

# Evolution of trophic transmission in parasites: the need to reach a mating place?

S. P. BROWN,\* F. RENAUD,† J.-F. GUÉGAN† & F. THOMAS†

\*Department of Zoology, University of Cambridge, Cambridge, UK

†Centre d'Etude sur le Polymorphisme des Micro-Organismes, CEPM/UMR CNRS-IRD 9926 Equipe: 'Evolution des Systèmes Symbiotiques' IRD, Montpellier Cedex, France

## Keywords:

complex life cycle;  
cross-fertilization;  
parasites;  
predators;  
self-fertilization;  
trophic transmission.

## Abstract

Although numerous parasite species have a simple life cycle (SLC) and complete their life cycle in one host, there are other parasite species that exploit several host species successively. From an evolutionary perspective, understanding the mix of adaptive and contingent forces shaping the transition from an ancestral single-host state to such a complex life cycle (CLC) has proved an intriguing challenge. In this paper, we propose a new hypothesis, which states that CLCs involving trophic transmission (i.e. transmission to a predator) evolved because they are an efficient way for parasites to meet a sexual partner, assuming that selective benefits are associated with cross-fertilization. Predators that eat a lot of prey in a relatively short time interval act to concentrate isolated parasites. We use an optimality model to develop our hypothesis and discuss further directions of potential research.

## Introduction

During the course of evolution, complex life cycles (CLCs) involving several host species have evolved independently in several large and distantly related groups of parasites (Anderson, 1984; Mackiewicz, 1988; Rohde, 1994; Schmidt-Rhaesa, 1997; Poulin, 1998). Among parasites with CLCs, a widespread mode of transfer from one host to the next is trophic transmission, with the definitive host (DH) being a predator of the intermediate host. This is for instance the case for several protozoans and nematodes, many trematodes, most cestodes and all acanthocephalans.

Compared with the huge effort that parasitologists have devoted to describe CLCs during the past decades, few studies have tried to understand their adaptiveness (Smith-Trail, 1980; Dobson, 1989; Combes, 1991; Dobson & Merenlender, 1991; Lafferty, 1992, 1999; Esch

& Fernandez, 1993; Morand, 1996). Current hypotheses fall within two main categories, those assuming that CLCs result from adjustments to historical events or accidents, and those arguing that they evolved because they are adaptive, i.e. fitness benefits are gained by adding hosts to the life cycle.

Smith-Trail (1980) suggested two main possible routes of evolution from a single to a two-host life cycle. In the first scenario, the present DH was once the only host in a simple life cycle (SLC). A species emerged that consumed a substantial number of parasite propagules. If this non-host species also became a regular part of the host's diet, parasites with the ability to survive passage through the intermediate would have a selective advantage over parasites that perished when eaten by the new species. In a second scenario, the present intermediate host was once the only host. Following the appearance of a new predator species, infected hosts frequently died from predation. Trophic transmission might have then evolved under strong selective pressure to survive the death of the host by predation, a feat most easily accomplished by parasitizing the host's predator (Smith-Trail, 1980; Lafferty, 1999). Such adjustments to historical contingencies may have played an important role in the evolution of CLCs, because parasites appeared

Correspondence: Frédéric Thomas, Centre d'Etude sur le Polymorphisme des Micro-Organismes, CEPM/UMR CNRS-IRD 9926, Equipe: 'Evolution des Systèmes Symbiotiques', IRD, 911 Avenue Agropolis, B.P. 5045, 34032 Montpellier Cedex 1, France.  
Tel.: +33 4 67 41 62 32; fax: +33 4 67 41 62 99;  
e-mail: fthomas@mpl.ird.fr

very early in the history of life (Conway Morris, 1981) and consequently had to adapt continuously to a large range of environmental changes including changes in faunal composition. However, as pointed out by Poulin (1998), these scenarios suggest that the evolution of CLCs would have been solely at the mercy of external factors, with parasite adaptation being limited to increases in the efficiency of exploitation of novel hosts.

Smith-Trail (1980) also suggested that two-host life cycles may have evolved from adaptive suicides of infected hosts in the context of kin selection. Kin selection theory suggests that an infected host can increase its inclusive fitness by reducing the risk of parasitic infection of its kin. From an infected host perspective, being eaten by a predator before the parasites mature and release propagules may be a solution to protect its kin from infection. As this kind of response became frequent in host populations, natural selection would have favoured parasites with the ability to survive and propagate within the predator.

Alternatively, CLCs could have evolved by parasite-selection, when fitness benefits are gained by adding new hosts to the life cycle. Parasites could, for instance, benefit from using intermediate hosts as a food base and DHs, which are usually large, long-lived and vagile, as an agent of dispersion (Ewald, 1995). CLCs could also have been selected because they represent ideal adaptations to exploit transient or ephemeral opportunities and to reduce intraspecific competition (Esch & Fernandez, 1993). It has been shown that adding a new host (the paratenic host) to an already established CLC may greatly enhance the success of transmission (Robert *et al.*, 1988; Morand *et al.*, 1995). This does not explain, however, why a transition from a SLC to a two-host life cycle has initially been an option favoured by selection.

In this paper, we would like to propose another adaptive hypothesis which stipulates that CLCs have been favoured by selection because in many cases it is a simple and cheap way for individual parasites to meet a sexual partner. We first develop this idea using verbal arguments and then we propose and analyse a model.

## Verbal arguments

### Parasites prefer cross-fertilization

Several works have shown that although numerous parasites are hermaphroditic (all Monogenea, most Digenea, all Aspidogastrea, all Gyrocotylidea, all Amphilinidea, the Eucestoda), cross-fertilization is the rule whenever possible, i.e. whenever two conspecifics meet (Esch & Fernandez, 1993; Nollen, 1993; Rohde, 1994; Combes, 1995; Trouve *et al.*, 1999). In addition, even in self-fertilizers, cross-fertilization may be necessary in the long run because numbers and/or viability of offspring may be reduced if cross-fertilization does not occur at least occasionally (Rohde, 1994; Wedekind *et al.*, 1998;

Lythgoe, 2000). Rohde (1977) even suggested that niche restriction inside the host (i.e. narrow habitat) has been favoured in some hermaphroditic helminths because it increases intraspecific contact and hence facilitates mating. Although we do not at the moment know the exact benefits gained by outbreeding compared with selfing individuals, these observations suggest that cross-fertilization may result in substantial fitness benefits for parasites.

### Predators act as concentrators

Finding a mate may be a major problem faced by parasitic organisms, especially when the density of the parasite population is low. Indeed, in contrast to free-living organisms which can find a sexual partner, or reach a mating place (e.g. salmon, lek species), simply by moving from one location to another, parasites are most of the time a prisoner of their habitat. Unless they are able to locate hosts harbouring a conspecific, they *a priori* rely on chance and/or patience for finding a mate. If the parasitic prevalence is high, and if the host can harbour more than one individual parasite, infective stages will be mostly successful in finding a mate when infecting a host at random. Otherwise, we might expect the evolution of alternate strategies. In very special cases, the parasite may leave its host and search for another one harbouring a sexual partner (e.g. Michaud *et al.*, 1999). Such situations are not the rule, however.

Numerous predators can eat a considerable number of prey in relatively short time intervals (e.g. aquatic birds foraging on invertebrates at low tide). From a parasite perspective, this could be an efficient and cheap way to find a mate. Indeed, by converting several patchily distributed habitats (i.e. the prey) into only one (i.e. the predator), predation inevitably concentrates isolated parasites. Hence, the probability for a given individual parasite of co-occurring with a conspecific can be high even when the prevalence of the parasite within the prey population is low. Transition from a SLC to a two-host life cycle (i.e. the prey and the predator) is therefore an option favoured by parasite-selection, assuming that cross-fertilization is beneficial.

### The model

The first assumption of the modelling section is that both SLC and CLC parasites are hermaphrodite. Thus, if individual parasites are able to reproduce by cross-fertilization, they receive a fitness return of  $w_c$ , whereas if they fail to mate, they receive a fitness return of  $w_s$ . Therefore, a simple fitness expression for an ancestral SLC parasite can be expressed as

$$w = mw_c + (1 - m)w_s. \quad (1)$$

Here  $m$  is the probability of mating within the host. An evolutionary transition from a SLC to a CLC requires the

consideration of mixed strategies of host exploitation. To incorporate mixed strategies, we introduce two key parasite variables, the probability of predation by a DH,  $p$ , and the efficiency of exploitation of a DH,  $e$ . More precisely,  $p$  represents the probability that a parasite in an intermediate host is consumed by a DH, before achieving sexual maturity. Thus changes in  $p$  will reflect changes in the predation rate of DHs on intermediate hosts.

Consider for example a transition from an ancestral SLC based in a snail host, to a CLC comprising the snail plus a snail predator. Imagine that infected snails are eaten by a potential DH with some probability  $p$ , and that if eaten, parasites are able to exploit the new host with some level of efficiency  $e$ . Conversely, infected snails escape predation with probability  $1-p$ , allowing the infection of further intermediate hosts with an efficiency  $1-e$ . Thus, there are two exclusive routes of transmission, via definitive (CLC) or intermediate (SLC) hosts. The efficiency parameter  $e$  represents antagonistic selection between SLC and CLC specialism, so that  $e = 1$  equals perfect adaptation to a CLC and zero adaptation to an SLC, and  $e = 0$  indicates the inverse.

Combining the new parameters  $p$  and  $e$  with the previous model of hermaphroditic reproduction (eqn 1), we find

$$w = pe [pm_d w_c + (1 - pm_d)w_s] + (1 - p)(1 - e) \times \{(1 - p)m_i w_c + [1 - (1 - p)m_i]w_s\}. \quad (2)$$

Here the first term represents the fitness via the CLC route of transmission (governed by  $p$  and  $e$ ), whereas the second term represents the fitness via the SLC route of transmission (governed by  $1-p$  and  $1-e$ ). The first square bracket captures the fitness return of a worm that achieves reproductive maturity within a DH (with probability  $pe$ ). The term  $pm_d w_c$  represents the mating probability of a worm in the DH ( $pm_d$ ), multiplied by the fitness of out-bred offspring ( $w_c$ ). The mating probability of a worm in the DH is here represented to be proportional to the probability of predation ( $p$ ), so that the higher the predation rate on infected intermediate hosts, the higher the chances that a worm in a DH will find a mate. The parameter  $m_d$  represents the mating coefficient within the DH, linking  $p$  to the mating probability of a worm in the DH ( $pm_d$ ). Finally, the term  $(1-pm_d)w_s$  represents the fitness of a worm that fails to mate in the DH, governed by the self-fertilizing fitness parameter,  $w_s$ .

The second term in curly brackets captures the fitness return of a worm that achieves reproductive maturity within an intermediate host [with probability  $(1-p)(1-e)$ ]. Mirroring the logic of the first square bracket  $(1-p)m_i$  represents the mating probability of a worm in an intermediate host, dependent on the probability that an infected parasite is not preyed-upon before the maturity of the parasite ( $1-p$ ), and the mating coefficient within an intermediate host,  $m_i$ .

Clearly the ancestral state is represented by  $p = e = 0$ , i.e. eqn 1. Note that the probability of mating is now governed by two life-cycle-specific mating parameters ( $m_d$  and  $m_i$ ), modified by the probability of parasite maturity in a given host class. Specifically,  $m_d$  and  $m_i$  can be viewed as aggregation coefficients, the higher the value of  $m$ , the faster the mating probability rises with the probability of maturity in a given host class ( $p$  or  $1-p$ ) in the relevant transmission route. A simple consideration of population densities between predators and preys gives the reasonable expectation that  $m_d$  will be larger than  $m_i$ , as predators are typically more scarce than the prey, and so are able to act as parasite concentrators (see prior section). For example, consider a value of  $p = 0.5$ . This means that parasites are equally likely to reach reproductive age in either class of host. However, should DHs be numerically more scarce than intermediate hosts, then the mature parasites in DHs will be more concentrated than the mature parasites in intermediate hosts. Nonetheless, generalist predators may outnumber specialist prey, so a range of conditions for  $m_d$  and  $m_i$ , are considered below.

A number of scenarios are presented in Figs 1 and 2 based on the simple model expressed in eqn 2. Figure 1 illustrates the fitness landscape for different combinations of  $p$  and  $e$ , given identical aggregation parameters for both the SLC and CLC pathways ( $m_d = m_i$ ). In Fig. 1a,b ( $w_s \leq w_c$ ), we see that the pure SLC and CLC strategies emerge as separate and strongly isolated adaptive peaks. The low fitness of ‘mixed’ strategies in Fig. 1a,b is guaranteed by the antagonistic specialism of the parameter  $e$ .

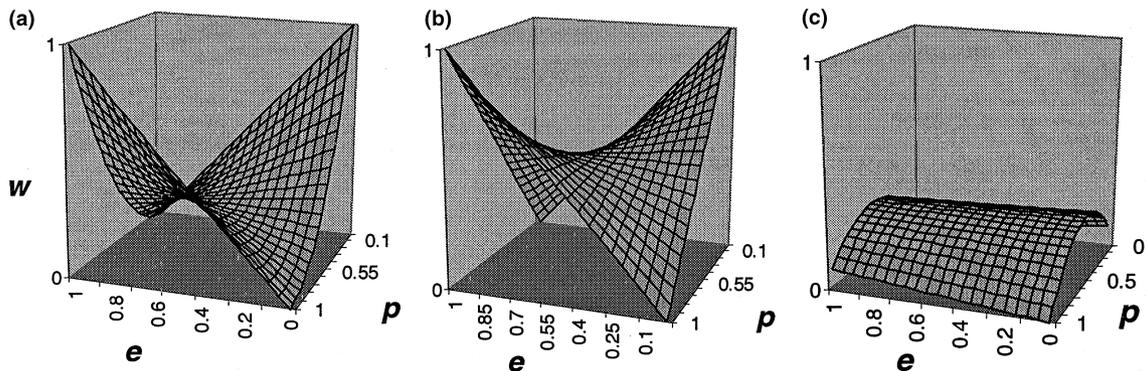
The potential for an evolutionary transition from an ancestral SLC specialization to a derived CLC specialization can be described by first finding a minimal value of DH predation ( $p$ ) that allows the invasion of increases in DH exploitation efficiency ( $e$ ), then inspecting the fate of further increases in  $p$ , given non-zero values of  $e$ . More formally, we find the differential of  $w$  (eqn 2) with respect to  $e$ , set to zero and solve for  $p$ . This step finds a contingent threshold of  $p$  ( $p^*$ ), above which selection favours increases in the CLC specialization parameter,  $e$ .  $p^*$  is defined implicitly by eqn 3:

$$\left. \frac{dw}{de} \right|_{p=p^*} = 0 \quad (3)$$

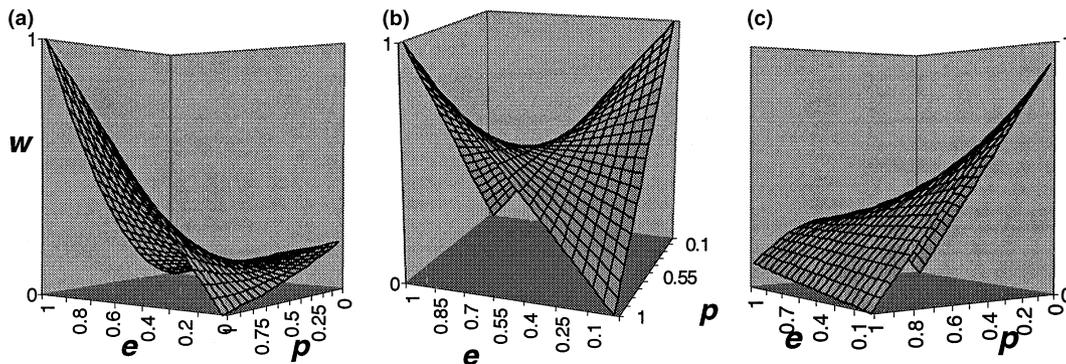
Which by rearrangement (taking the negative root for  $p^*$ ), yields eqn 4:

$$p^* = \frac{w_s - w_s m_i + w_c m_i}{(m_d - m_i)(w_s - w_c)} - \frac{\sqrt{(w_s m_i - w_s - w_c m_i)(w_s m_d - w_s - w_c m_d)}}{(m_d - m_i)(w_s - w_c)} \quad (4)$$

Experiencing  $p$  in excess of  $p^*$  is not sufficient to guarantee that selection would favour a transmission to a pure CLC strategy, as given even a transition to  $e = 1$ , further increases in  $p$  may not be favoured (see for



**Fig. 1** Parasite fitness as a function of the efficiency of exploitation of a definitive host (DH) ( $e$ ) and the probability of predation by a DH ( $p$ ), given equal mating coefficients,  $m_d = m_i = 1$ . (a) Cross-fertilization advantageous  $w_c = 1$ ,  $w_s = 0.1$ . (b) Cross-fertilization neutral  $w_c = 1$ ,  $w_s = 1$ . (c) Self-fertilization advantageous  $w_c = 0.1$ ,  $w_s = 1$ .



**Fig. 2** Parasite fitness as a function of the efficiency of exploitation of a definitive host (DH) ( $e$ ) and the probability of predation by a DH ( $p$ ), given unequal mating coefficients,  $m_d = 1$ ,  $m_i = 0.1$ . (a) Cross-fertilization advantageous  $w_c = 1$ ,  $w_s = 0.1$ . (b) Cross-fertilization neutral  $w_c = 1$ ,  $w_s = 1$ . (c) Self-fertilization advantageous  $w_c = 0.1$ ,  $w_s = 1$ .

example Fig. 1c, where  $P = e = 1$  carries a low fitness pay-off). To address this second transition issue, we find the differential of  $w$  (eqn 2) with respect to  $p$ , as presented in eqn 5:

$$\frac{dw}{dp} = 2\{e[p(m_d - m_i)(w_c w_s) + w_s + w_c m_i - w_s m_i] - m_i[w_c + w_c p + w_s - w_s p]\} - w_s, \quad (5)$$

and inspect the range of  $p$  over which this differential is positive for non-zero values of  $e$ . Combining these two analytical steps, we see that  $p^* = 0.5$  and  $dw/dp > 0$  for all  $p$  when  $e = 1$  (Fig. 1a,b). In other words, a contingent DH predation rate of greater than 50% would allow selection to favour specialization on CLC.

When self-fertilization is more profitable than cross-fertilization ( $w_c < w_s$ ; Fig. 1c), a 'mixed strategy' of CLC and SLC (i.e. intermediate  $p$ ) becomes optimal, irrespective of the ancestral point of specialization,  $e$ . Given a contingent value of DH predation of 0.5, increased  $e$  can invade an ancestral SLC population (i.e.  $p^* = 0.5$ ). However,  $dw/dp$  becomes negative as  $p$  approaches 1, hence exclusive CLC specialization is not a stable strategy. This can be understood as a selection for life cycle diversifica-

tion, to escape the likelihood of costly cross-fertilization. In theory, this provides an 'adaptive bridge' between different levels of  $e$  (hence a way to cross the adaptive valley in Fig. 1a,b, subject to environmental changes favouring self-fertilization). In practice, it is more plausible that selection would enforce asexuality in the ancestral host(s), thus stopping the selective pressure favouring host diversification as a mate-avoidance strategy.

Figure 2 illustrates the fitness landscape on  $p$  and  $e$ , given elevated aggregation in DHs ( $m_i < m_d$ ). When cross-fertilization and self-fertilization fitness are equal, changing the aggregation parameter has no effect on the fitness landscape (comparison of Figs 1b and 2b). In Fig. 2b, cross-fertilization is largely curtailed in the SLC, because of the low aggregation in this life cycle. Nonetheless, the adaptive landscape remains unchanged from Fig. 1b, as the fitness of cross-fertilization and self-fertilization offspring is defined to be identical. In contrast, when raised aggregation in DHs is coupled with differences in cross- vs. self-fertilization fitnesses, the adaptive landscape changes (comparison of Figs 1 and 2).

Figure 2c illustrates that given preferential aggregation in DHs, the 'adaptive bridge' between SLC and CLC

specialism in self-fertilization-friendly environments (see Fig. 1c) disappears, in favour of a single SLC adaptive peak. This shift to a single SLC optimum is because of single hosts becoming a relative refuge from costly aggregations, allowing a specialism to develop on single-host exploitation. For the parameters in Fig. 2c,  $p^* = 0.85$ , that is if 85% of parasites in the intermediate host are consumed by the potential DH before reaching maturity, then specialization on DH exploitation (i.e. raising  $e$ ) is favoured. However, even if  $e$  reaches 1, selection on host-manipulation would still favour the avoidance of DH, as  $dw/dp$  is negative when  $e = p = 1$ , hence CLC is not a stable strategy.

In contrast, in cross-fertilization-friendly environments, the same preferential aggregation in DHs leads to an increase in the CLC adaptive peak, and a concurrent drop in the adaptive barrier between the SLC and the CLC peaks (contrast Figs 1a and 2a). For the particular values in Fig. 2a,  $p^* = 0.30$ , hence a contingent rate of DH predation of as low as 30% would be enough to favour a shift in  $e$  towards the CLC optimum (i.e. would favour specialization on a CLC). This in turn would favour further increases in  $p$ , as  $dw/dp > 0$  for all  $p$  when  $e = 1$ . In other words, parasite-selection would favour parasite-induced host-manipulation to promote predation by the new DH, leading to a gradual climb up the CLC adaptive peak, towards the summit, where  $w(P = 1, e = 1) = 1$ .

## Discussion

Our hypothesis does not pretend to explain the evolution of all CLCs involving trophic transmission. For instance, the self-fertilizer cestode *Taenia solium* is a good counter-example to our suggestion, because this parasite obviously does not have a CLC in order to practise cross-fertilization. Nevertheless, we think that our hypothesis is likely to be relevant to explain the evolution of CLCs in other situations. For instance, it is common (e.g. in trematodes or cestodes) to find systems in which the parasite prevalence is extremely low within the first intermediate host population whereas it is almost 100% among DH. These situations are in accordance with the ideas that (i) opportunities for cross-fertilization would be rare without a concentrating host and (ii) predators indeed concentrate individual parasites. For most parasites with trophic transmission, the adult reproductive phase is reached only in the digestive tract of the DH and cross-fertilization only occurs inside this host. When reproduction occurs in other hosts, it is asexual. This is also in agreement with our hypothesis. It is also interesting to remark that adult flukes usually occupy restricted habitats in the digestive tracts of predators, a behaviour hypothesized to increase the probability of intraspecific contact and hence mate finding (Rohde, 1977). Reaching a restricted microhabitat in the DH may be viewed as the final task in the concentrating process needed before genetic exchange becomes possible,

i.e. after having reached a concentrating host, parasites reach a mating place.

Our model showed how a transition from a SLC to a two-host life cycle can be favoured by parasite-selection. Once a two-host life cycle is established, selection can *a priori* favour the addition of other intermediate hosts especially when this increases the efficiency of the concentration process. This could for instance be achieved when the added host is a more common prey for the target predator than the first host. A study by Robert *et al.* (1988) on two sympatric marine cestodes (*Bothriocephalus barbatus* and *B. gregarius*, Renaud *et al.*, 1983) seems to illustrate this statement. The larval stages of the two species live in a planktonic copepod. *Bothriocephalus barbatus* has a two-host life cycle and finishes this life cycle when the copepod is ingested by the final host, a flatfish. Although *B. gregarius* can be transmitted in the same way, it usually goes through a gobiid fish which feeds on copepods. Because gobiid fishes are a more common prey for flatfish than copepods, the addition of a paratenic host increases the efficiency of the concentration process. In the field, *B. gregarius* is much more prevalent and abundant than *B. barbatus* among flatfish.

Assuming that CLCs are parasitic adaptations for mate finding, several predictions could be tested in future studies. For instance, we expect the life expectancy of parasites inside DHs to be adjusted to the probability of finding a conspecific. This probability depends *a priori* on at least three parameters: the level of preference of the predator for the prey, the prevalence of the parasite within the prey population and whether or not the parasite is able to alter the phenotype of the prey in order to increase its susceptibility to the predator. For instance, we can predict that a manipulative parasite having a high prevalence within the prey population should also be short-lived within the predator as its probability of mate finding shortly after its arrival in the predator is high. Conversely, a rare parasite exploiting a relatively uncommon prey of the target predator (and which does not manipulate the prey to increase its predation risk) should live longer within the predator as more time is needed before the concentration process permits mate finding.

Assuming that CLCs evolve because of mate finding problems, we also expect that first intermediate hosts of CLC parasites rarely harbour infrapopulations of genetically distinct parasite individuals. As a corollary, SLC parasites practising cross-fertilization should exploit host species which are large/rich enough to at least temporarily support an infrapopulation of the parasite (i.e. opportunity for cross-fertilization exists), or evolved sophisticated mechanisms of mate finding.

According to our hypothesis, we might be tempted to predict that hermaphroditic parasites should have less tendency to have CLCs than obligately outcrossing dioecious parasites. Indeed, if SLCs are associated with low mate finding probabilities, hermaphroditism provides a reproductive insurance. Conversely, if CLCs concen-

trate parasites, CLC parasites may be expected to become dioecious because of an increased certainty of mate finding. However, the reality may be more complex. Indeed, not all parasites with SLCs have mate finding problems, and so these species may have both SLCs and dioecy. Similarly, SLC parasites encountering mate finding problems may invest in both hermaphroditism and CLCs as parallel adaptations. Consequently, predictions on the association between dioecy and CLCs remain delicate in the absence of additional information on mating probabilities, both current and historic.

Finally, we do not expect an evolutionary trend in adding or losing hosts. The number of hosts should be adjusted to the efficiency of the concentration process. This prediction could be tested for instance by analysing the characteristics of the infestation (i.e. prevalence and intensity) on the different hosts involved in more or less CLCs.

The creation of an analytic framework is useful in highlighting the relative roles of historical contingency and parasite adaptation in a shift from SLC to CLC. The model highlights that some level of predation by a DH is essential to begin a transition from SLC to CLC. This 'contingent' level of predation ( $p^*$ ) is made lower (i.e. the transition is made easier) when cross-fertilization is beneficial, and DHs act as parasite aggregators (i.e. Fig. 2a), in keeping with the mate-finding hypothesis. In addition, the model highlights that parasite-induced host-manipulation may play an important role in a transition from SLC to CLC, as it may act to adaptively increase  $p$ , once  $e$  has increased in response to  $p^*$ . In other words, host manipulation can be viewed not just as an adaptation simply to *complete* a parasite life cycle (for an introduction to the host-manipulation hypothesis, see Poulin, 1998 and references therein), but on occasion (i.e. historically) an adaptation to *extend* a parasite life cycle, driving the evolution of CLCs.

## Acknowledgments

We thank two anonymous referees for constructive comments on an earlier manuscript.

## References

- Anderson, R.C. 1984. The origins of zooparasitic nematodes. *Can. J. Zool.* **62**: 317–328.
- Combes, C. 1991. Evolution of parasite life cycles. In: *Parasite–Host Associations: Coexistence or Conflict?* (C. A. Toft, A. Aeschlimann & L. Bolis, eds), pp. 62–82. Oxford University Press, Oxford.
- Combes, C. 1995. *Interactions Durables: Ecologie et Evolution Du Parasitisme*. Masson, Paris.
- Conway Morris, S. 1981. Parasites and the fossil record. *Parasitology* **82**: 489–509.
- Dobson, A. P. 1989. The population biology of parasitic helminths in animal populations. In: *Applied Mathematical Ecology* (S. A. Levin, T. G. Hallam & L. J. Gross, eds), pp. 145–175. Springer-Verlag, London.
- Dobson, A. P. & Merenlender, A. 1991. Coevolution of macro-parasites and their hosts. In: *Parasite–Host Associations, Coexistence or Conflict?* (C. A. Toft, A. E. Aeschlimann & L. Bolis, eds), pp. 83–101. Oxford University Press, Oxford.
- Esch, G. W. & Fernandez, J. C. 1993. *A Functional Biology of Parasitism: Ecological and Evolutionary Implications*. Chapman & Hall, London.
- Ewald, P. W. 1995. The evolution of virulence: a unifying link between parasitology and ecology. *J. Parasitol.* **81**: 659–669.
- Lafferty, K. D. 1992. Foraging on prey that are modified by parasites. *Am. Nat.* **140**: 854–867.
- Lafferty, K. D. 1999. The evolution of trophic transmission. *Parasitol. Today* **15**: 111–115.
- Lythgoe, K. A. 2000. The coevolution of parasites with host-acquired immunity and the evolution of sex. *Evolution* **54**: 1142–1156.
- Mackiewicz, J. S. 1988. Cestode transmission patterns. *J. Parasitol.* **74**: 60–71.
- Michaud, M., Thomas, F., Becheikh, S., Raibaut, A., Shykoff, J. A. & Renaud, F. 1999. Stage-dependent decisions in a parasitic copepod practising environmental sex determination. *Mar. Ecol. Progr. Series* **185**: 189–193.
- Morand, S. 1996. Biodiversity of parasites in relation to their life cycles. In: *Aspects of the Genesis and Maintenance of Biological Diversity* (M. E. Hochberg, J. Clobert & R. Barbault, eds), pp. 243–260. Oxford University Press, Oxford.
- Morand, S., Robert, F. & Connors, V. A. 1995. Complexity in parasite life cycles: population biology of cestodes in fish. *J. Anim. Ecol.* **64**: 256–264.
- Nollen, P. M. 1993. *Echinostoma trivolis*: mating behaviour of adults raised in hamsters. *Parasitol. Res.* **79**: 130–132.
- Poulin, R. 1998. *Evolutionary Ecology of Parasites: From Individuals to Communities*. Chapman & Hall, London.
- Renaud, F., Gabrion, C. & Pasteur, N. 1983. Le complexe '*Bothriocephalus scorpii*' (Mueller, 1776). Différenciation par électrophorèse enzymatique des espèces parasites du Turbot (*Psetta maxima*) et de la Barbuie (*Scophthalmus rhombus*). *C. R. Acad. Sci.* **296**: 127–129.
- Robert, F., Renaud, F., Mathieu, E. & Gabrion, C. 1988. Importance of the paratenic host in the biology of *Bothriocephalus gregarius* (Cestoda, Pseudophyllidea), a parasite of the turbot. *Int. J. Parasitol.* **18**: 611–621.
- Rohde, K. 1977. A non-competitive mechanism responsible for restricting niches. *Zool. Anzeiger* **199**: 164–172.
- Rohde, K. 1994. The origins of parasitism in the platyhelminths. *Int. J. Parasitol.* **24**: 1099–1115.
- Schmidt-Rhaesa, A. 1997. *Nematomorpha*. In: *Süßwasserfauna Mitteleuropas 4/4* (J. Schwoerbel & P. Zwick, eds), 124 pp. Gustav Fischer-Verlag, Stuttgart.
- Smith-Trail, D. R. 1980. Behavioural interactions between parasites and hosts: host suicide and the evolution of complex life cycles. *Am. Nat.* **116**: 77–91.
- Trouve, S., Jourdane, J., Renaud, F., Durand, P. & Morand, S. 1999. Adaptive sex allocation in a simultaneous hermaphrodite. *Evolution* **53**: 1599–1604.
- Wedekind, C., Strahm, D. & Schärer, L. 1998. Evidence for strategic egg production in a hermaphroditic cestode. *Parasitology* **117**: 373–382.

Received 23 May 2001; accepted 25 June 2001