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## Ecology of the meadow spittlebug *Philaenus spumarius* in the Ajaccio region (Corsica) – I: Spring

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**Short title:** Ecology of *Philaenus spumarius* in Corsica

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**Abstract:** The meadow spittlebug, *Philaenus spumarius* (L.) (Hemiptera: Aphrophoridae), is the main vector in Europe of the recently detected plant pathogen bacterium *Xylella fastidiosa* Wells et al. (Xanthomonadales: Xanthomonadaceae). While the ecology of continental populations is well documented, nothing is known about the insular populations of *P. spumarius*, such as in Corsica, where the bacterium was detected in 2015. Hence, in an epidemiological context, the ecology of *P. spumarius* has been studied in a maquis landscape in the Ajaccio region between 2017 and 2019. Adults and nymphs were almost exclusively collected on *Cistus monspeliensis* L. (Cistaceae). However, very few specimens were collected

25 in summer, suggesting a movement of the adults to sheltered habitats. Unfortunately, despite  
26 several trapping methods used, the location adult summer habitat remains unknown for the  
27 studied population. It might be tempting to destroy the central plant host of *P. spumarius*  
28 populations. However, as spittlebug nymphs are highly polyphagous on low-growing plant  
29 species and as the females can lay eggs in any dead plant tissues, such practice could have a  
30 limited the impact. Instead, the strong relationship between *P. spumarius* and *C. monspeliensis*  
31 could be used to monitor spittlebug populations, to limit/concentrate the means of insect  
32 control, or in an agronomic context to lure insects away from crops. Maintaining natural  
33 arboreal vegetation around agronomic systems could help decrease insect abundance – and  
34 potentially, pathogen load – on cultivated species. Such hypotheses need to be further studied  
35 by landscape experiments.

36

37 **Key words:** host plant diversity; host plant palatability; *Cistus monspeliensis*; summer habitat;  
38 sex ratio; nymphs behaviour

39

## 40 **Introduction**

41 The Aphrophoridae (Hemiptera) is a relatively poorly diversified family, with about 900  
42 described species worldwide, most of them inhabiting tropical regions (Richards & Davies,  
43 1977; Shih & Yang, 2002). In Europe, this family is represented by about 29 species (Jach,  
44 2013), of which only six are present in Corsica (Chauvel *et al.*, 2015; Albre & Gibernau, 2019).  
45 The meadow spittlebug, *Philaenus spumarius* (L.), is the most widespread species and can be  
46 found in the whole Palearctic region from Western Europe to Russia. The ecological plasticity  
47 of *P. spumarius* has enabled the spittlebug to be successful in various non-native regions such  
48 as Japan, North America (USA, Canada), Hawaii and New Zealand (Yurtsever, 2000b). It  
49 harbours such extremely variable dorsal colours and patterns that up to 16 phenotypes have  
50 been described. The genetic basis of this phenotypic diversity was thus intensively studied and  
51 relationships with several ecological constraints (climatic conditions, predation, or habitat  
52 composition) were found (Halkka *et al.*, 1973; Stewart & Lees, 1988; Yurtsever, 2000a;  
53 Rodrigues *et al.*, 2016; Borges *et al.*, 2018). In Europe, *P. spumarius* is actually studied mainly  
54 for hosting the Latin American bacterium *Xylella fastidiosa* Wells *et al.*, which was detected  
55 for the first time in Southern Italy (Salento, Puglia region) in 2013 (EPPO, 2013). Since then,  
56 this bacterial phytopathogen has been responsible for the death of thousands of olive and  
57 almond trees in the western Mediterranean region. In Italy, olive growers have already lost  
58 between 0.2 and 0.6 billion Euros in investments and, according to the different economic  
59 model, the premature death of the olive trees could cost between 1.9 and 5.2 billion Euros over  
60 the next 50 years if no resistant trees are developed (Schneider *et al.*, 2020). With hundreds of  
61 host plants recorded worldwide, *X. fastidiosa* is considered as a major threat for European flora  
62 (EFSA, 2018). While initially introduced via infected ornamental trees (e.g. coffee trees), it has  
63 been demonstrated that *P. spumarius* was the main vector of the bacterium in Europe,  
64 propagating efficiently the bacterium to a wide diversity of native, ornamental and cultivated

65 plant species (Saponari *et al.*, 2014; Cornara *et al.*, 2017). The ecology of *P. spumarius* has thus  
66 been intensively studied in this epidemiological context, particularly in European continental  
67 populations developing in cultivated areas. The adults can be observed from the end of spring,  
68 after the last molt, to the end of autumn (Yurtsever, 2000b). However, in some populations,  
69 adults find refuge in cool habitats, usually in the shady and humid foliage of the surrounding  
70 shrubs and trees. This behavior mainly concerns populations subjected to (extreme) drought  
71 and warm conditions, most often in the southernmost parts of the distribution area (Drosopoulos  
72 & Asche, 1991; Drosopoulos *et al.*, 2010). This sheltering phase, where it exists, ends at the  
73 end of summer – early autumn. Egg laying, induced by the daylight shortening and lower  
74 temperatures (Stewart & Lees, 1988), occurs in autumn on plants of the lower vegetation layers  
75 (herbaceous and small shrubs). Females can produce between 350-400 eggs, in clutches of up  
76 to 20 eggs aggregated in a cement-like secretion. Eggs are laid either directly on suitable host  
77 plants, or on dead plant tissues (Yurtsever, 2000b). The eggs of *P. spumarius* hatch in early  
78 spring after an overwintering period (Nickel & Remane, 2002). Nymphs produce a  
79 characteristic spittle mass on the leaves or on the twigs of the plants inside which they are  
80 protected against predators and desiccation. Highly polyphagous, nymphs consume xylem sap  
81 and can develop on almost any available plant, with a preference for the youngest tissues of  
82 herbaceous plants and small shrubs. When mature at the end of spring, they set up a cavity in  
83 the spittle mass in which they molt into imagoes. As with the nymphs, adults are highly  
84 polyphagous, with hundreds of host plants recorded worldwide, belonging to a wide diversity  
85 of families from grasses to trees, including conifers (Yurtsever, 2000b; EFSA, 2018).

86 While *P. spumarius* is present in the whole Mediterranean region including the islands, such as  
87 Corsica, Sicily, Sardinia, the Balearic Islands and Crete, defined ecological parameters are  
88 almost exclusively based on continental populations developing in agricultural landscapes  
89 (Yurtsever, 2000b; Cornara *et al.*, 2018; Morente *et al.*, 2018; Bodino *et al.*, 2019; Dongiovanni

90 *et al.*, 2019). However, field surveys in Corsica highlighted that the adults of *P. spumarius*  
91 collected were found almost exclusively on a single plant species – *Cistus monspeliensis* L. –  
92 which is an unusual observation for this highly polyphagous species (Chauvel *et al.*, 2015;  
93 Cruaud *et al.*, 2018). In order to contribute to the knowledge of the epidemiology of *X.*  
94 *fastidiosa*, we studied the ecology and biology of the meadow spittlebug in a non-agricultural  
95 maquis habitat with weak anthropogenic perturbations. We present original data on one insular  
96 population of *P. spumarius* from South-West of Corsica near Ajaccio. The abundance and  
97 temporal variation of this spittlebug species was studied as well as the host plant diversity and  
98 palatability for the nymphs during their ontogenesis. Finally, the mobility of the adults among  
99 vegetation strata was studied during emergence, using different trapping experiments. Our  
100 specific questions were: (1) is *P. spumarius* specialized on *C. monspeliensis* as suggested by  
101 previous field surveys (Chauvel *et al.*, 2015; Cruaud *et al.*, 2018)?; (2) does the plant-host  
102 specialization, if any, concern adults and/or nymphs?; and (3) does *P. spumarius* find refuge in  
103 a sheltered habitat during summer since Corsica, beside been an island, belongs to the southern  
104 range of its distribution?

105

## 106 **Materials and methods**

### 107 **1. Survey**

108 The studied site is located near the University campus outside of Ajaccio (GPS coordinates:  
109 41.913492N, 8.655433E). The habitat is a typical thermomediterranean shrubby vegetation (i.e.  
110 maquis) dominated by *Pistacia lentiscus* L. (Anacardiaceae), *Cytisus laniger* (Desf.) DC.  
111 (Fabaceae) and *Cistus monspeliensis* with sparse trees *Olea europaea* L. (Oleaceae) and  
112 *Arbutus unedo* L. (Ericaceae) and weak anthropogenic perturbations during the past 35 years.  
113 A 34-month-long survey (from March 2017 to December 2019) was conducted in ~1100 m<sup>2</sup>  
114 maquis habitat to record the temporal population pattern of adults of *Philaenus spumarius*.

115 Simultaneously, the Auchenorrhyncha fauna present in the locality, belonging mainly to the  
116 Cicadellidae and Issidae families, were collected. Every 2-3 weeks, insects present in the low  
117 (under 120 cm) and high (above 120 cm) vegetation strata were separately collected using a  
118 sweep-net; a 20 minutes sampling was conducted in both strata. In total, 54 insect samples were  
119 collected for each vegetation stratum. At our studied site, the low vegetation stratum  
120 corresponded to the herbaceous and shrub species such as *Cistus monspeliensis*, *C. creticus* L.  
121 (Cistaceae) and *Myrtus communis* L. (Myrtaceae). The high vegetation stratum corresponded  
122 to trees mainly *Olea europaea*, *Arbutus unedo*, *Pistacia lentiscus* and *Phillyrea* L. spp.  
123 (Oleaceae). All the insects were identified and sexed by examining their genitalia under  
124 dissecting microscope (Albre & Gibernau, 2019).

125

## 126 **2. Adult ecology and behaviour**

127 Different experiments were performed soon after the emergence of *P. spumarius* adults, during  
128 the period when extremely few specimens were collected using the sweep-net approach. In order  
129 to verify whether the adults of *P. spumarius* took refuge in the tree foliage, intensive sweep-net  
130 captures were thus performed up to 6 meters high in 10 trees for each main species of the studied  
131 area, *Olea europaea*, *Arbutus unedo* and *Pistacia lentiscus*.

132 Interception traps were also used in order to passively capture the adults during the same period  
133 (soon after their emergence) and to study their mobility. We thus placed 54 yellow sticky traps  
134 (25 x 11 cm) in the low vegetation stratum, including grasses, *Cytisus laniger*, *C. monspeliensis*  
135 and *Myrtus communis* and in the high vegetation stratum, including *Arbutus unedo*, olive trees,  
136 *Pistacia lentiscus* and *Phillyrea* sp., close by or in the foliage of each species. The experiment  
137 was performed from May 25 to June 28, 2018, i.e. soon after adults emerged in our study site,  
138 when adult movements were more likely. Traps were checked every 3 days, and the insects  
139 identified and counted, using stereo microscope when necessary.

140 In order to verify whether adults were looking for shady and humid habitats to survive the  
141 summer conditions, we constructed shelters consisting of two green overlaid sticky plates of  
142 cardboard separated by 2 cm; a recipient filled with water was placed between the plates. This  
143 artificial system was supposed to represent a shaded and relatively humid (micro-)habitat as the  
144 natural reported shelter required for the survival of *P. spumarius* in summer.

145 The nymphs of *P. spumarius* produce conspicuous self-generated white foam nests in which  
146 they obligatory develop, from early February to the end of April. As neonate nymphs are  
147 relatively immobile, it has been considered that these foams could constitute a proxy to identify  
148 the females' choice for egg laying. We thus recorded the presence or absence of foams on all  
149 the plants of the studied area in early spring. In order to understand the progression of the foam  
150 distribution in the habitat throughout the season, foam presence or absence and the number of  
151 foams per plant were recorded along a 100 m long transect from March 9<sup>th</sup>, when most of the  
152 foams were visible, through April 24<sup>th</sup>, before the emergence of the adults. The range of  
153 movement exhibited by medium to full-sized nymphs was estimated by placing nymphs on a  
154 flat surface covered with paper. Fully exposed and deprived of food, nymphs searched for a  
155 plant and released some humidity on the paper, allowing us to follow their (sinuous) tracks.  
156 This experiment was repeated with 73 nymphs (body size range: 2.86-5.98 mm) and movement  
157 was tracked for 20 minutes trials.

158

### 159 **3. Nymph behaviour and survival**

160 Once per week from March 15<sup>th</sup> to May 3<sup>rd</sup>, 2017, which was near the end of the season during  
161 which foams were present in our studied site, 13 foams from the same area were sampled  
162 randomly. All the nymphs contained within the foams were counted and their body length  
163 measured using a stereo microscope.



164 In order to verify the polyphagy of the nymphs of *P. spumarius*, development experiments were  
165 performed by bagging the foliage of different plant species in the presence of natural foams or  
166 by transferring single neonate nymphs (all collected on *C. monspeliensis*) on a suite of the  
167 aforementioned plant species. Success was considered when the nymph completed its  
168 developmental cycle into an adult.

169

#### 170 4. Data analyses

##### 171 *Survey*

172 The abundances of *P. spumarius* in the vegetation strata were studied by comparing the number  
173 of individuals captured in low or high plants (Chi square test). Temporal variations of the  
174 number of adults (male or female) or the sample sex ratios were tested by fitting linear  
175 regressions. The mean sex ratio of the samples were also compared among seasons with a non  
176 parametric test (Kruskall-Wallis).

##### 177 *Nymphs*

178 The temporal variations of nymph number or size per foam in natural conditions were tested  
179 with linear regressions. The nymph travelled distance in laboratory conditions were also tested  
180 for linear relationship with their size.

181 All statistical analyses were performed with the statistical software Past 4.02 (Hammer *et al.*,  
182 2001).

183

184 **Hammer, Ø., Harper, D.A.T., Ryan, P.D.** (2001) PAST: Paleontological statistics software  
185 package for education and data analysis. Palaeontologia Electronica 4(1): 9pp. [http://palaeo-  
186 electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-<br/>186 electronica.org/2001_1/past/issue1_01.htm)

187

## 188 **Results**

## 189 1. Survey

### 190 a. Relative abundances

191 Among the 1848 Auchenorrhyncha specimens collected during the survey (fig. 1), the  
192 Aphrophoridae *Philaenus spumarius* was the most abundant species (n = 653; 35%), followed  
193 by the Cicadellidae *Euscelis lineolata* Brullé (n = 442; 24%) and the Issidae *Latilica maculipes*  
194 (Melichar) (n = 164; 9%). The only other known potential vector of the bacterium *Xylella*  
195 *fastidiosa* in the studied area was the species *Neophilaenus campestris* (Fallén)  
196 (Aphrophoridae), which accounted for only 1% (n = 10) of the total collected specimens. The  
197 total diversity list of Auchenorrhyncha present in the studied site represented 37 species  
198 including three alien species for Europe (Albre & Gibernau, 2019).

199

### 200 b. Temporal pattern of *Philaenus spumarius* population

201 An annual pattern was observed, with 2 main peaks of adult abundances: in spring, from late  
202 April to the end of June, and in autumn, from early October to the end of November (fig. 2,  
203 green bars). The second peak abundance was the most important one in terms of number of  
204 insects collected, representing 72%, 79% and 75% of the specimens collected in 2017, 2018  
205 and 2019, respectively. Thereafter, the number of adults reduced during the survey (range: 0-3  
206 individual(s) captured) in summer and increased massively only in autumn.

207 The annual temporal pattern of *P. spumarius* appeared to be different from the mean  
208 Auchenorrhyncha pattern (fig. 2, blue shaded curve). In spring, *P. spumarius* and the other  
209 Auchenorrhyncha species presented a peak of abundance. On the contrary in autumn, *P.*  
210 *spumarius* presented its maximum abundance, while the Auchenorrhyncha community is  
211 strongly decreasing or at its minimum abundance.

212

### 213 c. Vegetation strata

214 Overall, the adults of *P. spumarius* were far more abundant in the low vegetation stratum than  
215 in the high one, as up to 90.5% (n = 591) of specimens were collected from low-level vegetation  
216 (table 1). This habitat preference was even more important between July and December, with  
217 more than 96.6% of the insects being collected on low plants (< 120cm) during all three years  
218 of the survey. Interestingly, the insect's low vegetation tendency was less pronounced between  
219 January and June when 76.7% and 74.4% of the adults of *P. spumarius* were collected on low  
220 plants in 2018 and 2019, respectively. No significant difference was found in the number of  
221 adults of *P. spumarius* captured between January and June 2017 on low and high plants ( $\text{Chi}^2_1$   
222 = 0.05,  $p = 0.83$ ). It is also important to note that in the low vegetation stratum of the studied  
223 area, the insects were almost exclusively collected on plants of *Cistus monspeliensis*.

224

225

#### 226 **d. Sex-Ratio**

227 The number of males and females were strongly positively related (fig. 3;  $R^2 = 0.86$ ,  $p = 3.7 \times$   
228  $10^{-4}$ ), and there was no major sex ratio bias (line slope not different from one,  $F_{1,105} = 0.11$ ,  $p =$   
229  $0.74$ ). The only sample with a significant biased sex ratio was on November 22<sup>th</sup> 2018 with 21  
230 males and 40 females ( $\text{Chi}^2_1 = 6.03$ ,  $p = 0.014$ ).

231 There was a strong seasonal effect on sex ratio (fig. 4) independent of sample sizes and despite  
232 large variation (Kruskal-Wallis:  $H(\text{Chi}^2) = 12.6$ ,  $p = 0.005$ ) with winter and summer periods  
233 presenting significantly lower male proportions ( $13.3 \pm 23.1\%$  and  $19.8 \pm 28.6\%$  respectively)  
234 than during the spring and autumn periods ( $57.6 \pm 25.8\%$  and  $52.7 \pm 13.8\%$  respectively).

235

## 236 **2. Adults ecology**

### 237 **a. Summer adult habitat**

238 Only 3 adults of *P. spumarius* were collected during all the summer using the different trap  
239 systems specifically designed, suggesting they were not adapted (table 2). Sweep-net captures  
240 at about 6m high in the foliage of the 30 trees present in the vicinity of the surveyed area resulted  
241 in 217 insects, most of them (95.4%) belonging to the Cicadellidae family. Only 3 adult  
242 specimens of *P. spumarius* were collected on *Arbutus unedo* (n = 2) and olive tree (n = 1).  
243 Similarly, the yellow sticky traps placed in the surveyed site, both in the trees and in the low  
244 vegetation, trapped mainly Cicadellidae specimens (n = 252; 99.2%); no *P. spumarius* was  
245 trapped. Finally, only 1 insect (Cicadellidae) was collected in the shaded sticky shelters,  
246 suggesting the latter were not well-adapted to attract Auchenorrhyncha.

247

#### 248 **b. Host plants diversity for foams**

249 Our survey was performed during the early ontogenesis of *P. spumarius* (e.g. small sized foams)  
250 when neonate nymphs were hardly mobile. Hence, we hypothesised that the foam distribution  
251 reflected female host choice for oviposition. Among the 3672 plants included in our survey that  
252 belonged to 37 species, we recorded foams in 977 individual plants and 10 different plant  
253 species (fig. 5). However, most of the foams were observed on two Cistaceae species, namely  
254 *C. monspeliensis* (93.2%) and *C. creticus* (3.3%). A few foams were also observed on  
255 Asteraceae (*Dittrichia viscosa* (L.) Greuter, *Urospermum dalechampii* (L.) Scop. ex F.W.  
256 Schmidt, *Senecio vulgaris* L. and *Sonchus oleraceus* L.), Fabaceae (*Cytisus laniger*),  
257 Lamiaceae (*Lavandula stoechas* L.), Anacardiaceae (*Pistacia lentiscus*) and Ericaceae (*Arbutus*  
258 *unedo*). It is worth noting that foams were only present on *P. lentiscus* and *A. unedo* when  
259 foliage contacted with leaves of *C. monspeliensis* harbouring foams.

260 Moreover, up to 52% of the *C. monspeliensis* (1737 plants observed) and 13% of the *C. creticus*  
261 (246 plants observed) specimens were observed to harbour at least one foam (fig. 5). Foams

262 were also recorded on 40% of the *Urospermum dalechampii* (Asteraceae) specimens, but only  
263 15 individuals were observed in the studied area.

264

### 265 **3. Nymphs**

#### 266 **a. Foam density**

267 While in early March all of the observed foams were exclusively found on *C. monspeliensis*,  
268 this proportion decreased at the end of April (86%), with foams also appearing on *C. creticus*,  
269 *Dittrichia viscosa* and on other plant species (table 3a). Interestingly, this decrease of the  
270 proportion of foams on *C. monspeliensis* was accompanied by an increase of the proportion of  
271 *C. monspeliensis* plants (51%) hosting at least one foam (table 3b).

272

#### 273 **b. Nymphal development**

274 During the first month of spring, the body size of the nymphs increased regularly from 2.3mm  
275 to about 5.3mm, but then remained relatively constant over the last month of development (fig.  
276 6 – blue curve). We were not able to correlate body size differences with the different known  
277 nymphal instars of *P. spumarius*.

278 The number of nymphs per foam appeared to be significantly negatively correlated with the  
279 size of the nymphs ( $R^2 = 0.62$ ,  $P = 0.020$ ; fig. 6 – orange curve), with  $1.86 \pm 1.35$  neonate  
280 nymphs per foam in mid-March and  $1.08 \pm 0.86$  nymph per foam in early May. Up to 6 nymphs  
281 were found in the same foam in one occasion.

282

#### 283 **c. Nymphs capacity movement**

284 When removed from their foam and deposited on a flat paper surface, nymphs walked an  
285 average of 38.5 cm in 20 minutes; the maximum distance travelled was 89 cm (fig. 7). No  
286 relationship was found between the nymph size of the nymphs and the distance travelled ( $R^2 =$

287 0.022). The distribution of distances travelled is clearly not unimodal, but instead seems  
288 multimodal, with many spittlebugs travelling either short or relatively longer distances (fig. 7).  
289

#### 290 **d. Host plants of the nymphs**

291 In total, 158 neonate nymphs were individually collected from *C. monspeliensis* and manually  
292 transferred to and bagged on one of 15 common plant species at the studied site (table 4). The  
293 manual depositions of nymphs on the Cistaceae *C. monspeliensis*, the main natural host plant  
294 of *P. spumarius* in Corsica, but also on *C. creticus* resulted in 100% full development into  
295 adults. Hence, it can be considered that manual depositions had an insignificant effect on the  
296 survival and development of the nymphs; and that observed survival differences were likely  
297 due to differences in host plant palatability rather than to experimental effects. Asteraceae  
298 species also appeared to be average to excellent host species for nymphs of *P. spumarius*, with  
299 success rates ranging from 54% to 100% according to the species (table 4). On the other hand,  
300 *Plantago* L. species (Plantaginaceae) and *Cytisus laniger* appeared not to be very suitable host  
301 species with only 33-50% of the nymphs completing their development. Similarly, the  
302 strawberry tree, *Arbutus unedo* (Ericaceae), was also not a good host plant with only 10% of  
303 nymphal developmental success. At last, it was not possible to obtain any adult from nymphs  
304 on the other tested trees *Pistacia lentiscus* and *Olea europaea* or the perennial herb *Asphodelus*  
305 *ramosus* L. (Asphodelaceae).

306

## 307 **Discussion**

### 308 **Survey**

309 A survey of the Auchenorrhyncha fauna was performed over 3 consecutive years in a maquis  
310 landscape of the Ajaccio region of Corsica. Our main focus was on the Cicadellidae,  
311 Aphrophoridae, Issidae and Tettigometridae families. A total of 1848 adult specimens  
312 belonging to 32 species was recorded (Albre & Gibernau, 2019). The Cicadellidae was the most  
313 diversified family (27 species) and accounted for 50.1% of the Auchenorrhyncha fauna, with  
314 *Euscelis lineolata* the most represented Cicadellidae species (47.7% of the specimens). While  
315 poorly diversified (3 species), it appeared that the Aphrophoridae represented 35.9% of the  
316 collected insects and was almost exclusively represented by one species, *Philaenus spumarius*  
317 (98.5% of the Aphrophoridae). The Issidae (4 species and 11.1% of the collected insects) was  
318 mainly represented by *Latilica maculipes* (79.6% of the Issidae). Finally, with only 2.9% of the  
319 collected insects and 3 species, the Tettigometridae was the least represented family in the  
320 Ajaccio region (Albre & Gibernau, 2019).

321 A cyclic pattern of abundances was observed over the three years of survey, with a general peak  
322 of abundances from early April to the end of May, corresponding to the general plant blooming  
323 in spring, leaving few active insects into summer (July and August), which are the warmest and  
324 driest weeks of the year. In autumn, from early October to the end of November, *P. spumarius*  
325 “reappeared” in high abundances in the surveys and created a second peak, much more  
326 important than the first one and accounting for 61-81% of the total Auchenorrhyncha  
327 community in the habitat. However, the vertical distribution of *P. spumarius* in the vegetation  
328 differed according to the season. While 51.2-76.7% of the individuals were collected in the  
329 lower stratum in the spring, low vegetation contained 96.6-97.3% of all *P. spumarius*  
330 throughout the autumn peak. This habitat preference suggests that at the end of May / early  
331 June, the young adults left their nymphal habitat, corresponding to the lower stratum of the

332 vegetation (< 120cm, cf later), and disappeared from the vegetation till the end of September.  
333 Then, adults reappeared in the lower vegetation and could be observed in high numbers till the  
334 end of November. The transitional phases, i.e. the disappearance from and the return to the  
335 lower stratum, were rapid phenomena (less than 2 weeks), making it difficult to determine in  
336 what type of habitat the adults spend the summer period. A similar pattern of abundances has  
337 already been recorded for *P. spumarius* in different parts of its distribution range, particularly  
338 in the southernmost areas. In summer, adults were often captured in shrubs and trees in Italy,  
339 Greece, Spain or Turkey, but most often in low numbers (Yurtsever, 2001; Drosopoulos, 2003;  
340 Cornara *et al.*, 2017; Morente *et al.*, 2018).

341 The sex ratio with even males: females remained relatively constant in all samples throughout  
342 the year (fig. 3), which is consistent with the literature (Bodino *et al.*, 2019). Only one sample  
343 had a significantly biased sex ratio, 40 females to 21 males, on November 22<sup>th</sup>; interestingly  
344 this date corresponded to the period when the annual adult cycle of *P. spumarius* ended (fig. 2).  
345 When pooling the capture samples per season, a significant sex ratio difference was observed  
346 (fig. 4). In winter (January-March) and summer (July-September) four times more females were  
347 captured than males, suggesting a phenological and/or survival difference based on gender. On  
348 the contrary in spring (April-June) and autumn (October-December) the sex ratio was balanced.  
349

### 350 **Summer adult habitat**

351 Despite intensive surveys and experiments, it was almost impossible to find any adult in Corsica  
352 in the summer, where both nymphs and freshly-emerged adults were present in high densities  
353 the previous spring. The drastic diminution of the adults from the ground vegetation in summer,  
354 common in the Mediterranean region, is considered to be a consequence of the extreme dry and  
355 warm conditions of the region (Cornara *et al.*, 2017; Morente *et al.*, 2018; Bodino *et al.*, 2019;  
356 Santoiemma *et al.*, 2019). As the summer goes on, the spring host plants of *P. spumarius* (both



357 nymphs and young adults) dry out or are severely water-stressed. It is possible that these plants  
358 are no longer suitable for consumption. In the continental USA, where conditions in summer  
359 are less extreme, it has been shown that the turgor decrease of the host plants, or their  
360 disappearance, lead to a migration of adults to more turgid plants present in the close vicinity  
361 (Weaver & King, 1954). In the Mediterranean region, and particularly in Corsica, most of the  
362 plants from the low stratum are dried out in summer and probably not enough turgid for an easy  
363 xylem sap consumption, and thus adults need to move farther and/or to exploit new habitats. In  
364 some parts of the Iberian Peninsula (Morente *et al.*, 2018) or in the Liguria region (Bodino *et*  
365 *al.*, 2019), insects can migrate vertically towards the neighbouring trees during the summer  
366 season. Several *Philaenus* species are also known to find refuge in the neighbouring trees  
367 (*Quercus ilex* L., *Q. suber* L.) and shrubs in the Mediterranean part of their distribution area  
368 (Drosopoulos, 2003; Drosopoulos *et al.*, 2010). However, in our surveys, it was not possible to  
369 find adults on trees present in the vicinity, suggesting migrations out of the studied zone over  
370 relatively longer distances. One possibility is that adults could migrate to some water streams  
371 present in the neighbouring valleys, as observed in Central Spain (Morente *et al.*, 2018), or  
372 towards the sheltered northern slopes of the relief. In such relatively humid habitats, plants,  
373 including low stratum species, remain turgid throughout the summer and thus could be used as  
374 food plants by adults. Populations could also migrate to higher altitudes or far to the north,  
375 where turgid species can be found even in summer (Drosopoulos, 2003). However, *P.*  
376 *spumarius* are not good flyers and, unless carried by the wind, cannot fly over long distances  
377 by themselves (Weaver & King, 1954), suggesting long northward migrations improbable. For  
378 our study, we were not able to find the summer habitat of *P. spumarius* in the maquis vegetation  
379 near Ajaccio.

380 For some authors, the meadow spittlebug survives the extreme summer conditions by  
381 aestivating in a sheltered habitat (Drosopoulos, 2003; Drosopoulos *et al.*, 2010; Chauvel *et al.*,

382 2015). However, by definition, aestivation, or summer dormancy, is a survival strategy to  
383 sustain lack of food or any extreme conditions (such as temperatures, desiccation) during which  
384 the animal is inactive and stops feeding (Masaki, 2009; Richard, 2009; Wang *et al.*, 2015).  
385 From our observations, adults did not survive more than 24h without feeding (Albre, per. obsv.)  
386 suggesting that *P. spumarius* might not be able to aestivate as mentioned in several works  
387 (Drosopoulos, 2003; Drosopoulos *et al.*, 2010; Chauvel *et al.*, 2015). Further studies on the  
388 summer adult strategy to survive the dry season are needed to assess whether *P. spumarius*  
389 aestivates or not in Corsica.

390  
391 In the Ajaccio region, most of the foams were observed on *Cistus monspeliensis* (93.2%); foams  
392 were also recorded on *C. creticus* (3.3%) and *Dittrichia viscosa* (1.3%). Moreover, 52% of the  
393 1737 *C. monspeliensis*, 13% of the 246 *C. creticus* and 6% of the 221 *D. viscosa* plants hosted  
394 at least one foam. Up to 40% of the Asteraceae *Urospermum dalechampii* also hosted foam;  
395 however only 15 individuals were found in the studied area. The predominance of foams on *C.*  
396 *monspeliensis* confirms previous observations recorded in recent years for the Corsican  
397 populations of *P. spumarius* (Cruaud *et al.*, 2018; Albre & Gibernau, 2019). However, such a  
398 strong host plant bias is in total contradiction with the literature. *P. spumarius* is described as  
399 highly polyphagous, with nymphs developing mainly on Asteraceae species. The species'  
400 polyphagy is considered as a key factor explaining the large distribution range of the species,  
401 native from the Palearctic region, and its success when introduced in foreign territories, such  
402 as New Zealand, Hawaii or Japan. Comparatively, the nymphs of numerous *Philaenus* species  
403 are oligophagous on arid vegetation (*P. arslani* Abdul-Nour & Lahoud and *P. loukasi*  
404 Drosopoulos & Asche) or monophagous on *Asphodelus microcarpus* (*P. signatus* Melichar, *P.*  
405 *italosignus* Drosopoulos & Remane, *P. tarifa* Remane & Drosopoulos and *P. maghresignus*  
406 Drosopoulos & Remane), and present more reduced distribution areas (Drosopoulos *et al.*,

407 2010). The manual transfer of neonate nymphs collected on field *C. monspeliensis* resulted in  
408 100% full development into adults when deposited on plant of the same species, suggesting  
409 such handling had an insignificant effect on the survival and development of the nymphs. The  
410 manual deposition experiments clearly demonstrated that they could achieve their development  
411 on most of the Asteraceae tested (54 to 100%), on *C. creticus* (100%), on *C. laniger* (Fabaceae;  
412 54%) and on *Plantago* spp. (Plantaginaceae; 33 to 50%). Some mold had been observed during  
413 the experiment on the leaves of some *Plantago* spp. and *Erigeron canadensis* L. (Asteraceae)  
414 suggesting the reduced success rates observed for these species (the lowest ones, 33-54%) could  
415 be attributed to the decay of the tested plants rather than to a rejection of the plants by the  
416 nymphs. Only one nymph (10%) became adult on the strawberry trees (*A. unedo*) and no adult  
417 had been obtained on other shrubs (*P. lentiscus*) or trees (olive trees). These results confirm  
418 that, despites their apparent monophagy on *C. monspeliensis*, the nymphs of the Corsican  
419 populations of *P. spumarius* still have the capability of developing on diverse herbaceous  
420 species, thus confirming their polyphagy as described in the literature. In Corsica, the specificity  
421 of the nymphs and, in spring and autumn, of the adults, can thus not be attributed to a  
422 physiological constraint of insular populations. During our field experiments in the Ajaccio  
423 region, we noticed that in autumn, when the adults reappeared in the habitat, vegetation of the  
424 lowest stratum had not yet been restored. The diversity of turgid plant species was thus limited  
425 to a few Mediterranean species, particularly well adapted to the long summer dryness. In the  
426 studied area, turgid plants mainly corresponded to *C. monspeliensis*, by far the most represented  
427 species, *D. viscosa* and some sparse individuals of *C. creticus*. Most of the foams encountered  
428 in early spring were also observed almost exclusively on these 3 species. So it could be argued  
429 that when adults came back from their unknown summer shelter to the low vegetation in  
430 autumn, there was a limited choice of plant species to feed on. And as these plants appeared to  
431 be suitable for the full development of the nymphs, the females did not need to find other species

432 on which to lay their eggs. We do not know if this observed behaviour is mainly due to climatic  
433 constraints on the vegetation or local insect ecological adaptation. Such statement needs  
434 complementary studies to be assessed. According to the literature, eggs are often observed on  
435 the anfractuositities of dead plant tissues (Weaver & King, 1954; Cornara *et al.*, 2018). However,  
436 such observations took place in cultivated areas such as olive groves or cereal crops, where the  
437 vegetation of the lower stratum is not fully restored at the end of summer because of the  
438 agricultural practices (labour, pesticides...) and/or the summer conditions. Consequently, no  
439 palatable plant is available for the adults when they got back from their summer site, and thus  
440 females lay eggs on any suitable substrate in absence of a suitable host plant.

441 In recent papers dealing with *Philaenus* species, the host plant, *Asphodelus microcarpus*, has  
442 been synonymised with *A. aestivus* Brotero, 1804 (Maryńska-Nadachowska *et al.*, 2010;  
443 Maryńska-Nadachowska *et al.*, 2012). However, *A. aestivus* Brot. is restricted to the Central  
444 and South-Western parts of the Iberian Peninsula ([http://powo.science.kew.org/taxon/531446-](http://powo.science.kew.org/taxon/531446-1)  
445 [1](http://powo.science.kew.org/taxon/531446-1)), while some of the monophagous *Philaenus* species (*P. signatus* and *P. italosignus*) are not  
446 present in this region, suggesting some incoherence in the plant synonymies. A possibility could  
447 be that these *Philaenus* species develop on a different *Asphodelus* species, whose identification  
448 has yet to be determined. Moreover, the *microcarpus* taxon has been used several times, at  
449 different taxonomic levels and associated to several *Asphodelus* species; incorrect synonymies  
450 are thus probable. However, most of the taxa refer to *microcarpus* Viviani, which is an  
451 established synonym of *A. ramosus* L.  
452 ([https://wmsp.science.kew.org/synonymy.do?name\\_id=312417](https://wmsp.science.kew.org/synonymy.do?name_id=312417)), a species represented in the  
453 whole distribution area of the *Philaenus* species. In this case, *A. ramosus* L. should be  
454 considered as the nymphs host plant of the monophagous *Philaenus* species. Interestingly, none  
455 of the 20 neonate nymphs of Corsican *P. spumarius* achieves its development on this plant.  
456 According to phylogenetic, karyotype and morphological studies, *P. spumarius* belongs to the

457 polyphagous or oligophagous “*spumarius*” group, also including *P. tesselatus*, *P. loukasi* and  
458 *P. arslani*; the other *Philaenus* species belong to the monophagous “*signatus*” group, including  
459 *P. signatus*, *P. italosignus*, *P. maghresignus* and *P. tarifa*. The shift in the nymph host plant  
460 appears to be an important trait closely related to the diversification of the genus *Philaenus* in  
461 Europe. However, it should be interesting to test whether the nymphs of monophagous species  
462 could develop on other plant species and reciprocally, but also whether the nymphs of the  
463 polyphagous and oligophagous species could accept *A. ramosus* as host plant.

464 In early spring, foams contained about  $1.86 \pm 1.35$  neonate nymphs; this number progressively  
465 decreased to  $1.08 \pm 0.86$  in early May at the end of the last immature stage, when nymphs were  
466 the biggest. Different factors could explain this clutch size decrease, such as the death of the  
467 nymphs by predation, parasitism or desiccation. However, such deaths are unlikely because of  
468 the presence of the foam within which the nymphs develop and whose role is to protect them  
469 against such dangers (Yurtsever, 2000b). Nymphs could also be killed by herbivorous mammals  
470 during their food intake, although this scenario is unlikely as *Cistus* ssp. herbivory has never  
471 been observed on the studied site. This observation may result from a behavioural change with  
472 neonate nymphs, likely siblings, living together within the same foam and becoming solitary  
473 towards the end of their development. It could also be supposed that some nymphs sharing a  
474 foam move to create a new one, farther on the same plant or onto a neighbouring plant. This  
475 split could be conceivable, as an increase in the proportion of *C. monspeliensis* plants hosting  
476 foams (26% vs. 51%) and in the diversity of plant species with foams (1 species vs. 8 species)  
477 was observed between the early March and the end of April in the surveyed transect. Moreover,  
478 our experiments demonstrated that despite the nymphs’ vulnerability outside the foam, nymphs  
479 were able to walk up to 89 cm in 20 min on a flat surface. A similar capability has been observed  
480 in greenhouse conditions, with nymphs moving up to 76 cm in the vegetation (Weaver & King,  
481 1954). Finally, a displacement of foams from place to place on the same plant was often

482 observed overnight (Albre, pers. obs.) or even during the day (Weaver & King, 1954). Different  
483 factors could be implicated in these movements, such as conflicts with congeners within the  
484 foam, better access to xylem sap, a decrease in the food quantity/quality or the search for  
485 more sheltered sites for the establishment of the foam. Also, the aggregation of some neonate  
486 nymphs within the same foam could be an advantage, allowing for the formation of bigger  
487 foams, more resistant to drying and providing better protection. These advantages could be  
488 reduced or counterbalanced by increased difficulty to access to the xylem sap for bigger  
489 nymphs, inducing a behaviour change with their departure/separation and the production of  
490 their own new foam.

491

## 492 **Conclusions**

493 We highlighted a strong insect-plant relationship between the nymphs of the meadow  
494 spittlebug, *Philaenus spumarius*, and *Cistus monspeliensis* in the Ajaccio region of Corsica,  
495 probably because this species was the most abundant turgid plant species available in early  
496 autumn. In the epidemiological context of the plant pathogen bacterium *Xylella fastidiosa*, it  
497 might be tempting to destroy the central plant host of *P. spumarius* populations, which are the  
498 main vector for the bacterium. However, our experiments confirmed that spittlebug nymphs  
499 were highly polyphagous on low-growing plant species, as also indicated in the literature.  
500 Hence, destroying *C. monspeliensis* in spring, i.e. when nymphs are developing, could result in  
501 a spread of the nymphs towards the neighbouring plants of the low vegetation, as we had  
502 observed in several occasions in spring after road banks mowing. Similarly, in absence of *C.*  
503 *monspeliensis* in autumn, it's likely that females of *P. spumarius* may lay their eggs in any dead  
504 plant tissues, as described in the literature, resulting in nymphs climbing and developing on any  
505 neighbouring turgid low plant species during the next spring. Instead, the strong relationship  
506 between *P. spumarius* and *C. monspeliensis* could be used to monitor spittlebug populations,

507 to limit/concentrate the means of insect control, or in an agronomic context, *C. monspeliensis*  
508 could be planted to lure insects away from crops. Unfortunately, the location adult summer  
509 habitat remains unknown for the studied population. However, *P. spumarius* likely move to  
510 humid habitats (e.g. riverine vegetation) and/or areas with high densities of turgid trees, making  
511 well-watered cultivated groves an ideal habitat for this pathogen vector to seek refuge in  
512 Mediterranean climates. Maintaining natural arboreal vegetation around agronomic systems  
513 could help decrease insect abundance – and potentially, pathogen load – on cultivated species.  
514 Such hypotheses need to be further studied by landscape experiments.  
515

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522



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659 **Figure legends**

660 **Figure 1.** Cumulative abundance (%) of Auchenorrhyncha at the studied site near Ajaccio, from  
661 March 2017 to December 2019.

662

663 **Figure 2.** Temporal abundance of *P. spumarius* (black bars) and the other Auchenorrhyncha  
664 species (grey shaded curve) at the studied site near Ajaccio, between March 2017 and December  
665 2019 collected twice a month.

666

667 **Figure 3.** Relationship between the number of males and female of *P. spumarius* for the 54  
668 sampled dates between March 2017 and December 2019.

669

670 **Figure 4.** Proportion of adult males of *P. spumarius* captured during different seasons.

671

672 **Figure 5.** Frequency distributions of the plants with foams observed in the studied area. Black  
673 histograms: proportion of specimens per species with foams (total number of specimens  
674 observed indicated on the top). Grey histograms: distribution of the foams among all the  
675 recorded plant species.

676

677 **Figure 6.** Spring temporal variations of the nymphs during their growing season. Empty squares  
678 and plain curve: average size of the nymphs' body length (in mm). Black dots and dashed curve:  
679 average number of nymphs per foam.

680

681 **Figure 7.** Distribution of the distances travelled by nymphs of *P. spumarius* (n = 73) on a flat  
682 paper surface in 20 minutes.

683

684 **Tables**

685

686 **Table 1.** Relative abundance of adults of *P. spumarius* collected in the two sampled vegetation  
 687 strata: low plants (under 120cm) and higher plants (above 120cm) per semester during the three  
 688 years of survey.

689

	January - June		July - December	
	Low plants	Higher plants	Low plants	Higher plants
2017	51.2% (22)	48.8% (21)	97.3% (107)	2.7% (3)
2018	76.7% (56)	23.3% (17)	97.4% (264)	2.6% (7)
2019	74.4% (29)	25.6% (10)	96.6% (113)	3.4% (4)
Total	107	48	484	14

690

691 **Table 2.** Abundances of the collected Auchenorrhyncha in the various trapping experimental  
 692 designs soon after the emergence of the adults of *P. spumarius* (end of May – end of June).

693

	Net-sweeping tree foliage (6 m high)	Yellow sticky traps	Shaded sticky shelters
<i>Philaenus spumarius</i>	n = 3	n = 0	n = 0
Other Aphrophoridae	n = 0	n = 0	n = 0
Issidae	n = 7	n = 2	n = 0
Cicadellidae	n = 207	n = 252	n = 1

694

695



696 **Table 3.** Evolution of the foam distribution along a 100m survey between the March 09<sup>th</sup> and  
 697 April 24<sup>th</sup>. a. host plant distribution; b. proportion of observed plants for each species with at  
 698 least one foam.

699

	a		b		
	09/03/2017	24/04/2017	09/03/2017 24/04/2017		
	n = 33 foams	n = 103 foams	n plants		
<i>Cistus monspeliensis</i>	100%	86%	176	26%	51%
<i>Cistus creticus</i>	0%	2%	22	0%	10%
<i>Dittrichia viscosa</i>	0%	4%	21	0%	19%
Others (about 15 spp.)	0%	8%	111	0%	19%

700

701

702 **Table 4.** Developmental success rate of *P. spumarius* nymphs on different host plant species  
 703 (listed by alphabetical order). The success rate corresponds to the proportion of nymphs  
 704 achieving their full development on a bagged leaf (N success) out of the initial number of  
 705 nymphs tested (N baggings). \*: *C. monspeliensis* can be considered as a control experimental  
 706 for the nymph deposition.  
 707

Family	Species	Mode of deposition	N Baggings	N success	Success rate (%)
Anacardiaceae	<i>Pistacia lentiscus</i>	Manual	6	0	0%
Asteraceae	<i>Anthemis arvensis</i>	Natural	9	9	100%
-	<i>Pulicaria odora</i>	Manual	3	3	100%
-	<i>Tolpis umbellata</i>	Natural	2	2	100%
-	<i>Dittrichia viscosa</i>	Manual	35	26	74%
-	<i>Calendula arvensis</i>	Manual	13	9	69%
-	<i>Helichrysum italicum</i>	Manual	9	5	56%
-	<i>Erigeron canadensis</i>	Manual	13	7	54%
Cistaceae	<i>Cistus creticus</i>	Manual	9	9	100%
-	<i>Cistus monspeliensis*</i>	Manual	14	14	100%
Ericaceae	<i>Arbutus unedo</i>	Manual	10	1	10%
Fabaceae	<i>Cytisus laniger</i>	Manual	12	5	42%
Liliaceae	<i>Asphodelus ramosus</i>	Manual	20	0	0%
Oleaceae	<i>Olea europea</i>	Manual	12	0	0%
Plantaginaceae	<i>Plantago coronopus</i>	Natural	2	1	50%
-	<i>Plantago lanceolata</i>	Natural	3	1	33%