Dispersal of *Neophilaenus campestris*, a vector of *Xylella fastidiosa*, from olive groves to over-summering hosts

Running head: Dispersal ability of *Neophilaenus campestris*

Abstract

Neophilaenus campestris is one of the spittlebugs (Hemiptera: Cercopoidea) able to transmit *Xylella fastidiosa* to olive trees. Considering its vector ability and the wide distribution of this species in Spain, *N. campestris* should be considered a serious threat to key crops such as olive, almonds and grapevines. Migration and dispersal abilities of insect vectors have profound implications in the spread of vector-borne diseases. Thus, knowledge on the dispersal ability of *N. campestris* is essential to model, predict and limit the spread of the diseases caused by *X. fastidiosa*. A mass-mark-recapture technique was developed to track between-field movements of *N. campestris* during its late spring migration from the ground cover grasses within olive groves to sheltered areas dominated by pine trees. The fluorescent dust used for marking did not affect the survival nor the flying ability of *N. campestris*. Spittlebug adults captured in olive groves during late spring were dusted with fluorescent colours and released in different locations. Six recapture samplings were performed 23 to 42 days after release in 12 different sites located within a maximum distance of 2.8 km from the release point. Results indicated that *N. campestris* was able to disperse a maximum distance of 2473 m in 35 days. Furthermore, flight mill studies showed that *N. campestris* was able to fly long distances, reaching 1.4 km in an 82-minute single flight.

Altogether, our findings suggest that eradication measures are of limited value because vectors are able to disperse rapidly over distances much longer than expected.

KEYWORDS: Mass-mark-recapture (MMR), migration, fluorescent dust, insect vector, *Pinus pinea*, *Pinus halepensis*.

1. INTRODUCTION

Migratory journeys and dispersal abilities have profound implications in the spread of vector-borne diseases (Chapman, Reynolds, & Wilson, 2015; Fereres, Irwin, & Kampmeier, 2017; Irwin & Tresh, 1988). In a vector-borne pathogen system, the level of spread of a disease across the landscape is highly dependent on vector movement (Finke, 2012). Therefore, understanding patterns of vector movement is critical for the development of efficient control strategies focused on the vector management (Martini, Hoffmann, Coy, Stelinski, & Pelz-Stelinski, 2015). *Xyllela fastidiosa* Wells (1987) is a vector-borne plant pathogenic bacterium responsible for severe diseases of several economically important crops (Hopkins, 1989; Saponari, Boscia, Nigro, & Martelli, 2013). It is native to the Americas, but it has been detected recently in several European countries (EFSA, 2019). It first was found in Apulia, Italy (Saponari et al., 2013), and then in France, Germany, Spain, Portugal and Israel (EFSA, 2019; EPPO, 2019). *Xylella fastidiosa* is mainly transmitted to plants by xylem-sap feeding insects. It also can be transmitted by vegetative propagation material like grafting (Sanderlin & Melanson, 2008). Xylem-sap feeding insects which are able to transmit the bacterium, belong to the order Hemiptera, such as spittlebugs (Cercopoidea), cicadas (Cicadoidea) or sharpshooters (Cicadellidae: Cicadellinae), (Almeida, Wistrom, Hill, Hashim, & Purcell, 2005; Frazier, 1965; Krugner, Sisterson, Backus, Burbank, & Redak, 2019; Novotny & Wilson, 1997; Redak, Purcell, & Lopes, 2004). While sharpshooters are scarce in Europe, spittlebugs are abundant, thus they are considered the main potential vectors of *X. fastidiosa* in the European continent (Cornara et al., 2019; EFSA, 2015; Jacques et al., 2019). *Philaenus spumariu*s L. (1758), (Hemiptera:

Aphrophoridae) was identified as the main vector of *X. fastidiosa* in the olive groves of southern Italy (Cornara et al., 2016; Cornara, Cavalieri, Dongiovanni et al., 2017). Moreover, it has been found that *Neophilaenus campestris* Fallen (1805), which is widely distributed across the Iberian Peninsula (Morente et al., 2018), is able to transmit *X. fastidiosa* to olive trees under experimental conditions (Cavalieri et al., 2019). However, *N. campestris* is not usually taken into account in European vectors studies usually focus on *P. spumarius*. Therefore, research on *N. campestris* has the potential to contribute to the development of efficient strategies to mitigate the spread of *X. fastidiosa* across the European continent.

Regarding spittlebugs movement, Weaver & King (1954) observed that *P. spumarius* adults travel more than 30 m in a single flight, move as much as 100 m within 24 hours from the release point and fly at a height of 15 to 70 cm above the ground. In contrast, Freeman (1945) collected *P. spumarius* and *N. lineatus* at 84 m above ground and Reynolds, Chapman, & Stewart (2017) reported captures of *N. lineatus* at 200 m high**.** These captures in altitude, suggest that spittlebugs may be transported long distances due to low-level jet winds (Drake, 1985; Pienkowski & Medler, 1964; Sedlacek & Freytag, 1986; Wallin & Loonan, 1971; Zhu, Radcliffe, Ragsdale, MacRae, & Seeley, 2006). Moreover, spittlebugs spend most of their life cycle on ground cover vegetation, mainly grasses, where mating, oviposition and feeding occur (Bodino et al., 2019; Morente et al., 2018). However, they move from the ground cover to trees and shrubs in late spring when the ground vegetation dries out, and they return in the fall to lay their eggs (Antonatos et al., 2020; Cornara, et al., 2019; Cruaud et al., 2018; Dongiovanni et al., 2018; Mazzoni, 2005; Morente et al., 2018). Morente, et al., (2018) and Lopes, Landa, & Fereres, (2014) have reported that *N. campestris* are abundant

in pine trees (*Pinus halepensis* Mill., 1768) during the summer in mainland Spain. This suggests that pine trees could be an over-summering host plant exploited by *N. campestris* as a shelter when the grasses dry out. Since the process of transmission of *X. fastidiosa* may occur in few minutes (Cornara et al., 2020), non-colonizing spittlebug species may have an impact on disease epidemiology. This could be the case of *N. campestris* that is frequently found in ground cover vegetation in olive groves but is rarely found feeding on the olive tree canopy. They may play an important role in *X. fastidiosa* transmission when they move from grasses in the late spring to feed on woody hosts (Almeida, 2016; Bodino et al., 2019; Morente, et al., 2018).

Most of the information about the Cercopoidea dispersal abilities is based on studies about the behaviour of insects collected in landscapes different from the Mediterranean scrubland (Halkka & Halkka, 1971; Plazio et al., 2017; Weaver & King, 1954). However, the composition of the landscape and the climate conditions can influence the distribution of insects and their patterns of movement (Blackmer, Hagler, Simmons, & Henneberry, 2006; Crist, Guertin, Wiens, & Milne 1992; Haynes & Cronin, 2003; Jonsen & Taylor, 2000). Thus, information about the movement ability of *N. campestris* is crucial in the development of effective policies to contain the spread of *X. fastidiosa* in Europe.

Studying dispersal patterns and insect migration behaviour requires insect tracking in the field, which can be challenging due to their small size and general lack of specific return-migration sites (Chapman et al., 2015). Nevertheless, a combination of several methods can improve our knowledge of the movement and dispersal behaviour of the vectors of *X. fastidiosa* (Purcell, Gravena, & Donadio, et al., 1994). In flight mill studies, an insect is attached to an arm and it

flies in a circular trajectory allowing continuous measurement of flight parameters (Minter et al., 2018). Flight mills have been largely used to study the dispersal ability of serious insect pests, such as the red palm weevil (Ávalos-Masó, Martí-Campoy, & Soto-Tornero 2014) or the western corn rootworm (Yu et al., 2019). They also have been used to describe how several factors (humidity, temperature, age, sex, mated, no mated, etc.) influence insect displacement (Cheng, Luo, Jiang, & Sappington 2012; Jones et al., 2015; Riley, Downham & Cooter, 1997; Zhang, Wang, Wu, Wyckhuys, & Heimpel, 2008). Flight mills are a valuable tool to generate knowledge on the insects' flight potential under laboratory conditions, however these techniques should be combined with field tracking to give an accurate approach to insect movement in their natural habitat (Minter et al., 2018). Recent mass-mark-recapture (MMR) field studies on spittlebugs have given new insights on spittlebug dispersal abilities. Bodino et al., (2020) performed a MMR study in southern Italy, sampling in concentric circles from 10-120 m from the released point. They estimated 98% of *P. spumarius* population disperse in a radius of 400 m. In contrast, Conyers, Malumphy, De Marzo, & Down (2020) found that the maximum distance moved by *P. spumarius* was 10 m in two days. This great variation in the dispersal abilities of spittlebugs could be related to the differences in the composition of the landscape and the climate conditions which can affect the distribution of insects and their movement patterns (Blackmer et al., 2006; Crist et al., 1992; Haynes & Cronin, 2003, 2006; Jonsen & Taylor, 2000). MMR tests, specially using fluorescent dusts as markers, have been largely used to study the movement of important agricultural insect pests, including the leafhopper *Scaphoideus titanus* Ball, which is the vector of the Flavescence dorée plant

disease, and American vectors of *X. fastidiosa* such as *Homalodisca vitripennis* (Germar 1821),(Byrne, Rathman, Orum, & Palumbo, 1996; Coviella, Garcia, Jeske, Redak, & Luck, 2006; Hagler, 2019; Hagler & Jackson, 2001; Lessio, Tota, & Alma, 2014; Miranda et al., 2018; Northfield et al., 2009; Prasifka, Krauter, Heinz, Sansone, & Minzenmayer, 1999). One of the difficulties of MMR techniques is to evaluate the effect of marking on insect flight behaviour. However, this issue could easily be solved by performing flight mill tests with marked and non-marked insects. Thus, a combination of both techniques to study the dispersal ability of *N. campestris* could not only validate a MMR, but also give a general idea of their dispersal ability.

Therefore, the aim of this work was to understand *N. campestris* dispersal dynamics by combining two different techniques: (1) a flight mill assay and (2) a mass-mark-recapture assay.

2. MATERIAL AND METHODS

We conducted an indoor study to assess the persistence of fluorescent dusts (Day-Glo Color Corp. Cleveland, OH, USA) and its effect on the survivorship and flight ability of *N. campestris* before the mass-mark-recapture assay in the field. *Neophilaenus campestris* adults were collected by sweep net in Los Santos de la Humosa (Madrid, Spain) in late spring 2019; the location was the same where the mass-mark-recapture assay was performed. Spittlebugs collected were identified according to Ribaut, Quesne, & France (1952), Ossiannilsson, (1981), Giustina, (1989), Holzinger, Kammerlander, & Brill (2003) and Mozaffarian & Wilson, (2016). Insects collected were caged on *Bromus madritensis* L**.** for 3 days of acclimation in the greenhouse facilities at ICA-CSIC, Madrid, Spain set at 22.28 ± 0.23ºC and 54.64 ± 0.61% RH.

2.1. Persistence of fluorescent dusts and their effect on the survival of *Neophilaenus campestris*

To assess the effect of the fluorescent dusts on the survival of *N. campestris*, 200 individuals were randomly split into 5 groups of 40 individuals each: a dusted group which included one of each of the following colours: pink, blue, yellow and orange and a non-dusted control group. Insects were introduced in conical Falcon tubes (10 insects per tube) together with 2.8 mg of dust. The tubes were gently shaken and the same procedure was applied to the individuals of the control group without dust. Then, each group of 10 dusted and non-dusted insects was released in a single cage (10 adults per cage and four replicates per treatment) containing 4-week old potted *B. madritensis* plants (plants grown in a climatic chamber at 24:18°C of temperature and photoperiod 14:10). The number of alive and dead insects in each cage and the persistence of the dust on the insect's body were recorded twice a week for 35 days. A 4-level scale of dust coverage was established in relation to the intensity of the fluorescence on the insects: 1) completely dusted, 2) less dust but visible with the naked eye, 3) fluorescence not visible with the naked eye but visible by using UV light, 4) non-dusted. The assay was conducted in a greenhouse at ICA-CSIC, Madrid under the same environmental conditions described above. The plants were replaced every week to keep optimal conditions for insect rearing. A two-sample Cox proportional hazards model was performed to determine whether the colour of the fluorescent dust affected the survival of adults. Statistical analysis was performed in R software v.3.6.0 (R Core Team, 2019).

2.2. Effect of fluorescent dusts on the flight behaviour of *Neophilaenus campestris*

A commercial flight mill device (Insect FlyteMill, Crist Instruments, Hagerstown, MD, USA) with some adaptations to reduce friction and facilitate the flight of small insects was used to evaluate the effect of the dust on the flight potential of *N. campestris*. Flight mill recordings were taken 1-3 days after the insects were dusted with fluorescent dust using the same methodology for marking and the same 5 experimental groups (4 dusted and one non-dusted) described above. Individuals were exposed to greenhouse conditions until the experiments started. Experiments were carried out in the laboratory from 9:00h to 18:00h under controlled conditions: temperature (24±1Cº), artificial fluorescent light (10 μE m−2 s−1) and humidity (25-55%). Insects first were anesthetized by exposing them to CO_2 for 5 seconds. Then a pinhead was glued to the pronotum using a small drop of adhesive (Hot melt glue, NV98591 Nivel, Leganes, Madrid, Spain). Afterwards, the insects were placed on one side of the flight mill's arm (29.6 cm) with a suitable counter balance on the opposite side of the arm to make them fly in a circular trajectory. Insects that did not start to fly after 15 minutes were removed and discarded. The flight activity was recorded until the insect stopped flying for a time interval longer than 15 minutes. A total of 89 individuals were tested but only 50 out of the 89 tested performed successful flights. Thus, we recorded a total of 10 full flight recordings for each of the 5 experimental treatments (10 recordings per treatment). The data collected by the flight mill device were the following: the distance flown (m), the total flight duration (s) and the flight speed (m/s). A specific “mill_recorder” computer-based software and hardware device recorded the data and the “mill_processor” software calculated the flight descriptors (both developed by Marti-Campoy & Rodriguez-Ballester at the ITACA-Universitat Politècnica de València, Valencia, Spain). The flight

potential was evaluated according to the following flight descriptors: (1) Flight incidence: the ability of a given insect to perform a flight (Yes/No). (2) Number of flights**:** a new flight was assumed when the insect needed more than 20 seconds to complete one lap**.** (3) Total distance travelled: sum of the distance covered by all flights. (4) Total duration: sum of the duration of all flights. (5) Average speed: mean of the speed of each individual flight. The maximum distance travelled, flight duration and average speed also were recorded.

We analysed the effect of the sex and dust status (pink, blue, yellow, orange and non-dusted) on the flight incidence of *N. campestris* and the flight parameters: number of flights, total distance flown, total flight duration and mean speed. Flight incidence had a binary distribution (yes or no), we fit a general lineal model (GLM) with a binomial distribution of errors and link logit. Sex and dusted status were used as fixed factors. Moreover, number of flights, total distance flown and total flight duration were analysed through Generalized Linear Models (GLMs, negative binomial with logit link function) and on mean speed through linear models (LMs) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We compared the models by maximum likelihood (Zuur et al., 2009) and selected the best model relying on the AIC value (Akaike information criterion) (Burnham & Anderson, 2003). All the analyses were performed with the software R. v.3.6.0 (R Core Team, 2019).

2.3. Mass-Mark-Recapture assay (MMR)

The study was conducted at Los Santos de la Humosa, Eastern Madrid (Spain) (40° 30’ 04.08’’ N 3° 15.25’ 58’’ W, 850 m). We used 4 different colours (pink, blue, yellow and orange) for marking insects that were released in 4

different olive groves separated by 200 m (one colour per grove). The different colours were used to identify the distance travelled from each of the 4 release points to the recapture sites. The insect releases were carried out in olive groves with abundant ground cover vegetation, mainly dominated by grasses (Poaceae). The selection of the recapture sites was based on the presence of perennial natural woody vegetation which included known host species of *N. campestris* and other spittlebugs species (Lopes et al., 2014; Morente et al., 2018). Thus, the recapture sampling procedure was performed in 12 different sites where the dominant vegetation was *Pinus halepensis*, *Pinus pinea*, *Quercus coccifera*, *Quercus faginea*, *Retama sphaerocarpa*, *Foeniculum vulgare, Eryngium campestre* and *Prunus dulcis* (Figure 1). Recapture points were located at different distances, with the minimum distance being 94 m and the maximum distance of 2754 m from the most distant release point (Figure 1; Supporting information 1). The spittlebug MMR procedure was carried out on 23rd May 2019 following a methodology similar to the one described by Nakata, (2008). Adult individuals were captured by a sweep net from the ground cover vegetation in the four olive groves mentioned above and stored in 50 ml conical falcon tubes. Individuals captured were dusted in groups of 100 insects per falcon containing 7 mg of fluorescent dust. The same procedure was repeated with each of the 4 different colours. The dusted spittlebugs were released on the green ground cover of each olive grove. The first recapture event was carried out on 12th June 2019, 20 days after the release date, which matched the timing of the senescence of the ground cover vegetation. We performed five recaptures: 12th, 18th, 19th, 20th, 27th June and 5th July. Because the fluorescent dust was not visible with the naked eye, insects were recaptured by sweep net, caged on *B.*

madritensis plants and transferred to the laboratory. The presence of fluorescent dust on the body of every individual was addressed by using a UV lamp 13W (Halotec F6T5/BLB, Koala Components, Torrent (Valencia), Spain).

Regarding the high adherence of the fluorescence dust to the insects, several precautionary measures were carried out in order to avoid the contamination of the individuals recaptured. First, all materials used in the marking process were replaced each day (i.e. plastic bags and Falcon tubes). Second, the falcon tubes were replaced every day of recapture and the insect mouth aspirators were inspected by checking them under UV light looking for fluorescence traces. Third, the individuals recaptured in the field were stored in groups of 50 individuals in falcon tubes then caged on *B. madritensis* plants (one cage per location of recapture and date), for transportation to the laboratory. Finally, all the recaptured individuals were checked under UV light and screened for the presence of fluorescent dust on the insect's body. Only those individuals that showed clear trace of fluorescent dust were considered as marked insects (Figure 2A). Non-dusted individuals are shown in Figure 2B.

3. RESULTS

3.1. Persistence of fluorescent dusts and their effects on survival and flight activity of *Neophilaenus campestris*

3.1.1. Persistence of dusts and effects on *Neophilaenus campestris* survival

There was no statistical difference in the survival between dusted and non-dusted *N. campestris* maintained under greenhouse conditions (two-sample Cox proportional hazards model Z= -0.094, P= 0.925) (Figure 3). Moreover, none of

283 the marked individuals had a loss of marking dust beyond the level 2 during the
284 35-day period of the experiment, and all the marked insects were easily
285 distinguishable with the naked eye. It is worth noting that the indoor
286 environmental conditions where we raised the insects were different from those
287 in the field. Insects were maintained inside cages in a glasshouse with no
288 exposure to wind, rain or strong UV radiation.

289 3.1.2. Dust effect on the flight activity of *Neophilaenus campestris*

290 Flight mill assays showed that the overall proportion of individuals of *N.*
291 *campestris* that flew was 56.2% (50/89). The best fit GLMs and LMs, were always
292 the null models. Thus, neither the dusted status nor sex affected the flight
293 incidence, the number of flights, the total distance travelled, the total flight
294 duration, or the mean velocity. Therefore, we pooled together all the data of both
295 sexes, dusted and non-dusted individuals and we calculated the flight descriptors
296 for all insects (n=50) (Table 1). Results obtained showed that *N. campestris*
297 travelled 282 m in about 17 min on average in a single flight, and one individual
298 was able to travel almost 1.4 km in an 82-minute single flight. The mean speed
299 of flight was 0.26 m/s.

300 **3.2. Mass-Mark-Recapture assay (MMR)**

301 During the MMR assay (23rd May – 5th July) the temperatures averaged
302 23.4 ± 0.78°C. The wind conditions varied during the assay over the course of
303 the day with a mean of 2.5 ± 0.14 m/s with a maximum wind speed of 4.2 m/s
304 and a minimum of 1.8 m/s. Despite the changing wind conditions, the
305 predominant wind direction was southeast the day when marked insects were
306 released.

307 A total of 1315 individuals of *N. campestris* were released and 21 marked
308 individuals were recaptured representing a mark-recapture rate of 1.6% (Table
309 2). A total of 791 individuals of *N. campestris* (considering both marked
310 individuals and “wild” not marked insects) were captured from the 12-recapture
311 sampling sites. However, recaptures of marked individuals occurred only in three
312 (D, G and K) of the 12 sites sampled (Figure 1). The marked individuals that were
313 recaptured were found only on two different species of pine trees: *P. halepensis*
314 and *P. pinea*.
315 All the individuals recaptured were dusted with either orange or yellow
316 dusts. No individuals with a blue or pink dust were recaptured. *Neophilaenus*
317 *campestris* recaptured in points D (8 individuals) and G (8 individuals) were
318 marked with the orange colour (Figure 2A) which indicated that these insects flew
319 123 m from the orange release point to the D zone and 281 m to the G zone.
320 Furthermore, 5 dusted individuals of *N. campestris* were recaptured in the K
321 point, which was about 2400 meters away from the release point. Four of these
322 5 individuals had orange dust while 1 individual was marked with yellow
323 fluorescent dust.
324 The majority of the orange dusted insects had many orange dots and few
325 yellow or whitish dust particles on their body (Figure 2A) but for the purpose of
326 the analysis it was considered that all the marked individuals in zones D and G
327 came from the orange release site (Figure 1). In point D, recaptures occurred
328 throughout the whole assay. Thus, 3 orange-marked *N. campestris* were
329 recaptured on 12th June, 3 on 19th June and 2 individuals on 27th June. By
330 contrast, in point G the only date of recapture was 5th July when the 8 orange-
331 marked *N. campestris* were recaptured. Finally, in the point K, the 4 orange-

marked and the yellow-marked *N. campestris* were captured on 27th June. Recaptures at point D were done under variable climatic conditions while in point G and point K, recaptures matched with the two windiest and hottest days of the recapturing period: 27.94 °C of temperature and 2.9 m/s of wind speed and 30.96°C and 4.15 m/s respectively.

4. DISCUSSION

The indoor tests on survival, dust retention and flying capabilities of *N. campestris* showed that the methodology applied in our MMR field assay did not disturb the flight behaviour or survival of the dusted spittlebugs. However, insects exposed to natural conditions were different from those exposed to indoor facilities since they were not protected from rain and intensive UV light. This could explain why the marked insects collected in the field were not visible with the naked eye and a UV lamp was always needed for detection of the fluorescent dust. Moreover, the flight mill assay showed that *N. campestris* is able to travel much more than 100 m in less than an hour, which is a greater distance than previously observed for spittlebugs in other studies (Freeman, 1945; Weaver & King, 1954). Flight mill data are difficult to interpret because the insects' behaviour and flying ability might be influenced by experimental manipulation. However, flight mill assays give a general idea of insect flight behaviour and allow us to compare differences in flight behaviour between different groups (Ávalos-Masó et al., 2014; Dingle, 1965; Guo, Li, Shen, Wang, & Wu, 2020; Minter et al., 2018). It is known that the migration behaviour of insects is complex and can be influenced by multiple biotic and abiotic factors including sex (Minter et al., 2018). Moreover, previous studies stated that migratory behaviour can be influenced by

sex in spittlebugs (Cornara, Bosco, & Fereres, 2018). However, sex didn't influence any of the flight parameters of *N. campestris* in this study. Furthermore, we observed that the fluorescent dust did not have any effect on the flight behaviour of the spittlebug in the flight mill, which confirms the suitability of the mass-marking-recapture protocol used in this study.

Our results in the MMR assay support previous studies (Lopes et al., 2014; Morente et al., 2018) which proved that *N. campestris* move and settle on pine trees during late spring and summer (in our study *P. pinea* and *P. halepensis*). The spittlebugs recaptured in the K zone were able to travel distances longer than 2 km. Those that came from the orange release point travelled about 2282 m and those that came from the yellow release point moved a total of 2473 m, the longest distance covered by a spittlebug recorded in a field assay until now (Freeman, 1945; Reynolds et al., 2017; Weaver & King, 1954). Our results suggest that *N. campestris* is able to travel more than 2000 meters in 35 days. These results contrast with those obtained by Bodino et al., (2020) who estimated that 98% of the *P. spumarius* population moved within a radius of 400 m. However, they did not specify the distance moved by the remaining 2% of the population. One of the limitations of the MMR techniques is that a very high sampling effort is needed to recover marked insects at long distances from the release point. Likely, the long-distance movement of *N. campestris* could be dependent on wind speed and direction, and it likely is capable of flying up to the air currents where their migration becomes passive and displaced by tail winds (Freeman, 1945; Reynolds et al., 2017; Weaver & King, 1954). Bodino et al., (2020) performed recaptures at a maximum distance of 200 m from the release point, which may not represent the dispersal ability of *P. spumarius* over long

382 distance when aided by tail winds. Despite the changing wind conditions during
383 the MMR, the predominant wind direction was southeast the day when marked
384 insects were released. Interestingly, the furthest recapture point where marked
385 insects were found (more than 2km away) is located southeast of the release
386 points (Figure 1). This suggests that spittlebugs that were re-captured could have
387 travelled aided by tail winds present at the time when marked insects were
388 released. Regarding short-distance migration, we learned in our laboratory
389 studies that *N. campestris* was able to move more than 100 m in 24 hours. The
390 presence of sheltered habitats may favour its migration (Hunter, 2002). Some
391 orange dusted insects presented some yellow spots on their body. Thus, perhaps
392 some marked insects were able to contact each other during the sweep net
393 sampling and mate while they remained in falcon tubes after they were
394 recaptured. Moreover, insects remained in cages in the laboratory before sorting
395 them out in the microscope. Thus, while they remained in falcon tubes and cages
396 they may have transferred some dust particles from yellow marked to orange
397 marked insects and the other way around. Less likely, yellow and orange dusted
398 *N. campestris* could have met in a middle resting point within the migration track
399 where they could mate and thus transfer the dust from one individual to another.
400 These insect species are polyandrous and females mate frequently with multiple
401 couples during all their adult life. Therefore, the transfer of dust from one insect
402 to another is a possibility that cannot be excluded. Finally, no *N. campestris* was
403 found on the rest of oversummering host plants sampled in the study such as
404 oak trees. This result may indicate that, despite the polyphagous character of the
405 insect, it has a strong migratory preference for pines in the summer. It has been
406 recently described that *N. campestris* tend to return back to olive groves in the

fall to lay eggs (Bodino et al., 2019; Morente et al., 2018). Thus, the presence of pines in the landscape surrounding the crop may favour the establishment and proliferation of *N. campestris* in a given area throughout the year. Accordingly, nymphs develop on ground cover, mainly grasses, in olive groves and the emerged adults spend most of the summer on the surrounding pine trees, returning to the olive grove after the first rains in the fall to mate and lay their eggs on the emerging grasses. This has been observed in several areas of Spain including the Alicante region where *N. campestris* was very abundant in the grasses during the fall (Morente et al., 2018).

The migration capacity of *N. campestris* is only one of the difficulties that hamper the implementation of effective measures of disease containment. Our results, showing that *N. campestris* can migrate and fly more than 2 km in 5 weeks, together with the polyphagous habit of this species and its long-life cycle, provide additional information that can be useful to mitigate disease spread. In fact, a recent modelling study by Strona et al., (2020) shows that even limited probabilities of long-distance dispersal of infectious vectors dramatically affected disease outbreaks caused by *X. fastidiosa* in olive groves in Andalusia (southern Spain). They concluded that identifying and disrupting long distance dispersal processes may be much more effective to contain disease epidemics than surveillance and intervention concentrated on local scale transmission processes. Thus, the eradication measures that are being adopted as a general rule in the EU to fight against the disease by up-rooting infected plants and all plants, regardless of infection, within a 100 m radius, might be of limited value to contain pathogen spread. So, the fact that vectors of *X. fastidiosa* are able to move much more than 100 m, the persistence of the disease in the vector for

their entire adult stage (almost 9 months), together with the polyphagous nature of most xylem-feeders, suggest that vector management should be a critical component of the overall strategy to reduce the spread of *X. fastidiosa* across the European continent.

Additionally*, X. fastidiosa* symptom onset is variable depending on the plant species, from three to four months (in grapevines) to years (in the case of olive trees) (Almeida, 2016). Moreover, the detection of the pathogen in the plant is a difficult task, which requires certain concentrations of the bacterium and the right collection of samples (at least 4 leaves per sample from different trees in a large-scale sampling in the case of olive trees) (Loconsole et al., 2014). Additionally, vectors may acquire *X. fastidiosa* from infected asymptomatic hosts. Another important finding is that the transmission of *X. fastidiosa* by their vectors is a very fast process (inoculation occurs in 2 to 7 minutes after the onset of the first probe) (Almeida & Purcell, 2003; Cornara et al., 2020). Therefore, despite the fact that *N. campestris* adults do not colonize olive trees (Bodino et al., 2019; Cornara, Saponari, Zeilinger et al., 2017; Mazzoni, 2005; Morente, et al., 2018) they could easily land and probe briefly on olive canopies in late spring and summer when they disperse towards their over-summering hosts. In this process, they could rapidly transmit *X. fastidiosa* from one tree to another.

In summary, one of the critical components of the overall strategy against *X. fastidiosa* should be the management of vector populations in their early stages of development. This could avoid or reduce the presence of adults in areas were the disease is present and limit the risk of long-distance dispersal. This goal should be addressed in the most sustainable way by understanding the ecology, biology and behaviour of spittlebugs. Cultural control tactics such as

conservation tillage in the right moment could be effective for disrupting the life cycle of spittlebugs. In addition, removal of infected plants that may act, as disease foci should also be considered to reduce disease spread.

Finally, our study was focused on *N. campestris,* which was the most abundant vector species in our area of study. However, the main vector of *X. fastidiosa* in Europe is *P. spumarius* (Cornara et al., 2019). Thus, further investigation is needed to determine the migration behaviour of *P. spumarius* in areas where this vector is the dominant species.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTION

CL, MM, DH-B, AM and AF conceived research. CL, DH-B, AM, MP and AF conducted experiments. AM-C and FR-B designed the dashboard and the flight mill application software. CL and MM conducted the statistical analysis. CL, MM, AF and AM wrote the manuscript; all authors edited. AM and AF secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study were uploaded the 4th of November in 2020 and are openly available in:

https://drive.google.com/file/d/1hxRZud4a7j85gWJg9i9tMVW8cp19cuEu/view?usp=sharing

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778 **FIGURE LEGENDS**
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780 **FIGURE 1.** Mass-Mark-recapture (MMR) study zone. 1) Coloured circles: release
781 points (pink, blue, yellow and orange) 2) Letters: recapture points. A: *Quercus*
782 *coccifera*; B: *Foeniculum vulgare*, *Eryngium campestre* and Asteraceae; C:
783 *Retama sphaerocarpa* and *E. campestre*; D: *Pinus halepensis*; E: *Prunus dulcis*;
784 F: *P. dulcis*; G, H and I: *Pinus halepensis*; J: *Q. faginea* K: *P. halepensis* and *P.*
785 *pinea*; L: *Foeniculum vulgare* and *Retama sphaerocarpa*. 3) Points L and K
786 shown in the upper left and lower right corner, respectively are out of the map
787 scale because they were located too far away from the release points (Point L

788 was 1.7-2.3km far from the release points; Point K was 2.3-2.8 km far from the
789 release points). The distances between the release points and the recapture
790 points are shown on the supporting information 1.
791 Maxar Technologies, Map data © 2020, Spain. Retrieved from:
792 https://www.google.es/maps/place/28817+Los+Santos+de+la+Humosa,+Madrid
793 /@40.5020998,-
794
795 **FIGURE 2**. (1) An orange marked *Neophilaenus campestris* recaptured in the
796 zone D and exposed to UV light. Orange fluorescent particles were clearly visible
797 (a). Other particles were found that could be either yellow fluorescent particles
798 (b) or dust (c) covering some parts of the insect's body. (2) A non-dusted
799 individual of *N. campestris* exposed to UV light.
800
801 **FIGURE 3**. Survivorship curves for insects marked with fluorescence dust
802 (dashed line) and non-dusted control insects (continuous line). Standard error
803 bars are shown.