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Is population density a species character? Comparative analyses of the nematode parasites of mammals

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An increasingly popular approach to the question of what determines population density is to compare the characteristics of common and rare species. However, if densities vary wildly between populations or through time, or are poorly sampled, the search for species level traits may be fruitless, and perhaps not even justified. For example, parasite densities have been considered too variable for comparative analyses. Here, we use repeatability analysis on data of 62 species of mammalian nematodes where population density of each species was measured in at least two different host populations, and analysed three measures of parasite density: intensity, abundance and prevalence (abundance = prevalence × intensity). About half of the variation in population intensity was found between parasite species rather than between populations within species. For abundance there were significant, but less pronounced differences between parasite species. Population intensity and abundance also differed significantly across the 25 host species sampled. For prevalence, interpopulation variation within both parasite and host species may be too dominating for cross-species analyses to be fruitful. In line with this, prevalence and intensity were only weakly correlated, and had different frequency distributions. Intensity followed a log-normal distribution across both population estimates and species means; population prevalence estimates were bimodally distributed, but species means were normally distributed. Thus, despite striking variation within species, differences in population intensity between mammalian nematode species are identifiable from literature surveys, suggesting that comparative studies may be important for understanding intensity variation. More generally, repeatability analyses may also guide meaningful comparisons of cross-species analyses made in different species assemblages.

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What determines population density is one of the most fundamental issues in ecology. An exciting and increasingly popular approach to this question is to compare the characteristics of common and rare species (Damuth 1981, Nee et al. 1991a, Gaston 1994, Brown 1995, Cotgreave 1995, Silva and Downing 1995, Blackburn et al. 1996). But can estimates of population density be used to measure species commonness? If population densities are measured inaccurately or vary wildly across space or time, variation between species may be small relative to that found within species, so that attempts to identify species-level factors responsible for population abundance may be futile. This may not be a problem across extremely diverse taxa (e.g. from minute crustaceans to elephants, Damuth 1987), where we may expect variation in population density within species to

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be small relative to that across species. But such repeatability comes at a price: variation in population densities could be due to any of the huge suite of traits which differ between highly diverse taxa. Ideally, attempts to examine species differences in commonness require comparisons of ecologically and taxonomically comparable organisms. Here the issue of the repeatability of population density estimates for a species becomes crucial. Several ecologists, for example, have argued that much can be learnt from comparative analyses of parasite densities (Hamilton and Zuk 1982, Anderson and May 1991, Read 1991, John 1995, Møller 1996, Poulin 1996). Yet, several parasitologists have been sufficiently impressed by (often very large) within-species fluctuations in density to argue that cross-species analyses of parasite abundance are meaningless (Cox 1989, Weatherhead and Bennett 1991, 1992, Weatherhead et al. 1991, Yezerinac and Weatherhead 1995). Impressions are, of course, insufficient. What matters is the relative magnitude of variation within and between species for the group of organisms under study. In principle, this is a relatively easily addressed empirical question, yet we are unaware of previous attempts to do so by either proponents or critics of cross-species analyses. A related approach is the study of spatial or temporal concordance of rank abundances (Gaston 1994 and references therein). Concordance of rank abundances exists if the abundances of a set of species has similar ranks across locations or through time, and is a meaningful way to analyse commonness when there is at least some co-occurrence of species. Repeatability analyses may be applied to species that live in different habitats and never co-occur, which are frequently the kind of assemblages that are subject to macroecological research (e.g. Silva and Downing 1995, Blackburn et al. 1996).

Comparative analyses of species commonness typically seek associations between species characteristics (e.g. fecundity, size, metabolic rate) or characteristics of habitats they occupy (e.g. productivity, levels of competition, predator densities). Repeatability analyses will, if they reveal substantial variation between species rather than within them, make it harder to dismiss non-significant correlations as a consequence of noisy abundance data. Equally, an absence of significant repeatability demonstrates which null results may be considered uninformative. Furthermore, comparative analyses often seek to describe and explain variation in commonness by looking at the distribution of species densities. Clearly it is of interest to know whether these patterns represent largely cross-population or cross-species variation.

Here, we focus on the commonness of species of nematodes parasitising wild mammals. Populations of these parasites are often sampled in different geographic locations and substantial fluctuations in the abundance of single species through time or space are frequently reported (e.g. Fig. 1). We begin by asking whether, despite this often impressive variation observed within species, there are nonetheless detectable differences in population densities between nematode species.

Assessing habitat directly may also be important. For example, for a given body mass, non-tropical mammals are generally more abundant than tropical ones (Damuth 1987). Indeed, when applied to parasite population density, repeatability analyses may offer a way of assessing whether there is a repeatable influence of habitat, and hence whether habitat characters may need to be employed in comparative analyses. If host-type is an important determinant of parasite population density, the density of different species of parasites within the same host species should be more similar than expected by chance. We therefore ask the second question: is parasite population density repeatable within host species? This is not a trivial question; even across as different hosts as the wood mouse (*Apodemus sylvaticus* L.) and the black bear (*Ursus americanus* Pallas) variation between parasite population density estimates within host species appears to dominate (Fig. 2). Because particular parasite species are likely to occur in particular host species, significant repeatability of parasite densities for both parasite and host species would prompt another question: are there differences between parasite species that are independent of differences between host species?

Parasite populations are fragmented into individual hosts, so that two separate aspects of population density have typically been measured: (1) prevalence, the fraction of hosts in a population that is infected, and (2) intensity, the mean number of parasites in the infected hosts. These aspects have also been subject to separate comparative analyses (e.g. Read 1991, Poulin 1996). We therefore ask our questions independently for intensity and prevalence. Another measure of parasite density is abundance (the mean number of parasites in all hosts in a population). This measure is a combination of prevalence and intensity (abundance = intensity × prevalence), but because a substantial body of theoretical work has been developed using abundance (e.g. May and Anderson 1979, Dobson 1990), we also looked at the repeatability of abundance estimates.

For ecologists used to working with free-living organisms, it might seem puzzling that we do not express densities as number of worms per unit of host body mass or some equivalent. There are several reasons for this. First, theoretical work frequently uses intensity, abundance and prevalence (Anderson 1982, Anderson and May 1991). Second, any transformation of the data we use into units more frequently used to free-living organisms, such as number per unit area, necessarily introduces another source of variation (e.g. from estimates of host population density, see Blackburn and Gaston 1996). Here we are trying to determine whether comparative analyses are feasible given the potential

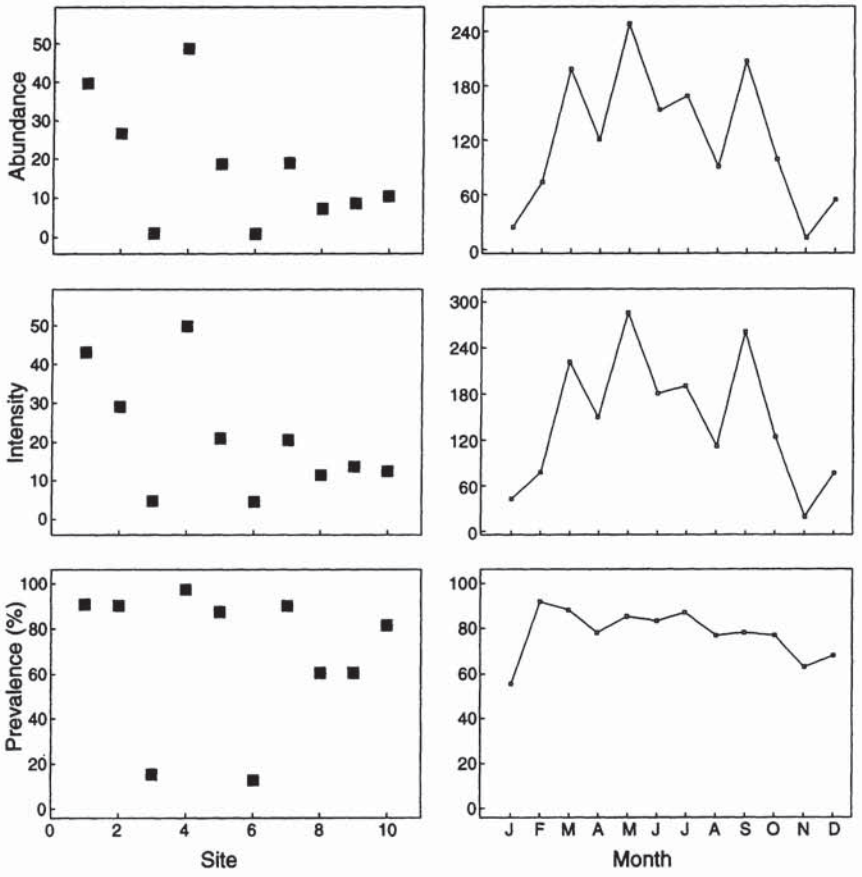

Fig. 1. Variation across time or space in abundance (mean number per host), intensity (mean number per infected host) and prevalence (proportion of hosts infected) of two species of mammalian nematodes. To the left *Gongylonema pulchrum* across sites in *Odocoileus virginianus* (white-tailed deer) and to the right *Obeliscoides cuniculi* across time in *Lepus americanus* (snowshoe hare). Data are from Prestwood et al. (1970) and Erickson (1944).

noise already in the data. We note that this difference in units does not affect the application of repeatability analyses to data from free-living organisms. Third, there may not be simple relationships between host body size and nematode population density (see for example Fig. 2). Establishing whether population estimates can be reliably used to detect differences in parasite densities across parasite and host species is a first step to addressing such questions.

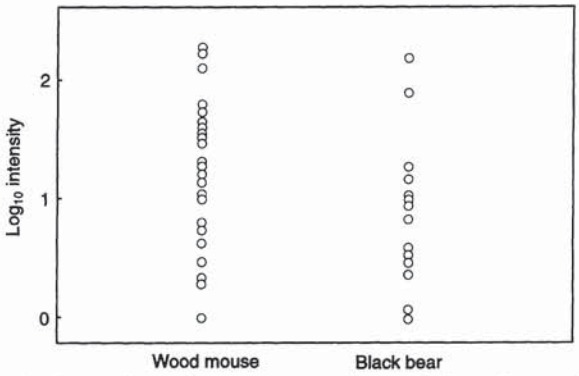

Fig. 2. Intensity estimates (mean number per infected host) of nematode populations in the wood mouse (*Apodemus sylvaticus*, 39 estimates) and in the black bear (*Ursus americanus*, 18 estimates). See Appendix for a list of nematode species and the number of population estimates from each species. The geometric mean of population intensity is slightly higher in the wood mouse (13 and 7 worms per infected host in wood mouse and black bear, respectively).

Materials and methods

The data

The dependent variable in this study was either the prevalence, the intensity or the abundance of individual parasite populations. We searched the literature for estimates of population sizes of nematodes of mammals. Measures from the same parasite population taken at different points in time may be correlated and cause us to overestimate the similarity of prevalence, abundance or intensity within species. We therefore focus on spatial variation, and repeated measures within populations were averaged to single estimates. Similarly, when a parasite species is shared by sympatric populations of different host species, estimates may be repeated measures of single parasite populations, and were therefore excluded. We included data if 30 host individuals or more had been sampled and if only adult parasites were included in the estimates. Parasite species with two or more estimates were included. Sources are given in the Appendix.

The data consisted of 217 parasite population estimates, representing 62 parasite species and 25 host species. Below, the number in brackets given with the median is lower and upper quartile and range. All nematode orders parasitising mammals were represented in the data. The median number of population estimates per parasite species was 2 (2, 4; 2–17), and the most frequently recorded species were *Gongylonema pulchrum* Molin, *Syphacia stroma* von Linstow and *Capillaria murissylvatici* Diesing, being recorded from 17, 15 and 11 host populations, respectively. Of the parasite species, 36 were recorded in single host species and the remaining 26 found in two to five host species each. The median number of hosts sampled to produce an estimate, was 58 (40, 117; 30–1650). The median number of population estimates per host species was (1, 8.5; 1–39). Wood-mouse (*Apodemus sylvaticus*), wild boar (*Sus scrofa* L.) and white-tailed deer (*Odocoileus virginianus* Rafinesque) were the most commonly recorded host species, being represented by 39, 31 and 20 parasite population estimates, respectively. The median number of parasite species recorded per host species was 4 (1, 5.5, 1–13). The number of organs examined varied between host populations, which may affect observed differences between host species. However, results from a separate analyses of data from the gastrointestinal tract, the most frequently sampled organ, were broadly similar to those from all data. The geographic range of each sample of hosts varied considerably, from a few hectares to several thousand square kilometres. The timespan of collection of hosts varied from a few days to several years, with 20% of the host samples (43 out of 217) being gathered in periods shorter than one season within a year. Prevalence is given as percentage of hosts infected with the upper and lower quartile and range, and intensity as absolute number of worms per host, with means of intensity as the geometric mean with standard errors in brackets. In the Appendix we list the host and parasite species with the number of population estimates for each parasite.

Data analyses

We $\log_{10}$ transformed intensity and abundance, and analysed the variables using unbalanced Model II Analysis of Variance. Parasite and/or host species were fitted as factors. A measure is said to be repeatable across species if the variance of means of population estimates among species is greater than expected on the basis of the variance of the population estimates within species. For intensity and abundance, we estimated the proportion of the variance that occurs among rather than within species by using the coefficient of intraclass correlation (r_I). With unequal number of populations in different species, exact confidence limits cannot be calculated to variance components, so only point estimates of r_I are usually given (Sokal and Rohlf 1981, Becker 1984). To obtain confidence intervals of the coefficient of intraclass correlation, we did separate analyses in a balanced dataset consisting of data from parasite species with two population estimates each. The confidence intervals were calculated following Becker (1984). Prevalence was analysed as $\log_e$ (the number of infected hosts/the number of uninfected hosts) using logistic regression with William's correction for overdispersion (Crawley 1993). The test statistic is change in deviance (ΔD), which is approximately χ^2-distributed with degrees of freedom equal to the number of species added to the model minus one. Again, parasite or host species were fitted as factors.

Population densities may differ between parasite species because they are found in different host species. We tested for the presence of an independent effect of parasite species by performing separate repeatability analyses within single host species. We used only host species where number of degrees of freedom due to error were equal or larger than number of degrees of freedom due to fitting parasite species as a factor. The host species used were (abbreviations given in the results); *Apodemus sylvaticus* (A.s.), *Capreolus capreolus* L. (C.c.), *Odocoileus virginianus* (O.v.), *Oryctolagus cuniculus* L. (O.c.), *Phoca largha* Pallas (Ph.l.), *Procyon lotor* Nelson and Goldman (Pr.l.) and *Sus scrofa* (S.s). Significance levels were adjusted according to the sequential Bonferroni technique (Rice 1989), which is conservative (Rothman 1990).

We estimated the predictive power of parasite species compared to that of host species on population density measures by first calculating the change in deviance by removing parasites from a model containing hosts and dividing by the change in degrees of freedom. Second, we calculated the change in deviance by removing hosts from a model containing parasites and divided it by the change in degrees of freedom. Difference in explanatory power was then calculated as the parasite term divided by the host term. For example, if removing parasites caused a deviance change of 50 on 10 degrees of freedom, and removing hosts caused a change of 10 on 4 degrees of freedom, parasites have $(50/10)/(10/4) = 2$ times the explanatory power of hosts.

Variation in sampling techniques

A nematode species typically lives in one organ of the mammalian body (e.g. gastrointestinal tract or heart, Anderson 1992). Parasitologists frequently examine the entire organ when estimating parasite densities. Alternatively, a portion of the organ may be examined, and prevalence and intensity estimated from such subsamples. Of the populations analysed here, 17% (36 out of 217 populations) were estimated using subsampling. If light infections are more often missed by subsampling,

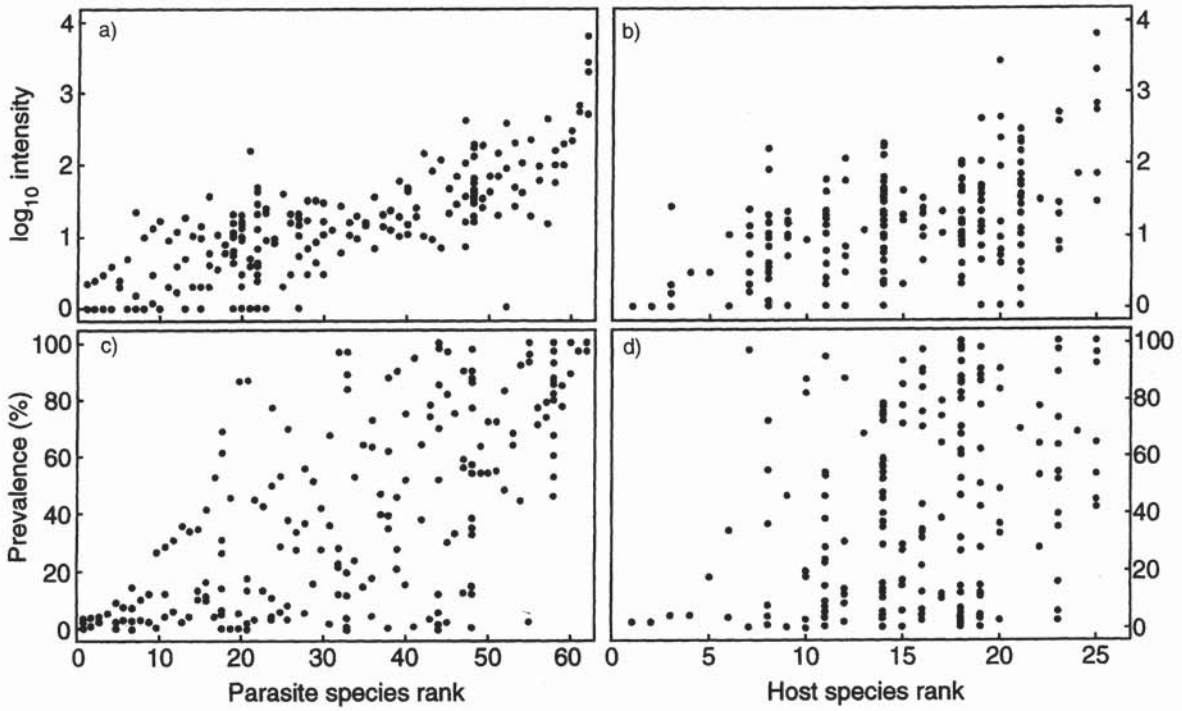

Fig. 3. Rank plots of $\log_{10}$ intensity and prevalence. The species were ranked after mean $\log_{10}$ intensity or mean prevalence, and all population estimates are plotted for each species. Rank 1 was given to the species with the lowest mean $\log_{10}$ intensity or mean prevalence. If variation is small within compared to between species, we would observe a narrow band from the lower left to the upper right corner. a) $\log_{10}$ intensity for parasite species, b) $\log_{10}$ intensity for host species, c) prevalence for parasite species and d) prevalence for host species.

prevalence may be underestimated and intensity overestimated. We checked for such bias by comparing, for the same parasite species, estimates produced by subsampling with those from complete examinations. Multiple estimates for a single species for either technique were averaged. Subsampling did not produce significantly lower estimates of prevalence (Wilcoxon matched pair test $n = 24$, $Z = 0.61$, $p = 0.54$, median 25 (13, 62; 3–97) and 40 (22, 59; 1–77) for subsampled and complete examination, respectively), or higher estimates of $\log_{10}$ intensity ($t_{23} = 1.1$, $p = 0.30$, mean 25 (-22, $+157$) and 18 (-14, $+53$) for subsampled and complete examination, respectively). We therefore pooled data based on subsampling and complete examinations.

In the absence of real differences between populations, prevalence estimates can be correlated with the numbers of hosts examined (Gregory and Blackburn 1991). If variation in number of hosts sampled generally causes parasite or host species to appear with repeatable different prevalence, there should be a correlation between mean number of hosts examined and mean prevalence across species. However, there was no such correlation across parasite or host species (Spearman rank order correlation, $r = 0.01$, $t_{60} = 0.1$, $p = 0.92$ and $r = -0.04$, $t_{23} = -0.2$, $p = 0.84$ for parasite and host species, respectively).

Results

Intensity

Of the total population variation in intensity, approximately half (52%) was associated with differences between parasite species, rather than differences between populations within species. Thus, estimates of intensity from different populations of the same parasite species are more similar to each other than expected by chance alone: estimates of species intensity derived from population estimates reported in the literature are repeatable ($F_{61,155} = 4.9$, $p < 0.0001$, $r_I = 0.52$, Fig. 3a). In a balanced dataset (the 34 parasite species with two population estimates), population intensities were also repeatable within parasite species ($F_{33,34} = 3.8$, $p < 0.0001$, $r_I = 0.59$), with the 95% confidence interval for r_I being (0.31, 0.77). Intensities of populations of nematodes harboured by the same host species are also more similar than expected by chance alone ($F_{24,192} = 3.4$, $p < 0.0001$, $r_I = 0.22$, Fig. 3b). Thus, intensity of parasite populations is significantly repeatable within the same host species. This host effect accounts for about 22% of cross-population variance in intensity. Thus, a population of parasites has more similar intensity to other populations of the same parasite species, and to populations of other parasite species in the same

host species, than expected by chance. Knowing the parasite species seems more important than knowledge of host species; parasite species has about 1.7 times the predictive power of host species.

Differences between parasite species are not simple consequences of poor sampling; they also exist in more thoroughly sampled subsets of the data. Considering just those parasite species where more than two population estimates were available, or those found in two or more host species, there are still pronounced differences in intensity between parasite species ($F_{27,121} = 6.7$, $p < 0.0001$, $r_I = 0.52$; $F_{25,88} = 5.0$, $p < 0.0001$, $r_I = 0.48$, respectively). Differences between host species may have been inflated by poor sampling. When considering just hosts where the median number of parasite species or more have been sampled (four or more), differences are less pronounced ($F_{13,185} = 2.7$, $p = 0.001$, $r_I = 0.11$).

Even within particular host species, there can be detectable differences between parasite species. Within five out of seven host species, there are significant differences between parasite species (A.s.; $F_{3,35} = 23.5$*, C.c.; $F_{8,8} = 15.7$*, O.v.; $F_{4,15} = 4.6$*, O.c.; $F_{2,3} = 26.8$*, Ph.l.; $F_{3,4} = 0.1$, Pr.l.; $F_{9,9} = 0.9$, and S.s.; $F_{12,18} = 5.8$*; * significant with table-wide $p < 0.05$).

Prevalence

Of the variation in parasite population prevalence, and looking across all parasite species, interpopulation variation within species was not so large as to swamp out differences between species ($\Delta D = 165.2$, d.f. $= 61$, $p < 0.0001$, Fig. 3c). Similarly, repeatable differences appear between host species; prevalence estimates from the same host species are more similar to each other than expected by chance ($\Delta D = 85.3$, d.f. $= 24$, $p = 0.0002$, Fig. 3d). However, these effects were much weaker in more thoroughly sampled species. Considering the 26 parasite species found in two or more host species, differences in mean prevalence between parasite species were only close to significant compared to variation between populations within species ($\Delta D = 35.9$, d.f. $= 25$, $p = 0.07$). Similarly, when considering host species with above or median number of parasite species, differences between host species were much less pronounced ($\Delta D = 25.9$, d.f. $= 13$, $p = 0.02$). Thus, prevalence appears to be a less repeatable measure than intensity.

Distributions of and relationships between prevalence and intensity

Prevalence and intensity were differently distributed across populations, with prevalence following a bimodal and intensity a log-normal distribution (Fig. 4). Across populations, geometric mean intensity was 15 worms per infected host (-2, $+2$) and median prevalence was 35% (6,73; 0.2–100). Population and species intensities were similarly distributed (Kolmogorov-Smirnov two sample test, $p > 0.05$), and neither was significantly different from a log normal distribution (Kolmogorov-Smirnov test for continuous distributions, $d = 0.06$, $p > 0.05$, $d = 0.11$, $p > 0.05$ for populations and species, respectively, Fig. 4). The distribution of species mean prevalence differed from the population prevalence distribution (Kolmogorov-Smirnov two sample test, $p < 0.01$): the former is not significantly different from a normal distribution whereas the latter is (Kolmogorov-Smirnov test for continuous distributions, $d = 0.08$, $p > 0.05$ and $d = 0.15$, $p < 0.01$ for species and populations, respectively, Fig. 4).

There were significant positive linear relationships between prevalence and intensity across both populations and species. However, in both instances, about two thirds of the variation in $\log_{10}$ intensity is unexplained by variation in prevalence (Fig. 5).

Repeatability of prevalence and intensity was reflected in repeatability of the combination of the two; abundance was repeatably different across both parasite and host species ($F_{61,155} = 3.0$, $p < 0.0001$, $r_I = 0.36$, $F_{24,192} = 2.8$, $p < 0.0001$, $r_I = 0.18$ for parasite and host species, respectively). The parasite and the host effect accounted for 36% and 18% of the population variation in abundance, respectively. Also in the balanced dataset of the 34 parasite species with two population estimates each, abundance was repeatable within parasite species ($F_{33,34} = 3.0$, $p = 0.0009$, $r_I = 0.49$), with the 95% confidence interval for r_I being (0.21, 0.72). There are also independent effects of parasite species on abundance, albeit less markedly than for intensity. Within three out of seven host species, there are significant differences between parasite species. (A.s.; $F_{3,35} = 20.7$*, C.c.; $F_{8,8} = 33.2$*, O.v.; $F_{4,15} = 2.0$, O.c.; $F_{2,3} = 11.3$, Ph.l.; $F_{3,4} = 1.4$, Pr.l.; $F_{9,9} = 1.3$, and S.s.; $F_{12,18} = 3.4$*, * significant with table-wide $p < 0.05$; see methods). We estimated parasites species to have 1.2 times the predictive power of host species on abundance.

As for prevalence, differences of abundance across parasite or host species were weaker in more thoroughly sampled species. Considering those parasite species sampled in two or more host species, differences were less pronounced ($F_{25,88} = 2.4$, $p = 0.001$, $r_I = 0.25$). Similarly, there are less clear differences between host species when considering just those host species where four or more parasite species have been sampled ($F_{13,185} = 2.9$, $p = 0.0006$, $r_I = 0.12$). Thus, abundance is a less repeatable characteristic of a parasite species than is intensity, but it is more repeatable than prevalence.

Discussion

Previously, cross-species analyses of population density have been justified by asserting that census

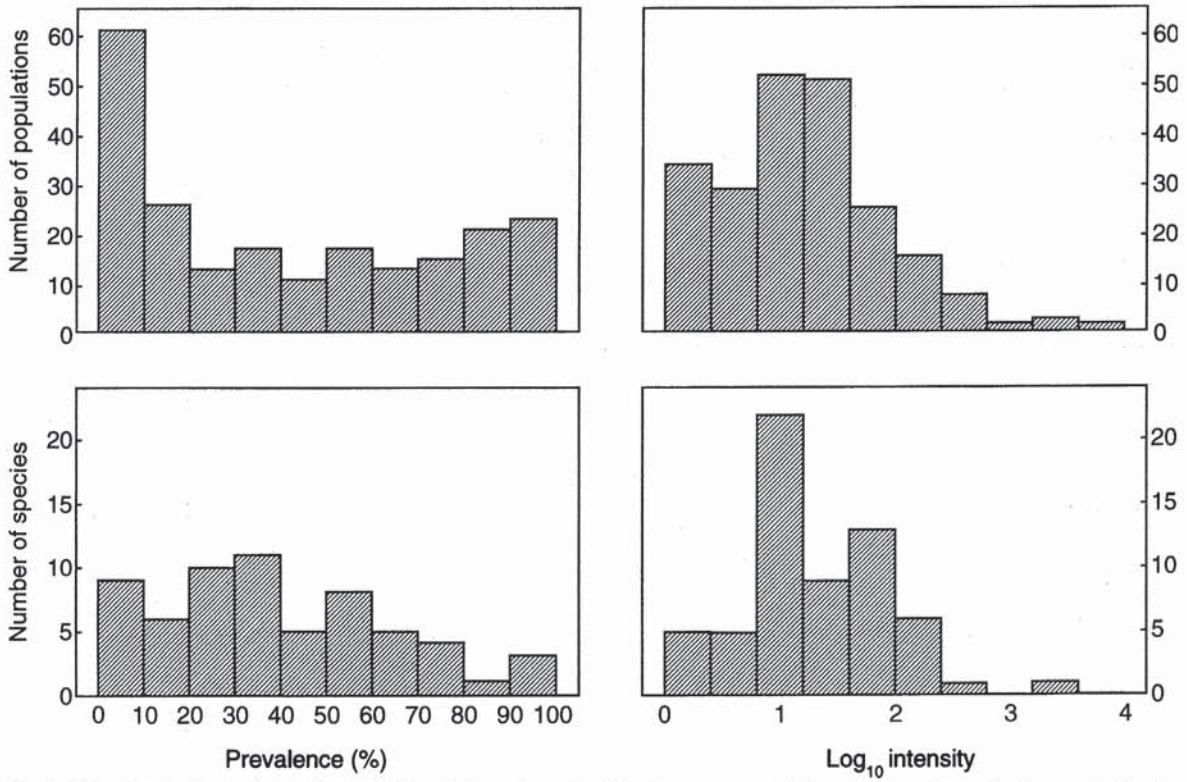

Fig. 4. The distributions of prevalence (left) and $\log_{10}$ intensity (right) across populations (top) and species (bottom). Species intensity was calculated as the logarithm of the arithmetic mean of population intensities, and species prevalence as the arithmetic mean of population prevalences.

data are reliable (e.g. Nee et al. 1991a). As we have shown, repeatability analysis may provide empirical justification for comparative analyses of the population densities of closely related species, even those which may appear too variable or too poorly sampled for such an undertaking. Measures of worm density gleaned from the literature are capable of identifying common and rare species of mammalian nematodes in terms of intensity: there is substantial variation in population intensity across all mammalian nematodes relative to within-species variation. We have also shown that there is a repeatable influence of habitat (i.e. host species) on intensity. For prevalence, differences between species are only marginally detectable above the variation within species. Indeed, with prevalence, negative results from comparative analyses may not require other explanations than large within-species variations. We note that this is consistent with the poor correlation between intensity and prevalence. The repeatability of abundance within parasite species is intermediate to

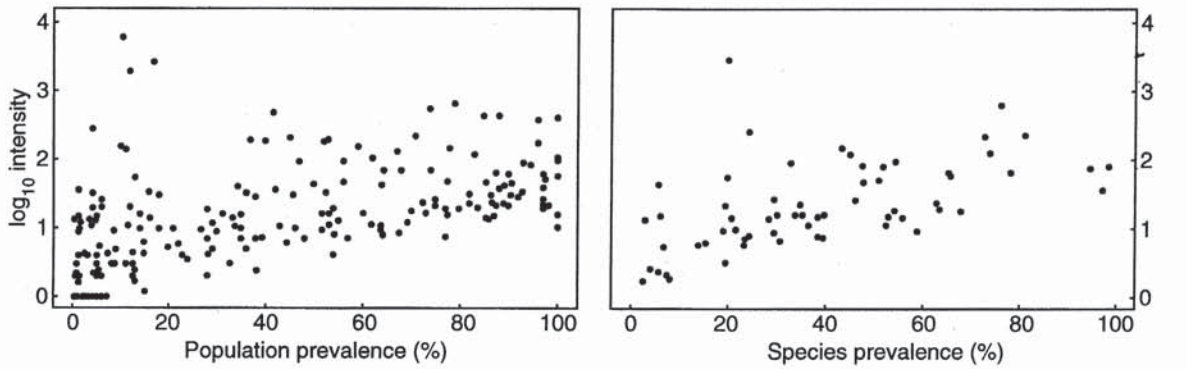

Fig. 5. Figure showing $\log_{10}$ intensity plotted against prevalence across populations (left) and species (right). Species intensity and prevalence were calculated as described in Fig. 5. There is a significant positive relationship between the two variables across both populations and species ($t_{215} = 11.0$, $p < 0.0001$, $r^2 = 0.28$ and $t_{60} = 6.2$, $p < 0.0001$, $r^2 = 0.29$ for populations and species, respectively).

that of intensity and prevalence, the two variables from which it was calculated.

High repeatability across species in an assemblage not only justifies cross-species analyses but also implies that a full understanding of variation in population density is not to be achieved without including explanations in terms of factors differing between species. What characteristics of parasite and host species might be important determinants of parasite population intensity? Generation time and fecundity vary between species and are important aspects of population increase, making these aspects of parasite life history obvious candidates. Body size covaries with life history parameters among the mammalian nematodes (Skorping et al. 1991), and body size has in itself been considered a determinant of population density (e.g. Damuth 1981, Peters 1983). Host size may also 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. On theoretical grounds, host birth and death rates and population density have also been identified as important factors (May and Anderson 1979, Dobson 1990). We are currently investigating these possibilities.

Compared to variation between populations, intensity differences between parasite species were more obvious than differences between host species. The relative explanatory power of parasites on intensity was roughly 1.7 times that of host species. This estimate should be taken as a crude approximation, as it compares the variation between parasite species within host species with that between host species within parasite species. Particular parasite species are generally found in similar host species, whereas a host species may harbour very different parasite species (Anderson 1992), so that the estimate may inflate the explanatory power of parasite species. Nevertheless, the higher estimated explanatory power of parasites could mean that characteristics of parasite species are more important than those of the host species they exploit. Consistent with this, we were able to detect repeatable differences between parasite species in population intensities even within single host species. These results may imply that habitat is a less important determinant of species commonness, or that the important component of the habitat is something other than the host species, such as organ system. For example, whether parasitic nematodes develop within the gastrointestinal tract or in some other part of the mammalian body has effects on nematode growth rates, size and hence fecundity (Skorping et al. 1991, Read and Skorping 1995). Even so, a critical issue in comparative ecology is whether patterns found between large number of species sampled in different communities reflect patterns within single communities (e.g. Lawton 1989, Blackburn et al. 1993, Currie 1993, Silva and Downing 1995). We found here that population density measures are repeatable also within a given community type (i.e. host species), opening the prospect that overall patterns may also be found within single communities of mammalian nematodes.

The debate on the underlying causes of the log-normal distribution of abundances and the causes and even existence of bimodal distributions of patch occupancy (here prevalence) addresses fundamental questions in population and community ecology (Sugihara 1980, Maurer 1990, Tokeshi 1990, Nee et al. 1991b, Pagel et al. 1991, Hanski and Gyllenberg 1993, Gaston 1994, Brown 1995). For mammalian nematodes, log-normal distributions are found both across populations and across mean species values. This, together with the high repeatability of intensity, is consistent with explanations of log-normal distributions of abundance in terms of species having different niches (Sugihara 1980, Tokeshi 1991). In contrast, the bimodal distribution of prevalence evident across all the populations is not found across species means (Fig. 4). An implication of this striking difference is that a particular parasite species can be found in a high proportion of hosts in some populations and only in a small proportion in others. This might provide an explanation for the low repeatability of prevalence, and is consistent with certain metapopulation models predicting that low prevalence populations are extinction prone and that species hence must be found with high prevalence elsewhere in order to persist (Hanski and Gyllenberg 1993). In contrast, this is not consistent with a model of bimodality arising as a consequence of species having different niches (Maurer 1990). This latter models predict that bimodality should be observed between species means, not only between populations.

In general, repeatability analysis may have several applications for comparative analyses. The first is to assess the relevance of negative results in cross-species analyses of abundance. For example, body size has been considered an important determinant of species abundance (see Blackburn et al. 1996 for a recent summary), even though body size is usually a poor predictor of species abundance, at least within groups of closely related species (Blackburn et al. 1993, Blackburn and Lawton 1994). If we know that repeatability of estimates of species abundance are low, then we could explain these results in terms of highly varying populations or sampling errors. On the other hand, repeatable differences between species estimates of abundances would imply that body size is indeed unimportant. In those situations we can begin to look at other factors (e.g. life history characters, Blackburn et al. 1996).

Second, phylogenetic information may be used in comparative analyses of abundance to control for effects of confounding factors (e.g. Blackburn et al. 1996, Harvey 1996), and repeatability analysis may be used to identify sensible taxonomic units for such analyses. For example, if population density is repeatable across genera, but not among species

within genera, contrasting taxonomic units below the generic level makes little sense. For example, there may be no justification for comparing species averages, and analysing populations within genera may be more appropriate. Of course, if large differences between populations come about because of sampling errors, the data are unsuitable even for cross population analysis.

Third, repeatability analysis may facilitate comparison between different cross-species analyses. If population density is a species character in some taxa but not others, comparisons of several taxa may overlook the importance of particular characters if groups with low repeatability of species abundance are used in the comparisons. For instance, Blackburn et al. (1993) tested the prediction from the energetic equivalence hypothesis that the logarithm of population density scales to the logarithm of body size with a slope of -0.75 by comparing slopes from 14 animal assemblages. This represents one of the largest body of data used to test this important idea. They rejected the hypothesis because most slopes differed significantly from the predicted value. However, in their data there was a strong positive relationship across the 14 assemblages between the R-squared and how close the slope was to -0.75 (Spearman rank order correlation $r = 0.94$, $p < 0.0001$). Indeed, the two assemblages with the highest R-squared values had slopes not significantly different from -0.75. Thus, the weaker the correlation, the less likely the data supported the energetic equivalence hypothesis. Repeatability analysis of those data would allow an assessment of whether that was simply because density estimates from some taxa were less repeatable, either because densities are truly variable or because they are poorly estimated.

Finally, repeatability analyses may also be helpful in justifying data used to measure other ecological variables that we know little about, but want to compare across species, for example population cycle period, resilience, persistence, resistance and temporal variability (Krukonis and Schaffer 1991, Pimm 1991). Are population estimates of these variables reliable estimates of species values?

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Appendix

1. Literature sources for nematode population density estimates

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2. The host species sampled (bold italics) and the parasite species from each host (italics) with the number of population estimates for each parasite species in brackets

Species designations are as given in the source papers, except for *Placoconus lotoris* which is synonymous with *Arthrocephalus lotoris* and *Uncinaria lotoris*.

Alopex lagopus; *Uncinaria stenocephala* (1)
Apodemus sylvaticus; *Capillaria murissylvatici* (10), *Heligmosomoides polygyrus* (10), *Syphacia stroma* (15), Trichuris *muris* (4)
Canis latrans; *Ancylostoma caninum* (2), *Dermatoxys veligera* (1), *Dirofilaria immitis* (2), *Physaloptera rara* (1), *Toxascaris leonina* (1), *Uncinaria stenocephala* (1)
Capreolus capreolus; *Haemonchus contortus* (2), *Nematodirus europaeus* (2), *Ostertagia leptospicularis* (2), *Ostertagia ostertagi* (1), *Rinadia mathevossiani* (2), *Skrjabinagia kolchida* (2), *Spiculopteragia boehmi* (2), *Trichostrongylus axei* (2), *Trichostrongylus capricola* (2)
Cervus elaphus; *Trichostrongylus axei* (1)
Clethrionomys glareolus; *Capillaria murissylvatici* (1)
Felis canadensis; *Ancylostoma caninum* (1), *Capillaria aerophila* (1), *Physaloptera rara* (1), *Toxascaris leonina* (1), *Uncinaria stenocephala* (1)
Lepus americanus; *Dirofilaria scapiceps* (1), *Obeliscoides cuniculi* (2), *Passalarus ambiguus* (1), *Protostrongylus boughtoni* (2), *Trichuris leporis* (1)
Lepus townsendi; *Obeliscoides cuniculi* (1)
Neofiber alleni; *Strongyloides sigmodontis* (1)
Odocoileus virginianus; *Gongylonema pulchrum* (10), *Gongylonema verrucosum* (5), *Haemonchus contortus* (2), *Oesophagostomum venolosum* (2), *Ostertagia ostertagi* (1)
Onychomys leucogaster; *Litomosoides carinii* (1), *Mastophorus muris* (1)
Oryctolagus cuniculus; *Graphidium strigosum* (2), *Passalarus ambiguus* (2), *Trichostrongylus retortaeformis* (2)
Oryzomys palustris; *Capillaria forresteri* (2)
Phoca largha; *Acanthocheilonema spirocauda* (2), *Anisakis simplex* (2), *Phocascaris cystophorae* (2), *Terranova decipiens* (2)
Podomys floridanus; *Litomosoides carinii* (1)
Procyon lotor; *Baylisascaris procyonis* (2), *Capillaria aerophila* (1), *Capillaria plica* (1), *Capillaria putorii* (1), *Dracunculus insignis* (2), *Gnathostoma procyonis* (2), *Molineus barbatus* (2), *Physaloptera maxillaris* (2), *Physaloptera rara* (3), *Placoconus lotoris* (3)
Rangifer tarandus; *Trichostrongylus axei* (1)
Sigmodon hispidus; *Litomosoides carinii* (1), *Mastophorus muris* (1), *Strongyloides sigmodontis* (1), *Trichostrongylus affinis* (1)
Stenella graffmani; *Anisakis simplex* (1)
Sus scrofa; *Ascaris suum* (3), *Ascarops strongylina* (3), *Capillaria putorii* (1), *Globocephalus urosubulatus* (3), *Gongylonema pulchrum* (3), *Haemonchus contortus* (1), *Metastrongylus apri* (3), *Metastrongylus pudendotectus*

(3), *Oesophagostomum dentatum* (2), *Oesophagostomum quadrispinulatum* (2), *Physocephalus sexalatus* (3), *Stephanurus dentatus* (2), *Trichuris suis* (2)
Sylvilagus floridanus; *Dermatoxys veligera* (1), *Dirofilaria scapiceps* (1), *Gongylonema pulchrum* (1), *Obeliscoides cuniculi* (1), *Passalarus ambiguus* (1), *Trichostrongylus affinis* (1), *Trichostrongylus calcaratus* (2), *Trichuris leporis* (2)
Tayassu tajacu; *Gongylonema pulchrum* (1), *Parabronema pecariae* (2), *Physocephalus sexalatus* (1), *Texicospirura turki* (1)
Ursus americanus; *Ancylostoma caninum* (1), *Baylisascaris transfuga* (2), *Capillaria aerophila* (1), *Capillaria putorii* (2), *Dirofilaria immitis* (2), *Dirofilaria ursi* (2), *Gongylonema pulchrum* (2), *Molineus barbatus* (2), *Physaloptera rara* (2), *Placoconus lotoris* (2)
Vulpes vulpes; *Capillaria aerophila* (1), *Capillaria plica* (1), *Physaloptera rara* (1), *Toxascaris leonina* (2), *Uncinaria stenocephala* (2)