Evolutionary Biology of Host-Parasite Relashionships: Theory Meets Reality
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# Adaptive diversity, specialisation, habitat preference and parasites

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## 1. INTRODUCTION

The evolution and maintenance of adaptive diversity has interested many investigators since the early studies of Levene (1953) and Dempster (1955). These works suggested that adaptive polymorphism should only be maintained in populations regulated within the resource involved in the ecological variation (soft selection). The conditions required are very stringent unless individuals display some kind of habitat selection (Maynard-Smith 1966; Maynard-Smith and Hoekstra 1980; Hoekstra *et al.* 1985; Hedrick 1990a,b; De Meeûs et al. 1993). Such theoretical approaches quickly proved to be relevant both for the study of habitat specialisation as for the maintenance of adaptive diversity and sympatric speciation (Maynard-Smith 1966; Rice 1987; de Meeûs et al. 1993; Erlandsson et al. 1999). Within such frameworks it was suggested (Renaud et al. 1996; De Meeûs et al. 1998) that parasitic organisms represent ideal illustrations of such processes. In this paper, I will briefly revisit the theoretical basis on the maintenance of adaptive diversity and the evolution of resource preference through populations genetics based models. I will then try to apply the main conclusions of these theoretical studies to biological examples taken from the parasitic world. I will then try to discuss, by developing a new family of models, what can be changed when considering complex life cycles as those often encountered in parasites.

## 2. BASIC MODELS

Assume an heterogeneous environment composed of two different resources (namely *1* and *2*) which respectively occupy $c$ and 1-$c$ of the total environment. These resources are exploited by organisms that differ in their ability to use one or the other of these available resources. For the sake of simplicity I will only consider the case in which two morphs (genotypes, species) are confronted. Let these morphs be $A$ and $a$. At any time, the frequency of these morphs in the population is $p$ and 1-$p$ for $A$ and $a$ respectively. They colonise, exploit these resources and then produce the next generation (no overlap). Such a pattern can correspond to organisms with a dispersal phase and a colonisation phase such as parasites, many marine organisms and many plants. The whole population will be considered at its carrying capacity. The constant size (say $N$) at which it is maintained allows a simpler tractability of the equations (population genetics model). Population size is supposed to be big enough to prevent drift. This supposes that regulation occurs (see below). Individuals freely colonise resources *1* and *2* with probabilities *c* and 1-*c* respectively. There they are submitted to a viability selection as described in table 1.

Table 1
Survival probabilities of the different morphs in the different available resources.

| | Resources | |
|---|---|---|
| | *1* | *2* |
| Survival of *A* | $w_{1A}$ | $w_{2A}$ |
| Survival of *a* | $w_{1a}$ | $w_{2a}$ |

Thus, the within resource relative frequencies of *A* and *a* are:

$cNpw_{1A}$ and $(1-c)Npw_{2A}$ for *A* in resource *1* and *2* respectively, and

$cN(1-p)w_{1a}$ and $(1-c)N(1-p)w_{2a}$ for *a* in resource *1* and *2* respectively.

If the regulation occurs within the resource (soft selection) then resource *1* contributes to a proportion *c* and resource *2* to a proportion 1-*c* of the pool of individuals getting out from these resources. The frequencies of *A* at the next generation becomes:

$$p' = c\frac{cNpw_{1A}}{cNpw_{1A} + cN(1-p)w_{1a}} + (1-c)\frac{(1-c)Npw_{2A}}{(1-c)Npw_{2A} + (1-c)Npw_{2a}}$$

which reduces to

$$p' = p\left[c\frac{w_{1A}}{pw_{1A} + (1-p)w_{1a}} + (1-c)\frac{w_{2A}}{pw_{2A} + (1-p)w_{2a}}\right]$$

If the regulation occurs outside the resources (hard selection), then

$$p' = \frac{cNpw_{1A} + (1-c)Npw_{2A}}{cNpw_{1A} + (1-c)Npw_{2A} + c(1-p)Nw_{1a} + (1-c)(1-p)Nw_{2a}}$$

which reduces to

$$p' = p\frac{cw_{1A} + (1-c)w_{2A}}{c\left[pw_{1A} + (1-p)w_{1a}\right] + (1-c)\left[pw_{2A} + (1-p)w_{2a}\right]}$$

Note that the within resource regulation mode corresponds to a very strong competition between individuals, contrarily to the outside resource regulation where competition for the resource is totally absent. These assumptions respectively correspond to Levene's (1953) and Dempster's (1955) models (or to soft and hard selection models, Wallace 1975). In each case the evolution of frequencies is described by the sign of:

$\Delta p = p' - p$

$\Delta p$ has the same sign as $\Delta p'$:

$$\Delta p' = p(w_{1a} - w_{1A})(w_{2a} - w_{2A}) + w_{1a} w_{2a} \left[ c \frac{w_{1A}}{w_{1a}} + (1-c) \frac{w_{2A}}{w_{2a}} - 1 \right] \quad (1)$$

for the within resource regulation case and

$$\Delta p' = c w_{1A} + (1-c) w_{2A} - \left[ c w_{1a} + (1-c) w_{2a} \right] \quad (2)$$

for the outside regulation case.

Polymorphism will be maintained if $p$ increases when close to 0 and decreases when close to 1. It is easily seen that in the outside resource regulation case this is never possible and that the morph displaying the bigger arithmetic mean fitness ($c w_{1i} + (1-c) w_{2i}$) will dominate the population. For the within resource regulation we obtain:

$$c \frac{w_{1A}}{w_{1a}} + (1-c) \frac{w_{2A}}{w_{2a}} > 1 \text{ (}A\text{ protected)}$$

and

$$c \frac{w_{1a}}{w_{1A}} + (1-c) \frac{w_{2a}}{w_{2A}} > 1 \text{ (}a\text{ protected)}$$

in which case the population converges to a unique equilibrium:

$$\hat{p} = \frac{c w_{1A} w_{2a} + (1-c) w_{2A} w_{1a} - w_{1a} w_{2a}}{(w_{1A} - w_{1a})(w_{2a} - w_{2A})}$$

A rather classical way to present this result is to transform these expressions into the harmonic and arithmetic means of relative fitnesses (e.g. relative to *A*) which gives:

$$\frac{1}{c\frac{1}{\frac{w_{1a}}{w_{1A}}}+(1-c)\frac{1}{\frac{w_{2a}}{w_{2A}}}} < 1 < c\frac{w_{1a}}{w_{1A}}+(1-c)\frac{w_{2a}}{w_{2A}} \tag{3}$$

or $HAR(a/A)<1<ARI(a/A)$ (e.g. Levene 1953).

This is a simple way to see that polymorphism is indeed possible since the harmonic means are always lower than the corresponding arithmetic means (e.g. Sokal and Rohlf 1981).

This double inequality is fulfilled in only very stringent conditions, i.e. when the selective advantages are large and divergent for *A* and *a*, or when these selective advantages are nicely adjusted to niche size (Maynard-Smith 1966). This is better seen in the simplified case where $w_{1A}$=1, $w_{2A}$=1-*s*, $w_{1a}$= 1-(1-*x*)*s* and $w_{2a}$=1-*xs*, with (*x*, *s*) in [0..1] (*x* representing the similarity between the two morphs). With these new assumptions the condition for protected polymorphism becomes:

$x\neq 1$ ($A\neq a$) and $\frac{1-s(1-x)}{2-s} < c < \frac{1}{2-s}$

It can be seen from Figure 1 that the adaptive diversity is stable only for strong selective costs (*s*) and low similarities between *A* and *a* (*x*), or *c* close to 1/2.
This is probably why such models often use either strong dissimilarities between the two competitors (e.g. Kisdi and Geritz 1999) or *c*=1/2 (e.g. Kawecki 1996) for sympatric speciation to occur.

For the outside resource regulation mode it can be seen from equation (2) that the sign of $\Delta p$ is independent of morph frequencies (no stable equilibrium). The morph that will dominate is the one displaying the highest arithmetic mean fitness. For the special case described above (with parameters *x* and *s*) the sign of $\Delta p$ is the same as:

$$\Delta p' = -s(1-x)(1-2c)$$

Here it is easily seen that, for *s*>0 (selection exists) and *x*<1 (*A* and *a* are different), the morph surviving better in the most frequent resource invades the population.

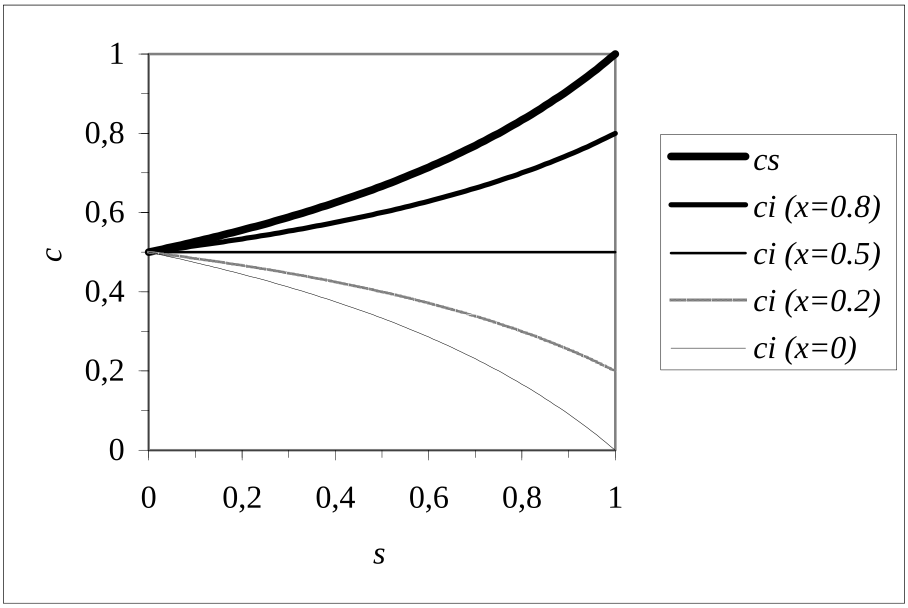

Figure 1: Conditions on *s* (survival cost in resource *2*) and *c* (frequency of resource *2*) for the stable maintenance of morphs *A* and *a* and for different values of *x* (adaptive similarity between the two morphs). Polymorphism is maintained between *cs* and *ci*. Above *cs* corresponds to the domination of morph *A* and below *ci* corresponds to the domination of *a*.

## 3. RESOURCE PREFERENCE

### 3.1. Description and consequences of resource preference

Resource preference changes the outcomes described above (e.g. De Meeus et al. 1993). This habitat preference (symbolised by *B* in the foffowing) can be modelled as a Markovian process of trials and error that fits what can be expected for parasitic or marine organisms with planktonic larvae (Doyle, 1975). If *i* is the maximum number of trials allowed and *d* is the survival probability while dispersing (choice is costly) then the probability to settle in the different resources are:

$$P_{B1} = \frac{cd\left[1-\left((1-c)d\right)^i\right]}{1-(1-c)d} \approx \frac{cd}{1-(1-c)d} \text{ ($i$ high) in resource $1$ if it is preferred,}$$

$$P_{B2} = \left((1-c)d\right)^i \approx 0 \text{ ($i$ high) in resource $2$ if it is not preferred,}$$

$$P_{B1}' = \left(cd\right)^i \approx 0 \text{ ($i$ high) in resource $1$ if it is not preferred,}$$

$P_{B2}{}' = \frac{(1-c)d\left[1-(cd)^i\right]}{1-cd} \approx \frac{(1-c)d}{1-cd}$ (*i* high) in resource *2* if it is preferred.

It is easy to see that in the case where say *A* prefers *1* and *a* prefers *2* then polymorphism is always maintained in the within resource regulation case since the population reaches the stable equilibrium $\hat{p} = c$ in one generation. For the outside regulation case, the sign of $\Delta p$ is the same as:

$$\Delta p' = c(1-cd)w_{1A} - (1-c)(1-(1-c)d)w_{2a}$$

If preference is not costly ($d \approx 1$) then the morph displaying the highest survival in the resource it settles in invades the population. If preference is highly costly ($d \approx 0$) then survivals and resource size are equally relevant, and if the survivals in the preferred resource are equal ($w_{1A} \approx w_{2a}$) then the morph choosing the most frequent resource will spread (De Meeûs et al. 1993). Habitat preference does not enhance adaptive diversity in this regulation mode.

All this however says nothing about the probability of evolution of resource preference.

## 3.2. Evolution of resource preference

Let us now consider that preference can evolve independently from what determines adaptation (*A*/*a*). Let *B* be the determinant of preference and *b* the determinant of indifference with frequencies *q* and (1-*q*) respectively. We have now four different morphs, *AB*, *Ab*, *aB* and *ab*, with respective frequencies *pq*, *p*(1-*q*), (1-*p*)*q* and (1-*p*)(1-*q*) for a complete independence between adaptation and preference. Let phenotype *AB* show a preference for resource *1* and *aB* for resource *2*. Morphs *Ab* and *ab* do not display any preference (probabilities *cd* and (1-*c*)*d* to settle in resources *1* and *2* respectively).

First I will consider the case of no initial polymorphism (*A* fixed).

In the next generation the frequency of the choosy allele will be:

$$q' = c\frac{\frac{cd}{1-(1-c)d}qw_{1A}}{\frac{cd}{1-(1-c)d}qw_{1A} + cd(1-q)w_{1A}} + (1-c)*0 = c\frac{q}{1-(1-c)d(1-q)}$$

in the within resource regulation mode, and

$$q' = \frac{\frac{cd}{1-(1-c)d}qw_{1A}}{\frac{cd}{1-(1-c)d}qw_{1A} + cd(1-q)w_{1A} + (1-c)d(1-q)w_{2A}}$$

in the outside regulation mode.

The evolution of resource preference is then described by:

$\Delta q' = -(1-c)(1-(1-q)d)$ which is always negative or null in the within regulation mode.

Refusing to settle in a competitor free niche is detrimental.

For the outside regulation mode, the condition for preference to invade is:

$$\frac{cd}{1-(1-c)d} > \frac{w_{2A}}{w_{1A}}$$

It can be seen from figure 2 that the evolution of resource preference requires either a strong selective advantage in the preferred resource or a moderate (*d* large) to a strong (*d* small) domination of the neglected resource. Remember that no competition exists within the resources. The advantage of preference is only a function of survivals in the preferred resource and while dispersing. If choosing is costly, it will be even more costly when choosing a frequently encountered resource. In any case, it is better that dispersal survival is high.

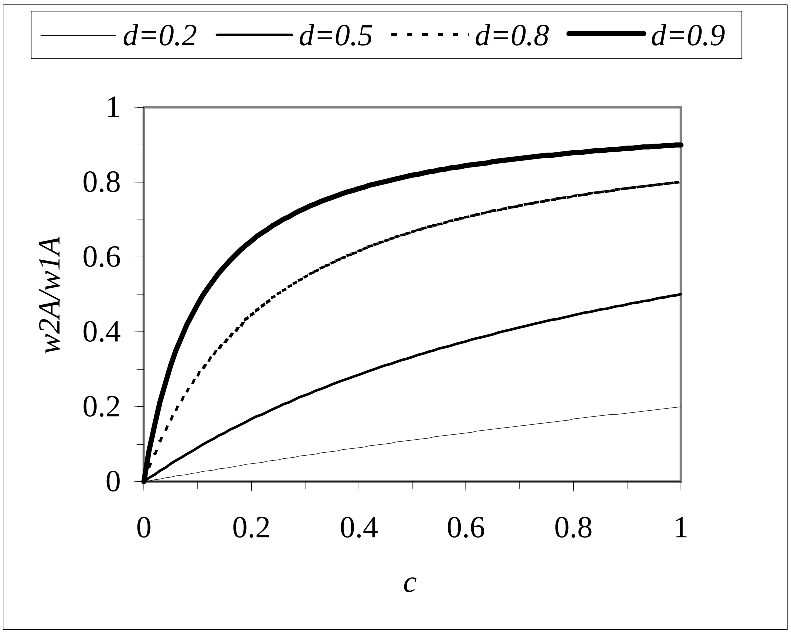

Figure 2: Upper limits for the ratio between survivals in the neglected to preferred resource ($w_{2A}/w_{1A}$) and $c$ (frequency of the preferred resource in the environment) for the evolution of resource preference in the outside resource regulation mode and for different values of $d$ (dispersal survival rate). The initial population is only composed of the *A* morph.

Consequently, resource preference can only evolve within the outside regulation mode, without no adaptive diversity maintenance. In the within resource regulation mode the evolution of resource preference critically depends on the presence of a previously installed adaptive diversity. We can set the best possible conditions for that polymorphism to be maintained, say in the $c$=1/2, $s$=1 and $x$=0. In that case we can compute that the equilibrium frequency of $A$ (without preference) is $\hat{p} = 1/2$ and that the condition on $d$ for $B$ to be protected when rare is:

$$d > \frac{2(1-s)}{2-s}$$

A glance at figure 3 reveals that in that very favourable case, the evolution of resource preference is not easy unless the selective costs within the wrong resource or dispersal survival are high.

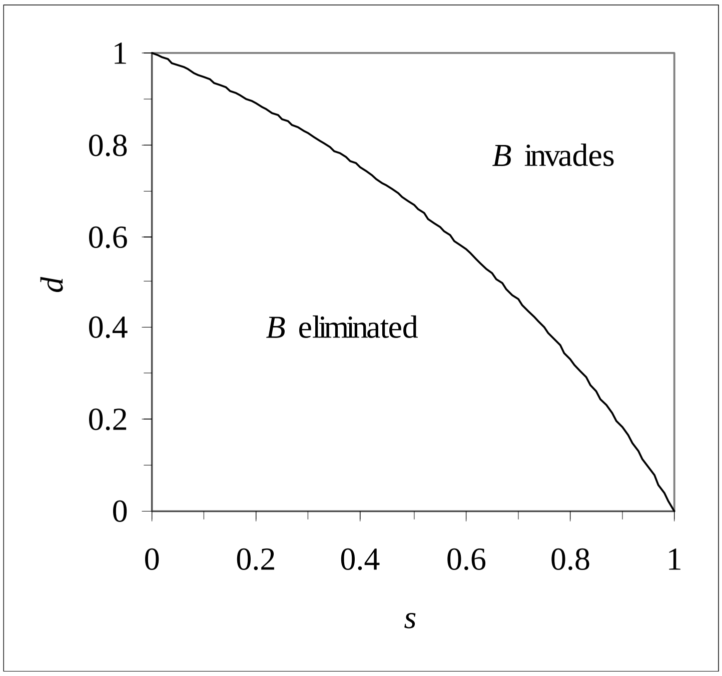

Figure 3: Conditions on $d$ (dispersal survival) and $s$ (selective costs of settling in the wrong resource) for the evolution of resource preference in the within resource regulation mode. The initial population is at adaptive equilibrium frequency of ½ for the $A$ morph in the case of $c$=1/2, $w_{1A}=W_{2a}$=1 and $w_{2A}=w_{1a}$=1-$s$ .

## 4. THE SOFT SELECTION/HARD SELECTION DILEMMA

Thus the maintenance of adaptive diversity is only possible in the within resource regulation case. The conditions required are stringent however, except when individuals display resource preference, in which case diversity is always maintained. However, resource preference can not evolve without a previous and strongly stable adaptive polymorphism unless regulation occurs outside the resources. In that case adaptive diversity is not maintained anymore. This is what I call the soft selection/hard selection dilemma.

Nevertheless, these results allow some predictions on what can be expected in natural populations.

## 5. PREDICTIONS FOR PARASITE POPULATIONS

As already suggested by Futuyma and Moreno (1988) the above models show clearly that soft selection (within resource regulation) favours generalists while hard selection (outside resource regulation) promotes resource specialisation. We thus expect organisms exploiting all the available resources to be regulated (at least partially) within their resource. Alternatively, organisms exploiting only one resource (hopefully the most favourable one out of several available) are expected to be mainly (if not totally) regulated outside their resource.

These perspectives can be applied to parasitic organisms. In that case the resource is the host and specialisation correspond to specificity. Parasites represent favourable case studies in this context. Indeed, the host comprises almost all the ecological requirements of the parasites (habitat-resource system of the parasite, Renaud 1992) (i.e. strong selective pressures) and parasites usually display strong dispersal potentials (high dispersal survival rates). Theoretically, such parasites should display a positive correlation between specificity and the time spent in or on the host. This should require a deeper comparative analysis but this seems roughly to be true if one compares the specificity displayed by monogeneans (always strong, Combes 1995) to ticks (highly variable, Hoogstraal and Aeschlimann 1982). But the main concern here is to relate some well documented examples to the above theoretical considerations.

### 5.1. Direct cycles: apparent within resource regulation cases

Direct cycle parasites appear to fit the within regulation case. Monogeneans and parasitic copepods are good examples. They indeed display strong degrees of specialisation (specificity) and diversification (at least monogeneans) (e.g. De Meeûs et al. 1998, Sasal et al. 1999). The exploitation of apparently all the available resources by specific but coexistent parasites suggests a within resource regulation mode with resource preference. Unfortunately, the postulated regulation mode is speculative in most cases. One parasitic copepods case may however provide a good illustration. The three congeneric copepods *Lepeophtheirus thompsoni*, *L. europaensis* and *L. pectoralis* are parasitic on three flat fishes in their area of distribution (from Northern Atlantic to Northern Mediterranean). *L. thompsoni* only exploits the turbot (*Psetta maxima*) in all the area, *L. europaensis* exploits the brill (*Scophthalmus rhombus*) in the Atlantic and both brill and flounder (*Platichthys flesus*) in the Mediterranean. *L. pectoralis* exploits the flounder in the Atlantic and is absent from the Mediterranean. It was shown that *L. europaensis* is perfectly able to colonise turbot and eliminate *L. thompsoni* but does not do so because of a strong preference of infective stages (De Meeûs et. al. 1995). Such a phenomenon can explain the stable coexistence of both parasites in the same environments where turbot and brill both live. However, this should require the existence of some within host regulation. Within host competition is suggested by the behaviour of *L. europaensis* with respect to the available hosts. During the Mediterranean colonisation, the flounder lost its original copepod *L. pectoralis.* This allowed the shifting of *L. europaensis* on that new host. Thus, in the Atlantic the presence of a competitor on flounder leads *L. europaensis* to settle only on brill (while being able to colonise all three hosts) but loses this feature when flounder loses *L. pectoralis* (De Meeûs et. al. 1995). This is exactly what is expected through a within host regulation mode and indeed, recent experiments (submitted manuscript) show evidence of a asymmetrical competition between the specialist and the generalist (*L. thompsoni* is indeed known to be much more specialised than *L. europaensis*, De Meeûs et al. 1995).

### 5.2 More than one generation within the host

Perhaps more spectacularly, direct cycle parasites that exhibit more than one generation on (in) a single individual host often display strong specialisation and diversification. This concerns all the terrestrial lice, skin acarians, pinworms etc… Their cycle corresponds to extensions of the Levene (1953) model found in the literature (e.g. Balkau and Feldman 1973, Christiansen 1975, Walsh 1984). Such models display two interesting properties: (i) the condition for adaptive polymorphism may be considerably widened and (ii) hard selection becomes a continuum from true hard selection, in the Levene/Dempster framework (total migration between patch), to true soft selection, for an absence of migration between patches (see De Meeûs and Renaud, 1996). In certain cases, niche diversification appears even easier than in the Levene (soft) model (Walsh, 1984). Such parasites appear to confirm these conclusions. The three human lice are each specialised to a particular kind of hair (Ludwig, 1982) as are the species of Myobiidae acarians (hair mites) (Fain, 1982) on their mammalian hosts. This appears to be the case for the other acarians of the genus *Demodex* on human hosts (Desch and Nutting 1972). The bird *Ibis falcinellus* harbours no less than seven species of mallophagous insects, each specialist of a particular kind of feather (Dogiel, 1964).

### 5.3. Apparent outside regulated parasites and indirect cycles

Many herbivorous insects appear as generalists throughout their geographical range but as local specialists (host shifts) (e.g. Fox and Morrow 1981, Traxler and Joern, 1999). This would illustrate the existence of a strong regulation outside the host-plants as suggested by the theoretical hard selection predictions. This is however difficult to demonstrate. Nevertheless, if we focus on indirect cycle parasites, more information can be gathered for that particular purpose. Indirect cycles may be interesting here because in one compartment competition may be such that the parasite population is mainly regulated there (within host regulation) and thus experiences no competition in the subsequent compartment. The two compartments should thus each display the characteristics of each regulation mode described above. For instance, trematodes are known to typically (i.e. most of the time) use three host compartments. Trematodes generally exhibit a much stronger specificity for the first intermediate host as compared to their definitive host (e.g. Combes 1995). For instance, three sibling species of the genus *Helicometra* found in the Etang de Thau (Southern France) are each specific to one mollusc species (Trochidae) as the first host but can all parasitise the intestine of *Gobius niger* (teleost fish). It is known that the energetic requirements of the parasite are greater in the first than in the definitive host where the trematode is often commensal (Bartoli, 1987). This may support the existence of a strong competition for the mollusc as far as the diversity maintenance is concerned, but the contrary as far as the evolution of specialisation is concerned. Here, we need further theoretical and biological information.

### 5.4. Indirect cycles in parasitic copepods

The Pennelidae copepod *Lernaeocera lusci* presents a two host life cycle, with the common sole as the first host where development and mating occur (fertilisation host) and a second host (gadid fishes) where fertilised females mature and produce their eggs (maturation host) (Tirard et al. 1994). *L. lusci* is able to exploit two different maturation hosts along its geographical range (Tirard et al. 1993). While it is found only on *Trsisopterus luscus* and never on *Merluccius merluccius* in the Atlantic, it is 8 times more abundant on the latter in the Mediterranean. *M. merlucius* seems to be a secondary host on which the parasite shifted in response to demographic changes of *T. minutus* in this area (Tirard et al. 1993). Interestingly, the parasite densities at which this copepod is found on the fertilisation host are more than ten times those found on the maturation hosts. This strongly suggests that regulation is fulfilled within the reproduction host and thus promotes the outside host regulation pattern found on the maturation hosts.

However, it may be interesting to investigate further the theoretical consequences of adding one more compartment in the Levene/Dempster models.

## 6. EXTENSION OF BASIC MODELS TO INDIRECT CYCLES

Let us then consider that regulation is fulfilled in one compartment $S$ (soft selection compartment) so that no competition exists in the second compartment $H$ (hard selection compartment). Both compartments consist of two resources each with frequencies $c_S$, $(1-c_S)$ and $c_H$, $(1-c_H)$ respectively, and survival rates as described in table 1, but with the corresponding subscripts ($S$ for soft and $H$ for hard).

The analytical steps are the same as in one compartment cases but require fastidious computations. I will not give the details and focus only on specific cases. In this new context the condition for diversity to be protected becomes:

$$HAR_S(a/A) < \frac{ARI_H(A)}{ARI_H(a)} < ARI_S(a/A) \qquad (4)$$

The ratio between the arithmetic means of the survivals in the hard regulated compartment must lie between the harmonic and the arithmetic means of relative survivals in the soft regulated one. This result is very similar to the result obtained for one compartment in the within (soft) resource regulation case shown in (3). If the centre of the double inequality (4) is more variable than the one found in (3), the width of conditions stays exactly the same.

From this it can be stated that the evolution and consequences of host preference are the same if considered as independent between the two compartments. We simply expect preference to evolve faster in the hard regulated compartment and that a previous stable diversity must establish itself before preference can appear. As soon as it appears, diversity becomes highly stable, each parasite being maintained in their respective host. In that case, preference should evolve for the same host (the most favourable one) in the hard regulated compartment. Trematodes seem to be good candidates for that pattern, but much more remains to be investigated before a definitive conclusion can be reached.

If host preference (e.g. the preference for the best host) is the same in the two compartments, things are altered. In the absence of an initial adaptive diversity (say *A* fixed) the condition for the propagation of host preference becomes.

$$\frac{c_S}{1-(1-c_s)d} > \left(1-(1-c_H)d\right)\left[1+\frac{(1-c_H)w_{2AH}}{c_H w_{1AH}}\right] \tag{5}$$

The best conditions are clearly for high values of $c_S$ and *d* and high degrees of specialisation on the preferred resource. To get clearer conditions on $c_H$ we need to study special situations.

For $d \approx 1$, condition (5) is always fulfilled for any $c_H<1$ if $w_{1AH}>w_{2AH}$ as in the pure outside resource regulation model.

For $w_{1HA}\approx 1$ and $w_{2HA}\approx 0$ (total specialisation of *A* on $1_H$), the condition (5) reduces to:

$$\frac{c_S}{1-(1-c_s)d} > 1-(1-c_H)d \Leftrightarrow c_H < \frac{\dfrac{c_S}{1-(1-c_S)d}-(1-d)}{d}$$

The Figure 4 leads to the same but much more pronounced conclusions than for the outside resource regulation model.

However, and in such conditions (*A* fixed), it is easy to see that indifference (phenotype *b*) is always protected. Indeed, *b* is always produced at the rate $1\text{-}c_s$ in compartment *S* at each generation, whatever its initial frequency is. This means that if both alleles are protected they will converge to a stable equilibrium.

Thus, to provide a good chance for an adaptive polymorphism to be protected by *B*, preference must previously reach high equilibrium frequencies. This will be possible for very high $c_s$, low $c_H$, high *d* and a strong specialisation as regard to hard regulated resources. In the hard regulated compartment, where no competition takes place, closely related parasites will probably tend to specialise on the same resource as previously suggested. However, in the absence of adaptive diversity, an incomplete specificity is expected in both compartments. Such patterns appear difficult to connect with the biological examples cited above. This furthermore requires highly constrained conditions to emerge

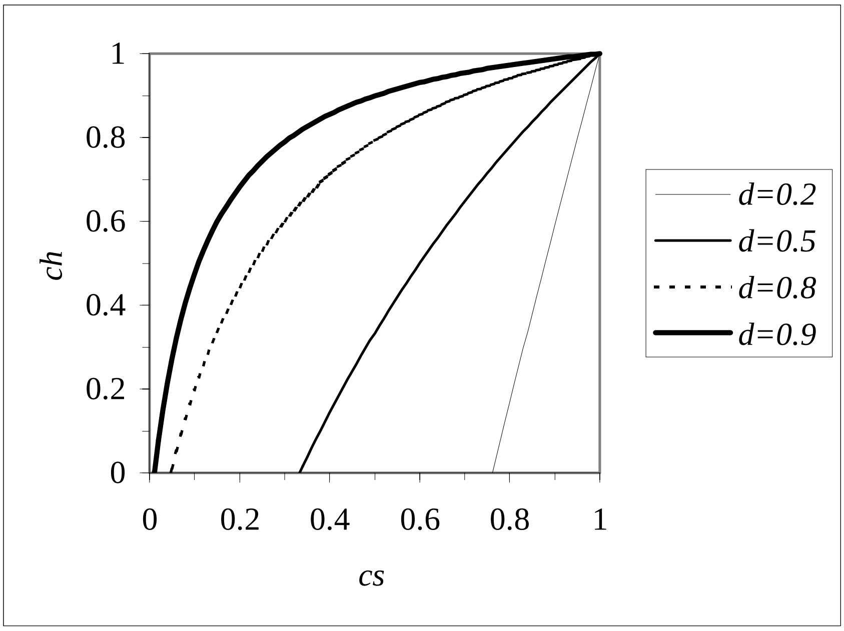

Figure 4: Upper limits for $c_H$ (frequency of the preferred niche in the hard regulated compartment) as a function of $c_s$ (frequency of the preferred niche in the soft regulated compartment) and for different dispersal survival rates (*d*).

## 7. CONCLUSIONS

To conclude, the complex life cycles do not appear to enhance significantly, within the theoretical framework envisaged here, either adaptive diversity or specificity. It only provides a rather convincing way to get soft and hard regulated patterns in the different compartments of the parasite cycle.

The patterns expected are thus simply those expected from pure models for the compartment of interest. There is one big difference however. If adaptive diversity is selectively maintained in the soft regulated compartment, the different morphs (phenotypes, species) will be lead to coexist also in the hard regulated one. This will provide quite different patterns with or without resource preference (Figure 5).

When no diversity exists and preference is present in both compartments, a critical validation of the above considerations will rely on the existence of empty though available hosts belonging to the hard regulated compartment. In theory these empty but less favourable hosts are expected to be frequently encountered by parasite infective stages, because of differences in host body and/or host population sizes.

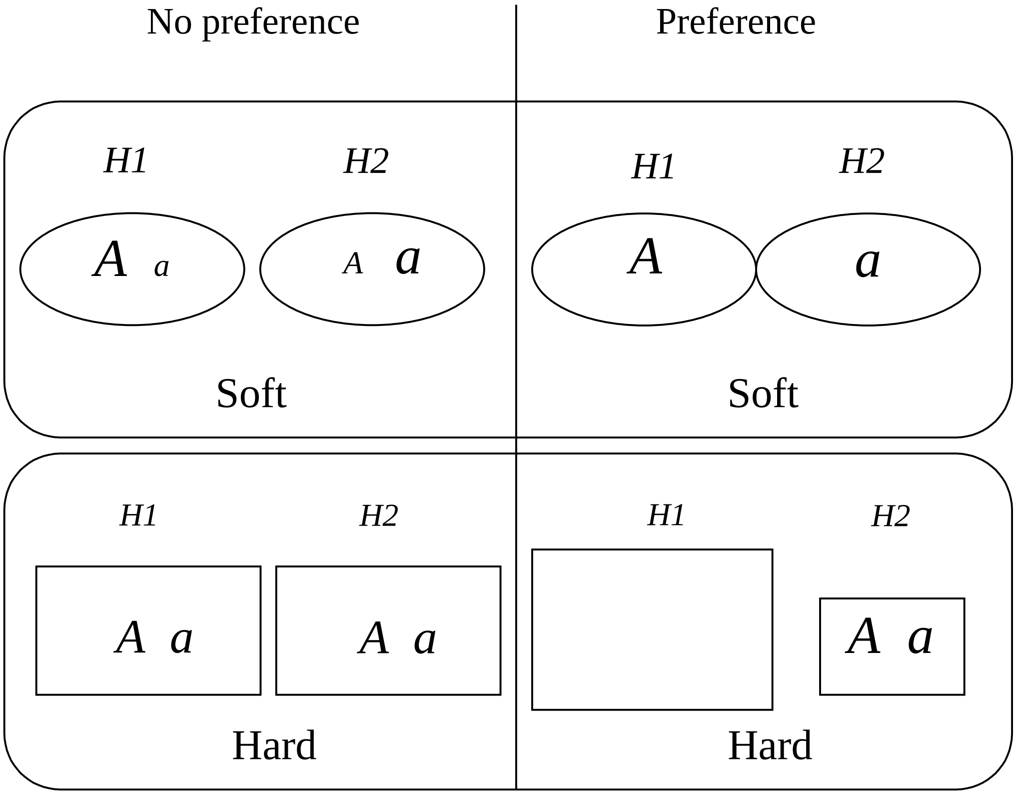

Figure 5: Expected patterns of distributions of coexisting morphs *A* and *a* in the soft and hard regulated compartments of an indirect parasitic cycle. The size of the fonts for *A* and *a* reflects the relative expected abundances of both morphs in each host (*H1* or *H2*) in each compartment. Size of resources are represented by the size of circles (soft) and squares (hard) and are set in the most favourable patterns for the maintenance of adaptive diversity in the soft compartment, and for the evolution of host preference in the hard compartment.

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