Encounter rate between local populations shapes host selection in complex parasite life cycle

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The present study aimed to understand how a parasite with a complex life cycle selects a given host succession when several potential hosts are present. *Ligula intestinalis* (Cestoda, Pseudophyllidea) was considered, which presents a life cycle with three hosts: copepod, fish, and piscivorous bird. Encounter probability between each pair of hosts was calculated for Lavernose-Lacasse gravel pit (France) using a sum of the product of the host abundances over time. Among four potential copepod hosts, two potential fish hosts, and six potential bird hosts, the results demonstrate that the copepod *Eudiaptomus gracilis*, the roach (*Rutilus rutilus*), and the great crested grebe (*Podiceps cristatus*) had a maximal encounter probability due to their abundance, but also due to the similarities of the temporal dynamics of their life cycles. These results agree with previous experiments and field work identifying a high specificity of *L. intestinalis* to *E. gracilis*, *R. rutilus*, and *P. cristatus* in the study site. This suggests that the abundance of potential hosts and the temporal dynamics of their life cycles act together to determine encounter rates between hosts and parasites, and thus could constitute a crucial determinant in local host selection by parasites with a complex life cycle.   © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, **89**, 99–106.

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INTRODUCTION

Over evolutionary time, parasites have added hosts and steps to their life cycles, thus increasing their complexity (Combes, 1995). In parasitic platyhelminths, nematodes, and acanthocephalans, complex life cycles involving transmission by predation from one or several intermediate invertebrate hosts to a definitive vertebrate host are extremely common (Poulin, 1998). At each step in the temporal sequence of the cycle, a range of potential hosts can be used, allowing parasites to specialize on one or more hosts (Lymbery, 1989). Such selection is crucial for parasite survival that aims, as for any organism, to exploit its environment as completely as possible to produce sufficient offspring. Host specificity, as illustrated by the filter concept of Combes (1991), stipulates that the parasite life cycle is shaped by two selective filters: (1) an encounter filter (i.e. the probability of encounter between hosts and parasites) and (2) a compatibility filter (i.e. physiological and immunological compatibility between hosts and parasites). Such theoretical concepts have been illustrated by numerous field and experimental studies assessing host specificity (Rohde, 1980, 1994; Lymbery, 1989; Poulin, 1998), determinants of host specificity (Combes, 1991; Rohde, 1994; Thompson, 1994; Morand *et al.*, 1999; Barger & Esch, 2002; Desdevises, Morand & Legendre, 2002; Krasnov *et al.*, 2004), and the evolution of host specificity (Ward, 1992). For example, Desdevises *et al.* (2002) investigated the determinant of host specificity in the genus *Lamellodiscus* (Monogenea), and concluded that one of the most important determinants of host specificity is the abundance of hosts, which positively influences the probability that the parasite come in contact with a host (Arneberg *et al.*, 1998). Such processes have already been illustrated in direct parasite life cycles

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(i.e. only one host), but little information is available for parasites having more complex life cycles. Using an optimality model, Choisy *et al*. (2003) have demonstrated that selection favoured a complex cycle only if the intermediate hosts were more abundant than the definitive hosts. However, host abundance may not be sufficient to explain host specificity when considering complex parasite life cycles. Indeed, the temporal dynamics of the host life cycle is probably important to consider, especially for invertebrate hosts that usually present one or more generations per year and therefore have highly variable temporal abundance dynamics. Such a tendency may be triggered in heteroxenous parasites that require a certain succession of several hosts to accomplish their life cycle. Accordingly, the potential determinants of host selection have to take into account the temporal dynamics of potential hosts that could strongly influence the probability of parasite transmission from one host to the next. To date, such issues have been underestimated, certainly because difficulties in assessing the relationship between different host dynamics over time.

In the present study, the encounter probability between potential hosts of the tapeworm *Ligula intestinalis* (L.) was quantified to provide insights into the potential influence of the temporal dynamics of host abundance on host selection by parasites. This cestode parasite presents a complex life cycle with three distinct hosts in succession in a predator–prey system. Free-swimming coracidia larval stages are eaten by the first intermediate host, a planktonic copepod, and develop in the haemocoel cavity into procercoid forms. Infected copepods are ingested by a cyprinid fish in which the procercoid larvae develop into plerocercoids located in the host's abdominal cavity. The final host is a fish-eating bird in which the parasites acquire their sexual maturity. Parasite eggs are released into the water with bird faeces (Dubinina, 1980).

Many reports have listed the potential hosts of *L. intestinalis* in natural aquatic environments and give the impression that it has a broad host range. However, this should be considered with caution, as according to Poulin (1998), using lists of published records does not provide an accurate measure of the host specificity in a given local parasite population.

In the present study, a site was selected with a large range of potential hosts for each stage of the parasite life cycle (i.e. two cyprinid fish, four copepods, and six aquatic birds, already listed as potential *L. intestinalis* hosts), aiming to: (1) measure host encounter rates and predict host-parasite specificity; (2) validate these results with previous work using experimental infestation; and (3) discuss the importance of temporal dynamics in host selection and the pressures acting on the evolution of host specificity at different stages in the parasite life cycle.

MATERIAL AND METHODS

Lavernose-Lacasse gravel pit is located in the southwest of France, near the city of Toulouse, on the alluvial plain of the Garonne River. This eutrophic artificial lake is 190 m above sea level, with a total area of 23 ha and a mean depth of 2.7 ± 0.4 m. The average annual water temperature is approximately 14 °C (range 5–25 °C). For the purpose of this study, the three host compartments necessary to complete the *L. intestinalis* life cycle were surveyed: copepod, fish, and bird populations. For each of the three compartments, each potential host species in the parasite life cycle was taken into account.

Samples of zooplankton were collected monthly from April 1998 to April 2000 using a plankton net (mesh size 100 µm) vertically hauled up from the bottom of the gravel pit to the water surface. The approximate volume of water filtered was 120–130 L. Zooplankton samples were immediately preserved in a 4% formaldehyde solution. In the laboratory, the density of each cyclopoid and diaptomid species in the samples was determined, using a microscope (8×50 magnification), according to the identification keys of Dussart (1967).

Fish were collected monthly from April 1998 to April 2000 using clear nylon monofilament gill-nets (length 30 m, height 1.7 m). A set of six nets with different mesh sizes (10, 12, 14, 17, 21, and 27 mm) was used to catch the entire range of fish sizes. Fish captures are expressed as catch-per-unit-effort (CPUE) (i.e. numbers of individuals m^{-2} min^{-1}).

Waterbird species were counted weekly for 2 h in the morning, from April 1998 to April 2000, using a telescope (20×60 magnification) and binoculars (8×30 magnification).

Encounter probability between each pair of hosts was calculated using a sum of the product of the host abundances over time. This procedure was repeated for each pair of potential hosts (bird–copepod, copepod–fish, and fish–bird) to provide encounter scores. High scores within a potential host pair predict a high encounter probability.

RESULTS

In Lavernose-Lacasse, the two most abundant cyprinid fish species were the roach *Rutilus rutilus* (65.7% of the total number of fish) and the silver bream *Blicca bjoerkna* (31.9%) (Loot *et al*., 2001). Roach was significantly more abundant than bream (Fig. 1A) (*t*-test, $P < 0.05$). CPUE estimations of roach and bream revealed that maximal catches occurred during summer for both species (Fig. 2A). Four copepod species were present in Lavernose-Lacasse gravel pit (Fig. 1B): *Eudiaptomus gracilis* (Sars, 1863),
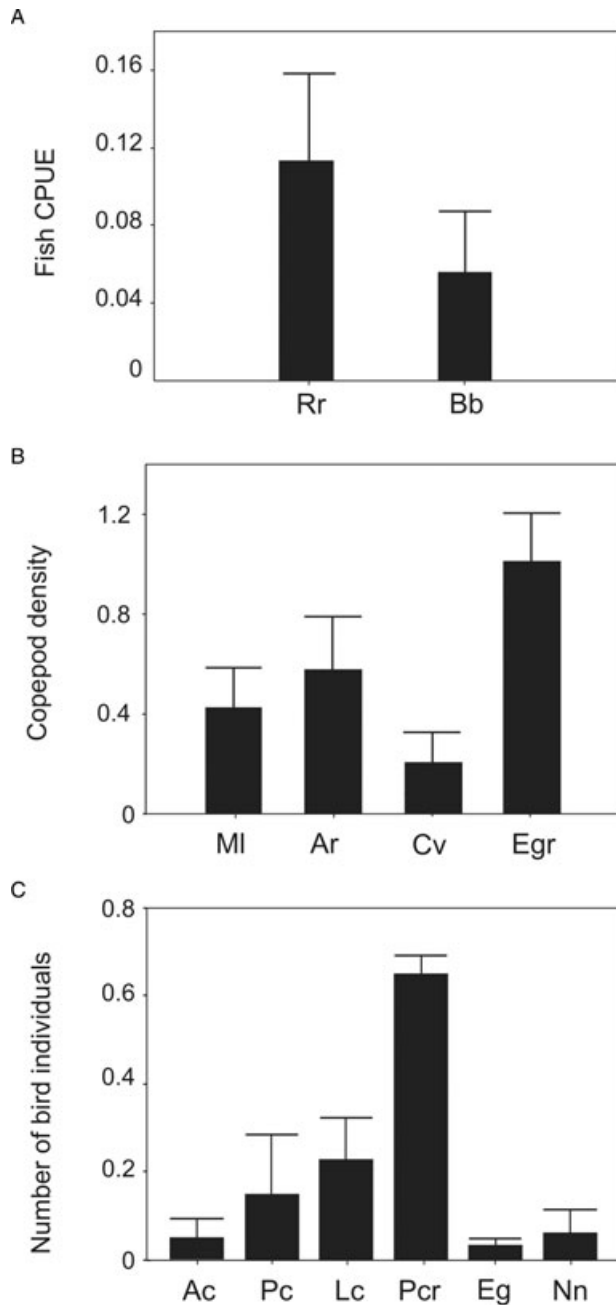
Figure 1. Mean relative abundance of fish, copepods and birds present within Lavernose-Lacasse gravel pit. A, cyprinid fish catch-per-unit-effort (CPUE; numbers of individuals m^{-2} min^{-1}). B, copepod density (number of individuals per litre). C, numbers of birds. Rr, *Rutilus rutilus*; Bb: *Blicca bjoerkna*; Ml, *Mesocyclops leuckarti*; Ar, *Acanthocyclops robustus*; Cv, *Cyclops vicinus vicinus*; Egr, *Eudiaptomus gracilis*; Ac, *Ardea cinerea*; Pc, *Phalacrocorax carbo*; Lc, *Larus cachinnans*; Pcr, *Podiceps cristatus*; Eg, *Egretta garzetta*; Nn, *Nycticorax nycticorax*.

Acanthocyclops robustus (Sars, 1863), *Mesocyclops leuckarti* (Claus, 1857), and *Cyclops vicinus vicinus* (Ulianine, 1875). *Eudiaptomus gracilis* was the most abundant copepod species [analysis of variance (ANOVA), $F = 14.697$, d.f. = 3, 96, $P < 0.001$; Tukey's test, $P < 0.001$]. The density of each species varied along the year and each species exhibited its own temporal dynamics (Fig. 2B) (for more details, see Loot *et al*., 2001). Six species of aquatic birds were recorded during the surveys (Fig. 1C): the grey heron, *Ardea cinerea* (Linnaeus, 1758); the cormorant, *Phalacrocorax carbo* (Linnaeus, 1758); the yellow herring gull, *Larus cachinnans* (Pallas, 1811); the great crested grebe, *Podiceps cristatus* (Linnaeus, 1758); the egret, *Egretta garzetta* (Linnaeus, 1758); and the night heron, *Nycticorax nycticorax* (Linnaeus, 1758). The great crested grebe was the most abundant bird species (ANOVA, $F = 39.862$, d.f. = 5, 114, $P < 0.001$; Tukey's test, $P < 0.001$), whereas the other species were slightly less abundant in the gravel pit. The great crested grebe, and to a lesser extent the yellow herring gull, inhabited the gravel pit throughout the year, whereas the four other species were occasional visitors (Fig. 2C). Detailed information on the life cycles and temporal dynamics of these species is provided in Loot *et al*. (2001).

Encounter scores between the 12 species (birds, fish, and copepods) showed a clear association between three species pairs: *P. cristatus* and *E. gracilis* (Table 1), *E. gracilis* and *R. rutilus* (Table 2), and *R. rutilus* and *P. cristatus* (Table 3). Encounter scores for these species were clearly higher than for other species associations. These results predict that *P. cristatus* (bird), *E. gracilis* (copepod), and *R. rutilus* (fish) are the most probable hosts in the *L. ligula* life cycle.

DISCUSSION

One of the most fundamental characteristics of a parasite's life cycle is the spectrum of hosts species used at each stage. Such information is available only for a limited number of parasite species and, even when potential hosts are known, the determinism of host selection is not yet understood (Poulin, 1998). However, Norton & Carpenter (1998) and Arneberg *et al*. (1998) demonstrated that host population density and parasite abundance are positively correlated, suggesting that host population density increases the probability that a parasite transmission stage (e.g. egg per larvae) will contact a host. This hypothesis is supported by Dybdahl & Lively (1998), who demonstrated that common host genotypes are more susceptible to parasite infection than rare genotypes, thus suggesting that local parasite adaptation results from parasite tracking of locally common host genotypes (Lively & Dybdahl, 2000). However, studies on this
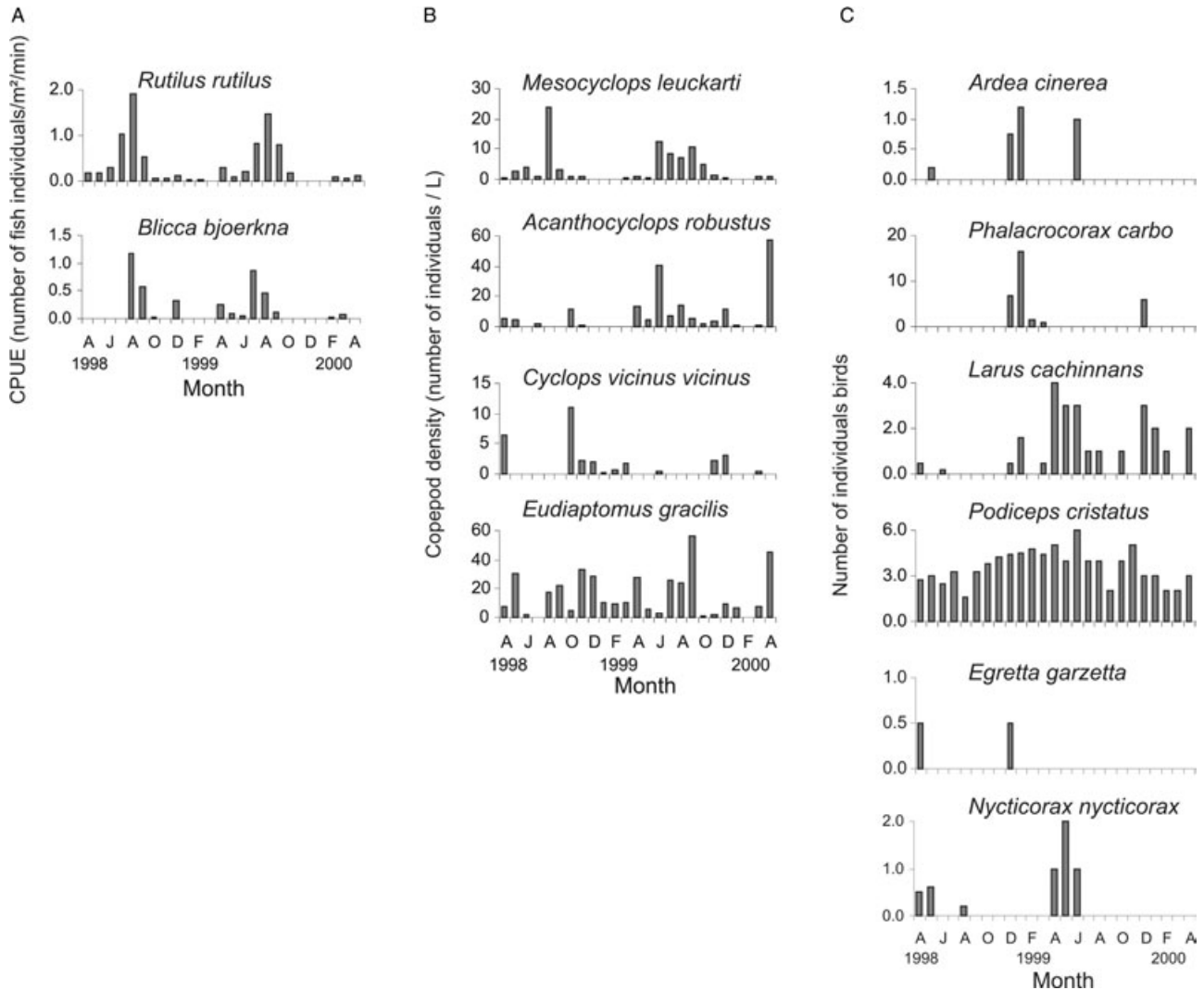
Figure 2. Monthly dynamics (from April 1998 to April 2000) of fish, copepods and birds present within Lavernose-Lacasse gravel pit. A, cyprinid catch-per-unit-effort (CPUE). B, copepod density. C, numbers of birds.

Table 1. Encounter probability scores between potential hosts in the *Ligula intestinalis* life cycle: aquatic bird and copepod

	Aquatic bird					
Copepod	*Ardea cinerea*	*Phalacrocorax carbo*	*Larus cachinnans*	*Podiceps cristatus*	*Egretta garzetta*	*Nycticorax nycticorax*
Mesocyclops leuckarti	12.71	3.67	65.27	270.88	0.18	20.01
Acanthocyclops robustus	41.32	70.23	366.57	741.03	2.71	68.54
Cyclops vicinus	2.28	38.88	15.85	112.81	4.21	3.63
Eudiaptomus gracilis	41.95	435.28	357.03	1336.08*	18.07	66.26

*Higher scores predict a high encounter probability (see methods).

Table 2. Encounter probability scores between potential hosts in the *Ligula intestinalis* life cycle: copepod and fish

| Fish | Copepod | | | |
	Mesocyclops leuckarti	*Acanthocyclops robustus*	*Cyclops vicinus vicinus*	*Eudiaptomus gracilis*
Rutilus rutilus	79.82	55.36	2.21	175.86*
Blicca bjoerkna	46.77	19.58	0.95	95.08

*Higher scores predict a high encounter probability (see methods).

Table 3. Encounter probability scores between potential hosts in the *Ligula intestinalis* life cycle: aquatic bird and fish

| Fish | Aquatic bird | | | | | |
	Ardea cinerea	*Phalacrocorax carbo*	*Larus cachinnans*	*Podiceps cristatus*	*Egretta garzetta*	*Nycticorax nycticorax*
Rutilus rutilus	0.38	1.32	5.18	26.36*	0.15	1.27
Blicca bjoerkna	0.29	2.22	2.98	13.33	0.16	0.74

*Higher scores predict a high encounter probability (see methods).

subject deal with directly transmitted parasites (i.e. the parasite life cycle has only one host), or only one stage of the parasite life cycle in the case of complex cycles. Considering parasites with complex life cycles, such as *L. intestinalis*, it can be hypothesized that a similar process could occur at each stage of the parasite life cycle. Although numerous reports showed that *L. intestinalis* is able to exploit a large range of host species at each stage in the life cycle (Dubinina, 1980; Gerdeaux, 1986; Bean & Winfield, 1992; Museth, 2001; Barus & Prokes, 2002), field studies have demonstrated that *L. intestinalis* presents a high local host-specificity (Harris & Wheeler, 1974; Bean & Winfield, 1989; Loot *et al.*, 2001). Indeed, field work and experimental infestation showed that the copepod *E. gracilis*, the roach (*R. rutilus*), and the great crested grebe (*P. cristatus*) were the most favourable hosts for continuation of the parasite life cycle in Lavernose-Lacasse gravel pit (Loot *et al.*, 2001). These three host species were the most abundant in the gravel pit (Fig. 1), therefore demonstrating that the trends reported for directly transmitted parasites are also valid for parasites with complex life cycles. Indeed, host population density plays an important role because there is a 'cost of the distance' for the parasite (May & Anderson, 1978; Dobson, 1990; Grenfell & Harwood, 1997; Bustnes, Galaktionov & Irwin, 2000). For example, roach is the most widespread cyprinid species in Europe and is one of the most common intermediate hosts of *L. intestinalis* (Dabrowski & Szpilewski, 1980). In the same way, heavy infestation of bleak (*Alburnus alburnus*) has

been reported by Harris & Wheeler (1974) in the Thames river, where this species is the most abundant cyprinid fish.

However, considering parasites with complex life cycles, abundance may not be sufficient to explain host selection by parasites. Indeed, the temporal dynamics of potential hosts (Fig. 2) provided additional information on the frequency of host encounters. The final host (i.e. *P. cristatus*) is a sedentary bird (Santoul & Tourenq, 2000) with stable abundance throughout the year. Therefore, grebes do not represent a limiting factor for the accomplishment of the parasite life cycle (Fig. 2C). *Rutilus rutilus* shows a seasonal variation in fish CPUE, increasing in spring and decreasing in autumn (Fig. 2B). Hence, CPUE do not measure fish abundance, which is stable throughout the year, but an activity rate (Hamley, 1975). The roach were maximally active for 6 months per year and were therefore abundant prey for piscivorous birds during this period. In the same way, the coincidence between fish and copepods arises when both high fish activity rate and high zooplankton abundance (Fig. 2A).

Therefore, the synchrony of potential host temporal dynamics should be considered. Such criteria combining abundance and temporal dynamics can be calculated using a simple encounter score (Tables 1, 2, 3) which sums up the complex dynamics observed on the field (Fig. 2). In the present study *P. cristatus*, *E. gracilis*, and *R. rutilus* had the highest encounter score. This is consistent with our field and experimental results describing *L. intestinalis* hosts and life cycle in the Lavernose gravel pit (Loot *et al.*, 2001).

Similarities in host cycles could therefore be an important factor shaping host selection. Indeed, as a response to pressures generated by the life cycle itself, natural selection would favour *L. intestinalis* specimens present in hosts with similar population dynamics, therefore procuring a higher probability of completing the life cycle. According to Ward (1992), organisms tend to specialize on predictable resources (i.e. those that are stable through time), thus minimizing risk of extinction. Accordingly, the environmental stability provided by hosts with a long life expectancy (Sasal *et al*., 1999) may allow parasites to develop specific adaptations (Basset, 1992; Kitahara & Fujii, 1994). In the present study, abundant hosts (birds, fish, and copepods) with similar temporal dynamics and frequent associations between them may provide a stable environment that promotes the accomplishment of the parasite life cycle.

These results suggest a scenario for the evolution of *L. intestinalis* specificity (Fig. 3A). It can be hypothesized that host selection is primarily driven by encounter probability between successive hosts, thus facilitating parasite transmission from one host to the next. After host selection, a specialization process takes place between the parasite and the locally common host. This process probably involves biochemical or metabolic adaptations occurring after environmental selection, leading to an increase in host specificity as experimentally demonstrated by Loot *et al*. (2001).

However, alternative scenarios should also be considered. Among them, host selection driven by physiological and/or immunological factors can be proposed (Fig. 3B). In that case, host encounter probability would hardly affect selection and therefore transmission efficiency is not necessarily ensured. To compensate the low transmission efficiency, the specialization process may modify host behavioural and/or biological traits to increase the chances of the parasite completing its life cycle (Dobson & Merenlender, 1991). Such modifications have already been illustrated by Combes *et al*. (1994) and Poulin (1998) in digenean cycles. These authors described a reduction of free-living stage mortality as well as an increase of the number of intermediate stage individuals by parthenogenesis.

In our view, the first scenario, which stipulates that biochemical or metabolic adaptations are secondary processes occurring after environmental selection, is more realistic than the second one. This scenario is relevant in the light of both bibliographical studies and the results of present study and appears to provide a simple explanation for understanding host selection in complex parasite life cycles. However, further studies are required to explore the repeatability of our scenario to determine the evolutionary steps of host specificity.
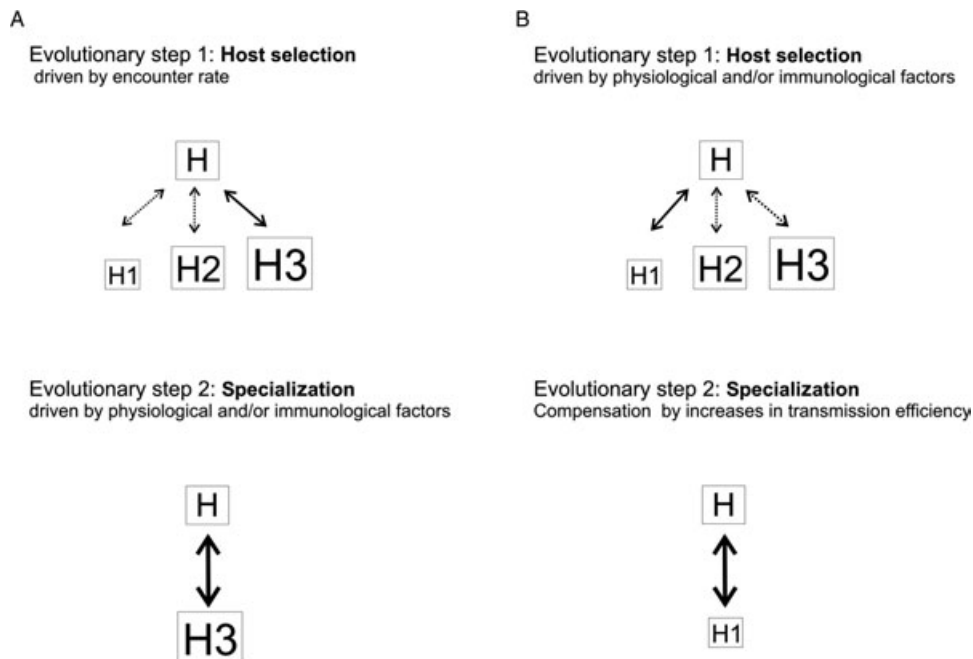

Figure 3. Illustration of two possible scenarios for the addition of a new host to the life cycle of *Ligula intestinalis*. Solid lines represent selected pathways (i.e. suitable host among the spectrum of potential species). Dotted lines represent pathways with low success of parasite transmission. The box size is proportional to the probability of encounter with the previous host (H). Scenarios were divided into two evolutionary steps: host selection and specialization.

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