship); the solid line, the slope ( $-0.19$ ) revealed by independent contrast analyses of all data; the broken line, a slope of  $-0.75$ . One outlier is not shown (body size range 0.3, slope 8.3 in A and 8.0 in B).

patency,  $9 \leq n \leq 14$  species). Nematode body size was negatively and significantly ( $P < .05$ ) correlated with intensity after the effects of adult nematode location (in two models) or prepatency period or life cycle (in one model each) were removed. When effects of parasite body size were controlled for in the same nine models, no other nematode life-history traits were significantly correlated with intensity (all  $P$  values  $> .14$ ). Thus, these nonphylogenetic analyses provide another piece of evidence that nematode body size has an independent effect on intensity within single communities.

### Slopes of Body-Size Intensity Relationships

In all analyses, slopes of nematode body size–intensity relationships were significantly shallower than  $-0.75$ , and when independent contrast analyses were used and/or confounding factors were controlled for directly, they consistently took values around  $-0.20$  (table 4). The negative upper-bound slopes (NUBS) were somewhat more negative, which was expected from the potential for artificially steep slopes using the method of Blackburn et al. (1992) here (see “Methods”). Still, even the NUBS were significantly shallower than  $-0.75$ .

Another pattern that is demonstrated for the first time here is that as body size range increases, within-community relationships between body size and intensity converge toward the global relationship (fig. 2A, B). Thus, among communities with large range in body size, slopes of size–intensity relationships are similar to those obtained across all species with confounding factors controlled for.

### Discussion

A large body of ecological literature stresses the importance of body size for determining animal abundance, yet macroecological empirical evidence exists for free-living animals only (e.g., Damuth 1987; Nee et al. 1991; Griffiths 1992). Most animal species are parasites, and here we show that size is important for population density also among parasites: small-bodied mammalian nematodes are generally commoner than larger ones. Nematode body size, which ranged over six orders of magnitude, could explain 10% of the variation in nematode species density, which is considerably less than the amount of variation in abundance explained by body size among mammals, where size range is similar (Damuth 1987).

Population intensity was also correlated with other traits of nematode life history, but these relationships were not significant when the effects of body size were controlled for or, alternatively, when independent contrast analyses were used. Traits of host species were also related to intensity, but again, not when independent contrast analyses were applied. Parasite body size, on the other hand, was related to intensity independently of all other factors considered and regardless of way of analysis. This differs from that found among British birds, where life span but not body size was an important determinant of population density (Blackburn et al. 1996). Among mammalian nematodes, significant size–intensity relationships were seen when life-history traits were controlled for directly, and, most important, body size and

**Table 4:** Slopes of relationships between parasite body size (female body volume) and population intensity (mean number of parasites per infected host)

Way of analysis	df	OLS slope (95% CI)	SR slope (95% CI)
All data pooled, nonphylogenetic	90	-.12**** (-.22, -.02)	-.12**** (-.23, -.01)
All data pooled, nonphylogenetic, controlled for host size	89	-.19**** (-.31, -.07)	Not determined <sup>a</sup>
All data pooled, independent contrasts	52	-.18**** (-.35, -.01)	-.19**** (-.37, -.01)
Within communities, nonphylogenetic	19	-.18**** (-.34, -.03)	-.19**** (-.34, -.05)
Within communities, independent contrasts	19	-.21**** (-.35, -.07)	-.22**** (-.36, -.07)
NUBS, within communities, nonphylogenetic	9	-.46* (-.70, -.23)	-.46* (-.70, -.23)

Note: Slopes were estimated using ordinary least-squares regression (OLS) or the structural relation (SR); see "Methods." Six different slopes were calculated: using all data and nonphylogenetic analyses; same data and way of analysis, but with the effects of host body mass removed by partial correlation; same data using independent contrasts analyses (see "Methods"); using nonphylogenetic analyses within nematode communities where parasite body size ranged over more than two orders of magnitude; same data using independent contrasts analyses; and NUBS within communities with six or more species (nonphylogenetic; see "Methods"). Within-community slopes are averages of all slopes from all communities; 95% CI = 95% confidence interval of mean regression coefficient; significance level for difference from  $-0.75$ .

<sup>a</sup> SR slope cannot be estimated without bias because nematode body size and host body size are correlated ( $n = 92$ ,  $r = 0.41$ ,  $P < .0001$ ; Harvey and Pagel 1991, pp. 198–202).

\*  $P < .05$ .

\*\*\*\*  $P < .000$ .

intensity were significantly correlated within single nematode communities and when independent contrast analyses were used. Relationships between nematode body size and population intensity are therefore not generated by biased sampling from the literature (see Lawton 1989), by confounding effects of a range of habitat variables, such as densities of host populations, or by other characters shared by closely related nematode taxa. Although certain life-history traits are measured with more error than body size (Skorping et al. 1991), there is no evidence that any other trait than size is correlated with intensity.

Results were less consistent from nonphylogenetic analyses. In particular, the size-intensity relationship was not significant when effects of host population density were controlled for. This result may be a spurious one caused by the use of species values as independent data points (e.g., Harvey 1996) or imply that effects of host population density on parasite intensity (P. Arneberg, A. Skorping, B. Grenfell, and A. F. Read, unpublished manuscript) are too strong for any size-intensity relationship to be detectable when data are pooled from host species living at very different densities. These difficulties may also affect the large number of studies that have assessed size-density relationships by using nonphylogenetic analyses on data pooled from different habitats (e.g., Damuth 1981, 1987, 1993; Peters 1983; Peters and Raelson 1984; Robinson and Redford 1986; Brown and Maurer 1987; Carrascal and Telleria 1991; Blackburn et

al. 1993; Silva and Downing 1994; Ebenman et al. 1995; Marquet et al. 1995), where the problems known to arise from the use of species as independent data points have generally been ignored.

Here, relationships between nematode body size and population intensity had slopes around  $-0.20$  when confounding factors were controlled for and appropriate statistical techniques were used. Thus, they are consistently shallower than the value of  $-0.75$  predicted by the energetic equivalence rule (Damuth 1981). This was observed also for slopes among the most common species in each community (see Lawton 1989). The relationship between body mass and energy usage does not appear to be different for nematodes than for, say, birds and mammals. Among free-living nematodes, metabolic rate scale to body mass with a slope around 0.75 on log-log scales (Schiemer 1987), and for parasitic species, although the sample contained only four species, the slope was 0.65 (Von Brand 1979). Thus, there is no evidence of energy equivalence among nematodes parasitizing mammals: the shallow slopes of size-intensity relationships suggest that populations of large-bodied parasite species use more energy than populations of small-bodied ones in nematode communities.

This pattern of energy usage implies that relationships between body size and intensity among mammalian nematodes are not generated by processes related to population energy usage in the manner envisaged by the evolutionary model underlying the energetic equivalence rule

(Damuth 1981; Maiorana and Van Valen 1990). However, this model has been criticized for making unrealistic assumptions (Marquet et al. 1995). One of the key assumptions, that species have shared a common resource base through evolutionary time (see Marquet et al. 1995), is nevertheless realistic here, because mammalian nematodes have a long history of engagement with their hosts and each other (Anderson 1992). In another respect, the model is unrealistic if the evolutionary outcome of biotic interactions depends on body size. For example, with large-bodied species being superior to small ones in controlling energy, evolutionary processes related to population energy usage may still give the shallow size-density relationships found here.

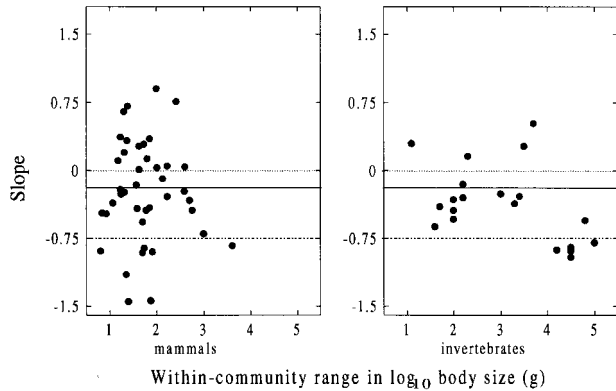
Focusing on how relationships between body size and abundance can be generated by processes acting in ecological time (Lawton 1989; Blackburn 1993), we can take the lack of energy equivalence found here to imply that mammalian nematode populations are generally not constrained by energy availability. The weakness of this interpretation is that there is no formal theory linking energy equivalence to energy limited populations in ecological time. Among mammalian nematodes, however, other evidence indicates that energy availability is not limiting populations. Within the mammalian body there is often a continuous excess of energy that is not exploited by the parasites, which suggests that nematode populations could reach higher intensities if their populations were not limited by some other factor than energy (Calow 1983; Wharton 1986).

If processes related to population energy usage are not important in determining the form of the relationship between nematode body size and population density, why does parasite body size still affect intensity? Space limitation is not a likely cause because the total volume of all nematodes in a host typically takes up only a small portion of the host body. Even if we added together the body mass of all nematode individuals of a species found in a host population (assuming  $100 \text{ mm}^3$  body volume = 1 g nematode body mass, and using averages of male and female nematode body mass), this typically makes up only a tiny fraction of the body mass of a single host individual (average 1% of host body mass; maximum, 46%). An alternative process, which could be valid for animals in general, is size-dependent intraspecific competition. If large-bodied nematode individuals affect each other more severely than do smaller parasites, then intraspecific competition could constrain densities of large parasites to lower levels than smaller ones. The size-intensity relationship may also be generated by processes that are more specialized to parasites. For example, if a single large worm causes more damage to its host than

a more small-bodied parasite, then effects on both host mortality and fecundity could constrain densities of large nematodes to lower levels than smaller ones (Anderson and May 1978; May and Anderson 1978). Also, intraspecific-specific apparent competition (Holt 1977) may prevent high intensities of large-bodied parasites, if the amount of antigen produced increases with parasite body size. If so, there is some interesting allometry of immunogenicity to be revealed.

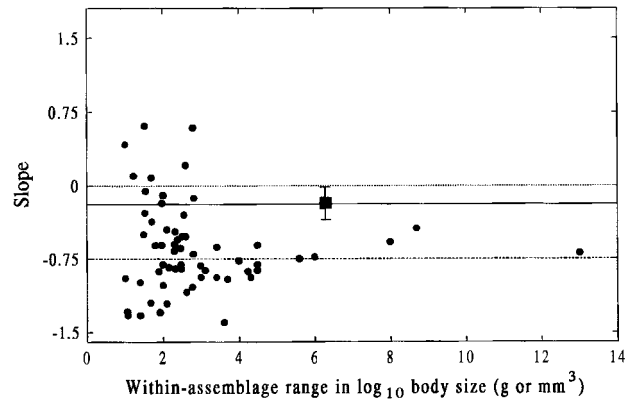
If the processes generating size-density relationships among parasites are the same as those generating them among free-living animals, then slopes of the relationships ought to be similar. However, considerable discussion in the literature on size-abundance relationships concerns whether slopes found in global relationships are also found within single communities and also whether global slopes attain any particular value (e.g., Lawton 1989; Damuth 1991; Currie 1993). Here, we found for the first time that slopes of size-density relationships within communities converge toward the global relationship as body size range increases within communities, which suggests that community relationships between size and density do indeed represent truncated samples of the global relationship between nematode body size and population density, as suggested by Currie (1993) and Damuth (1981). Is this a general trend, seen also for free-living animals? In figure 3 we compare body size range and slopes of size abundance relationship from single communities of free-living animals, and the picture resembles that found for mammalian nematodes, except for different convergence. Slopes vary wildly among communities of evenly sized species, and as size range increases, slopes converge toward a value around  $-0.75$ . This is seen both for mammals and invertebrates (fig. 3). Global relationships also exhibit this pattern: much of the discussion about the general shape of global cross-species relationships between size and abundance may stem from variation in body size range among assemblages studied, and again there is a trend for convergence toward values around  $-0.75$  (fig. 4). Thus, as revealed by nonphylogenetic analyses (i.e., ordinary regression), relationships between body size and population density apparently have a common underlying slope among free-living animals tending toward a value of about  $-0.75$ . At comparable ranges, the relationship is shallower for parasitic nematodes of mammals (fig. 4).

One implication of this is that the processes generating size-density relationship may generally differ between free-living and parasitic animals. For example, parasite-specific mechanisms like immune responses and parasite-induced host mortality may be important determinants among mammalian nematodes. However, such conclu-



**Figure 3:** The relationship between range in log body size and slope of linear least-square regression relationships between the logarithms of body size and population density within communities. Relationships are shown for mammals (*left*) and free-living invertebrates (*right*). The dotted line denotes a slope of 0 (i.e., no relationship); the solid line, the slope of  $-0.19$  observed among nematodes parasitizing mammals; and the broken line, a slope of  $-0.75$ . Sources are Strayer and Likens (1986), Marquet et al. (1990), Blackburn et al. (1993), Gaston et al. (1993), Strayer (1994), Dugan et al. (1995), and Silva and Downing (1995).

sions may be premature, because the form of size-abundance relationships when phylogenetically based statistical methods are used to address the statistical problems posed by multispecies data sets, and hence possibly to control for the effects of a range of confounding factors, is largely unresolved among free-living animals (Harvey 1996). The only group other than mammalian nematodes where this has been done extensively is birds, where the use of phylogenies has revealed novel aspects of size-abundance relationships. For example, Cotgreave and Harvey (1992) showed that size and density were unrelated within bird communities when independent contrast analyses were used, even though nonphylogenetic analyses revealed a significant excess of negative relationships (although they did not pay attention to size range within communities). Also, when independent contrast analyses are used, bird abundance may be unrelated to body size but correlated with other life-history traits (Blackburn et al. 1996). Although this lack of overall relationship between size and abundance within bird taxa may stem from the fact that relationships tend to be positive at low taxonomic levels and negative at higher ones (Nee et al. 1991; Cotgreave and Harvey 1994), these patterns suggest that functional links between body size and population density are fundamentally different between birds and the group of parasites studied here. More detailed macroecological examination of other taxa may tell us whether this difference is particular to mammalian



**Figure 4:** The relationship between range in log body size and slope of linear least-square regression relationships between the logarithms of body size and population density among assemblages of free-living animals (*solid circles*) and nematodes parasitizing mammals (*solid square*, with 95% confidence interval). For free-living animals, slopes were estimated using nonphylogenetic analyses (ordinary regression); and for nematodes, phylogenetically independent contrasts (see Methods). The dotted line denotes a slope of 0 (i.e., no relationship); the solid line, a slope of  $-0.19$  observed among nematodes parasitizing mammals; and the broken line, a slope of  $-0.75$ . Sources are Peters and Wassenberg (1983), Robinson and Redford (1986), Damuth (1987, 1993), Macpherson (1989), Carrascal and Tellería (1991), Nee et al. (1991), Cambefort (1994), Ebenman et al. (1995), and the present study. (Note: The datapoint with range value of approximately 9 is misplaced. The correct value is 3.4. This does not alter any conclusions.)

nematodes and birds, and hence whether generalizations about single factors as determinants of animals abundance are possible.

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#### APPENDIX

##### Phylogenetic Tree Used in the Analyses

Figures A1–A4 show the phylogenetic tree used in the analyses. Sources are given in “Methods.” Branch lengths are arbitrary.

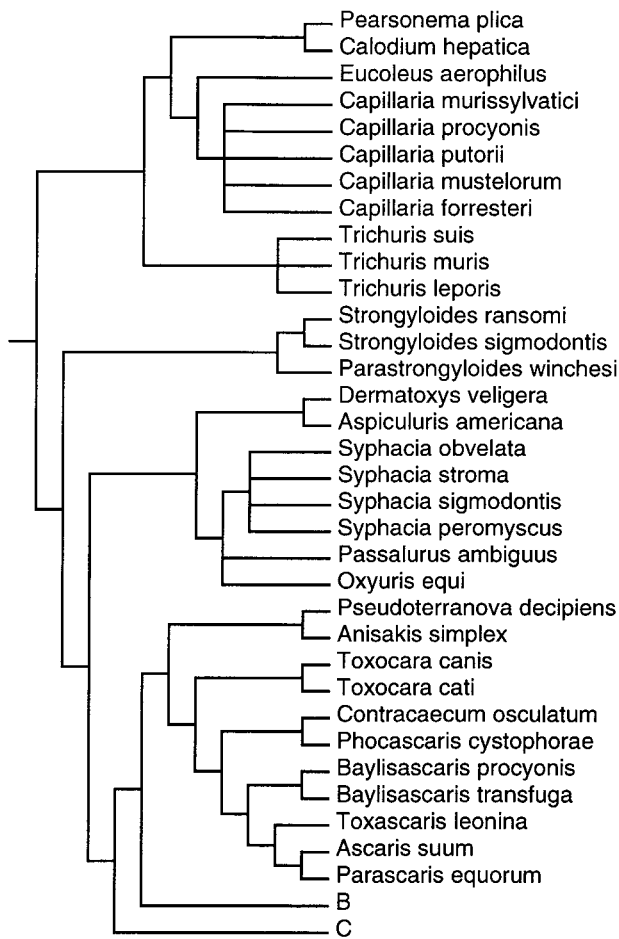


Figure A1: Key to clade topology and phylogenetic relationships within the orders Ascaridida, Enoplida, Oxyurida, and Rhabditida. Detailed topology of clades B, C, and D (position shown in fig. A3) are shown in the subsequent figures (figs. A2–A4).

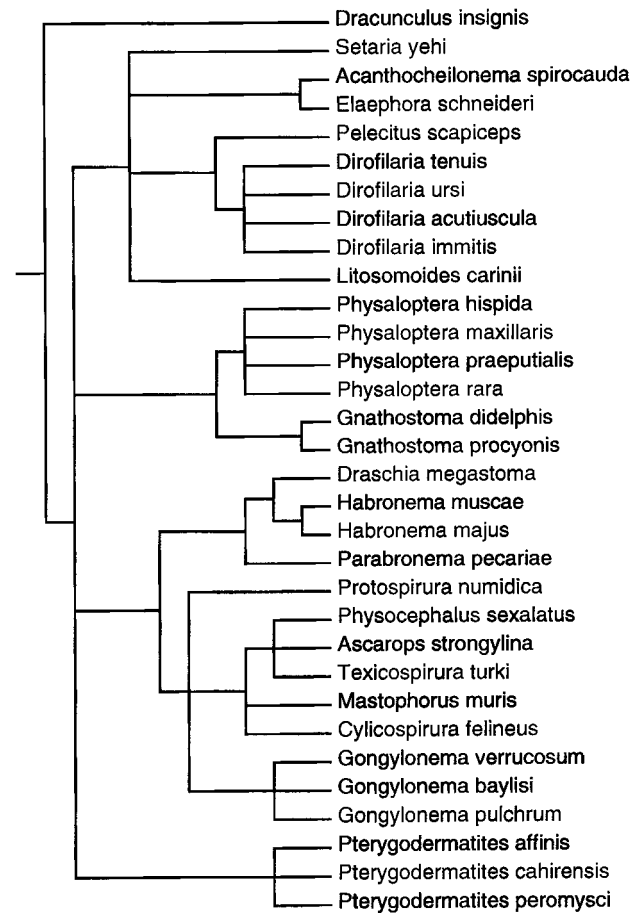


Figure A2: Clade B, order Spirurida. The tree is rooted at the end of the branch leading to taxon B in figure A1.

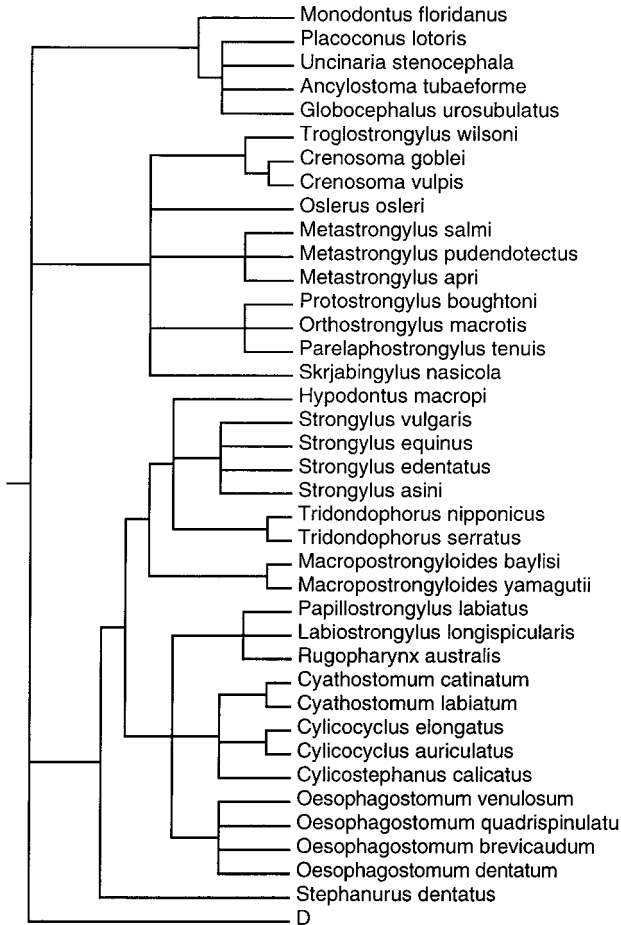


Figure A3: Clade C, order Strongylida (in part): superfamilies Ancylostomatoidea, Strongyloidea, and Metastrongyloidea. The tree is rooted at the end of the branch leading to taxon C in figure A1.

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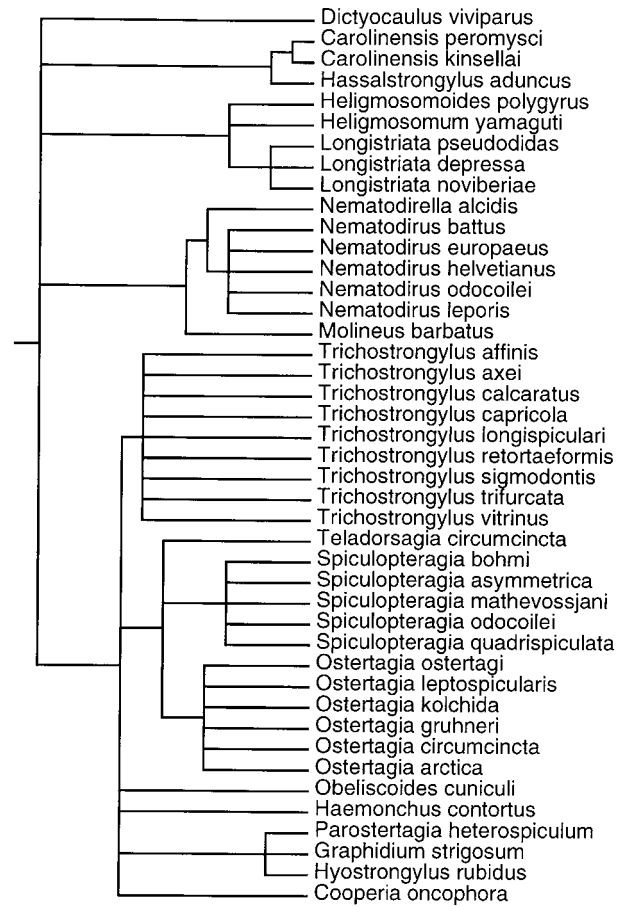


Figure A4: Clade D, order Strongyloidea (in part): superfamily Trichostrongyloidea. The tree is rooted at the end of the branch leading to taxon D in figure A3.

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