

# Relationships between the distribution of *Galba truncatula* (Gastropoda: Lymnaeidae) climatic conditions and the altitude of municipalities in Haute Vienne (France)

Gilles Dreyfuss\*, Philippe Vignoles and Daniel Rondelaud

Laboratory of Parasitology, Faculty of Pharmacy, 2, rue du Docteur Raymond Marcland, 87025 Limoges, France

Received: 11 January 2018; Accepted: 6 March 2018

**Abstract** – A retrospective study on 7407 populations of *Galba truncatula* found in the department of Haute Vienne for 37 years (1970–2006) was carried out to determine if altitude and climate on acid soils had an effect on the distribution of populations and the characteristics of their habitats. Out of a total of 13 478 water points surveyed in 179 municipalities, the overall frequency of snail populations was 54.9% but varied with the habitat type and the municipality on which these water points are located. The frequency of snail populations significantly decreased when the mean altitude of municipalities or their mean annual rainfall increased. Conversely, this frequency significantly increased with increasing mean annual temperature. The characteristics of habitats were analysed for 6281 populations in relation to the mean altitude of municipalities. The area of *G. truncatula* habitats and the density of overwintering snails per m<sup>2</sup> of habitat significantly decreased with increasing altitude. On the acid soils of Haute Vienne, the distribution of *G. truncatula* populations is closely related to the altitude and climatic conditions of municipalities.

**Keywords:** Altitude / climate / distribution / *Galba truncatula* / habitat / Haute Vienne

## 1 Introduction

The snail *Galba truncatula* O.F. Müller (Mollusca Pulmonata: Lymnaeidae) is known as the common intermediate host of the parasite *Fasciola hepatica* Linnaeus (Platyhelminthes Digenea: Fasciolidae) in numerous countries of the world (Torgerson and Claxton, 1999; Mas-Coma *et al.*, 2009). This lymnaeid has a large geographic range, including Africa, Asia, Europe and North America (Seddon *et al.*, 2015). In South America, this snail is also present in several countries and has reportedly been introduced from Europe (Bargues *et al.*, 2017). In France, the distribution of *G. truncatula* is still uncertain. According to Germain (1930/1931), the species was common throughout the country, but less widespread in south-eastern France and Corsica. The presence of many empty shells found in archaeological excavations during the past decades has confirmed this distribution of *G. truncatula* in France (Limondin and Rousseau, 1991; Guitter *et al.*, 2003; Granai *et al.*, 2011; Magnin and Bonnet, 2014), as shown on the map published by the National Museum of Natural History in Paris (Muséum National d'Histoire Naturelle, 2003–2017). However, this appears to have changed over time. The presence of the species is currently probable or real in many

departments, whereas its absence is probable or real in the Paris region, the Côtes d'Armor, Finistère, Ille et Vilaine, and Yonne (Muséum National d'Histoire Naturelle, 2003–2017). Knowing the distribution of the host snail in a given region therefore enables to specify the local characteristics of the disease in the definitive host and to better target the measures to be taken to control it.

The development of *G. truncatula* populations and, consequently, the transmission of *F. hepatica* are dependent on the climate in the country where lymnaeids live. The most favourable conditions are temperatures ranging between 10 and 25 °C and high relative humidity depending on atmospheric precipitations (Taylor, 1965). As a result, the disease is common in temperate regions like most European countries (Torgerson and Claxton, 1999). However, the existence of snail habitats also depends on geological formations and the topography of a land (Rapsch *et al.*, 2008). These last factors enable to determine whether or not snail habitats can be present in a given area (Ollerenshaw and Smith, 1969; Ollerenshaw, 1971). Climatic factors and soil conditions were used by several authors (Malone *et al.*, 1998; 2001; Malone and Yilma, 1999) to develop predictive models to estimate the risk caused by fasciolosis. Using different techniques including the Geographic Information System, endemic areas for fasciolosis were specified in different countries of the world like Ireland (Selemetas *et al.*, 2015), Sweden (Novobilský *et al.*, 2015),

\*Corresponding author: [gilles.dreyfuss@unilim.fr](mailto:gilles.dreyfuss@unilim.fr)

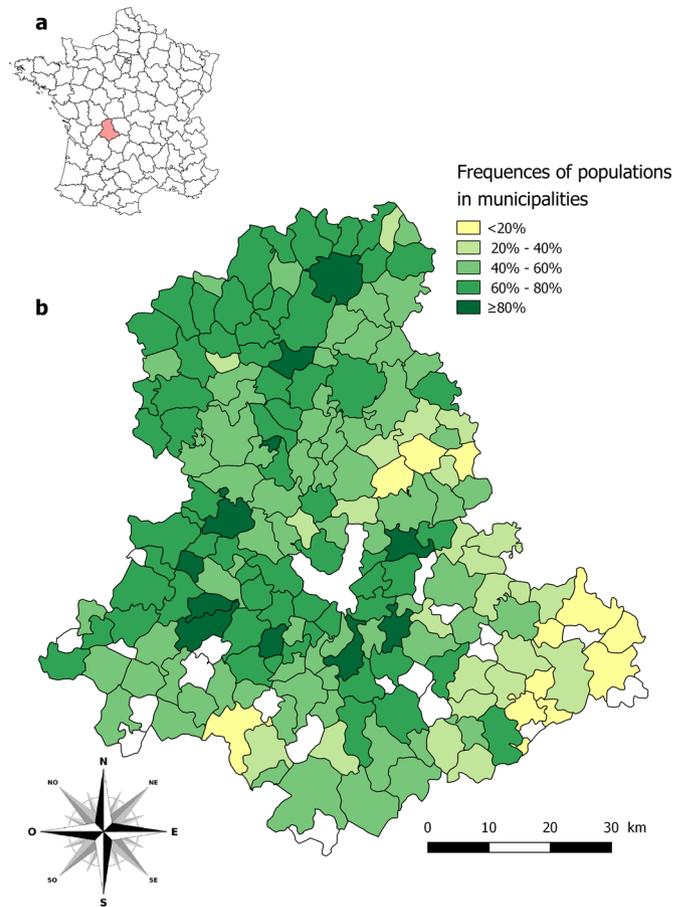
Switzerland (Rapsch *et al.*, 2008; Baggenstos *et al.*, 2016) or the United Kingdom (Fox *et al.*, 2011). Most models were mainly validated by means of surveys on the prevalence of *F. hepatica* infection in the definitive host (Malone *et al.*, 1998; Tum *et al.*, 2007). In contrast, those using data on the intermediate host are much less numerous (Rapsch *et al.*, 2008; Baggenstos *et al.*, 2016).

In Central France, the populations of *G. truncatula* were quite numerous on the cristallophyllian soils of Limousin. Seven habitat types have been described in this region by Vareille-Morel *et al.* (1999, 2007). The distribution of snail habitats according to their size and abundance of overwintering snails has been refined in subsequent works (Rondelaud *et al.*, 2011; Dreyfuss *et al.*, 2015). However, these results concern all the stations colonized by the lymnaeid on acid soils in the three departments of Limousin (Corrèze, Creuse, Haute Vienne) and one may wonder whether there were any variations in the number and characteristics of these habitats in relation to the geographic data and climatic conditions of the department. This assumption is based on the report by Vignoles *et al.* (2017). According to these authors, the prevalence of *F. hepatica* infection in *G. truncatula* significantly decreased in Haute Vienne with the increase in altitude or the decrease in the mean annual temperature of municipalities. In view of this result, the following two questions arose: did the populations of *G. truncatula* show variations in their number according to the relief and climate of the Limousin municipalities? Did the characteristics of their habitats also change in relation to the altitude of municipalities? To answer these two questions, a retrospective study was carried out on snails that our team collected between 1970 and 2006 in Haute-Vienne. This department was chosen for this study because of numerous samples of snails collected by our team in this area from the 1970s.

## 2 Materials and methods

### 2.1 Study area

The department is located in the north-western part of the Massif Central (Fig. 1). The latitude of this region ranges from 45°26' to 46°21' N, whereas its longitude ranges from 0°48' to 1°34' E. Its surface area is about 5520 km<sup>2</sup>. In this department, there are three larger districts: the Basse Marche (altitude, 150–300 m) in the northern third, the valleys of the Vienne river and its tributaries (altitude, 150–400 m) largely located in the central part, and the plateaus and mounts of Limousin (altitude, 300–777 m) along the eastern, south-eastern and south-western borders of the department (Chèvremont, 2008). The subsoil is mainly composed of granite or gneiss, with some outcrops of mica-schist or serpentinite. The result is the presence of numerous rivers (>7000 km). In the Basse Marche district, the pH of the water flowing through *G. truncatula* habitats ranges from 5.9 to 7.8 depending on the habitat type, with a mean value of 6.5 ± 0.8. When habitat altitude is increasing, the pH value decreases and varies from 5.6 to 6.8 in the Mounts of Ambazac, with a mean value of 6.1 ± 0.3. In contrast, the concentration of calcium ions dissolved in water showed great variations: 18.4 ± 5.7 mg/L in the Basse Marche district, and 6.7 ± 4.4 mg/L in the Mounts of Ambazac (Guy, 1996; Guy *et al.*, 1996).



**Fig. 1.** Geographic location of the department of Haute Vienne in France (a) and frequency of *Omphiscola glabra* populations according to 179 municipalities (b).

The continental type climate is attenuated by moist winds coming from the Atlantic Ocean. However, in its eastern part, the climate undergoes a mountainous influence due to the proximity of the Massif Central (Chèvremont, 2008). The Haute Vienne is predominantly rural and the human activity is mainly focused on livestock and forestry: this department comprises 168 000 ha of natural grassland and 149,996 ha of wood, which corresponds to 33.1% and 29.6% of its area, respectively.

### 2.2 Snail populations

Figure 1 shows the 179 communes on which the populations of *G. truncatula* involved in this study are located. The other 20 municipalities were excluded due to the low number of water points (see below) surveyed between 1970 and 2006.

Table 1 shows the different studies carried out by our team in the department of Haute Vienne during these 37 years and specifies the number of water points investigated. Most populations were identified between 1970 and 2006 in a total of 234 cattle- or sheep-breeding farms (Rondelaud *et al.*, 2011). Other populations were found (i) between 1986 and 1995 in 25 other farms to study experimental transplantations of snails into new potential habitats (Vareille-Morel *et al.*,

**Table 1.** Snail investigations performed for 37 years (1970–2006) in the department of Haute Vienne with indication of their purpose and the number of water points investigated.

Purpose of investigations	Stations	Number of water points investigated
Detection of snail habitats in 234 farms with a problem of animal fasciolosis	Grasslands and their vicinity (road ditches, ponds, streams, rivers)	7831
Experimental transplantations of snails in other 25 farms	Grasslands only	624
Mapping of snail populations in 106 municipalities in northern Haute Vienne	Mainly road ditches, ponds, streams and rivers	3606
Other investigations:		
Wild watercress beds at the origin of human fasciolosis cases	Small ponds, man-made basins	252
The Vienne river and its main tributaries	River banks	464
Other ponds and streams	Pond and stream banks	701
Total	–	13 478

**Table 2.** Stations investigated from 1970 to 2006 in the department of Haute Vienne and number of positive sites for *Galba truncatula*.

Type of stations	Number of sites investigated	Number of sites with snails (%)	Frequency (%)
Open drainage furrows	5232	3986	76.0
Springs (meadows)	1601	1176	73.4
Open drainage ditches	1539	525	34.1
Road ditches	2174	1138	52.3
Trampled areas	279	20	7.1
Pond banks	910	283	31.0
Brooks	903	184	20.3
River banks	840	95	11.3
Totals	13 478	7407	54.9

2002) and (ii) between 1998 and 2000 during another study to map the distribution of *G. truncatula* in the north of the department (Rondelaud *et al.*, 2000b). The remaining populations have been discovered in smaller studies focused on wild watercress beds, ponds, streams and rivers (Dreyfuss *et al.*, 1997; Rondelaud *et al.*, 2000a; Hourdin *et al.*, 2006).

Table 2 shows the total number of these populations, taking into account the type of their habitats. Most populations were found in swampy meadows: at the peripheral end of open drainage furrows (3986), along the main drainage ditch (525), around/in temporary or permanent springs, each surrounded by a rush bed (1176) or in cattle-trampled areas (20). Another group of 1138 populations was living in road ditches when a spring head is present. The other populations were identified on pond banks (283), in permanent streams measuring less than one metre in width (184) or on river banks (95).

### 2.3 Protocol of investigations

Snail habitats have been detected in March or April using the indicator plant method (Over, 1962) because the presence of these plants points out favourable conditions under which *G. truncatula* can live (Taylor, 1965). Six species: *Juncus acutiflorus* (Ehrhart) ex-Hoffmann, *Juncus effuses* Linnaeus,

*Lotus uliginosus* Schkuhr, *Agrostis stolonifera* Linnaeus, *Dactylis glomerata* Linnaeus and *Glyceria fluitans* (Linnaeus) R. Brown, were used as indicator plants. The first three were selected because they represented more than 75% of the plant species found by Ghestem *et al.* (1974) or Guy *et al.* (1996) in the swampy meadows of northern Haute Vienne. In road ditches, the two rush species, *A. stolonifera* and *G. fluitans* were chosen because of their predominance in the study by Jourdin *et al.* (1985) in the same area. On the banks of ponds, streams and rivers, *D. glomerata* and *G. fluitans* were chosen (Dreyfuss *et al.*, 1997; Hourdin *et al.*, 2006). The choice of March or April for these investigations was based on the following observations: (i) all points were watered during these two months, (ii) the vegetation was sufficiently developed for the identification of Poaceae species, (iii) the populations of *G. truncatula* were only composed of adult individuals of the overwintering generation, and (iv) no predation of *G. truncatula* by the land snail *Zonitoides nitidus* O.F. Müller occurred in March–April (this only occurs in June–July in grasslands on acid soils: Rondelaud, 1975; Rondelaud *et al.*, 2006).

When an indicator plant was found near a water point, the corresponding area was studied to detect the presence of the snail. If *G. truncatula* was observed, the abundance of the population was determined by counting overwintering snails

**Table 3.** Results provided by the Pearson's correlation test in the analysis of mean altitude, mean annual rainfall and mean annual temperature in the different municipalities of Haute Vienne. CI, confidence intervals.

Pearson's correlation coefficients (95% CI)			
Parameters	Mean altitude	Mean annual rainfall	Mean annual temperature
Mean altitude	1	0.794(0.726;0.846)***	-0.749(-0.812;-0.670)***
Mean annual rainfall	0.794(0.726;0.846)***	1	-0.735(-0.800;-0.652)***
Mean annual temperature	-0.749(-0.812;-0.670)***	-0.735(-0.800;-0.652)***	1

\*\*\*  $p < 0.001$ .

on the area of each habitat because this generation is mainly composed of adults (>4 mm shell height) in March or April. Depending on the water level, these snails were counted at sight or after their collection using a sieve (3 mm mesh size). Habitat detection and snail counting in each meadow were carried out by two people for 30–40 min. In road ditches and along the banks, these operations were carried out by a single person for 15–20 min per habitat. The area of each habitat was then determined. Measurement of areas occupied by snails was easy for furrows, ditches, ponds, streams and rivers. Snail habitats in springs and trampled areas were mapped and their area was determined based on geometric shape and size.

The number of water points investigated when conditions are favourable for snail life was dependent on the surface area of each municipality. This number was at least 60 points for each of the 108 small municipalities (<30 km<sup>2</sup>), 90–100 points for each of the 53 municipalities of intermediate size (31–50 km<sup>2</sup>) and 120 points or more for each of the 18 largest ones (>50 km<sup>2</sup>).

Species identification was performed on the morphology of the shell according to our experience on the lymnaeids. No molecular biology study was carried out during the period of snail investigations (1970–2006) to confirm this identification. In this study, snails present in each habitat were considered as one population.

## 2.4 Geographic and climatic data

The mean altitude of each municipality was obtained by considering that of its main city and was determined using the Carte-de-France website (<http://www.cartesfrance.fr>). As the mean altitude of these municipalities ranged from 160 to 570 m, we have used four categories of altitude (<300 m, 300–400 m, 401–500 m, and >500 m) to classify individual values provided by the study of several parameters. The other two variables were the mean annual rainfall and the mean annual temperature recorded in the 200 municipalities of Haute Vienne between 1971 and 2000. The latter data came from maps published by Météo France (Météo France, 2016). Five categories were used for mean annual rainfall (<900 mm, 900–1000 mm, 1001–1100 mm, 1101–1200 mm, and >1200 mm), whereas five other categories (<9.5 °C, 9.5–10 °C, 10.1–10.5 °C, 10.6–11 °C, and >11 °C) were used for the mean annual temperature.

## 2.5 Parameters studied

The first was the frequency of snail habitats in each municipality and was calculated using the ratio between the number of sites with live snails and the number of water points

detected by the presence of an indicator plant. The other two parameters were the surface area of each habitat and the density of overwintering snails per m<sup>2</sup> of habitat. They were only calculated for open drainage furrows, springs and road ditches because these snail habitats are the most numerous in Haute Vienne (a total of 6300, Tab. 2). As 19 of these habitats were occupied by a mixed community with *G. truncatula* and another lymnaeid (*Omphiscola glabra* O.F. Müller, *Stagnicola palustris* O.F. Müller) or a physid (*Aplexa hypnorum* Linnaeus), they were excluded from this study so that habitat characteristics were only calculated for 6281 populations of *G. truncatula*.

Values for altitude, annual rainfall and annual temperature were first subjected to a Pearson's correlation test to assess the degree of relationship between these three parameters. As the latter were highly correlated with each other (Tab. 3), the frequencies given in the above categories of altitude, annual rainfall or annual temperature were subjected to a simple linear regression instead of being processed by multiple linear regression. All frequencies are given with their 95% confidence intervals. Individual values noted for the surface area of habitats and the density of overwintering snails were also classified in the different categories as above, but only for the mean altitude of municipalities. They were averaged and standard deviations were established, whatever the habitat type. Normality of these last values was analysed using Shapiro-Wilk normality test (Shapiro and Wilk, 1965). As the distributions of these values were not normal, the Kruskal-Wallis test was used to establish levels of significance. We have also used the *pgirmess* r package (Siegel and Castellan, 1988) as a post-hoc test to do pairwise multiple comparisons. The different analyses were performed using the R 3.3.0 software (R Core Team, 2016).

## 3 Results

### 3.1 Frequency of snail populations

Out of a total of 13 478 water points surveyed in the 179 municipalities of Haute Vienne, the overall frequency of snail populations was 54.9% (Tab. 2). The highest frequency was noted at the peripheral extremity of open drainage furrows in grasslands (76.0%), followed by springs (73.4%), road ditches (52.3%), open drainage ditches (34.1%) and the banks of ponds (31.0%) by decreasing order. The frequency of snail populations in each of the other four habitat types was less than 25% (Tab. 2). However, this frequency also varied with the mean altitude of municipalities, as shown in Figure 1. Values

**Table 4.** Frequency of habitats occupied by *Galba truncatula* in the department of Haute Vienne between 1970 and 2006 in relation to different categories for the mean altitude, mean annual rainfall and mean annual temperature of municipalities.

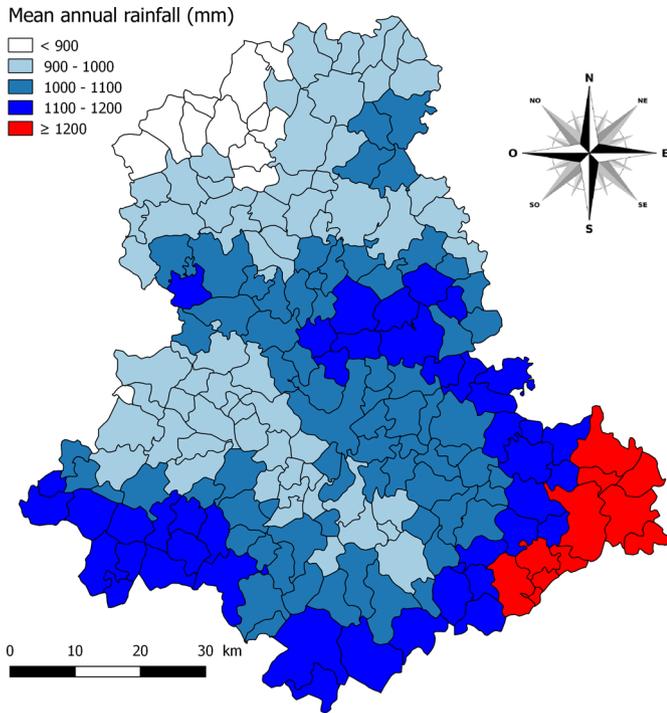
Parameter and categories	Number of habitats with <i>Galba truncatula</i>	Number of water points surveyed	Frequency (%) of snail habitats [95% confidence intervals]
<b>Mean altitude</b>			
<300 m	3721	5212	71.39 [70.10; 72.62]
[300;400 m[	2980	5415	55.03 [53.60; 56.36]
[400;500 m[	598	2067	28.93 [26.90; 30.94]
≥500 m	108	784	13.78 [11.40; 16.39]
Total	7407	13 478	54.96 [54.10; 55.80]
<b>Mean annual rainfall</b>			
<900 mm	511	755	67.68 [64.20; 71.01]
[900;1000 mm[	3166	4815	65.75 [64.30; 67.09]
[1000;1100 mm[	2371	4395	53.95 [52.40; 55.43]
[1100;1200 mm[	1172	2884	40.64 [38.80; 42.46]
≥1200 mm	187	629	29.73 [26.10; 33.47]
Total	7407	13 478	54.96 [54.10; 55.80]
<b>Mean annual temperature</b>			
<9.5 °C	7	54	12.96 [5.37; 24.90]
[9.5 °C;10 °C[	60	361	16.62 [12.90; 20.87]
[10 °C;10.5 °C[	563	1734	32.47 [30.20; 34.73]
[10.5 °C;11 °C[	2861	5479	52.22 [50.80; 53.55]
≥11 °C	3916	5850	66.94 [65.70; 68.15]
Total	7407	13 478	54.96 [54.10; 55.80]

**Table 5.** Values provided by a simple linear regression when used to calculate the relationship between the frequency of habitats with *Galba truncatula* and the mean altitude, mean annual rainfall or mean annual temperature in different municipalities of Haute Vienne. Abbreviation: df, degrees of freedom.

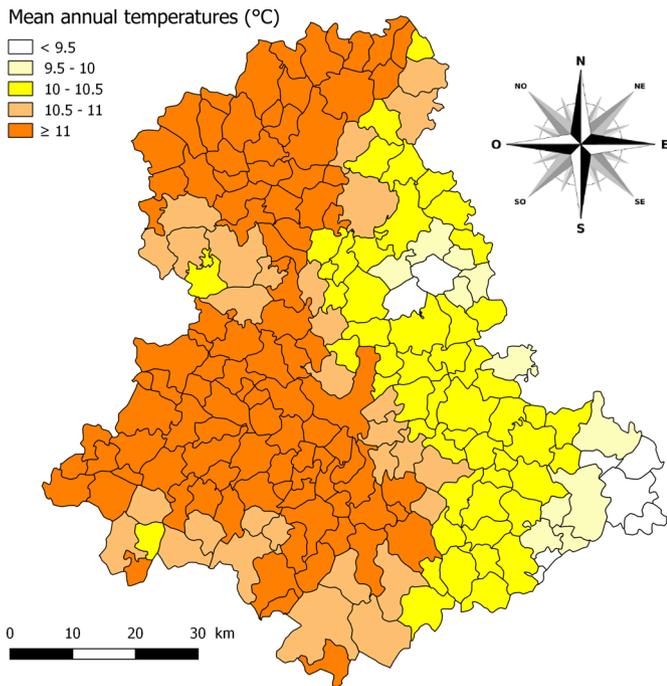
Equation and coefficients	Estimate	Standard error (S.E.)	95% confidence intervals	t value	p-value
<b>Frequency = a.altitude + b</b>					
a	$-1.79 \times 10^{-3}$	$8.83 \times 10^{-5}$	$[-1.96 \times 10^{-3}; -1.62 \times 10^{-3}]$	-20.26	$p < 0.001$
b	1.14	$3.03 \times 10^{-2}$	[1.08; 1.20]	37.70	$p < 0.001$
Residual S.E.: 0.106; df: 177					
Multiple $R^2$ : 0.699; adjusted $R^2$ : 0.697					
<b>Frequency = a.rainfall + b</b>					
a	$-1.07 \times 10^{-3}$	$1.17 \times 10^{-4}$	$[-1.30 \times 10^{-3}; -8.39 \times 10^{-4}]$	-9.161	$p < 0.001$
b	1.65	0.12	[1.41; 1.89]	13.65	$p < 0.001$
Residual S.E.: 0.159; df: 177					
Multiple $R^2$ : 0.322; adjusted $R^2$ : 0.318					
<b>Frequency = a.temperature + b</b>					
a	0.36	0.03	[0.31; 0.41]	14.46	$p < 0.001$
b	-3.40	0.27	[-3.94; -2.86]	-12.44	$p < 0.001$
Residual S.E.: 0.131; df: 177					
Multiple $R^2$ : 0.542; adjusted $R^2$ : 0.539					

above 80% were recorded in only 11 municipalities in the west and north of this department. In contrast, the lowest values (<20%) were noted for the municipalities (in pale yellow) located in the Mounts of Limousin located along the eastern, south-eastern and south-western borders of the department. Table 4 shows this decrease in frequencies with the increase in

altitude: from 71.3% in municipalities under 300 m to 13.7% in those above 500 m altitude. This decrease was significantly correlated ( $p < 0.001$ ) with the increasing altitude of municipalities, as shown in Table 5 (linear regression). This model can explain 69.7% of total variance in the frequency of snail populations.

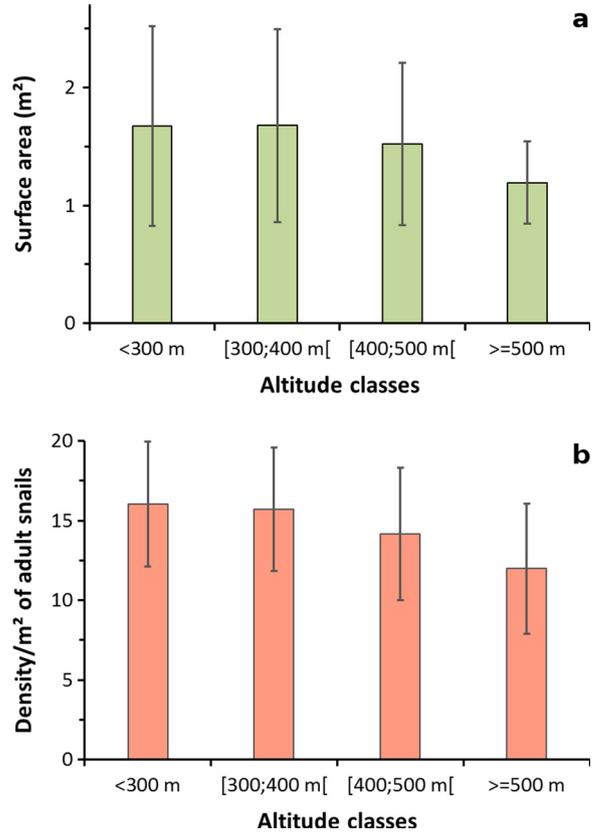


**Fig. 2.** Mean annual rainfall from 1971 to 2000 in the 200 municipalities of the Haute Vienne department.



**Fig. 3.** Mean annual temperature from 1971 to 2000 in the 200 municipalities of the Haute Vienne department.

Figure 2 shows variations in mean annual rainfall in the 200 municipalities of Haute Vienne. Annual rainfall was closely related to the mean altitude of the communes (Tab. 3). The lowest precipitations were noted in the communes at the northern limit of Haute Vienne and these values increased in



**Fig. 4.** Surface area of habitats (a) and density.m<sup>-2</sup> of overwintering snails (b) for 6281 populations of *Galba truncatula* identified between 1970 and 2006 in the department of Haute Vienne. These mean values and their SDs are presented for four altitude categories.

intensity towards the south of the department. The most abundant precipitations (>1200 mm per year) were noted in the communes on the eastern, south-eastern and south-western borders of the department where the Limousin Mounts are located. A significant relationship ( $p < 0.001$ ) between the decrease in the frequencies of snail populations and the increase in mean annual precipitations was noted, as shown in Tables 4 and 5. However, this model based on the annual precipitations can only explain 31.8% of total variance in the frequencies (Tab. 4). On the other hand, the mean annual temperature (Fig. 3) has an inverse distribution in the department, with the highest values in the municipalities located in the north and west, while the lower ones are on the eastern and south-eastern borders. There was also a positive and significant ( $p < 0.001$ ) relationship between the increase in frequencies and that of the mean annual temperature in municipalities (Tabs. 4 and 5). The latter model explains 53.9% of total variance in the frequencies (Tab. 5).

### 3.2 Characteristics of snail habitats

As altitude was the best factor to explain total variance in the frequency of snail populations, it was chosen to analyse potential changes in habitat area or the density of overwintering snails in relation to the relief of Haute Vienne. Figure 4 shows the mean values of the two parameters and their

standard deviations in relation to the four altitude categories. The surface area of *G. truncatula* habitats decreased significantly ( $H_3 = 52.59$ ,  $p < 0.001$ ) with the increase in altitude, ranging from  $1.67 \text{ m}^2$  in municipalities under 300 m to  $1.19 \text{ m}^2$  in those above 500 m (Fig. 4a). Apart from the difference between the mean values recorded in the <300 m and 300–400 m categories, the differences between the other categories were all significant. Similarly, the density of overwintering snails per  $\text{m}^2$  of habitat decreased significantly ( $H_3 = 166.85$ ,  $p < 0.001$ ) with the increase in altitude, ranging from  $16.0 \cdot \text{m}^{-2}$  in municipalities under 300 m to  $11.9 \cdot \text{m}^{-2}$  in those above 500 m (Fig. 4b). Pairwise comparison of mean densities revealed that all differences were significant.

## 4 Discussion

The results reported in the present study were mainly compared with those that Vareille-Morel *et al.* (2007) and Rondelaud *et al.* (2011) provided during their investigations in a total of 361 farms raising cattle or sheep on the acid soils of northern Corrèze, Creuse and Haute Vienne. The percentages reported in our study for the habitats with *G. truncatula* in open drainage furrows, springs and trampled areas are lower than those provided by Rondelaud *et al.* in 2011: 76.0%, 73.4% and 7.1% of water points investigated (Tab. 2), respectively, instead of 84.1%, 81.4% and 14.8% (out of 5546, 1454 and 233 water points for Rondelaud *et al.* in 2011). Conversely, the habitats located on the banks of watercourses (streams + rivers) are higher in our study (a total of 31.6%: Tab. 2, instead of 22.4%), while the percentages of snail habitats in open drainage ditches, road ditches and pond banks are close to each other. These variations in percentages must be reported to the stations studied because Rondelaud *et al.* (2011) carried out their investigations only in the meadows of 361 farms and their immediate vicinity, while our study focused on a higher number of water points located in 179 communes of Haute Vienne. These results demonstrate that swampy grasslands with their open drainage networks, springs and trampled areas were the best sites for the development of *G. truncatula* populations on the acid soils of Limousin: 81.6% of the 7709 habitats identified by Vareille-Morel *et al.* (2007) in this region. On the other hand, the banks of the main rivers constitute unfavourable habitats for this species, especially in the sections located to the east of the department (Dreyfuss *et al.*, 1997).

On the acid soils of Haute Vienne, the frequency of *G. truncatula* populations significantly decreased when the mean altitude of municipalities increased: from 71.3% in municipalities under 300 m to 13.7% in those above 500 m (Tab. 4). This decrease in frequencies was also noted when the mean annual rainfall increased or when the mean annual temperature decreased. This result is rather difficult to interpret due to a relative lack of information on this point in the literature. In South Africa, De Kock *et al.* (2003) reported results similar to ours by examining the distribution of 723 *G. truncatula* populations in relation to altitude, mean annual rainfall and mean annual temperature of habitats. According to these authors, temperature was an important determinant in the geographical distribution of the species, while altitude only had a limited role due to the diversity of landscapes and

climatic conditions (De Kock *et al.*, 2003). The decrease in the number of populations noted in the present study above 500 m altitude may be due to the effect of temperature alone on the development of *G. truncatula*, as a minimum temperature of  $10^\circ\text{C}$  is required for the growth of the snail (Kendall, 1953; 1965). Two arguments support this approach: (i) the existence of a single annual generation for *G. truncatula* (instead of two per year usually in lowlands) in the department of Creuse, near Haute Vienne, above 500 m (Rondelaud and Mage, 1992) or in the French Jura and Alps when altitude rises (De Massias *et al.*, 1996); (ii) the slower development of *F. hepatica* larval forms in *G. truncatula* in the alpine regions of Switzerland: up to two years for Eckert *et al.* (2005). But the foregoing explanation is far from satisfactory and another factor must be sought to explain this decrease in *G. truncatula* populations in Haute Vienne above 500 m altitude. In fact, the snail has already been observed at higher altitudes in Western Europe: up to 1200 m in the French Jura (De Massias *et al.*, 1996), 2100 m in Switzerland (Eckert *et al.*, 1975) and 2600 m in the French Alps (De Massias *et al.*, 1996) and the Pyrenees (Combes, 1968). Under these conditions, it is necessary to assume the existence of specific ecological conditions for *G. truncatula* in the municipalities of Haute Vienne. One of these factors could be the abundance of peat bogs found above 500 m altitude in the Limousin region: 2359 in the Corrèze, Creuse and Haute Vienne departments, sometimes extending over 12 hectares or more (Conservatoire d'Espaces Naturels du Limousin, 2012). According to Allée *et al.* (1997), this high frequency of peat bogs on these acid soils would be linked to the disappearance of many forests in the Limousin watersheds over the centuries and, consequently, to water accumulation in these areas due to changes in water circulation. However, another explanation based on the predominance of conifers in areas above 500 m altitude and the effect of their needles on the acidification of runoff (Hornung, 1985) cannot be completely excluded.

The characteristics of *G. truncatula* habitats located in open drainage furrows, springs and road ditches significantly decreased with increasing altitude of municipalities. In those under 300 m, the mean surface area of snail habitats was  $1.67 \text{ m}^2$  and gradually decreased up to  $1.19 \text{ m}^2$  in municipalities above 500 m (Fig. 4a). This result must be related to the type of habitat found in the municipalities studied according to altitude. Habitats in road ditches were numerous under 400 m altitude. Their number sharply decreased between 400 and 500 m altitude to be very low above 500 m. As the habitats located in these ditches may have an area exceeding  $5 \text{ m}^2$  on the acid soils of Limousin (Rondelaud *et al.*, 2011), the decrease in their number from 400 m altitude may explain the smaller areas that we noted between 400 and 570 m. The decrease in the density of overwintering snails per  $\text{m}^2$  of habitat can partly be explained by the winter conditions, which are more severe in municipalities above 500 m altitude than in those with lower altitude, which would have a negative effect on the survival of overwintering snails. Another assumption is that the lower density of overwintering snails noted above 500 m altitude would be due to more acid soils. This latter hypothesis is supported by the low pH values in running water (pH 5.4–5.6) noted in several habitats of *G. truncatula* in the Mounts of Ambazac and those of Limousin (Rondelaud, personal observation).

In conclusion, the distribution of *G. truncatula* populations on the acid soils of Haute Vienne is closely related to the relief and climatic conditions of municipalities. Their number showed a gradual decrease when the mean altitude and mean annual rainfall of municipalities are increasing, or when the mean annual temperature is decreasing. The characteristics of snail habitats also showed the same decrease with the increase in altitude. Further observations are needed to confirm these results in other French regions or other temperate countries on acid soils.

**Acknowledgements.** The authors gratefully thank M. Abrous, D. Bouix-Busson, B. Didier and C. Vareille-Morel for providing their data on the snail populations they have investigated in the Haute Vienne department during their studies. They are also grateful to several PharmD students: C. Apostoloff, L. Farge, C. Granet, D. Guichard, F. Guy, C. Lacourarie, S. Nauche, L. Vareille and F. Xuereb, for their assistance in the field.

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**Cite this article as:** Dreyfuss G, Vignoles P, Rondelaud D. 2018. Relationships between the distribution of *Galba truncatula* (Gastropoda: Lymnaeidae) climatic conditions and the altitude of municipalities in Haute Vienne (France). *Ann. Limnol. - Int. J. Lim.* 54: 19