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Complex life cycle and body sizes at life-history transitions for macroparasites

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ABSTRACT

Questions: Macroparasites often require multiple hosts. (1) What are the conditions under which a complex life cycle (using both definitive and intermediate hosts) is more advantageous than a simple life cycle (using definitive host only)? (2) What are the optimal body sizes at life-history transitions? (3) Can a complex life cycle co-exist with a simple life cycle in the same population?

Mathematical method: We study the evolutionary dynamics of phenotypes that differ in their life cycles and in their body sizes (size at birth, at transition between hosts, at maturity, etc.)

Key assumptions: Evolution of the life-cycle pattern is linked to the evolution of body sizes at life-history transitions. Mortality, growth rate, host finding success, and hatching success are given as functions of body size.

Conclusions: (1) The results are usefully illustrated graphically. (2) Size at birth, size at transition between hosts, and size at maturity depend on the productivity and mortality of parasites within different hosts. (3) The co-existence of phenotypes with different life histories is possible if the density dependence works both in an intermediate host and in a definitive host.

Keywords: body size, complex life cycle, evolution, macroparasite.

INTRODUCTION

Many marine invertebrates adopt a littoral, sedentary adult stage in benthic habitat and a planktonic larval stage in pelagic habitat. This is termed a 'complex' life cycle because such organisms need to spend time in two or more widely different habitats to complete their life cycle. Sometimes, closely related species that have a simple life cycle are able to skip the planktonic larval stage. They give birth to offspring of a benthic form by direct development, and they can complete their life cycle in a single benthic habitat.

Even clearer examples of complex life cycles are shown by helminth parasites. They perform sexual reproduction in a definitive host, but in many cases their larvae spend some time in one or two intermediate hosts before entering the definitive host (Dobson, 1988; Lafferty, 1999). For example, Bothriocephalid cestodes require one intermediate host, which is a

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copepod (Jarroll, 1979; Granath and Esch, 1983), and their definitive host is marine fish (Robert *et al.*, 1990). In addition to the essential intermediate hosts, helminth parasites may also use paratenic hosts (such hosts are not obligatory to complete their life cycle, however). For example, *Bothriocephalus barbatus*, a species of Bothriocephalid cestodes of turbot, needs only one intermediate host to complete its life cycle, but *B. gregarius* requires an additional paratenic as well as the same intermediate host (Robert and Gabrion, 1991). The transition between stages in different hosts is often accompanied by an ontogenetic transformation and niche shift (Loreau and Ebenhoh, 1994).

Evolution of the complex life cycles of parasites has been addressed. For example, Dobson and Merenlender (1991) studied the population dynamics of parasites with two different life cycles – one that uses a definitive host only and another that uses both an intermediate host and a definitive host. The parasite that uses two hosts was at an advantage when its basic reproductive ratio was larger than that of the parasite with a single definitive host only. Morand *et al.* (1995) examined the case in which the definitive host has an opportunity to be infected by larval stages of the parasite localized in both its natural intermediate and a paratenic host. Brown *et al.* (2001) claimed that the complex life cycles involving trophic transmission evolved because they are an efficient way for parasites to meet a sexual partner, assuming that selective benefits are associated with cross-fertilization. Lafferty (1999) suggested that an evolutionary origin for complex life cycles might be predation of a parasitized host, which provides the opportunity for the parasite to make the predator an additional host when the parasite gains the ability to infect the predator. However, whether or not adding one more host to the life cycle is beneficial to the parasite will depend on the growth advantage and the cost of mortality of parasites, which in turn are affected by the host's susceptibility and immunity.

Trade-offs between different life cycles and different timings of life-history transitions are closely linked with body sizes. The reproductive resources of a parasite increase greatly with size at maturity (Morand, 1996). The ability to search for a suitable host and survivorship may also depend on the parasite's body size. To evaluate the relative advantage of a parasite that exploits both an intermediate host and a definitive host (complex life cycle) over a parasite that exploits a definitive host only (simple life cycle), we need to know the growth advantage gained by spending time in an intermediate host, and the cost of finding that host or the loss incurred during an additional host search.

A parasite that reproduces earlier reduces the risk of being killed before maturation, but it has a smaller body size and fewer resources available for reproduction. Hence size at sexual maturity should be determined by weighing the benefit of a further increase in size with the risk of mortality by postponing reproduction. Producing a large number of eggs is beneficial if all of them survive. However, since small larvae from small eggs experience high mortality in the early life stages, producing fewer larger eggs could be advantageous (Smith and Fretwell, 1974). In addition, large larvae enjoy an advantage after settling in the host, because they spend less time developing and hence experience lower mortality than small larvae. A different size at which a larva leaves an intermediate host and transfers to a definitive host would affect the mortality experienced in the two hosts.

To understand the diversity of complex life cycles in helminth parasites, we study the evolution of parasites with complex life cycles by considering the growth of each individual, and discuss the evolution of size at life-history transitions, such as egg size, larval size during transitions between hosts, and size at maturity. Our basic assumption is that the hatching success of an egg, the survivorship of a larva, growth rate within each host, and

the reproductive resources of an adult are given as functions of parasite body size. We also discuss the conditions for a complex life cycle and a simple life cycle to co-exist.

MODEL

We consider two types of parasites that have different life cycles, as illustrated in Fig. 1. A glossary of terms is given in Table 1.

Simple life cycle

We first consider a parasite with a simple life cycle, the 'type 1' parasite. It completes its life cycle in a definitive host in which individuals reproduce sexually (Fig. 1). For simplicity, we assume that it is hermaphroditic. Let x_e be the size of a newly produced offspring. Since its size is determined by egg size, it has suffix e indicating 'egg'. Larvae are distributed over the environment and then picked up by individuals of the definitive host species.

Let $f(w)$ be the hatchability of an egg if the parasite egg size is w. We assume that there is a minimum egg size below which the larvae cannot hatch. Hatchability increases with size, but saturates to an asymptotic level for very large egg sizes. For example, it may be $f(w) = \gamma(w - m)/\{1 + \delta(w - m)\}$ for $w > m$, and $f(w) = 0$ for $w \leq m$, where m is the minimum egg size for hatchability. γ and δ are positive parameters. Assuming random encounters, $1 - e^{-a_d H_d}$ is the rate of host encounter for a parasite, where H_d is the total number of definitive hosts and a_d is searching efficiency. For simplicity, we assume that the host encounter rate is independent of the body size of parasites. Let N_1 be the number of eggs in the population. Here the number of individuals that can encounter a definitive host is

$$N_1^d = N_1 f(x_e)(1 - e^{-a_d H_d}) \tag{1}$$

Once the parasite succeeds in encountering a host, it remains in the host and grows until it reaches size x_r. During this period, daily mortality is $\mu_d(w)$ and the growth rate per day is

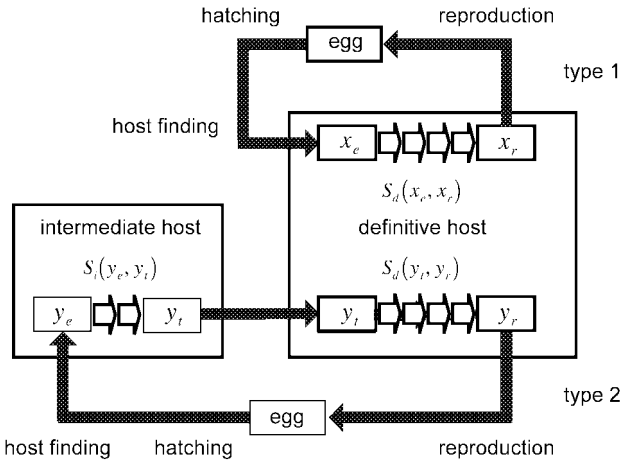


Fig. 1. Schematic representation of the model. The type 1 parasites have a simple life cycle and use the definitive host only. The type 2 parasites have a complex life cycle and use both an intermediate host and a definitive host to complete their life cycle.

Table 1. Glossary of variables, parameters, and functions used in the model

Type 1 parasite	
Number of eggs in the population	N_1
Number of individuals that can encounter the definitive host	N_1^d
Critical body sizes of the type 1 parasite:	
egg size	x_e
size at maturity	x_d
Type 2 parasite	
Number of eggs in the population	N_2
Number of individuals that can encounter the intermediate host	N_2^i
Number of individuals that can encounter the definitive host	N_2^d
The critical body sizes of the type 2 parasite:	
egg size	y_e
size at transition between the two hosts	y_t
size at maturity	y_d
Number of definitive hosts	H_d
Number of intermediate hosts	H_i
Success encountering definitive hosts	$1 - e^{-a_d H_d}$
Success encountering intermediate hosts	$1 - e^{-a_i H_i}$
Searching efficiencies	a_d and a_i
Functions (which depend on body size *w*)	
Hatchability of eggs	$f(w)$
minimum hatchable size	m
parameters in the hatchability function	δ and γ
Survivorship of parasite in the definitive host while growing from size w_1 to size w_2	$S_d(w_1,w_2)$
Mortality rate in the definitive host	μ_d
Growth rate in the definitive host	$g_d(w)$
maximum size in the definitive host	K_d
exponential growth rate when size is small	r_d
Survivorship of parasite in an intermediate host while growing from size w_1 to size w_2	$S_i(w_1,w_2)$
Mortality rate in the intermediate host	μ_i
Growth rate in the intermediate host	$g_i(w)$
maximum size in the intermediate host	K_i
exponential growth rate when size is small	g_{0i}
Reproductive resources	$R(w)$
proportionality constant	R_0
Competition coefficient within a definitive host	c_d
Competition coefficient within an intermediate host	c_i
Parameter in a negative binominal distribution	k
Equilibrium population of type 2 only parasite	$\hat{N}_2$
Number of type 1 parasites that can encounter definitive hosts when there are type 2 parasites only	$\hat{N}_1^d$
Number of type 2 parasites that can encounter definitive hosts when there are type 2 parasites only	$\hat{N}_2^d$
Number of type 2 parasites that can encounter intermediate hosts when there are type 2 parasites only	$\hat{N}_2^i$
Population of type 2 parasites that can co-exist	$\tilde{N}_2$
Fitness of type 1 parasite (simple life cycle)	W_{simple}
Fitness of type 2 parasite (complex life cycle)	$W_{complex}$
Density-independent component of the fitness of the type 1 parasite (simple life cycle)	$\overline{w}_{simple}$
Density-independent component of the fitness of the type 2 parasite (complex life cycle)	$\overline{w}_{complex}$

$g_d(w)$, both of which are functions of size (see Table 1). In the numerical examples below, we assume logistic growth: $g_d(w) = g_{0d}w(1 - w/K_d)$. K_d is the maximum size and g_{0d} is the exponential rate of growth of the parasite when small. We also assume mortality μ_d is independent of size w. Then we have

$$\frac{dw}{dt} = g_d(w), \tag{2a}$$

$$w(0) = x_e \qquad \text{and} \qquad w(T) = x_r \tag{2b}$$

where T is the time spent within a host. Survivorship during the period in which size increases from x_e to x_r is

$$S_d(x_e,x_d) = \exp\left[-\int_0^T \mu_d\,dt\right] = \exp\left[-\int_{x_e}^{x_r} \frac{\mu_d}{g_d(w)}\,dw\right] \tag{3}$$

Survivorship depends on the growth rate because faster growth shortens this period and reduces mortality.

Let $R(w)$ be the amount of reproductive resources possessed by a parasite of body size w. It is an increasing function of body size w. In the numerical example for illustration, we use $R(w) = R_0w$, showing that the amount of resources is proportional to body size, where R_0 is a proportionality constant. The number of eggs produced is $R(x_r)/x_e = R_0x_r/x_e$.

In addition, we consider density-dependent mortality in the host, represented by a factor, $\phi_d(N^d_{total})$, which satisfies $\phi_d(0) = 1$ and $0 < \phi_d(N^d_{total}) \le 1$, and is a decreasing function of the total number of parasites in the definitive host N^d_{total}. Then the number of parasites of type 1 in the next generation is

$$N_1^{next} = N_1^d S_d(x_e,x_r)\{R_0x_r/x_e\}\phi_d(N^d_{total}) \tag{4}$$

Combining equations (1) and (4), the rate of multiplication of the population size per generation, or the ratio of N_1^{next}/N_1, is

$$W_{simple} = f(x_e)(1 - e^{-a_dH_d})S_d(x_e,x_r)\{R_0x_r/x_e\}\phi_d(N^d_{total}) \tag{5}$$

This is equivalent to the basic reproductive ratio (Dobson, 1988), or the fitness. What is notable in equation (5) is that the fitness W_{simple} is given as a function of critical body sizes x_e and x_r.

Complex life cycle

Next, we consider a parasite with a complex life cycle, a 'type 2' parasite. It spends time in an intermediate host before entering the definitive host (Fig. 1). For simplicity, we first consider the case in which the parasite does not reproduce asexually in an intermediate host.

Let y_e be the size of a newly produced offspring of the parasite. The hatchability multiplied by the survivorship in the early stages increases with egg size and is expressed as $f(y_e)$, the same function as for a type 1 parasite. The larva succeeds in finding an intermediate host with rate $1 - e^{-a_iH_i}$, where H_i is the total number of intermediate hosts, assuming random encounters. Symbols with the suffix i represent the time spent by the parasite in the intermediate host. The parasite remains in the intermediate host until it reaches transfer size y_t. During this period, daily mortality in the intermediate host is μ_i, and the growth rate per

day is $g_i(w)$, given as a function of size. The survivorship of parasites in the intermediate host is a density-independent factor

$$S_i(y_e, y_t) = \exp\left[-\int_{y_e}^{y_t} (\mu_i / g_i(w)) \mathrm{d}w \right] \tag{6}$$

multiplied by a density-dependent factor $\phi_i(N^i_{total})$. $\phi_i(N^i_{total})$ is a decreasing function of the total number of individuals in the intermediate host, N^i_{total}.

When juveniles reach size y_t, they leave the intermediate host and start searching for definitive hosts to settle in. The probability of meeting a definitive host (or per capita transmission rate) is $1 - e^{-a_d H_d}$, where H_d is the number of definitive hosts in the area. Thus the number of parasites of type 2 that can encounter a definitive host is

$$N_2^d = N_2 f(y_e)(1 - e^{-a_i H_i}) S_i(y_e, y_t) \phi_i(N^i_{total})(1 - e^{-a_d H_d}) \tag{7}$$

Once the parasite succeeds in encountering a definitive host, it remains in the definitive host and grows until it reaches size at maturation y_r. The amount of reproductive resources for an individual parasite is an increasing function of body size y_r, and is $R(y_r) = R_0 y_r$. The number of eggs of the type 2 parasite in the next generation is

$$N_2^{next} = N_2^d S_d(y_i, y_r)\{R_0 y_r / y_e\} \phi_d(N^d_{total}) \tag{8}$$

Hence the fitness (or the rate of multiplication per life cycle) of type 2 parasites is the ratio N_2^{next}/N_2, which is given by

$$\begin{aligned} W_{complex} = {} & f(y_e)(1 - e^{-a_i H_i}) S_i(y_e, y_t) \phi_i(N^i_{total}) \\ & \times (1 - e^{-a_d H_d}) S_d(y_t, y_r)\{R_0 y_r / y_e\} \phi_d(N^d_{total}) \end{aligned} \tag{9}$$

OPTIMAL CRITICAL SIZES FOR A SIMPLE LIFE CYCLE

Consider recurrent mutation or invasion of genotypes that have different life-history parameters from the resident type. These invaders may succeed in spreading and might replace the resident. After many invasions and subsequent replacements, the population should reach a state that is an evolutionarily stable strategy, which can be calculated by choosing critical sizes x_e and x_r ($0 < x_e \le x_r$) to maximize the fitness W_{simple} (with N_{total} fixed).

The logarithm of equation (5) is

$$\ln W_{simple} = \ln(f(x_e)/x_e) - \int_{x_e}^{x_r} (\mu_d / g_d(w)) \mathrm{d}w + \ln x_r + [\text{other terms}]$$

where the last terms are independent of x_e or x_r. By taking the derivative and setting it equal to zero, we have

$$1/x_e - f'(x_e)/f(x_e) = \mu_d / g_d(x_e) \tag{10a}$$

and

$$\mu_d / g_d(x_r) = 1/x_r \tag{10b}$$

Equation (10a) indicates how optimal egg size is determined. The right-hand side of equation (10a) indicates hatching success and larval survivorship before entering the host. A large egg produces a large larva with a high survivorship both before and after its encounter with the host. The right-hand side of equation (10b) is the advantage gained by a larva when starting from a large size in terms of a reduced mortality in the host, and can be called the 'growth advantage of having a larger initial size'.

Equation (10b) represents optimal size at maturity. If there are multiple solutions of equation (10b), then the one nearest the saturation size K_d at which growth rate slows down is the local optimum. A faster increase in reproduction with size (greater R_0), a higher growth rate, and lower mortality in the host would increase optimal reproductive size.

Graphical representation

The results can be illustrated graphically, as shown in Fig. 2. The horizontal axis represents body size. The three curves are $\mu_d/g_d(w)$, $1/w$, and $1/w - f'(w)/f(w)$. The optimal size at maturity x_r is given by equation (10b) as a cross point of two curves $\mu_d/g_d(w)$ and $R'(w)/R(w)$. Only the larger of the two cross points is the optimum x_r, because the smaller cross point is the local minimum of the fitness shown by the second derivative. In a similar manner, the optimal egg size x_e is given by the smaller of the two cross points between curves $\mu_d/g_d(w)$ and $1/w - f'(w)/f(w)$ (see Fig. 2). The range of the parasite's body size is indicated by a horizontal arrow below the x-axis.

Suppose that the productivity of the habitat is enhanced or that the mortality is reduced. Then the function $\mu_d/g_d(w)$ becomes smaller, and as a result the optimal egg size x_e is reduced (change from dotted curve to solid curve in Fig. 2) and the optimal size at maturity x_r is increased.

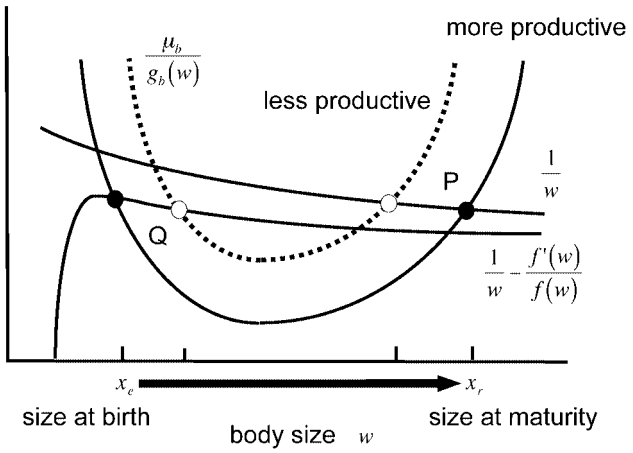


Fig. 2. Optimal body sizes at birth and at maturity for a type 1 parasite adopting a simple life cycle. The horizontal axis represents body size w. The three curves are: $\mu_d/g_d(w)$, $1/w$, and $1/w - f'(w)/f(w)$. The cross point of curve $\mu_d/g_d(w)$ and curve $1/w$ (labelled 'P') gives the optimal size at maturity x_r. The cross point of curve $\mu_d/g_d(w)$ and curve $1/w - f'(w)/f(w)$ (labelled 'Q') has the optimal egg size x_e. The dotted curve indicates the case with a reduced growth rate or enhanced mortality. The arrow below the x-axis indicates the range of body sizes used by the parasites.

OPTIMAL CRITICAL SIZES FOR COMPLEX LIFE CYCLE

If all the mutants have a complex life cycle (type 2), the natural selection working on the critical sizes y_e, y_t, and y_r ($0 < y_e \le y_t \le y_r$) would realize the values that maximize the fitness $W_{complex}$ given by equation (9). In a similar manner as in the last section, the conditions for the optimal body sizes at life-history transitions (y_e, y_t, and y_r) are

$$1/y_e - f'(y_e)/f(y_e) = \mu_i/g_i(y_e) \tag{11a}$$

$$\mu_i/g_i(y_t) = \mu_d/g_d(y_t) \tag{11b}$$

and

$$\mu_d/g_d(y_r) = 1/y_r \tag{11c}$$

Equation (11a) is the condition for the optimal egg size y_e. It is similar to equation (10a). The only difference is that the growth advantage of having a larger initial size should be evaluated using the mortality and growth rate of parasites in an intermediate host instead of those in a definitive host.

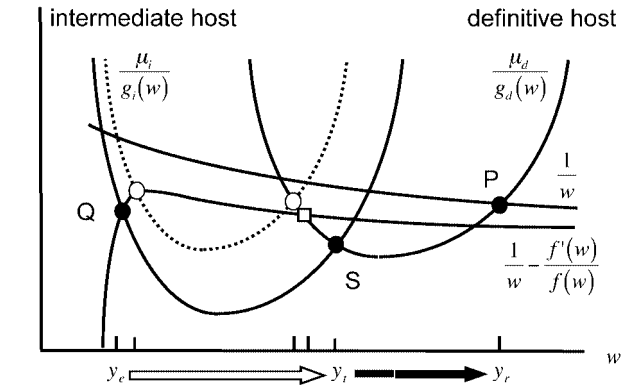
Equation (11b) represents the size at which the parasite transfers from an intermediate host to a definitive host. If the larva leaves the intermediate host and enters the definitive host at a smaller size, it will experience less mortality in the intermediate host, but greater mortality in the definitive host. Equation (11b) indicates that the optimal size of host transfer should be the one at which these two balance. The optimal transfer size is larger (or the transfer should be delayed) for a lower mortality and a faster growth rate in the intermediate host, and for a higher mortality and a slower growth rate in the definitive host.

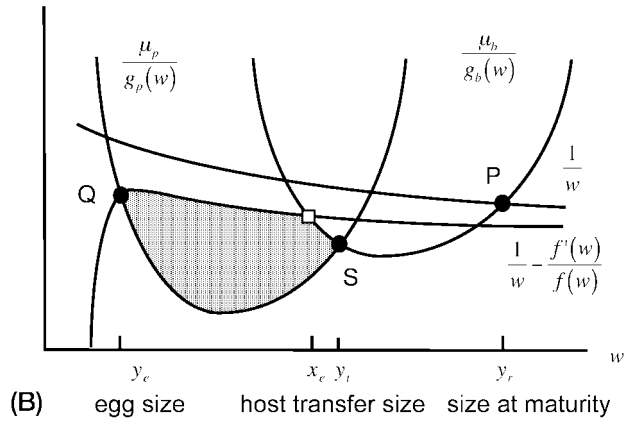
Equation (11c) determines the size at maturity in the definitive host. This is equivalent to equation (10b).

Graphical representation

Again a graphical representation is useful. Figure 3A illustrates four curves: $\mu_i/g_i(w)$, $\mu_d/g_d(w)$, $1/w$, and $1/w - f'(w)/f(w)$. The optimal egg size y_e is the body size at the smaller of the two cross points of $1/w - f'(w)/f(w)$ and $\mu_i/g_i(w)$; the optimal size at transfer between two hosts y_i is the cross points of $\mu_i/g_i(w)$ and $\mu_d/g_d(w)$; and the optimal size at maturity in the definitive host y_r is the larger of the two cross points between $\mu_d/g_d(w)$ and $1/w$.

Fig. 3. Optimal body sizes for a type 2 parasite with a complex life cycle. The horizontal axis represents body size w. The four curves are: $\mu_d/g_d(w)$, $\mu_i/g_i(w)$, $1/w$, and $1/w - f'(w)/f(w)$. (A) The cross point of curve $\mu_d/g_d(w)$ and curve $1/w$ is labelled 'P', and its w is equal to the optimal size at maturity y_r, which is the same as x_r of the type 1 parasite. The cross point of curve $\mu_i/g_i(w)$ and curve $1/w - f'(w)/f(w)$ (labelled 'Q') gives the optimal egg size y_e. The cross point of curve $\mu_d/g_d(w)$ and curve $\mu_i/g_i(w)$ (labelled 'S') has the optimal size of host transfer y_t of the type 2 parasite. The open and solid arrows below the horizontal axis are the ranges of body size in an intermediate and in a definitive host, respectively. An open square indicates the optimal egg size of the corresponding type 1 parasite. (B) The shaded area surrounded by three curves corresponds to the integral in equation (15), which indicates the benefit of using an intermediate host before entering the definitive host. A complex life cycle is beneficial if this area is large enough to compensate the loss related to finding an intermediate host. (C) The optimal complex life cycle if parasites in an intermediate host divide and increase in number before entering the definitive host.


intermediate host
definitive host
$\frac{\mu_i}{g_i(w)}$
$\frac{\mu_d}{g_d(w)}$
P
Q
S
$\frac{1}{w}$
$\frac{1}{w} - \frac{f'(w)}{f(w)}$
w
y_e
y_t
y_r
(A)
egg size
host transfer size
size at maturity


$\frac{\mu_p}{g_p(w)}$
$\frac{\mu_b}{g_b(w)}$
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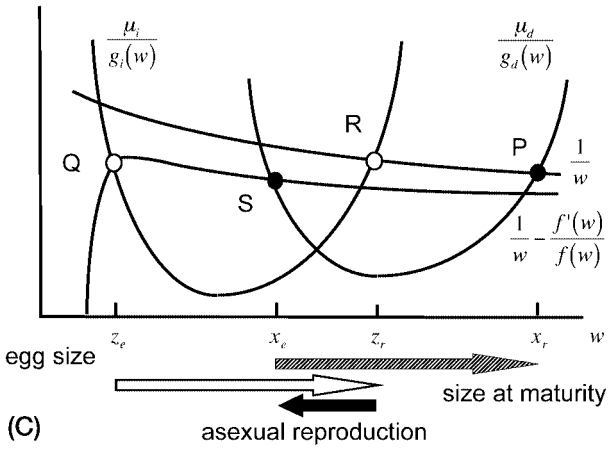
$\frac{1}{w}$
$\frac{1}{w} - \frac{f'(w)}{f(w)}$
w
y_e
x_e y_t
y_r
(B)
egg size
host transfer size
size at maturity


$\frac{\mu_i}{g_i(w)}$
$\frac{\mu_d}{g_d(w)}$
R
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$\frac{1}{w} - \frac{f'(w)}{f(w)}$
w
z_e
x_e
z_r
x_r
egg size
size at maturity
(C)
asexual reproduction

Suppose that growth rate in an intermediate host is improved or mortality in an intermediate host is reduced. Then the function $\mu_i/g_i(w)$ becomes smaller than before (shift from dotted curve to solid curve in Fig. 3A). Then the optimal egg size y_e becomes smaller and the size at host transfer y_t becomes larger than before, but the size at maturity y_r remains unchanged.

In Fig. 3, we also indicate by an open square the optimal size at birth for a simple life cycle (definitive host only). Size at maturity is the same between a complex life cycle and a simple life cycle ($y_r = x_r$), which can be proved by the fact that equations (11c) and (10b) are the same. Hence we conclude that if multiple parasites use the same definitive host, they tend to mature at similar sizes, even if one uses an intermediate host and the other does not.

Egg size of a complex life cycle should be much smaller than that of a simple life cycle ($y_e < x_e$). However, egg size at transition between the two hosts for a complex life cycle can be larger than, smaller than, or equal to that of a simple life cycle.

Asexual reproduction within an intermediate host

In this paper, we assume that the parasite grows in its intermediate host but proliferates only in its definitive host. This might be a good assumption for filaria, *Brugia malayi* and *Wuchereria bancrofti* (Miyazaki, 1991), but many species of trematoda multiply within an intermediate host asexually, by fission or budding. We may treat this as an additional step in the model, by assuming that a single individual in the intermediate host divides into n individuals asexually, and that the propagules of smaller size should start searching for definitive hosts.

Here, we consider that a parasite multiplies in its intermediate host. The parasite grows from initial size z_e to final size z_r in the intermediate host (see Fig. 3C). Then, the parasite divides into a number of individuals each of which attempts to enter a definitive host. Let the size of this parasite be x_e. Then, the number of individuals produced by division is simply z_r/x_e. In the definitive host, the parasite grows from initial size x_e to the size at maturity x_r. In this setting, we have the following fitness:

$$\begin{aligned} W_{complex} = f(z_e)(1 - e^{-a_i H_i}) S_i(z_e, z_r)\{z_r/x_e\}\phi_i(N^i_{total}) \\ \times (1 - e^{-a_d H_d}) S_d(x_e, x_r)\{R_0 x_r/z_e\}\phi_d(N^d_{total}) \end{aligned} \tag{12}$$

Natural selection works on four critical sizes (z_e, z_r, x_e, and x_r) to achieve those that maximize equation (12) under the constraint that $z_r \geq x_e$. The optimal solution is illustrated graphically in Fig. 3C. The initial size for parasites in a definitive host x_e and size at maturity x_r are the same as those of the simple life cycle species in the same environment.

RELATIVE ADVANTAGES OF A COMPLEX LIFE CYCLE AND SIMPLE LIFE CYCLE

The density-dependent reduction in survivorship occurs both in the intermediate host and in the definitive host. Since only type 2 parasites use an intermediate host, the number of parasites in an intermediate host is equal to that in a complex life cycle:

$$N^i_{total} = N^i_2 = N_2 f(y_e)(1 - e^{-a_i \mathrm{H}_i}) \tag{13}$$

To show the density dependence of the fitness clearly, we introduce density-independent components of the fitness: $\bar{w}_{simple} = W_{simple}/\phi_d(N^d_{total})$ and $\bar{w}_{complex} = W_{complex}/$

$(\phi_i(N^i_{total})\phi_d(N^d_{total}))$. Using these components, we can express the fitness as a product of the density-independent component and a density-dependent factor: $W_{simple} = \overline{w}_{simple}\phi_d(N^d_{total})$ and $W_{complex} = \overline{w}_{complex}\phi_i(N^i_{total})\phi_d(N^d_{total})$. Hence, the populations in the next generation are

$$N_1^{next} = N_1\overline{w}_{simple}\phi_d(N_1^d + N_2^d), \tag{14a}$$

$$N_2^{next} = N_2\overline{w}_{complex}\phi_i(N_2^i)\phi_d(N_1^d + N_2^d) \tag{14b}$$

The ratio of the fitness of a complex life cycle and that of a simple life cycle is:

$$\begin{aligned}\frac{W_{complex}}{W_{simple}} &= [(1 - e^{-a_i H_i})\phi_i(N^i_{total})] \times \frac{f(y_e)S_i(y_e,y_t)S_d(y_t,y_r)y_r/y_e}{f(x_e)S_d(x_e,x_r)x_r/x_e} \\ &= [(1 - e^{-a_i H_i})\phi_i(N^i_{total})] \times \exp\left[\begin{array}{l}\displaystyle\int_{y_e}^{x_e}\{1/w - f'(w)/f(w) - \mu_i/g_i(w)\}\mathrm{d}w \\ \displaystyle+\int_{x_e}^{y_i}\{\mu_d/g_d(w) - \mu_i/g_i(w)\}\mathrm{d}w\end{array}\right]\end{aligned} \tag{15}$$

where we assume that the body sizes at life-history transitions are optimized. The first term of equation (15) is the success of encountering an intermediate host. It is likely considerably smaller than 1, because host encounters are normally a difficult step for parasites. The second term is the growth advantage of spending some time in an intermediate host, and is larger or equal to 1. The terms in the integral of equation (15) are represented by the shaded area in Fig. 3B. The size of this area is large when growth is fast and mortality is low in the intermediate host. A complex life cycle will be beneficial if this area is large enough to compensate the mortality related to finding an intermediate host.

If density dependence occurs only within the definitive host, different types cannot co-exist stably. Then the ratio of two types N_2/N_1 follows a geometric series with common ratio $\overline{w}_{complex}/\overline{w}_{simple}$, which is given by equation (15) and is a constant. Type 1 wins if $\overline{w}_{complex}/\overline{w}_{simple} < 1$, and type 2 wins if $\overline{w}_{complex}/\overline{w}_{simple} > 1$. There is no possibility of co-existence.

As explained in Appendix 2, we can calculate the equilibria of equation (14) and their stability. The model has an equilibrium composed only of type 1 parasites (simple life cycle) and another equilibrium composed only of type 2 parasites (complex life cycle). In addition to these single-species equilibria, there may be an equilibrium in which both type 1 and type 2 parasites have positive abundance, indicating their co-existence. Figure 4 shows the parameter regions for an illustrative example. There is a parameter region for existence in which $\overline{w}_{complex} > \overline{w}_{simple}$ (see Appendix 2 for derivation).

DISCUSSION

The basic assumption of the model presented here is that reproductive rate, hatching success, mortality, and the growth rate of parasites are all given as functions of body size. Based on this assumption, the trade-offs between fitness components are satisfied in a plausible manner. Producing eggs of a larger size improves the hatching success and the survivorship of larvae, but it reduces the number of eggs produced. An earlier transfer from an intermediate to a definitive host reduces the mortality in an intermediate host but increases mortality in a definitive host. Finally, a larger size at maturity increases fecundity at the cost of an enhanced risk of being killed before reproduction.

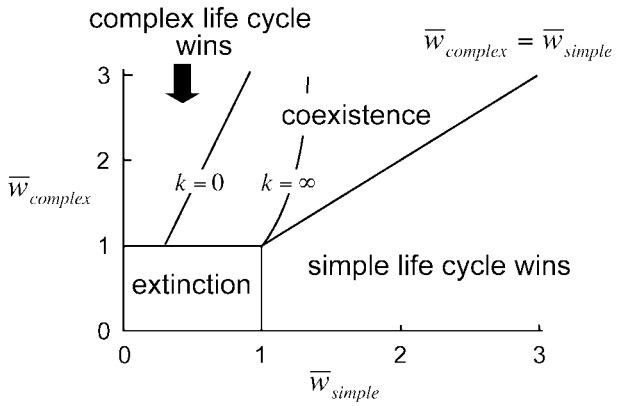

Fig. 4. Parameter regions for different outcomes of competition. $\overline{w}_{simple}$ and $\overline{w}_{complex}$, the density-independent components of fitness in a simple life cycle and complex life cycle, respectively. The outcome of competition is indicated. Density dependence works both in the intermediate host and in the definitive host. There is a region in which the stable co-existence of the two types is possible. The limiting cases of $k \to 0$ and $k \to \infty$ are indicated. The fixed parameters are: $a_d = 5.0$, $c_d = c_i = 0.3$, $H_d = 50$, and $H_i = 50$.

The evolution of body sizes at life-history transitions should achieve the optimal body sizes that maximize the fitness function (W_{simple} or $W_{complex}$). The relative advantage of two life cycles is also judged by comparing the fitness between the best type 1 species (W_{simple}) and the best type 2 species ($W_{complex}$). If density dependence works only in the definitive host, the larger of the two types will occupy the whole population. This is equivalent to stating that the life-history pattern that evolves is the one that achieves the maximum basic reproductive ratio (Dobson, 1988). Parasites with different life cycles cannot co-exist stably.

The evolutionarily stable sizes at life-history transitions (such as egg size, larval size at host transfer, and size at maturation) depend on growth rate as a function of size, mortality, efficiency in host finding, and host density. Lafferty (1999) and Lafferty and Kuris (2002) suggested that, when a parasite begins to infect a new host, an initially small typical parasite should evolve eventually to the size that allows it to consume the maximum amount of host possible without seriously compromising the longevity of the host, thus becoming a large-sized parasitic castrator. This scenario is consistent with the result in this paper on the evolutionarily stable body size at maturity in the definitive host, denoted by x_r or y_r. It is close to but a little smaller than K_d, the saturation size.

If density regulation occurs only in the definitive host, only a single type remains in the population; but co-existence of two types is possible if density dependence works in both hosts. However, the co-existence of multiple parasite species using the same host can be explained by the aggregation and the independence of the number of parasites between different species (Roberts and Dobson, 1995). Since a negative binomial distribution is realized by a mixture of Poisson distributions with different parameters, the observed aggregation can be caused by any heterogeneity of hosts concerning susceptibility – whether exposure to the parasite, behavioural differences, habitat structure, or the strength of the immune response. We did not consider the heterogeneity of host susceptibility explicitly, but assumed a negative binominal distribution, because the focus of our study was on the evolution of

critical sizes and the advantage of different life-history patterns, rather than the co-existence mechanism.

In the current paper, we assumed that the parasite would leave the intermediate host when it reaches size y_r. Then, the parasite searches for a definitive host and enters its host's body. This is a model suitable for *Schistosoma japonicum* with percutaneous infection from the intermediate host to the definitive host (Tanaka and Tsuji, 1997). In contrast, in some species of cestode, parasites are transferred to the definitive host when the intermediate host is eaten by the definitive host (Robert *et al.*, 1988; Robert and Gabrion, 1991). If the intermediate host is a prey of the definitive host, the transition event from the two hosts may not be a strategy of the parasite but simply a fortuitous event. However, parasites may be able to modify the host's behaviour to increase its exposure to the predator, which is the definitive host for the parasite (Dobson, 1985). Modification of the host's behaviour by parasites has been a major research topic recently in parasitology. For example, red grouse with nematode parasites are more vulnerable to mammalian predators (Hudson *et al.*, 1992). The avian predators prefer roach infected by a tapeworm to uninfected roach (Loot *et al.*, 2002). The parasite in the intermediate host may keep the host somewhere less exposed until it reaches a size suitable for its own transfer. When the parasite reaches its transfer size, it may manipulate the host's behaviour to enhance the likelihood of the host being eaten by the predator. If this is the case, the timing of the behavioural switch from cryptic to exposure to the predator evolves to occur when the parasite reaches the size suitable for its transition from one host to the other.

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APPENDIX 1

Here we consider that density regulation occurs only in the definitive host. Let N be the total number of parasites that could encounter a definitive host, and H be the total number of hosts in the population. Due to competition within a host, survivorship is discounted by a crowding factor $e^{-\bar{c}x}$ where x is the number of competitors in the same host and $\bar{c}$ is a positive constant.

The number of parasites in a host often follows an aggregated distribution (Shaw and Dobson, 1995). If the number of parasites per host follows an aggregated distribution and is independent between species, multiple species of parasite can stably co-exist on a single host species (Dobson, 1985; Roberts and Dobson, 1995). Here we assume that the number of parasites in a host follows a negative binomial distribution, with mean N/H. The number of competitors in the same host for a chosen parasite also follows the same negative binomial distribution:

$$p_x = \left(\frac{k+x-1}{x}\right) p^{-k}(1+p)^{-k-x}$$

where $p = N/kH$ and k is a positive constant. The reciprocal of k indicates the degree of aggregation of the distribution. The average survivorship due to crowding is

$$\phi(N) = \sum_{x=0}^{\infty} e^{-\bar{c}x} p_x = \frac{\{1+p(1-e^{-\bar{c}})\}^{-k+1}}{1+p} = \frac{(1+cN/kH)^{-k+1}}{1+N/kH} \tag{A1}$$

where we set $c = 1 - e^{-\bar{c}}$, which is a constant satisfying $0 < c < 1$. For the case in Fig. 4, the density dependence in an intermediate host and in a definitive host is given by replacing the symbols by those with suffix *i* and *d* respectively.

APPENDIX 2

Analysis of the case in which density dependence works both in the definitive host and in the intermediate host.

Equilibria

At equilibrium, $N_1^{next} = N_1$ and $N_2^{next} = N_2$ hold. There are four kinds of equilibria:

(i) Equilibrium with $N_1 = 0$ and $N_2 = 0$. This equilibrium always exists, indicating that neither species exists in the system.

(ii) Equilibrium with only type 1 ($N_1 > 0$ and $N_2 = 0$). The abundance of type 2 parasites is zero ($N_2 = N_2^i = N_2^d = 0$). From equation (14a) with $N_1^{next} = N_1$, we have

$$1/\overline{w}_{simple} = \phi_d(N_1^d) \tag{A2}$$

The right-hand side decreases monotonically with N_1^d, from 1 to 0 (as N_1^d increases from 0 to infinity). Hence if $\overline{w}_{simple} \leq 1$, there is no solution with positive N_1^d. If $\overline{w}_{simple} > 1$, equation (A2) has a unique positive solution ($N_1^d > 0$). The population size at the beginning of a year N_1 is determined using equation (1).

(iii) Equilibrium with only type 2 ($N_1 = 0$ and $N_2 > 0$). The type 1 parasite is absent ($N_1 = N_1^d = 0$). From equation (14b) with $N_2^{next} = N_2$, we have

$$1/\overline{w}_{complex} = \phi_i(N_2^i)\phi_i(N_2^d) \tag{A3}$$

Using equations (7), (13), and (A3), we can calculate a solution for N_2^i and N_2^d numerically. N_2^d is a continuous function of N_2^i and $N_2^d = 0$ when $N_2^i = 0$. Hence if $\overline{w}_{complex} \leq 1$, there is no positive solution. In contrast, if $\overline{w}_{complex} > 1$, there is at least one equilibrium. Note, however, if the competition in the intermediate host is very strong, N_2^d is not a monotonic function of N_2^i, and there can be multiple equilibria. The population size at the beginning of a year N_2 is determined from equation (7).

(iv) The co-existence equilibrium ($N_1 > 0$, $N_2 > 0$). Here, the populations of each type parasite are

$$1/\overline{w}_{simple} = \phi_d(N_1^d + N_2^d) \tag{A4a}$$

and

$$1/\overline{w}_{complex} = \phi_i(N_2^i)\phi_d(N_1^d + N_2^d) \tag{A4b}$$

From these, we have

$$\overline{w}_{simple}/\overline{w}_{complex} = \phi_i(N_2^i) \tag{A5}$$

If $\overline{w}_{complex} \leq \overline{w}_{simple}$, there is no positive solution of N_2^i, implying that co-existence is not possible. In contrast, if $\overline{w}_{complex} > \overline{w}_{simple}$, the equilibrium population N_2^i of the type 2 parasite exists and is determined as the positive solution of equation (A5). We can then calculate N_2 and N_2^d from equations (7) and (13). On the other hand, $N_1^d + N_2^d$ can be obtained from equation (A4a). From this, we obtain N_1^d, which must be positive. Otherwise, there is no co-existence equilibrium.

Invasion condition and the stability of equilibria

Now we examine the condition for a rare type to invade the equilibrium in which the other type dominates.

(i) Invasibility of type 2 to the equilibrium dominated by type 1. Suppose that a small number of type 2 parasites invade the equilibrium population composed of type 1 parasites only, which is given by equation (A2). Since N_2 is small, we have

$$N_2^{next} = N_2 W_2 \phi_d(\hat{N}_1^d) \tag{A6}$$

Together with equation (A2), this gives

$$N_2^{next}/N_2 = \overline{w}_{complex}/\overline{w}_{simple} \tag{A7}$$

Hence, a type 2 parasite can invade the population dominated by the type 1 parasite when $\overline{w}_{complex} > \overline{w}_{simple}$, but not when $\overline{w}_{complex} < \overline{w}_{simple}$.

(ii) Invasibility of type 1 to the equilibrium dominated by type 2. In a similar manner, we consider the case in which a small number of type 1 parasites invade the equilibrium population dominated by type 2 parasites. Equation (A3) is satisfied. Since N_1 is small, we have

$$N_1^{next} = N_1 \overline{w}_{simple} \phi_d(\hat{N}_2^d) \tag{A8}$$

Combined with equation (A3), this gives

$$\frac{N_1^{next}}{N_1} = \frac{\overline{w}_{simple}}{\overline{w}_{complex}} \phi_i(\hat{N}_2^i) \tag{A9}$$

$\hat{N}_2^d$ is the number of parasites of type 2 that can encounter a definitive host and $\hat{N}_2^i$ is the number of parasites of type 2 that can encounter an intermediate host, both of which are in the equilibrium that includes only type 2 parasites. When the fitness of the type 1 parasite is greater than that of the type 2 parasite multiplied by the reduction in density dependence in the intermediate host ($W_1 > \phi_i(\hat{N}_2^i) W_2$), the type 1 parasite can invade the population of the type 2 parasite. However, when the fitness of the type 1 parasite is lower than that of the type 2 parasite, the type 1 parasite cannot invade.

Summary of the analysis

We have the following cases in which different patterns of equilibria are indicated. The results are confirmed by direct computer simulation of the dynamics for the case illustrated in Fig. 4.

1. *Co-existence of two types*

There exists an equilibrium in which both types co-exist when the following inequality holds:

$$\overline{w}_{complex} > \overline{w}_{simple} > \phi_i(\hat{N}_2^i)\overline{w}_{complex} \tag{A10}$$

where $\hat{N}_2^i$ is the abundance of the type 2 parasite in the intermediate host at the time of transition to the definitive host in the equilibrium composed only of the type 2 parasite. The type 1 parasite can invade the type 2 only population, and the type 2 parasite can also invade the type 1 only population. Based on numerical analyses, the co-existing equilibrium is stable.

2. *Type 1 (definitive host only) wins*

Suppose that the following condition holds:

$$\overline{w}_{simple} > \overline{w}_{complex} \tag{A11}$$

The type 1 parasite can invade the type 2 only population, but the type 2 parasite cannot invade to the equilibrium population dominated by the type 1 parasite.

3. *Type 2 (both definitive host and intermediate host) wins*

Suppose we have the following inequality:

$$\phi_i(\hat{N}_2^i)\overline{w}_{complex} > \overline{w}_{simple} \tag{A12}$$

In this case, the type 1 parasite cannot invade the type 2 only population, but the type 2 parasite can invade the population dominated by the type 1 parasite. There is no equilibrium in which the two types can co-exist.

In the example illustrated in Fig. 4, we used the density-dependent factor in Appendix 1. When k is infinitely large, a negative binominal distribution converges a Poisson distribution. If k converges to 0, $\phi_i(\hat{N}_2^i)$ reaches the saturation point c_i. If k is infinitely large, $\phi_i(\hat{N}_2^i)$ reaches the limit $\exp[-c_i\hat{N}_2^i/H_i]$. We illustrate when k is 0 and when k is infinity (a Poisson distribution) in Fig. 4.