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Omphiscola glabra (Gastropoda, Lymnaeidae): Changes occurring in natural infections with *Fasciola hepatica* and *Paramphistomum daubneyi* when this snail species is introduced into new areas

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Abstract – Cross-transplantations of *Omphiscola glabra* between two French departments (Haute-Vienne and Indre) were carried out to study snail settlement in these new sites during six years and to determine if this snail species was well adapted to its local parasites (*Fasciola hepatica* and *Paramphistomum daubneyi*). Local snails placed in new sites for each department were used as controls. In Indre furrows, the number of adults per population and the area of each habitat peaked on the third year post-introduction. Similar findings were also noted in the Haute-Vienne furrows occupied by local snails but peaks were only observed on the fourth year. In contrast, in Haute-Vienne sites populated by introduced snails, there was a progressive decrease in snail abundance and habitat area from the second year. The local *O. glabra* transplanted in Haute-Vienne kept their same degree de susceptibility to *F. hepatica* and *P. daubneyi*, thus demonstrating a good adaptation of these snails to their parasites. In other groups of transplanted snails, the first natural infections were only noted from the second or third year post-introduction and their prevalence progressively increased over time. Local adaptation of these latter snails to parasites would be more progressive in time and would stretch over several snail generations.

Key words: Calcium / *Fasciola hepatica* / *Galba truncatula* / natural infection / *Omphiscola glabra* / *Paramphistomum daubneyi* / snail settlement

Introduction

According to the Red Queen hypothesis, parasites should be better at infecting sympatric (local) populations of snails than allopatric host populations (Lively and Dybdahl, 2000). Among the diverse investigations reported in the literature, parasites have been found to be more infective to their sympatric hosts in several systems (Lively *et al.*, 2004; Muñoz-Antoli *et al.*, 2010), thus demonstrating local adaptation between both partners. However, this hypothesis was not verified in other snail-parasite systems (*e.g.* Prugnolle *et al.*, 2006). This variable nature of results was also found in the *Galba truncatula*-*Fasciola hepatica* system. If local adaptation between these partners was verified in the field (Abrous *et al.*, 1999, 2000) and even during the larval development of *F. hepatica* within its snail host (Belfaiza *et al.*, 2005), other experiments performed by our team have demonstrated that Spanish and Moroccan isolates of *F. hepatica* were more infective to French populations of *G. truncatula* than miracidial isolates originating from central France (Gasnier *et al.*, 2000; Goumghar *et al.*, 2001). An explanation to interpret this set of conflicting results may be the change which had occurred in the infectivity of *F. hepatica* miracidia from the 2000s. According to Dreyfuss *et al.* (2007), miracidia originating from triclabendazole-treated cattle had a greater infectivity to their snail host than miracidia coming from ruminants treated with broad-spectrum anthelminthics.

Contrary to parasites which had been more studied before 2002, the transplantation of snails from a given area in another area was not still very used to verify the occurrence of local adaptation hypothesis in a snail-parasite system. Nevertheless, this technique is interesting because of the possibility of subjecting snail populations diversely susceptible or resistant to a digenean to another natural parasitic pressure exerted by the definitive host. Since 2003, this technique was used in a field experiment

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to answer the following three questions: Did *F. hepatica*-susceptible snails keep the same degree of susceptibility when they were locally introduced into new sites located in the same district as the population of origin? Did this susceptibility change if these snails were placed in another district differing by geology and, as a consequence, by parasitological profile? If snail samples little susceptible to *F. hepatica* were introduced into a district where highly susceptible populations of belonging to the same species were living, did the susceptibility of the former snails increase in time? Cross-transplantations of snails were thus made in 2003 and were followed during six years to study their settlement into new sites and changes occurring in their susceptibility to natural infections with *F. hepatica*. To verify these results, local transplantations of snails (controls) were also performed by placing them in new sites located in the same district.

Materials and methods

Lymnaeid species and French departments chosen for this study

As *G. truncatula* is the main snail host of *F. hepatica* in central France (Rondelaud *et al.*, 2009), the lymnaeid chosen was a close related species: *Omphiscola glabra*. Natural infections of this latter snail with *F. hepatica* and/or another digenean, *Paramphistomum daubneyi* were reported from the 2000s by several authors (Mage *et al.*, 2002; Dreyfuss *et al.*, 2003, 2005) on the acid soils of Haute-Vienne. If miracidia of both digenean species penetrate *O. glabra* during the same time interval (4 h) at exposure, the first parasite which enters the snail favours the development of the other digenean (Augot *et al.*, 1996) so that natural infections with *F. hepatica*, *P. daubneyi*, or both can be noted. According to Mage *et al.* (2002), this snail co-infection was frequent on acid soil because of the presence of both digenean species in the same cattle. Nevertheless, if single-miracidium infections were performed with *O. glabra*, only juvenile snails measuring less than 2 mm in height at exposure can sustain the larval development of *F. hepatica* (Boray, 1978; Bouix-Busson and Rondelaud, 1986), whereas all experiments made with *P. daubneyi* were negative.

Contrary to Haute-Vienne, the parasitic conditions were different in a close geographical area on sedimentary soil (department of Indre, subdistrict of south-eastern Brenne). No natural infections with *F. hepatica* and/or *P. daubneyi* were noted from 1996 to 2003 in local populations of *O. glabra*, whereas the first infections with *P. daubneyi* in cattle were detected from 2001 and in *G. truncatula* from 2003 (unpublished data).

Snail populations and sites chosen for the introduction of snail samples

In the department of Indre (Fig. 1), the population of *O. glabra* (46°40'27"N, 1°21'19"E) was living in a road ditch along the road D46, on the commune of Chitray, whereas that of northern Haute-Vienne was located in a small water collection (46°4'42"N, 1°6'47"E) along the road D72, on the commune of Saint-Junien-les-Combes. The distance between both populations was 55 km. In each population, 30 samples of snails, each comprising 100 adults (more than 14 mm in height), were collected in April 2003.

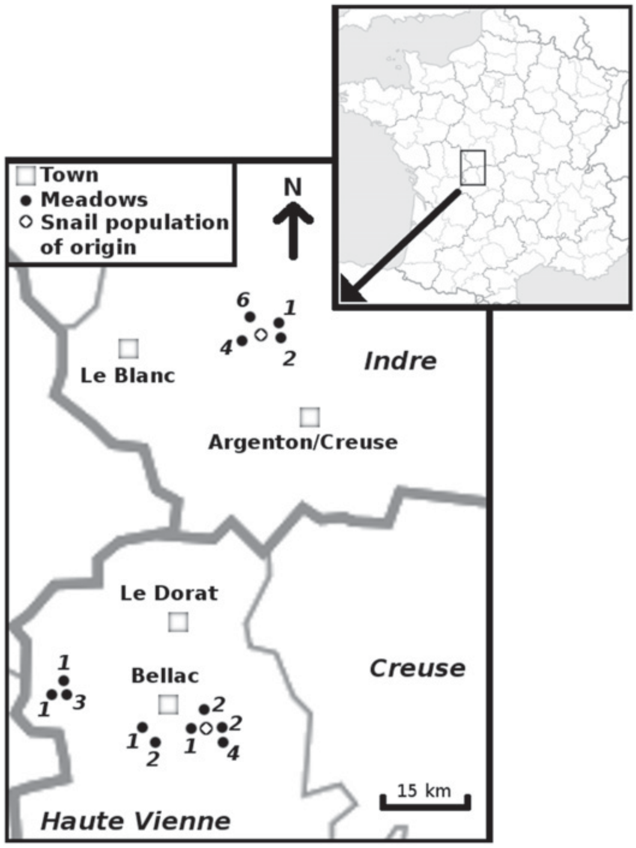

Fig. 1. Geographic location of study areas in central France. Each figure (in italics) indicates the number of meadows used for the experiment.

Snail samples were placed in new sites *i.e.* thirty hygro-mesophilous meadows in both departments (Table 1). In northern Haute-Vienne, the 17 meadows were each located at the bottom of a valley. As the underlying subsoil was composed of granite, an open drainage network was dug to allow water evacuation coming from spring heads and rains. In this department, the pH of running water ranged from 5.6 to 7 and the quantity of dissolved calcium in water was less than 20 mg.L^{-1} (Guy *et al.*, 1996). In contrast, the 13 meadows chosen in the department of Indre were flatter and their hygrophilous zone was more reduced so that there were few open drainage furrows. As the soils of these pastures were composed of silt and sand, supported by a calcareous subsoil, the pH of running water was higher (from 6.7 to 7.8) with 26–35 mg.L^{-1} of dissolved calcium. All meadows were grazed by cattle during the present study.

Table 1. Origin and number of snail samples placed in new sites in March 2003, with indication of the number of populations found at the end of the experiment (2009).

Snail samples			Number of snail populations		
Department (subdistrict)	Introduction into furrows located in	Number in April 2003	Two years after snail introduction	Four years after snail introduction	At the end of experiment (and %)
Indre (south-eastern	Indre* (local snails)	13	13	11	10 (76.9)
Brenne)	Haute-Vienne* (introduced snails)	17	12	10	8 (61.5)
Haute-Vienne	Haute-Vienne (local snails)	17	17	16	13 (76.4)
(Basse Marche)	Indre (introduced snails)	13	11	7	3 (17.6)

* Location of meadows: Indre (communes of Chitray, Migné and Nuret-le-Ferron), Haute-Vienne (communes of Berneuil, Blanzac, Breuilaufa, Mézières-sur-Issoire and Saint-Junien-les-Combes).

The furrows chosen in the present study were devoid of any *O. glabra* populations before the introduction of each sample. In contrast, *G. truncatula* was present in all thirty meadows, with populations living in furrows different from those in which *O. glabra* was placed. All meadows were subjected to the same climatic conditions, with a continental climate strongly modulated by wet winds which came from the Atlantic Ocean. The annual mean pluviometry ranged from 800 to 1000 mm, while the annual mean temperature was 10–11 °C.

Protocol used for snail introduction

In each meadow, one sample collected from the department of Indre and another from the Haute-Vienne were placed in two drainage furrows (one sample per furrow). This sequence was chosen to subject both snail samples to the same parasitic pressure during cattle grazing. Seventeen samples originating from Indre (Table 1) were thus introduced into 17 open drainage furrows on acid soil (introduced snails), while the 13 others were placed in local furrows in Indre (local snails). A similar protocol was used for snail samples collected from Haute-Vienne, with 13 introduced into furrows in Indre (introduced snails) and 17 into those of Haute-Vienne (local snails).

In each furrow, snails were placed on the bottom per groups of 10 individuals each at regular intervals of 3 m for a total length of 30 m. The zone chosen for snail introduction in Haute-Vienne was the middle part of the furrow because local populations of *O. glabra* often occupied this place in an open drainage network (Vareille-Morel *et al.*, 1999). In the case of Indre, snails were put in the lowest part of each furrow, generally close to the main ditch. As snails living on calcareous soils buried themselves in drying soil during summer months (Rondelaud *et al.*, 2003), the bottom of sites chosen in Haute-Vienne was covered by a >3 cm layer of sand and mud, while it was often constituted by marl in Indre.

Slaked lime (0.2 kg per furrow in 2003 and 2004) was added to the soil to facilitate the settlement of snails from Indre to the more acidic soils of Haute-Vienne. Vegetation was not mowed in the 30 meadows from 2003 to 2009 so that rushes and bulrushes growing on the borders of each furrow protected aestivating snails from the direct effects of sun. In addition, each site was fenced with barbed wire to avoid levelling of furrow walls by cattle trampling throughout the year.

Parameters studied

For each furrow colonized by a sample of *O. glabra*, three parameters were measured at mid-May from 2004 to 2009: (i) total number of adults by counting snails higher than 12 mm, (ii) area occupied by each lymnaeid population in the furrow, and (iii) maximum size of 50 adults to the nearest mm. Individual values noted for each parameter were averaged and standard deviations were established taking into account snail origin and the geographical location of meadows. These values were compared using a two-way analysis of variance.

As *O. glabra* shell heights naturally infected with *F. hepatica* and/or *P. daubneyi* often ranged from 5 to 10 mm (Abrous *et al.*, 1999, 2000), this scale of shell heights was chosen to study natural infections in local and introduced snails from 2004 to 2009. Samples of 100 *O. glabra* each were randomly collected from the 60 furrows at mid-May each year. Snails were then dissected under a stereomicroscope to find live rediae of each digenean and determine the overall prevalence of natural infection with *F. hepatica* or *P. daubneyi*. To verify if these frequencies differed from those existing in the local populations of *G. truncatula*, 100 adults of this last species (shell height, >4 mm) were also sampled from each meadow at the end of May in 2009. A χ^2 test was used to establish the levels of significance.

All statistic analyses were made using the Statview 5.0 software.

Results

Successful settlements of local *O. glabra* in 2009 were noted in more than 75% of cases. The results were not as good for introduced snails because 61.5% of populations were still present in furrows of Indre compared to 17.6% in those of Haute-Vienne (Table 1).

Outcome of snail samples introduced into new sites

In the Indre furrows colonized by local snails, the number of adults (Fig. 2a) and area occupied by each

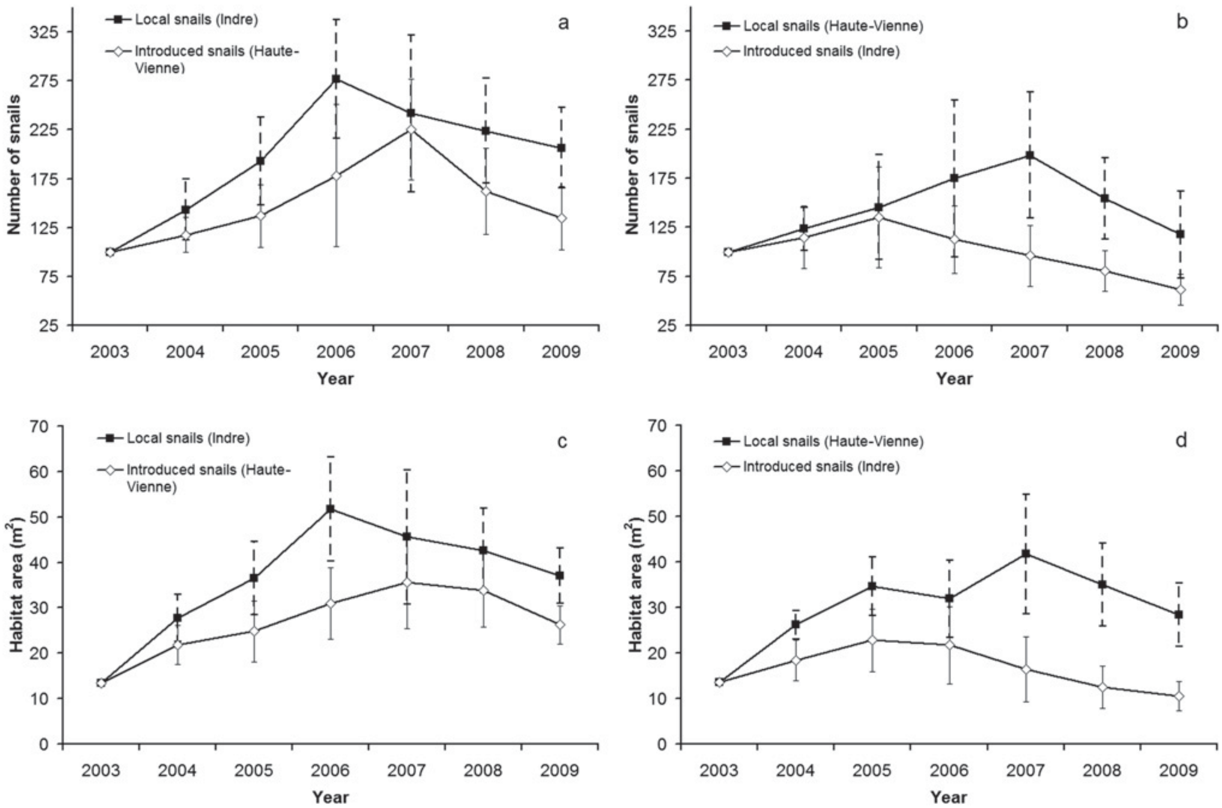

Fig. 2. Total number of adult snails counted in May (2a, 2b) and area of furrow occupied by each population (2c, 2d) in Indre (2a, 2c) and Haute-Vienne (2b, 2d).

population (Fig. 2c) increased up to 2006 and decreased afterwards. Similar findings were also noted for introduced samples but peaks were only observed in 2007. In the case of the Haute-Vienne meadows colonized by local snails, two peaks in adult number (Fig. 2b) and area of each habitat (Fig. 2d) were noted in 2007. In furrows colonized by introduced snails, mean values of both parameters increased during the first two years p.i. and then steadily decreased to figures lower than those noted in 2003. In 2009, the mode of snail transplantation ($F_{1,30} = 13.22$, $P < 0.001$) and its interaction with snail origin ($F_{1,30} = 28.73$, $P < 0.001$) had significant effects on the total number of adults, while the factor snail origin was not significant. Similar findings were also noted for habitat areas (snail transplantation: $F_{1,30} = 34.42$, $P < 0.001$; interaction with snail origin: $F_{1,30} = 24.66$, $P < 0.001$).

In May 2009, maximum shell height of *O. glabra* in the Indre meadows was 20.5 ± 2.0 mm for local snails and 18.8 ± 1.7 mm for introduced snails. On acid soil, respective values were 16.7 ± 1.9 mm and 17.5 ± 2.5 mm. All differences between these shell heights were not significant.

Natural snail infections

In snails collected from both departments, no co-infection with both digeneans was noted. The values of prevalence recorded from 2004 to 2009 are shown in Figure 3. In Haute-Vienne meadows colonized by local *O. glabra*, prevalences of natural infections in snails were close to each other over years: their values ranged from 4.4% to 7.0% for *F. hepatica* and from 2.8% to 4.2% for *P. daubneyi*. In the same pastures but populated by introduced snails, the frequencies were low in 2005 (0.6% for *F. hepatica*, 0.3% for *P. daubneyi*) and thereafter increased to greater than 3.0%. In Indre meadows, most natural snail infections with these digeneans were only detected from 2006. The number of infected snails also increased with the year and this process was more rapid for introduced snails than for local *O. glabra* (from 0.9% to 8.7% for *F. hepatica*, for example, in introduced snails instead of 0.5% to 2.7% in local *O. glabra*). In Indre, the prevalence noted in 2009 for *F. hepatica* infections was significantly higher ($\chi^2 = 31.90$, $P < 0.001$) in local snails than for introduced snails, while the difference between prevalences found in Haute-Vienne snails was not significant. Another significant difference ($\chi^2 = 5.08$, $P < 0.05$) between prevalences noted for *P. daubneyi*-infected snails was also noted in Indre, whereas the values found in Haute-Vienne in 2009 did not significantly differ from each other.

Table 2 gives the prevalences of natural infections with *F. hepatica* or *P. daubneyi* found in the different samples of *G. truncatula* and *O. glabra* after their collection from new habitats in 2009. In Haute-Vienne meadows, the *F. hepatica* prevalence was significantly greater in local *O. glabra* than in *G. truncatula*. In Indre furrows, another significant difference between the prevalences of *F. hepatica*

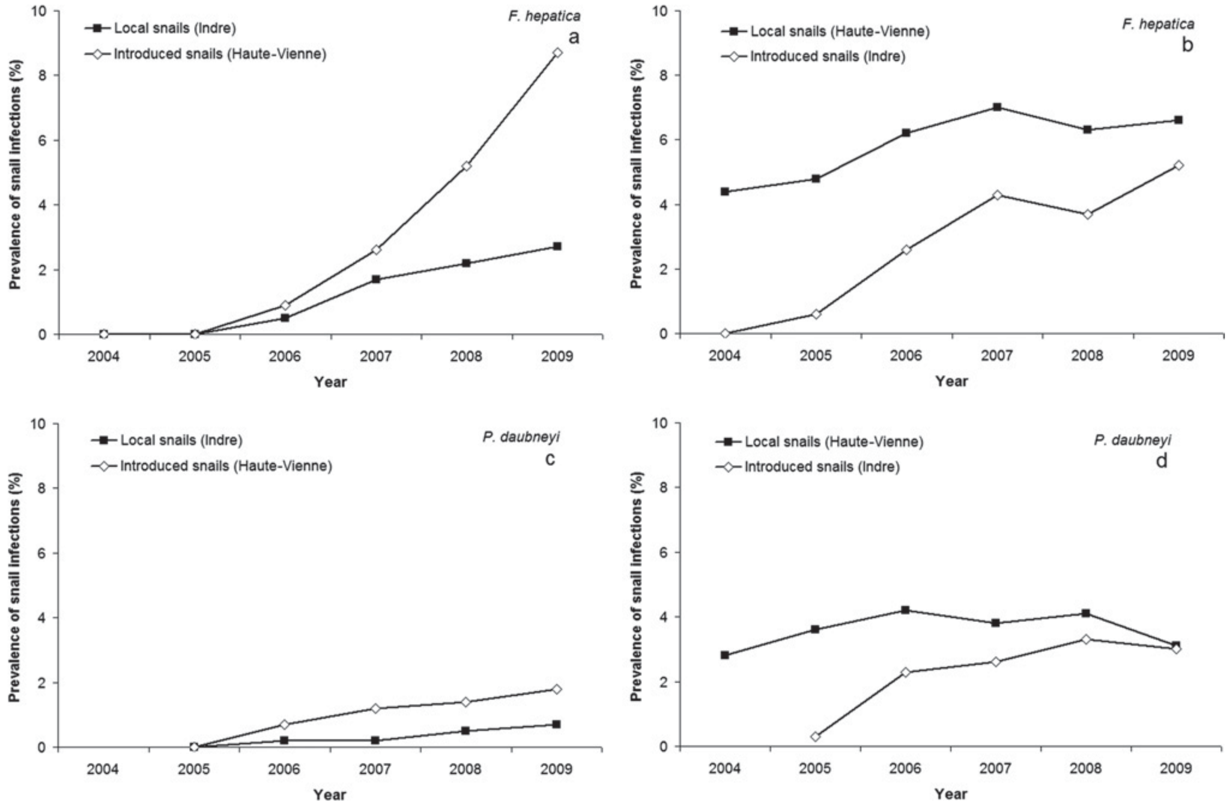

Fig. 3. Overall prevalence of natural infections with *F. hepatica* or *P. daubneyi* in the samples of *O. glabra* collected from the furrows of Indre (3a, 3c) and Haute-Vienne (3b, 3d) between 2003 and 2009.

Table 2. Prevalence of natural infections with *F. hepatica* or *P. daubneyi* noted in samples of *G. truncatula* and *O. glabra* after their collection in 2009. NS, not significant.

	Mean prevalence (%) of natural infections in 2009					
	F. hepatica			*P. daubneyi*		
Origin of *O. glabra*	*G. truncatula*	*O. glabra*	χ^2 test (*P*)	*G. truncatula*	*O. glabra*	χ^2 test (*P*)
Snails living in the department of Indre						
Local	3.3	2.7	NS	1.7	0.7	NS
Introduced		8.8	28.81 ($P < 0.001$)		1.9	NS
Snails living in the department of Haute-Vienne						
Local	4.6	6.6	5.85 ($P < 0.05$)	3.6	3.2	NS
Introduced		5.3	NS		3	NS

infections found in introduced *O. glabra* and local *G. truncatula* was noted. The differences between other prevalences were not significant.

Discussion

In Haute-Vienne, the prevalence of parasite infections found from 2004 in local snails (Figs. 3b and 3d) demonstrated that these *O. glabra* kept the same degree of susceptibility when they were transplanted in new sites. These snails were well adapted to their local parasites and this finding was in accordance with the Red Queen hypothesis. In contrast, in local snails living in Indre and in both groups of introduced snails, the first natural infections were only found from 2005 (Haute-Vienne) or from 2006 (Indre) and their prevalences were afterwards steadily increasing over time. As these findings seems to be in discordance with the above-mentioned hypothesis, two perhaps complementary explanations might be proposed. The first is the greater pressure in parasite eggs that infected cattle deposited in Haute-Vienne meadows. In the department of Corrèze, a French department close to Haute-Vienne, fasciolosis affected 11.2% to 25.2% of cattle between 1990 and 1999, whereas paramphistomosis was detected in 5.2–44.7% of cattle during the same period (Mage *et al.*, 2002). In contrast, in the different cattle-breeding farms of south-eastern Brenne used for the present study, the presence of *F. hepatica* and that of *P. daubneyi* were noted, respectively, in 8.3% and 4.5% of coproscopical examinations made at the beginning of this experiment (data not shown). The second hypothesis is to admit a progressive adaptation of these *O. glabra* to parasite infection during several snail generations, as demonstrated by Boray (1969) for *Lymnaea peregra* and *F. hepatica*. Two arguments supporting this interpretation were the report by Bouix-Busson and Rondelaud (1986) on *O. glabra* and that by Dreyfuss *et al.* (1994) on *Stagnicola palustris*. According to these authors, prevalences of *F. hepatica* infections increasing over several successive years were already noted for these species when miracidia of *F. hepatica* were experimentally introduced in snail habitats on acid soil each year.

The other findings presented in this study were less important. However, they required special comments:

- In both types of Indre furrows and in Haute-Vienne furrows colonized by local *O. glabra*, the number of adults in each population peaked on the third or fourth year after introduction of snail samples into these new sites. Similar findings were also noted for habitat areas. These data agreed with those reported by Rondelaud *et al.* (2006) for other *O. glabra* populations when a biological control was applied during several years to numerous meadows on acid soil to eliminate *G. truncatula*. According to these authors, if the same furrows were occupied by separate communities of both lymnaeids, the number of surviving *O. glabra* and the area of their habitats also peaked on the third year after the disappearance of *G. truncatula*. In contrast, if snails coming from Indre were placed on acid soil, there was an increase in snail abundance and habitat area up to the second year post-introduction, followed by a progressive decrease of these parameters thereafter. The values noted during the first two years can be easily explained by the presence of slaked lime which had favoured snail growth. Those found during the following three years may be explained by the low quantity of calcium in the water and soil of these sites. Indeed, high calcium levels in soil and water had an influence on the distribution of land snail species within a country (*e.g.*, Boycott, 1934), abundance of each species (*e.g.*, Hotopp, 2002; Vadeboncoeur *et al.*, 2007), and also on the maximum shell height of adults, as demonstrated for local *O. glabra* in the present study. The intermediate values noted for introduced *O. glabra* in 2009 might be explained by the necessity of a longer than five year period in order to have a visible effect of calcium on nail height.
- Significantly greater prevalences with *F. hepatica* were noted in 2009 in the local *O. glabra* living in Haute-Vienne and in snails introduced in Indre. In contrast, other snail populations did not show such increase in infection rates. These findings are difficult to comment because the prevalences recorded by Abrous *et al.* (1999, 2000) in *F. hepatica*-infected snails were often less than 5% on acid soil. As samples of *O. glabra* for snail dissection were performed in mid-May (instead of March–April or September–October for above-mentioned authors), the most likely explanation is to correlate these findings with the period of snail sampling (mid-May). If this explanation is valid, this high number of *F. hepatica*-infected snails would decrease in June–July, probably due to the death of some *O. glabra* during cercarial shedding at the end of June (in central France). However, another assumption based on death of infected *O. glabra* during their burying in the soil in summer (Rondelaud *et al.*, 2003) cannot be excluded.

In conclusion, the local *O. glabra* transplanted in Haute-Vienne are well adapted to their parasites. In other groups of transplanted snails, the adaptation to local parasites would be more progressive over time. This last finding might be due to progressive extension of paramphistomosis in central France (the first natural infections of *G. truncatula* with *P. daubneyi* were found in Haute-Vienne from 1995 and in south-eastern Brenne from 2003).

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