Body size variation in tapeworms (Cestoda): adaptation to intestinal gradients?

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We describe patterns of variation in the body size of tapeworms (Cestoda) parasitizing rodents and shrews. Tapeworms display considerable interspecific variation in body size. Tapeworms also occur only in certain, species-specific parts of intestine. Empirical data on tapeworms suggest that these two phenomena are related: the biggest tapeworm species tend to occur in midgut. We put forward a hypothesis that the observed variation in body size and age-at-maturity reflects adaptation to specific levels of mortality and amount of nutrients in intestinal environment. We construct a simple energy allocation model in which we assume that optimal life-histories maximize the expected reproductive success (R_0). Under realistic intestinal gradients of mortality and amount of nutrients, the predicted patterns of variation in body size resemble those observed in tapeworms of small mammals.

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Body size is one of the most important traits in the life history evolution of animals (Roff 1992). Parasites are no exception: the body size of parasitic nematodes correlates positively with developmental time, growth rate, fecundity and length of reproductive period (Skorping et al. 1991). The evolutionary forces affecting body size in parasites have seldom been studied. However, the body size of oxyurid nematodes is known to correlate positively with the body size of their hosts, suggesting that larger hosts provide more energy and live longer, which favours long-living, larger parasites (Morand et al. 1996).

Tapeworms (Cestoda) display considerable interspecific variation in body size. The smallest tapeworms of mammals reach hardly a length of 1 mm (e.g. *Urocystis prolifer* (Villot) in *Sorex* shrews; Vaucher 1971), whereas the largest species may exceed a length of 20 m (e.g. *Diphyllobothrium latum* (Linnaeus) in man; see von Bonsdorff 1977). Moreover, cestodes representing the same family may show a 250-fold difference in body size even within a single host species (e.g. hymenolepi-

did cestodes in the shrew *Blarina brevicauda* (Say); Vaucher and Durette-Desset 1978). Body size is known to affect the fecundity of tapeworms, at least in intraspecific comparisons (Boddington and Mettrick 1981). The feeding mode of cestodes – absorption of nutrients through the external wall – further increases the importance of body size in cestode life histories: body size greatly influences the rate at which nutrients are absorbed from the environment.

Intestinal helminths of vertebrates characteristically inhabit a limited, predictable region of available habitat. The structure of the intestinal wall, availability of nutrients, pH and other physico-chemical factors change radically along the length of the intestine (Mettrick and Podesta 1974), suggesting that species living in different parts of intestines are faced with very different "external" conditions (Stock 1985).

Our empirical observations on tapeworms of small mammals suggest that intestinal location and body size are related: within a tapeworm assemblage, the largest species tend to occupy the mid-intestine, and the

Table 1. Average intestinal positions and body dimensions (mm) for tapeworm species parasitizing voles and lemmings. Intestinal position refers to three sections of the small intestine.

Family Species	Position	Length	Width	Host species (locality)	Source
Anoplocephalidae					
Anoplocephaloides sp. 1	2.4	75	4.2	*M. agrestis* (S. Finland, Lapland)	1
Anoplocephaloides sp. 2	1.2	29	2.8	*Microtus* spp. (S. Finland, Lapland)	1
A. c.f. *variabilis*	1.1	29	3.0	*Microtus* spp. (Alaska)	1,2
A. mascomai	1.0	21	1.9	*M. carbrerae* (Spain)	3
A. dentata	3.0	14	4.8	*M. agrestis* (S. Finland)	1
A. troeschi	3.0	13	4.7	*M. miurus* (Alaska)	1
A. lemmi	3.0	19	6.5	*Lemmus* (Alaska)	1,2
Paranoplocephala sp. 1	1.2	137	2.7	*Dicrostonyx* (N. Siberia)	1
Paranoplocephala sp. 2	1.9	162	4.0	*M. agrestis* (S. Finland)	1
P. arctica	2.0	139	2.7	*Dicrostonyx* (N. Siberia, Alaska)	1,4
P. gracilis	1.1	178	2.9	*Microtus* spp., *Clethrionomys* spp. (Lapland)	1
P. janickii	1.0	100	2.5	*M. arvalis* (Hungary)	5
P. kalelai	2.3	191	2.4	*C. rufocanus* (Lapland)	6
P. omphalodes	2.1	240	5.5	*M. miurus* (Alaska)	1,7
Hymenolepididae					
Hymenolepis horrida	2.1	178	2.9	*M. oeconomus* (Alaska)	1,7
H. asymetrica	2.2	103	2.6	*M. agrestis* (S. Finland), *C. glareolus* (Bulgaria)	1,8
Catenotaeniidae					
Catenotaenia henttoneni	2.0	117	1.8	*C. glareolus* (Lapland)	9

Sources for body dimensions: 1) V. Haukisalmi and H. Henttonen unpubl.), 2) Rausch 1976, 3), Murai et al. 1980, 4) Rausch 1952, 5) Tenora et al. 1985b, 6) Tenora et al. 1985a, 7) Haukisalmi et al. 1995, 8) Genov 1984, 9) Haukisalmi and Tenora 1993.

smallest species the posterior intestine. We hypothesize that the observed interspecific variation in body size is adaptive: the differences in intestinal conditions, particularly those related to the mortality risk and nutrition, influence the optimal body size of cestodes inhabiting various parts of the intestine.

In this paper we first report the empirical patterns of body size variation in tapeworms of small mammals. We then present a simple resource allocation model for optimal body size along the intestinal gradients to test our hypothesis. Finally, the model predictions are compared with the observed patterns.

Helminth data

Our empirical data include intestinal positions and body dimensions for 34 species of tapeworms parasitizing arvicoline rodents (lemmings and voles; 17 species) (Table 1) and *Sorex* shrews (17 species) (Table 2). The specific and generic taxonomy of rodent cestodes is based primarily on Rausch (1976), Tenora and Murai (1980), Tenora et al. (1985a) and Haukisalmi and Tenora (1993). 14 of the 17 species parasitizing rodents belong to a single family, Anoplocephalidae. Three anoplocephalid genera, *Anoplocephaloides*, *Andrya* and *Paranoplocephala*, are thought to parasitize arvicolid rodents. However, the exact generic status of species

assigned to *Andrya* and *Paranoplocephala* is largely unsettled, and we therefore address all these species to a single genus, *Paranoplocephala* (s.l.). Moreover, the species traditionally assigned to *Anoplocephaloides* probably represent several different genera (Genov and Georgiev 1988). In the taxonomy of shrew cestodes, we follow Vaucher (1971) (species) and Czaplinski and Vaucher (1994) (genera). All but one species of shrew cestodes represent the family Hymenolepididae.

The phylogenetic relationships among cestodes are based primarily on prevailing taxonomy. However, we also assume that the armed and unarmed species of the family Hymenolepididae (shrew cestodes) represent different phyletic lines (Table 2) (Mas-Coma 1982), that the family Catenotaeniidae represents a different line from the other two families of rodent cestodes (Anoplocephalidae, Hymenolepididae) (Freeman 1973), and that the *Anoplocephaloides* species of rodents fall in two phylogenetically distinct groups (*A. dentata, A. troeschi* and *A. lemmi*, and *Anoplocephaloides* sp. 1, *Anoplocephaloides* sp. 2, *A.* c.f. *variabilis* and *A. mascomai*) (Genov and Georgiev 1988).

Intestinal positions

Intestinal positions for most of the helminth species come from our own studies from Finland, Siberia, Alaska and eastern USA (Haukisalmi and Henttonen

Table 2. Average intestinal positions and body dimensions (mm) for tapeworm species parasitizing shrews. Intestinal position refers to ten sections of the entire intestine.

Host species (locality) Family Species	Position	Length	Width	Source
Sorex araneus (Europe)				
Dilepididae				
Molluscotaenia crassiscolex	2.8	14.5	1.15	1,2,3
Hymenolepididae				
Ditestolepis diaphana*	3.2	3.1	0.22	1,2,3,4,5
D. tripartita*	2.9	3.2	0.26	2,6,7
Ditestolepis sp.*	6.3	4.0	0.34	13
Soricinia infirma*	9.2	0.78	0.13	1,2,4,7,8
Pseudobotrialepis globosoides*	5.0	60.0	0.90	2,9
Staphylocystis furcata	4.1	44.9	1.19	1,2,3,4
Urocystis prolifer	8.3	0.81	0.18	1,2,3,4,7
Neoskrjabinolepis schaldybini	6.2	8.1	0.35	1,2
N. singularis	6.1	24.0	0.50	2
Lineolepis scutigera	6.6	10.9	0.21	1,3
Vigisolepis spinulosa	3.1	29.2	0.65	1,2,3,5
Staphylocystoides stefanskii	4.2	3.6	0.45	2
Sorex cinereus (North America)				
Hymenolepididae				
Ditestolepis macyi*	2.3	2.0	0.50	10
Lineolepis parva	3.8	5.0	0.30	11
Staphylocystoides longi	1.4	1.3	0.39	12
S. serrula	2.8	2.0	0.29	12

* unarmed species (no hooks on the scolex).
Sources for body dimensions: 1) Genov 1984, 2) Vaucher 1971, 3) Kisielewska 1961, 4) Roots et al. 1994, 5) Soltys 1952, 6) Rybicka 1959, 7) Žarnowski 1955, 8) Mas-Coma and Gallego 1975, 9) Soltys 1954, 10) Locker and Rausch 1952, 11) Rausch and Kuns 1950, 12) Oswald 1951, 13) Own observations (V. Haukisalmi unpubl.).

1994, unpubl., Haukisalmi and Laakkonen unpubl.). The average intestinal positions for *Urocystis prolifer* and *Staphylocystoides stefanskii* (Žarnowski) were estimated from the data of Vaucher (1971) and intestinal position for *Paranoplocephala mascomai* from Murai et al. (1980). The typical position of *P. janickii* was received as a personal communication from F. Tenora.

The data on intestinal distribution of the shrew cestodes were obtained by dissecting the entire intestine in ten parts of equal length. In rodent hosts, tapeworms occur only in the small intestine, which was dissected in three parts, roughly corresponding to the three functional regions of the small intestine (duodenum, jejunum and ileum). For simplicity, we refer with "intestine" only to the part of intestine inhabited by tapeworms.

We calculated the median position (1–10 or 1–3) for each cestode species in each host individual. The mean of these median positions was used as the species' characteristic location within the intestine.

Body dimensions

For shrew cestodes the body dimensions were obtained mainly from literature (Table 2), and for rodent cestodes mainly from own (unpublished) sources (Table 1).

We used the product of body length and body width as an index of cestode body size. Body length and width were determined as the observed maximum values (rodent cestodes: own measurements) or as the mean of maximum values reported in various sources (shrew cestodes). If a cestode species occurred in more than one host species, we used data from the preferred host species, i.e. the one showing the highest prevalence of the particular parasite species.

Statistical analyses

Because of non-independence of species values in comparative studies (Harvey and Pagel 1991), we analyse the relationship between cestode body size and intestinal position using 'phylogenetic regression' of independent contrasts (Felsenstein 1985, Pagel 1992). Independent contrasts are differences that have evolved between daughter taxa (species or higher nodes in phylogeny) originating from a common ancestor; each comparison thus represents an independent evolutionary event. The calculations were performed using the CAIC statistical package (Purvis and Rambaut 1995). Branch lengths, which were unknown, were set to unity. All regressions were forced through the origin.

Table 3. Significance of interspecific differences in helminth body size (one-way parametric ANOVA). Species with at least two body size estimates were included in tests. Helminth body sizes were log-transformed. n, number of species. r_i, coefficient of intraclass correlation, i.e., the proportion of variation among species.

	N	df	F	p	r_i
Rodents					
All species	13	12,121	61.2	<0.0001	0.86
Paranoplocephala	6	5,60	41.4	<0.0001	0.84
Anoplocephaloides	5	4,43	17.7	<0.0001	0.64
Shrews					
All species	11	10,29	68.9	<0.0001	0.95
Hymenolepididae	10	9,26	74.1	<0.0001	0.95

Results

Is body size a species-specific characteristic?

Cestode body sizes often show pronounced intraspecific variation. Since our analysis aims at assessing the possible evolutionary relationship between cestode body size and intestinal position, it is crucial to know whether the body sizes of various cestodes species are truly species-specific.

We performed parametric one-way ANOVA for log-transformed body size data using various cestode species as categorical variables. Our own measurements (rodent cestodes; Table 1) or maximum values reported in literature (shrew cestodes; Table 2) formed replicates for each species. All analyses, either performed on species-rich families or genera or whole cestode assemblages, showed highly significant differences among cestode species (Table 3). Furthermore, the proportion of variation among species (coefficient of intraclass correlation; Sokal and Rohlf 1995) was invariably high (65–95%). We conclude that body size is a truly species-specific characteristic for cestodes of small mammals.

Empirical relationship between intestinal position and body size

Our data show a humped or triangular size distribution of cestodes within the intestine of both rodents and shrews (Fig. 1): the largest species occur in the middle intestine and the smallest species in the posterior intestine. We first analysed this pattern with a simple cross-species regression (ignoring the possible phylogenetic effects) performed on two sets of species: species in the anterior-middle intestine showing an apparent positive relationship between intestinal position and log(body size), and species in the middle-posterior intestine showing a negative relationship (these two groups are denoted as "A" and "B" in Fig. 1). All four regression analyses indicated a significant relationship between intestinal position and body size (constant fitted) (shrews, A: $b = 0.36$, $p = 0.048$; B: $b = -0.60$, $p < 0.001$; voles, A: $b = 0.39$, $p = 0.046$; B: $b = -0.81$, $p = 0.001$).

The regression analyses of independent contrast between intestinal position and log(body size) also showed the expected relationships for all sets of species, albeit only two sets out of four (shrews: B, and voles: A) showed a clearly significant correlation (Table 4). The apparently humped distribution of cestode body sizes along the intestine is thus reasonably well supported by statistical analyses controlling for the confounding effects of parasite phylogeny.

Model of optimal body size

We consider the simplest possible model of optimal body size. Our model acknowledges two basic factors influencing the expected reproductive success: mortality risk and growth rate. To make the model analytically tractable, we make a number of simplifying assumptions. First, because adult tapeworms are considered weakly pathogenic or non-pathogenic (Reese 1967), we assume that parasites do not influence the survival of their hosts. Second, the energy expenditure to maintenance in adult tapeworms is low (e.g., 4% in *Hymenolepis diminuta* (Rudolphi), Munger and Karasov 1989), and thus can be neglected. However, tackling with the host immune responses may require considerable energy expenditure. Finally, fitness can be measured as the expected reproductive success.

We now construct a simple resource allocation model to study optimal body sizes along intestinal gradients. We assume that the rate of energy intake is allometrically related to the body weight of an individual, $W(t)^\alpha$, where the exponent α is a scaling parameter, and to the concentration of nutrients in the intestine, c, assumed to be constant during the lifetime of a parasite. Immature worms use all available energy to body growth. The change in body weight is given by

$$\frac{dW(t)}{dt} = cW(t)^\alpha \qquad (1)$$

Because cestodes ingest their food through their body surface, we assume that the rate of energy intake is proportional to the surface area of a worm, yielding $\alpha = 2/3$. The body weight of an immature individual at
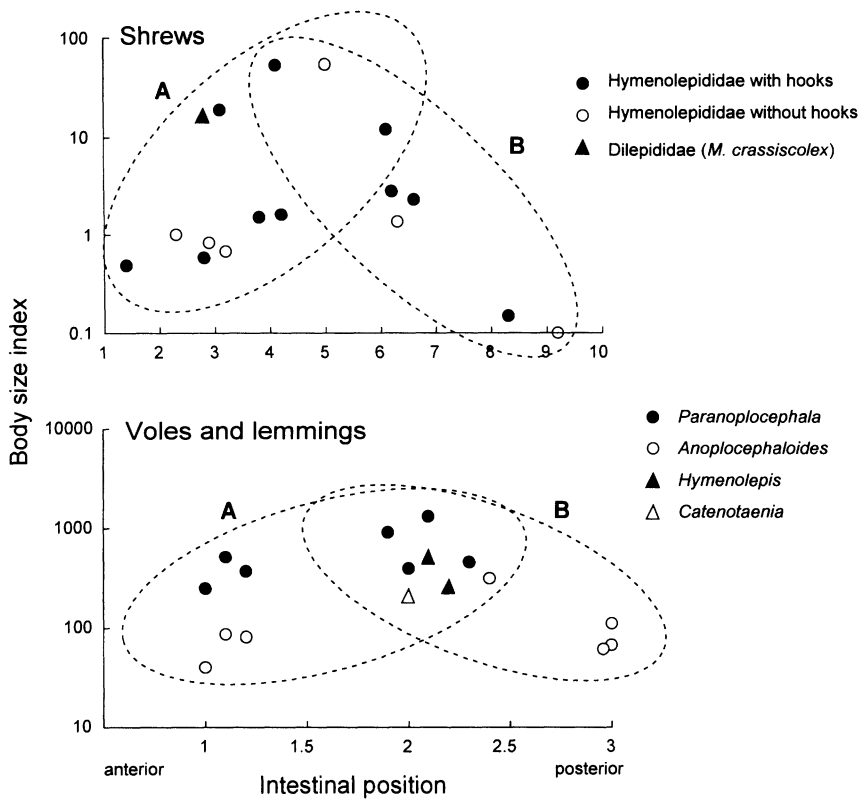
Fig. 1. Body sizes of tapeworms parasitizing shrews and rodents (voles and lemmings) in different parts of intestine. Each dot represents one parasite species. In rodents only the small intestine is inhabited by tapeworms; three different parts of small intestine were distinguished. In shrews the whole intestine was divided in ten sections. The dashed ellipses denote the sets of species (A and B) that were used for phylogenetic regressions (Table 4).

time t can now be solved from Eq. 1, assuming that weight-at-birth ($t = 0$) is w_0:

$$W(t) = \left(\frac{ct}{3} + \sqrt[3]{w_0} \right)^3. \qquad (2)$$

After maturity, all energy is channelled to reproduction. The expected production of eggs at maturity is achieved by summing up the egg production during the rest of the life, discounted with a survival probability to a given age:

$$\frac{1}{w_0} \int_{t_M}^{\infty} c W(t_M)^{2/3} e^{-\mu(t - t_M)} \, dt = \frac{c}{w_0 \mu} W(t_M)^{2/3},$$

where μ is a parasite mortality rate. Mortality rate is a composite parameter which depends both on the mortality risk of the host, and on the risk that a parasite dies even if the host survives. The latter risk may vary in different parts of intestine. The expected reproductive success $R_0(t_M)$ at the beginning of infection is given by

$$R_0(t_M) = \frac{e^{-\mu t_M} c}{w_0 \mu} W(t_M)^{2/3} = \frac{e^{-\mu t_M} c}{w_0 \mu} \left(\frac{ct_M}{3} + \sqrt[3]{w_0} \right)^2.$$

The only maximum of $R_0(t_M)$ for positive t_M is at

$$t_M^* = \frac{2}{\mu} - \frac{3}{c} \sqrt[3]{w_0}. \qquad (3)$$

Substitution of (3) to (2) yields optimal weight-at-maturity

$$W(t_M^*) = \left(\frac{2c}{3\mu} \right)^3. \qquad (4)$$

Table 4. Phylogenetic regressions based on standardized linear contrasts for intestinal position (predictor variable) and body size (dependent variable) in cestodes of shrews and voles. Regressions were forced through the origin. Separate analyses were performed for species from the anterior–middle intestine (A) and species from middle-posterior intestine (B); species included in analyses A and B are shown in Fig. 1. Cestode body sizes were log-transformed. n_s, number of species. n_i, number of independent contrasts.

	Slope	r^2	p	n_s	n_i
Shrews					
A	0.48	0.50	0.075	12	6
B	−0.70	0.95	0.005	8	4
Voles					
A	0.65	0.64	0.009	14	6
B	−0.80	0.38	0.111	11	7

From Eq. (3) it is seen that optimal age-at-maturity increases when the amount of nutrients increases or when mortality or egg weight decreases. The same is true for optimal weight-at-maturity (Eq. (4)), except
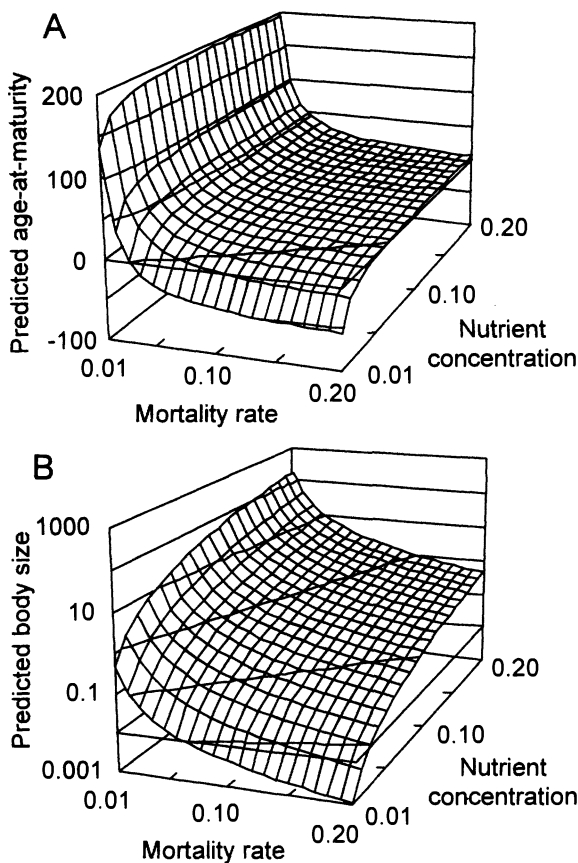
Fig. 2. Model predictions of age-at-maturity (A) and body size (B) as functions of mortality rate (μ) and nutrient concentration (c). Negative values of age-at-maturity and body weight below weight-at-birth ($w_0 = 0.01$) indicate that the parasite population is not viable.

that egg weight does not influence optimal body weight. Note that optimal age-at-maturity and body size are positively correlated. The dependence of optimal body size and age-at-maturity on mortality and nutrition is illustrated in Fig. 2.

Next we apply our model to tapeworms occurring on an intestinal gradient. First we have to characterize the intestine in terms of nutrition and mortality. The energetic demands of cestodes are primarily fulfilled by absorption of simple carbohydrates, particularly glucose (see a review by Mettrick and Podesta 1974). The concentration of glucose along the intestine varies according to the diet of the host, the highest concentrations being found either in the anterior intestine or the middle intestine (Dunkley 1972, cited in Mettrick and Podesta 1974). The posterior intestine has very low levels of carbohydrates. In Fig. 3 we assume a humped shape of nutrition gradient.

The measurement of mortality risk of cestodes along the intestine is less clear-cut, but we assume two alternative situations: either mortality is high in the anterior intestine and low in other parts of the intestine, or

mortality is low and constant throughout the intestine (Fig. 3A). High mortality risk in the anterior intestine may be caused by strong peristalsis, rapid flow of ingesta or abrasion by partly undigested food material in that region (Stock 1985). However, the mortality risk might depend also on species-specific characteristics, such as attachment structures.

Fig. 3 illustrates the optimal body size and age-at-maturity along a hypothetical intestinal gradient. Both traits show the highest values in the middle intestine. If mortality does not change along the intestine, the difference between anterior and middle intestine is small. The predicted pattern in body size qualitatively fits the patterns observed in tapeworms of small mammals (see Fig. 1). The predicted pattern is rather robust: if nutrient concentration decreases in a linear way along the intestine, we still observe a humped body size pattern, provided that mortality rate is highest in the anterior intestine.

Discussion

The fact that the intestinal body size distributions were roughly similar in different families of cestodes parasitizing two different groups of hosts suggests that the observed pattern is a real and general one. Furthermore, our model gives tentative support for the hypothesis that the observed variation in body size between different tapeworm species reflects adaptation in face of the different intestinal environments the different tapeworm species occupy. Unfortunately, we are not aware of any other empirical intra- or interspecific data set that would allow a comparison with the predictions of the model. There are, however, scattered data showing that the largest species within cestode assemblage tend to occupy the middle parts of the (small) intestine in other host groups as well (Crompton 1973).

Different species are likely to experience their environment in different ways. For example, nutrient concentration (c) and mortality (μ) are determined not only by environment, but also by characteristics of a tapeworm species: among other things, nutrient concentration may depend on the compounds ingested by a given species, and mortality on attachment structures. These factors decrease the applicability of our model in interspecific comparisons, as long as they cannot be controlled for. Nevertheless, our view is that the model is sufficiently robust to give insight to body size variation also on higher taxonomical levels. Particularly, the predictions concerning the effects of mortality risk and nutrient concentration on the optimal body size are very general, with similar predictions arising from a wide range of different models (see a review in Roff 1992).
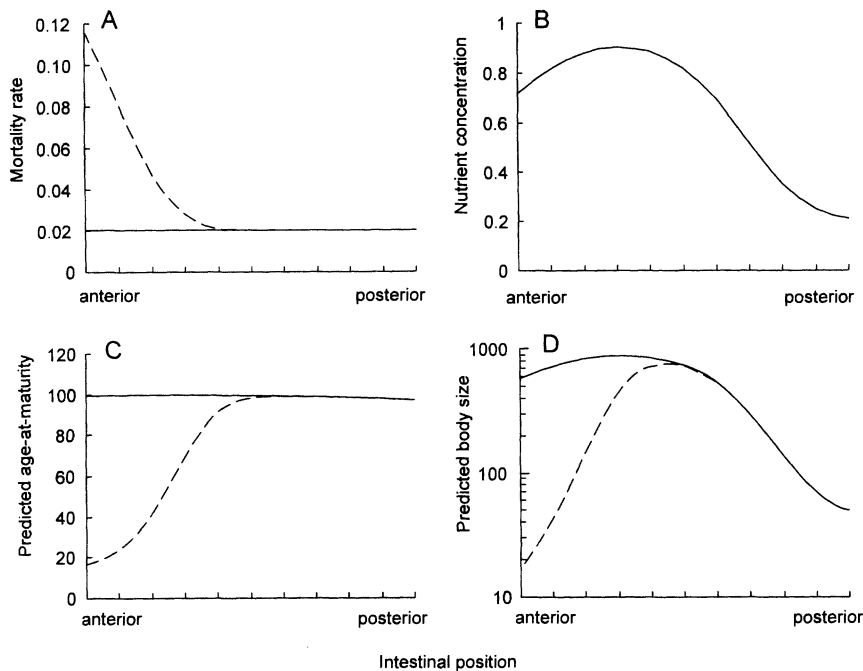
Fig. 3. Hypothetical mortality (A) and nutrient concentration gradients (B) in an intestine. For mortality we use two different scenarios: constant mortality (solid lines) or mortality decreasing towards posterior intestine (dashed lines). Model predictions of age-at-maturity (C) and body size (D) along the intestine. Variation in egg size do not influence the predicted body size. Compare the predictions with the patterns observed in our empirical data (Fig. 1). Parameter values: $w_0 = 0.01$.

We observed that rodent cestodes are on average much larger than shrew cestodes (Tables 1 and 2). Such a difference could be caused simply by differences in host body size: rodents are usually much larger than shrews (Harvey and Keymer 1991, Morand et al. 1996). However, rodent cestodes are also relatively larger than shrew cestodes (Haukisalmi and Henttonen 1994). The size difference between shrew and rodent cestodes could be partially explained by the host diet: rodents as herbivores consume more carbohydrates than primarily insectivorous shrews. It should be noticed, however, that some cestodes are adapted to extremely low prevailing concentrations of carbohydrates. For example, *Molluscotaenia hepatica* (Baer) is a relatively large species that dwells in the bile duct of shrews, a very carbohydrate-poor environment (cf. Wages and Roberts 1990). Furthermore, it is possible that also higher mortality rate has favoured smaller body size (and age-at-maturity) in shrew cestodes as compared to rodent cestodes.

Although the carbohydrate gradients within the mammalian small intestine are reasonably well studied, the patterns of mortality risk of cestodes are much harder to estimate. One of our alternative assumptions is that strong mechanical action increases mortality risk in the anterior intestine. Under this assumption, the model predicts a humped body size distribution along the intestine, a prediction supported by the empirical data. The presence of both small and large species in the anterior intestine (rodents) or in the anterior-middle intestine (shrews) suggests that the mortality gradients may be species-specific. For some cestode species the duodenum is evidently a low-mortality region, which

would favour large body size in species occupying that part of the intestine. A low mortality rate could be achieved by efficient attachment devices, i.e. by rostellar hooks. However, all rodent cestodes which inhabit the anterior small intestine are lacking hooks (in fact, all rodent cestodes in our data set, except *H. asymetrica* Janicki, are unarmed), and the small-sized shrew cestodes inhabiting the anterior intestine include both armed and unarmed species. Thus, the presence of attachment devices (other than suckers) does not seem to explain the variability of cestode body sizes in the anterior intestine.

An alternative explanation is that the shear bulk of the large-sized cestodes helps them to maintain the preferred position in the anterior intestine. On the other hand, a very small size may also enhance attachment, because miniature cestodes are able to hide among the long villi of the anterior intestine. According to our observations, this attachment strategy is adopted by the smallest species of tapeworms in the anterior intestine of shrews (*Staphylocystoides* spp.). If the body size does play a role in attachment, we would expect the intermediate-sized cestodes to be lacking in the proximal parts of the intestine; this appears to be the case in cestodes of small mammals. A corresponding situation is seen in nematodes: the species living in the anterior intestine are either very small, and attached to the intestinal wall (e.g. *Heligmosomoides* spp. in rodents and *Longistriata* spp. in shrews), or so large (Ascaridae) that specialized attachment devices are not needed (Bansemir and Sukhdeo 1996). The pronounced variation of body size in the middle intestine may also reflect species-specific constrains on body size evolution, although high vari-

ability is expected simply because of the high number of species living in that region.

Energy allocation models have proved to be useful in studying a variety of life history problems, e.g. age-at-maturity (Kozłowski and Wiegert 1986, Kawecki 1993), indeterminate growth (Kozłowski and Uchmanski 1987, Engen and Sæther 1994, Heino and Kaitala 1996), and paedomorphosis (Kozłowski 1996). Our model is similar to those used by Kozłowski and Wiegert (1986) and Engen and Sæther (1994). Particularly, our model arises as a special case of one of the models studied in Engen and Sæther (1994). However, we are not aware of previous attempts to explain interspecific patterns of body size variation along environmental gradients with energy allocation models.

We assumed that an optimal life history strategy maximizes the expected reproductive success. But is such a strategy also evolutionarily unbeatable, i.e. an evolutionarily stable strategy (ESS)? Under assumptions of density independence (within the life stage under consideration) and discrete life stages the answer is positive. The assumption of discrete life stages is justified since many tapeworms occur seasonally in their small mammalian hosts (Kisielewska 1961, Haukisalmi et al. 1988). However, density-dependent factors are likely to operate at some high densities at least. If this happens, an ESS life history may, but need not to, deviate from the one maximizing the expected density-independent reproductive success. An example in which this deviation occurs is given in Kawecki (1993). What really matters are details of competitive interactions. The extension of our model to account for density dependence is beyond the scope of this paper.

Because the model predictions match fairly successfully to the empirical data, we assume that the present model has captured the essential components of tapeworm body size evolution. The greatest difficulty in the application of the model is the realistic estimation of cestode mortality rate, a parameter that greatly affects the predictions of the optimal body size. The mechanical disturbance is probably important in this respect, but we could as well assume that some of the physiological gradients within the intestine (e.g. pH) is crucial for the survival of cestodes. In fact, overall mortality rate probably depends on several interacting factors, which are likely to vary among cestode (and host) species. We conclude that the present model gives insight into the evolutionary processes affecting the tapeworm body size, but more detailed information on the patterns of mortality are clearly needed.

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160