

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

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3	Ecology of the meadow spittlebug Philaenus spumarius in the Ajaccio region
4	(Corsica) – I: Spring
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12	Short title: Ecology of Philaenus spumarius in Corsica
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17	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 several trapping methods used, the location adult summer habitat remains unknown for the 26 27 studied population. It might be tempting to destroy the central plant host of P. spumarius populations. However, as spittlebug nymphs are highly polyphagous on low-growing plant 28 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.

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

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, 2013), of which only six are present in Corsica (Chauvel et al., 2015; Albre & Gibernau, 2019). 44 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

plant species (Saponari et al., 2014; Cornara et al., 2017). The ecology of P. spumarius has thus 65 66 been intensively studied in this epidemiological context, particularly in European continental populations developing in cultivated areas. The adults can be observed from the end of spring, 67 68 after the last molt, to the end of autumn (Yurtsever, 2000b). However, in some populations, adults find refuge in cool habitats, usually in the shady and humid foliage of the surrounding 69 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 to 20 eggs aggregated in a cement-like secretion. Eggs are laid either directly on suitable host 76 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).

While *P. spumarius* is present in the whole Mediterranean region including the islands, such as
Corsica, Sicily, Sardinia, the Balearic Islands and Crete, defined ecological parameters are
almost exclusively based on continental populations developing in agricultural landscapes
(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 population of P. spumarius from South-West of Corsica near Ajaccio. The abundance and 96 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**

The studied site is located near the University campus outside of Ajaccio (GPS coordinates:
41.913492N, 8.655433E). The habitat is a typical thermomediterranean shrubby vegetation (i.e.
maquis) dominated by *Pistacia lentiscus* L. (Anacardiaceae), *Cytisus laniger* (Desf.) DC.
(Fabaceae) and *Cistus monspeliensis* with sparse trees *Olea europaea* L. (Oleaceae) and *Arbutus unedo* L. (Ericaceae) and weak anthropogenic perturbations during the past 35 years.
A 34-month-long survey (from March 2017 to December 2019) was conducted in ~1100 m²
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

Different experiments were performed soon after the emergence of *P. spumarius* adults, during the period when extremely few specimens were collected using the sweet-net approach. In order to verify whether the adults of *P. spumarius* took refuge in the tree foliage, intensive sweep-net captures were thus performed up to 6 meters high in 10 trees for each main species of the studied 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.

In order to verify whether adults were looking for shady and humid habitats to survive the summer conditions, we constructed shelters consisting of two green overlaid sticky plates of cardboard separated by 2 cm; a recipient filled with water was placed between the plates. This artificial system was supposed to represent a shaded and relatively humid (micro-)habitat as the 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 the plants of the studied area in early spring. In order to understand the progression of the foam 149 150 distribution in the habitat throughout the season, foam presence or absence and the number of foams per plant were recorded along a 100 m long transect from March 9th, when most of the 151 foams were visible, through April 24th, before the emergence of the adults. The range of 152 153 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.

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3. Nymph behaviour and survival

160 Once per week from March 15th to May 3rd, 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. In order to verify the polyphagy of the nymphs of *P. spumarius*, development experiments were performed by bagging the foliage of different plant species in the presence of natural foams or by transferring single neonate nymphs (all collected on *C. monspeliensis*) on a suite of the aforementioned plant species. Success was considered when the nymph completed its developmental cycle into an adult.

169

170 4. Data analyses

171 Survey

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

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Hammer, Ø., Harper, D.A.T., Ryan, P.D. (2001) PAST: Paleontological statistics software
package for education and data analysis. Palaeontologia Electronica 4(1): 9pp. http://palaeoelectronica.org/2001_1/past/issue1_01.htm

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188 **Results**

189 **1.** Survey

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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).

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b. Temporal pattern of Philaenus spumarius population

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

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

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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 (Chi²₁ 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*.

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d. Sex-Ratio

The number of males and females were strongly positively related (fig. 3; $R^2 = 0.86$, p = 3.7 x10⁻⁴), and there was no major sex ratio bias (line slope not different from one, $F_{1,105} = 0.11$, p = 0.74). The only sample with a significant biased sex ratio was on November 22th 2018 with 21 males and 40 females (Chi²₁ = 6.03, p = 0.014).

There was a strong seasonal effect on sex ratio (fig. 4) independent of sample sizes and despite large variation (Kruskal-Wallis: H (Chi²) = 12.6, p = 0.005) with winter and summer periods presenting significantly lower male proportions (13.3 ± 23.1 % and 19.8 ± 28.6 % respectively) than during the spring and autumn periods (57.6 ± 25.8 % and 52.7 ± 13.8 % respectively).

236 **2.** Adults ecology

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.

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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.

Moreover, up to 52% of the *C. monspeliensis* (1737 plants observed) and 13% of the *C. creticus* (246 plants observed) specimens were observed to harbour at least one foam (fig. 5). Foams were also recorded on 40% of the *Urospermum dalechampii* (Asteraceae) specimens, but only
15 individuals were observed in the studied area.

264

- **3.** Nymphs
- 266

a. Foam density

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

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b. Nymphal development

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

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

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c. Nymphs capacity movement

When removed from their foam and deposited on a flat paper surface, nymphs walked an average of 38.5 cm in 20 minutes; the maximum distance travelled was 89 cm (fig. 7). No relationship was found between the nymph size of the nymphs and the distance travelled ($R^2 =$ 0.022). The distribution of distances travelled is clearly not unimodal, but instead seems
multimodal, with many spittlebugs travelling either short or relatively longer distances (fig. 7).

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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).

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 had a significantly biased sex ratio, 40 females to 21 males, on November 22th; interestingly 343 344 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

Summer adult habitat

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

For some authors, the meadow spittlebug survives the extreme summer conditions by 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 Palaearctic 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 anfractuosities 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 (Maryańska-Nadachowska et al., 2010; 443 Maryańska-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/531446-445 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 Α. L. ramosus 452 (https://wcsp.science.kew.org/synonomy.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 ± 1.35 neonate nymphs; this number progressively 465 decreased to 1.08 ± 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 research 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.

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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 <i>P. spumarius</i> (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 <i>P. spumarius</i> for the 54
668	sampled dates between March 2017 and December 2019.
669	
670	Figure 4. Proportion of adult males of <i>P. spumarius</i> 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 <i>P. spumarius</i> $(n = 73)$ on a flat
682	paper surface in 20 minutes.
683	

684 Tables

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

	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	

- **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).

	Net-sweeping tree	Vallary at alm trans	Shaded sticky	
	foliage (6 m high)	r enow sucky traps	shelters	
Philaenus spumarius	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	

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

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

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

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