

ORIGINAL ARTICLE

The rose flea beetle (*Luperomorpha xanthodera*, Coleoptera: Chrysomelidae), an alien species in central Poland – from an episodic occurrence in an established population

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Abstract

The rose flea beetle, RFB (*Luperomorpha xanthodera* Fairmaire 1888) is a new flower pest in Europe. In 2012, it was brought accidentally to central Poland. To search for this introduced species in the area adjacent to the site of the first finding, 29 plant species belonging to five botanical families (Lamiaceae, Brassicaceae, Asteraceae, Plantaginaceae, Crassulaceae) were monitored over a 3-year-long study (2016–2018). RFB were found on 11 herbaceous/ornamental plant species (Lamiaceae, Brassicaceae, Asteraceae) along with feeding damage to the flowers. White mustard (*Sinapis alba* L., Brassicaceae), hyssop (*Hyssopus officinalis* L.), and *Monarda* spp. (Lamiaceae) were its most preferred host plants. In each season, RFB females preferred host plants which bloomed abundantly and vividly. However, among the examined plant species there was a large variation in the year-to-year RFB abundance. Over the examined period the RFB extended its abundance exponentially, and its population survived and established itself in the area. The general sex ratio of the beetles was strongly female biased. In the female pool, females with conspicuously swollen abdomens predominated. The results of our study provide more insight into RFB behaviour, its establishment and spreading into new areas. To support the evidence for the RFB risk factor as an agricultural/horticultural pest, further research should focus on the beetles' biology, reproductive tactics, larval host plant preference, larva-inflicted damage and harmfulness, the impact of the RFB on the native fauna, as well as its further local and distant migration propensity. Presently our knowledge about these aspects is still fragmentary.

Keywords: Alticinae, Asteraceae, Brassicaceae, host plant preference, Lamiaceae, non-native flower beetle-pest

Introduction

The worldwide development of international horticultural/ornamental plant trade has increased the risk of alien herbivorous pest species being accidentally transferred from the site of their origin to new geographical areas (Baker *et al.* 2005; Hellmann *et al.* 2008; Davis 2009; Hulme 2009; Maxwell *et al.* 2014; Early *et al.* 2016; Orlova-Bienkowskaja 2017). Species brought accidentally or deliberately into new areas usually acquire

the status of "invasive" (Baker *et al.* 2005). Sometimes the introduced species are destructive to natural and agro-ecosystems by harming their native structure and functions (Kenis *et al.* 2009; Carvalheiro *et al.* 2010). If not eradicated early, such species may quickly grow in numbers and expand their range, becoming important agricultural, horticultural or forest pests (Genovesi 2005; Jerde and Lewis 2007; Liebhold *et al.* 2016).

A new alien species can colonize a new habitat and establish itself only when its environmental requirements are met. Factors such as natural/agricultural landscape structure, soil properties, climate (temperature, precipitation) and/or agricultural/cropping practices are cited as the most powerful factors affecting the biology, behaviour, abundance and distribution of a new alien species (Hill and Mayo 1980; Vilà *et al.* 2007; Hellmann *et al.* 2008; Roques *et al.* 2009; Walther *et al.* 2009; Kenis and Branco 2010; DeLucia *et al.* 2012).

The rose flea beetle, RFB (*Luperomorpha xanthodera* Fairmaire 1888, Coleoptera: Chrysomelidae: Alticinae) is native to China and Korea. Recently, it has been recorded in the European and Mediterranean Plant Protection Organization (EPPO) region, namely in the United Kingdom, Austria, France, Germany, Hungary, Italy, the Netherlands and Switzerland (EPPO Reporting Service 2012), as well as in Montenegro (Radonjić and Hrnčić 2017) and Russia (Bieńkowski and Orlova-Bienkowskaja 2018a, b). The RFB is a generalist, developing cryptically in soil but carrying out intensive and long-lasting adult supplementary feeding on shoots of taxonomically different plants (presumably other than the larval host plants) (Del Bene and Conti 2009). Adults can be found on flowers of various plants more often than on their leaves causing damage when abundant (Johnson and Booth 2004; Heal 2006; Del Bene and Conti 2009). Up until now, the beetles have been found on plant species from at least 21 botanical families (Heal 2006; Del Bene and Conti 2009; EPPO Reporting Service 2012).

In Poland, a single male RFB specimen was recorded for the first time in 2012 on oregano (*Origanum vulgare* L., Lamiaceae) cultivated at the experimental and educational collection of herbaceous and ornamental plants [the Experimental Station of Warsaw University of Life Sciences – SGGW (WULS – SGGW), Warsaw] (Kozłowski and Legutowska 2014). It had supposedly migrated to the oregano field from imported ornamental plants sold at a nearby gardening centre. Since then no further specimens of the RFB were recorded until 2016 when we observed some RFB feeding symptoms along with single individuals on flowers of the Baikal skullcap (*Scutellaria baicalensis* Georgi, Lamiaceae). This finding prompted us to determine if the population of the RFB had established itself and spread from the site of the first finding of the single individual. Furthermore, due to the diversity of medicinal and aromatic plant species in the examined area, it was possible to assess the host plant preferences of the beetle, thus contributing to knowledge about RFB host plant selection and colonization in a new geographical environment.

Materials and Methods

Three-year studies (2016–2018) were carried out at the Experimental Station of WULS – SGGW located in Wilanów (52°09'38.7"N 21°06'16.4"E), Warsaw, Masovia, central Poland. Over the following years the abundance of the beetles differed considerably, therefore different sampling methods were applied.

In the first year of the study (2016), between mid-June and mid-August (June 15 and 23; July 20, 28; August 5, 18) plant species cultivated on separated plots (2 m × 3.5 m; avg. 45 plants per plot) were swept by means of a sweeping net six times with no detailed observation of flower damage. Using this method, the RFB was monitored on 21 plant species belonging to four botanical families – Lamiaceae [Baikal skullcap, oregano, wild thyme (*Thymus serpyllum* L.), common thyme (*Thymus vulgaris* L.), of the *Monarda* genus (*Monarda media* Willd., *M. fistulosa* L., *M. citriodora* Cerv. Ex Lag., *M. didyma* L., *M. bradburiana* Beck), peppermint (*Mentha piperita* L.), common mountain mint (*Pycnanthemum virginianum* L. B.L. Rob. & Fernald), sage (*Salvia officinalis* L.), basil (*Ocimum basilicum* L.), hyssop (*Hyssopus officinalis* L.), lavender (*Lavandula angustifolia* L.)], Asteraceae [purple coneflower (*Echinacea purpurea* (L.) Moench.), China aster (*Callistephus chinensis* L.), common marigold (*Calendula officinalis* L.), Mexican marigold (*Tagetes erecta* L.)], Plantaginaceae [broadleaf plantain (*Plantago major* L.)], and Crassulaceae [roseroot (*Rhodiola rosea* L.)].

In 2017, from July 14 to August 19 the same plant species as in the previous season were carefully scanned and the beetles were manually collected five times (July 14, 28; August 4, 11, 19). However, some plant species had been relocated to new sites (for comparison see Figs. 1A–B). Some new Lamiaceae plants – *M. punctata* L., calamint (*Calamintha*), and catmint (*Nepeta* spp.), as well as some new Asteraceae and Rosaceae plants – dahlia (*Dahlia x cultorum*) and rugose rose (*Rosa rugose* Thunb.) were additionally monitored. At the beginning of August, 2017 white lupine (*Lupinus alba* L., Fabaceae) was sown in the area from which in early spring most of the Baikal skullcap plants had been removed. For details see the Figures 1A–B.

Upon noticing a beetle on a flower, an open Eppendorf tube (V = 2 ml) was carefully moved close to the flower to provoke the beetle to jump off it and straight into the tube. Then, the beetles in the tubes were immediately transferred to the lab and divided into three categories: physogastric females (those with swollen abdomens), non-physogastric females, and males



Figs. 1A–B. Topographic Google maps of the Experimental Station of WULS – SGGW located in Wilanów (52°09'38.7"N 21°06'16.4"E), Warsaw, central Poland illustrating a scheme of experimental plant plots and likely routes of rose flea beetle (RFB) migration (white arrows) in the seasons 2016 and 2017 (A and B, respectively); the bluish dimmed area is the site of a gardening centre; areas framed with blue are the plots surveyed for the presence of RFB; an open white circle indicates the site of the first RFB record in 2012; small coloured rectangles filled with numbers represent plant plots where the beetles were found in 2016, June 15: *S. baicalensis* (1); August 5: *Monarda fistulosa*, *M. media*, *M. citriodora* (2); August 18: *M. fistulosa*, *M. bradburiana*, *M. didyma* (3); in 2017, July 14: *M. media*, *M. didyma* (1); July 28: *Hyssopus officinalis* (2); August 4: *M. fistulosa* (3); August 11: *M. citriodora*, *M. bradburiana*, *H. officinalis*, *Scutellaria baicalensis* (4), August 18: *M. citriodora*, *M. fistulosa*, *M. bradburiana* and *Nepeta* spp. (5)

(Fig. 2). The RFB females could be easily distinguished from the males by the size of the antennae (Döberl and Sprick 2009). The physogastric females had visibly swollen abdomens extending behind elytrae unlike the non-physogastric ones (Fig. 2). We did not find any females with intermediate characteristics. Occasionally, sweepings and/or scans of plants relatively close to the experimental plots were carried out to determine if the beetles were spreading out of the area of the plots.

In 2018, from July 26 to August 30 the beetles were collected four times (July 26, August 2, 7, 30) from hyssop, *M. fistulosa*, oregano, common yarrow (*Achillea millefolium* L., Asteraceae) and white mustard (*Sinapis alba* L. subsp. *alba* (syn. *Brassica alba* (L.) Rabenh.,



Fig. 2. Rose flea beetle (RFB) male (♂) and female (♀) in a physogastric stage. Scale bar = 1 mm

Brassica hirta Moench, Brassicaceae) using the same technique as in the previous year. All plants were at the flowering stage. White mustard was sown as an intermediate crop in the area previously planted (2017) with white lupine.

In each season, monthly climatological conditions [temperature (°C) and rainfall (mm)] were measured at The Local Meteorological Station (Wilanów).

Chi-square test of goodness of fit was applied for sex ratio assessments assuming an expected sex ratio of 1 : 1. Computer software available from <http://quantpsy.org> was used (Preacher 2001) for the analyses. The total abundance of the beetles captured in the following years was presented as simple bars along with an exponential regression function. Relationships between the total number of beetles per month vs the 2 month climatic variables – temperature (°C) and rainfall (mm) were evaluated using linear regression. Statistical significance of the relationships was checked using Student's t-test (http://vassarstats.net/tabs_r.html). For all analyses the significance level was set at 0.05.

Results

In the season of 2016, among the seven captured individuals of the RFB, six were physogastric females (Fig. 3; Table 1). All the females were collected from plants of the mint family such as: *S. baicalensis*, *M. media*, *M. fistulosa*, *M. citriodora*, *M. didyma*, and *M. bradburiana* grown as shown in Figure 1A. The only male was spotted on *M. fistulosa*. The first beetle was observed on June 15 on the *S. baicalensis* plot situated

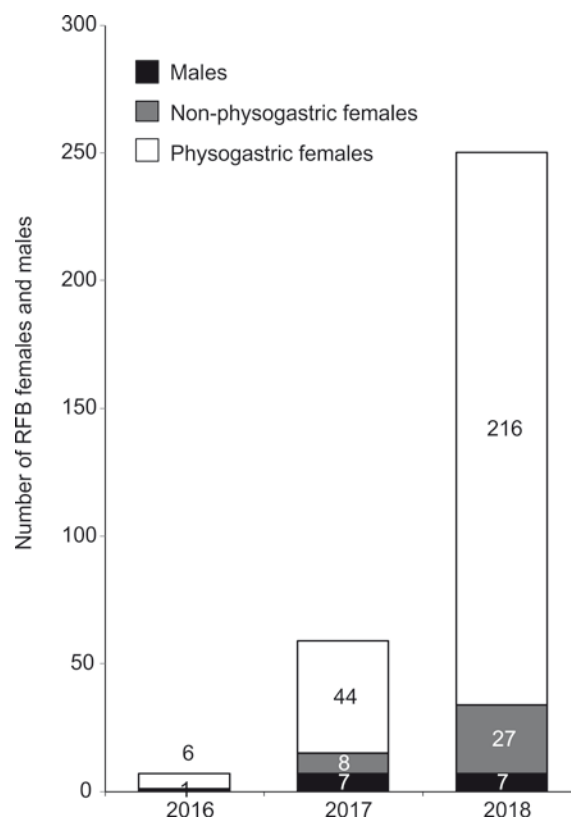


Fig. 3. The total number of rose flea beetle (RFB) individuals (physogastric and non-physogastric females and males) captured on the Lamiaceae, Brassicaceae and Asteraceae plants in the following years of study. The total beetle number shows an exponential increase ($y = 1.2875e^{1.7898x}$, $r = 0.9956$, $P_{(one-tailed)} = 0.02974$)

approximately 25 m away from the oregano plot where the first individual of the species had been recorded previously (Kozłowski and Legutowska 2014) and

Table 1. Total number of rose flea beetle (RFB) captured on the Lamiaceae, Brassicaceae and Asteraceae plant species over the seasons

Species	Family	2016		2017		2018		Total		Σ
		♀	♂	♀	♂	♀	♂	♀	♂	
<i>Scutellaria baicalensis</i>	Lamiaceae	1	0	1	0	0	0	2	0	2
<i>Monarda media</i>	Lamiaceae	1	0	9	1	0	0	10	1	11
<i>M. fistulosa</i>	Lamiaceae	1	1	11	2	14	1	26	4	30
<i>M. citriodora</i>	Lamiaceae	1	0	3	0	0	0	4	0	4
<i>M. didyma</i>	Lamiaceae	1	0	3	0	0	0	4	0	4
<i>M. bradburiana</i>	Lamiaceae	1	0	5	0	0	0	6	0	6
<i>Hysopus officinalis</i>	Lamiaceae	0	0	19	4	33	0	52	4	56
<i>Nepeta</i> spp.	Lamiaceae	0	0	1	0	0	0	1	0	1
<i>Origanum vulgare</i>	Lamiaceae	0	0	0	0	18	0	18	0	18
<i>Achillea millefolium</i>	Asteraceae	0	0	0	0	2	0	2	0	2
<i>Sinapis alba</i>	Brassicaceae	0	0	0	0	176	6	176	6	182
Total		6	1	52	7	243	7	301	15	316

♀ – female; ♂ – male

15 m away from the border of the gardening centre. Later in the season (August 5), other beetles were found either on the neighbouring *Monarda* plots (*M. fistulosa*, *M. media*, *M. citrodora*) situated some 30 m to the south of the first spotting, or on the *M. fistulosa*, *M. bradburiana* and *M. didyma* plots growing more to the west (Fig. 1A). The beetles might have migrated to the aggregated plots of the abundantly flowering species of the genus *Monarda* from the Baikal skullcap, at this point already out of bloom.

In 2017, we captured as many as 59 individuals (44 physogastric females, eight non-physogastric females and seven males), i.e. more than the second power of the number of the beetles caught in the previous year (n^2) (Fig. 3). From Figure 1B it is clear that between July 14 and 20, the beetles resided on hyssop and two *Monarda* species (*M. didyma* and *M. media*), whereas between August 4 and 11, the beetles spread to *M. fistulosa*, *M. citrodora*, *M. bradburiana* and *S. baicalensis*, and they were still present on the hyssop. On August 18, the beetles still fed on the flowers of the *Monarda* species and for the first time appeared on catmint flowers. The beetles, now in much higher numbers, extended their range and migrated either to the south east reaching the plots of hyssop and catmint (some 50 m away from the *Monarda* plots) or to the west, to the plots of *M. bradburiana* situated that year some 20 m away from the other *Monarda* plots (Fig. 1B). Thus, it is clear that the beetles could have relocated some 70 m away from the site of their previous occurrence.

Over the 2-year study (2016, 2017), hyssop, *M. fistulosa* and *M. media* plants had the most beetles, with 23, 15 and 11 individuals which corresponds to 35, 23 and 17%, respectively (Table 1; Fig. 4A). Much smaller numbers of females were found on *M. bradburiana* (six females), *M. didyma* (four females) and *M. citrodora* (four females), comprising 9%, 6% and 6%, respectively. Only a few beetles settled on *S. baicalensis* (two females) and catmint (one male) flowers, representing 3% and 1%, respectively.

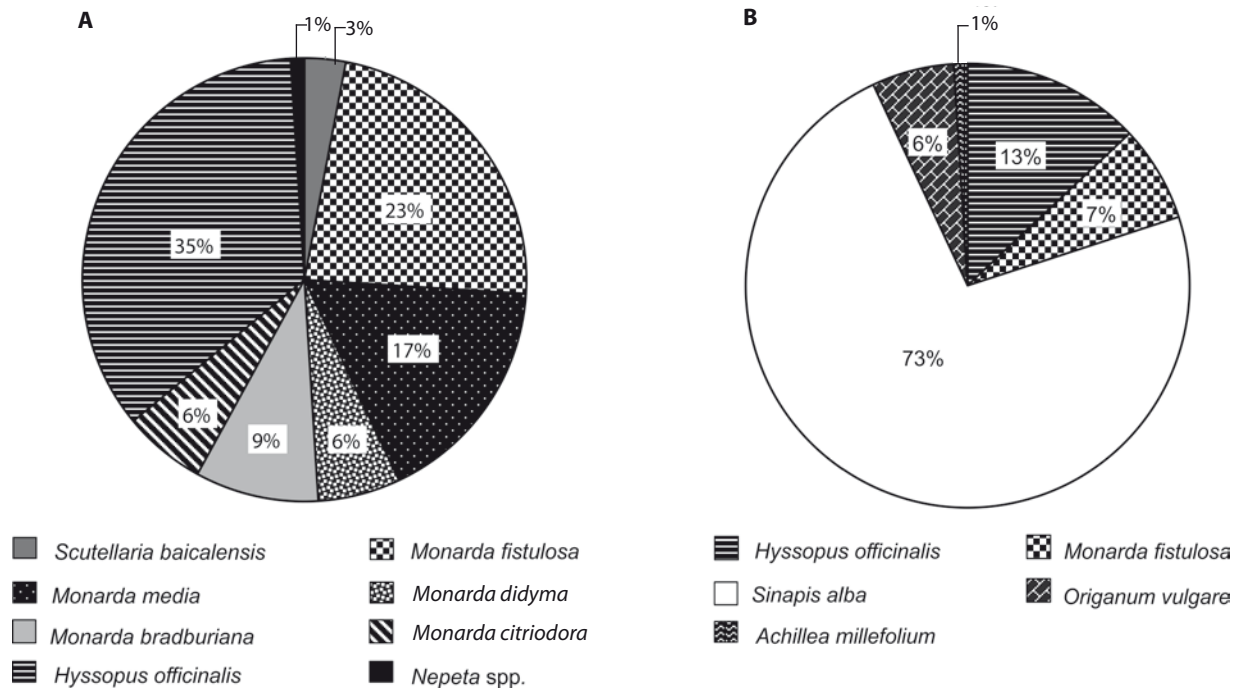
The plots of the mint plant family with negative scores all through the seasons of 2016 and 2017 were: thyme, oregano, *M. punctata* and *M. piperita*, *Pycnanthemum*, salvia, purple coneflower, basil, lavender, *Calamintha* Mill., as well as all the plant species other than those belonging to the Lamiaceae family (the China aster broadleaf plantain, common marigold, roseroot, dahlia, Mexican marigold and white lupine). In summary, in both seasons there were beetles only on the plants of the mint family found on the experimental plots and in the adjacent areas.

In 2018, 250 individuals (216 physogastric females, 27 non-physogastric females and seven males) were collected (Table 1; Fig. 3). On July 26, the beetles resided on the flowers of hyssop (14 females), oregano (two females) and *M. fistulosa* (two females).

With the exception of oregano, all the plants were at the full flowering stage. One week later (August 2), 16 females (15 physogastric and one non-physogastric) were found on the hyssop, three physogastric females were located on the oregano, two physogastric females fed on the *M. fistulosa* and one on the common yarrow. For the first time 64 beetles (48 physogastric and 13 non-physogastric females, three males) were detected on the nectar-rich white mustard plants at the flowering stage. Between August 7 and 30, the beetles still aggregated in large numbers (118 individuals: 107 physogastric, eight non-physogastric females, three males) in the white mustard field. Simultaneously, in much lower numbers, the beetles occurred on hyssop (two physogastric and one non-physogastric females), oregano (12 physogastric and one non-physogastric females), and *M. fistulosa* (8 physogastric and two non-physogastric females, and one male), as well as on common yarrow (one physogastric female). In 2018, 73% of the beetles were collected from the flowering plants of white mustard, 13% from hyssop, 7% and 6% oregano and *M. fistulosa*, respectively and only 1% from common yarrow (Fig. 4B). Thus, these results reveal that RFB dominated on the white mustard (Brassicaceae) which had appeared in the area for the first time. Moreover, in the season of 2018, the beetles occurred in much higher numbers than previously (2016, 2017) and relocated to the area where they had first been found on the Baikal skullcap in 2016. Surprisingly, in this season we found the RFB specimens on the oregano where the first beetle had been noticed in 2012.

In the course the study, the number of RFB in the area grew exponentially ($y = 1.2875e^{1.7898x}$, $r = 0.9956$, $P_{\text{(one-tailed)}} = 0.02974$; where y is the number of RFB and x is the subsequent year, $x = 1$ for year 2016) from the seven individuals captured in 2016 to 250 individuals in 2018 (Fig. 3). Generally, the sex ratio in the pool of the beetles captured in 2017 was, as in the previous year (2016), strongly female biased (52 females, 7 males) and as indicated by the chi-squared test ($\chi^2 = 34.2$, $p < 0.000001$) there was a significant difference between the observed and the expected values at the 5% significance level. Thus we can reject the null hypothesis that the sex ratio is 1 : 1. In the female pool (52 females), physogastric females predominated (44 : 8) ($\chi^2 = 24.9$; $p < 0.0001$). Similarly, the sex ratio in the pool of beetles collected in 2018 was strongly female biased (243 females, 7 males) ($\chi^2 = 222.8$; $p < 0.0001$). In the female pool (243 females), physogastric females predominated (216 : 27) ($\chi^2 = 135.2$; $p < 0.000001$). Interestingly, in our 3-year survey we did not notice any pairing beetles. We may have missed them, assuming mating had occurred earlier in each of the seasons.

In 2017, some damage to flowers suggesting nibbling by the beetles was noticed on the roses growing



Figs. 4A–B. The relative proportion of rose flea beetle (RFB) captured on the host plant species of the Lamiaceae family over two seasons (2016; 2017) (A). The relative proportion of RFB recorded on the host-plants of Lamiaceae and Brassicaceae families available in the season 2018 (B)

close to the hyssop and calamint, but no beetles were found. Therefore, the beetles from the hyssop were brought to the laboratory and transferred to rose flowers. Their feeding activity caused both window pane like and edge feeding damage (Fig. 5E). In the field, the beetles feeding on Baikal skullcap and *Monarda* spp. were easily visible on flowers (Figs. 5A and D) and three types of damage were distinguished: (1) feeding holes in petals (Fig. 5A), (2) elongated window pane like damage in petals (Figs. 5B and E) and (3) edge feeding damage in petals. Beetles also fed on the

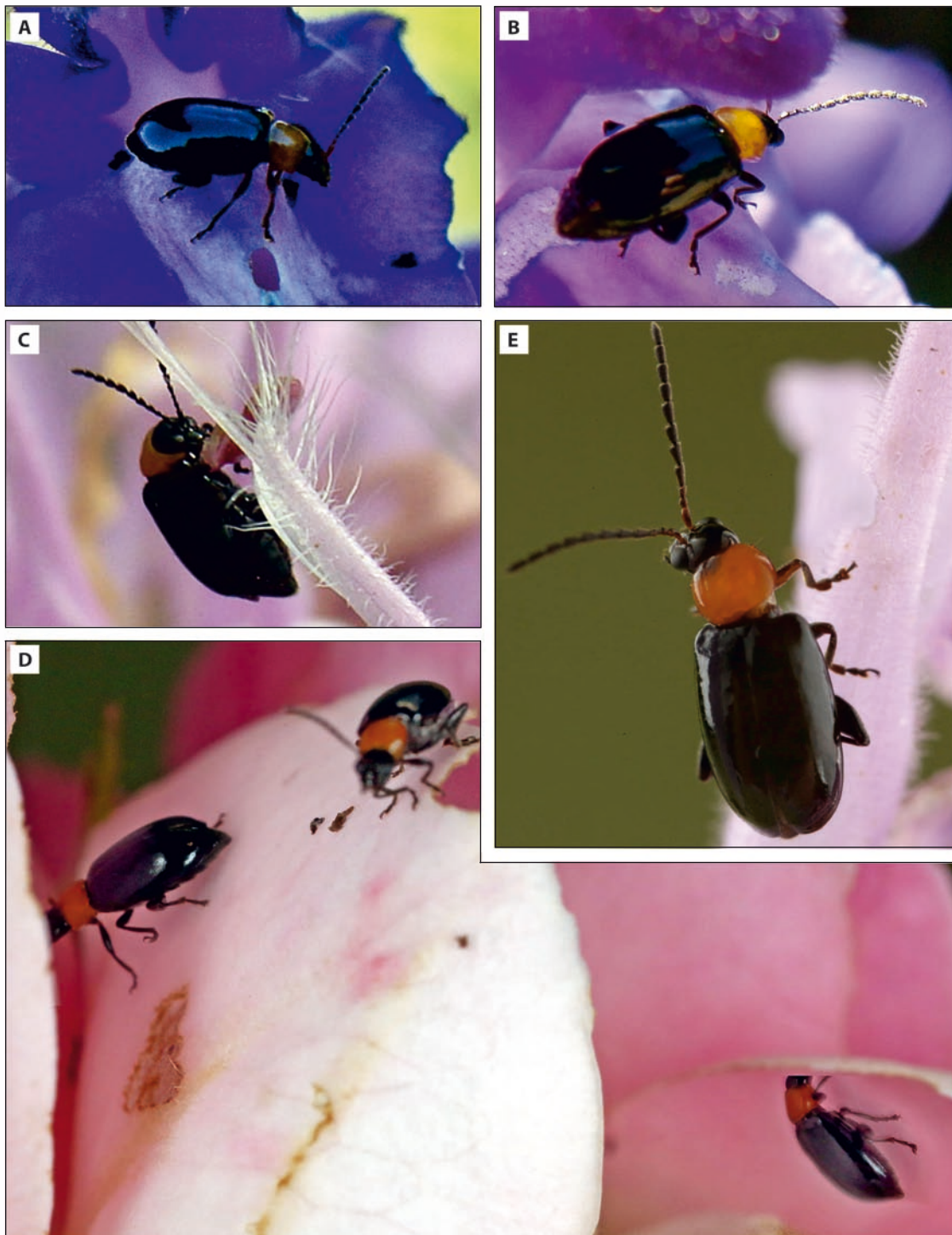
anthers of *Monarda* spp. flowers (Fig. 5C). In 2018, on the bright yellow petals of the white mustard flowers, actively feeding RFB individuals were very visible and produced either feeding holes or edge feeding damage in petals (Fig. 6).

The average temperatures and total precipitation for the same months varied over the researched period (Table 2). In 2016, the average monthly temperature was very similar between June, July and August, fluctuating from 18.4 to 19.8°C, and it was higher than the long-term average monthly temperature for these months.

Table 2. Summer weather conditions based on the measurements at the local Meteorological Station (Wilanów)

Year	Temperature [°C]			Precipitation [mm]		
	June x ± SD (min–max)	July x ± SD (min–max)	August x ± SD (min–max)	June x ± SD (min–max)	July x ± SD (min–max)	August x ± SD (min–max)
2016	19.2 ± 3.34 (2.9–33.6)	19.8 ± 2.61 (6.8–32.6)	18.4 ± 2.46 (4.2–31.0)	38.4 (0–14.4)	76.8 (0–48.4)	60.8 (0–17.2)
2017	–	18.8 ± 2.39 (6.8–32.3)	19.3 ± 3.57 (6.8–34.4)	–	106 (0–24.4)	50 (0–16.8)
2018	–	21.3 ± 2.77 (8.9–32.2)	20.5 ± 3.23 (7.5–32.3)	–	83 (0–18.6)	62.4 (0–30)
Long-term average*	16.5 (11–22)	18.5 (13–24)	17.5 (12–23)	70	90	65

*weather averages for Warsaw Okęcie Airport, Warsaw (Poland) during 1985–2015 (Available on: <https://www.timeanddate.com/weather/poland/warsaw/climate>)



Figs. 5A–E. Variety of the flower damage by rose flea beetle (RFB) feeding: (A) feeding hole in a petal of hyssop, (B) elongated window pane like damage on a petal of hyssop, (C) mode of the beetle feeding on the anther of *Monarda* spp., (D) edge feeding damage on a petal of *Monarda* spp., (E) both window pane like damage and edge feeding damage as a result of the rose flea beetles feeding on rose petals

June was the driest month, with a total month precipitation amounting to 38.4 mm, which was almost half of the long-term average. In 2017, the average monthly temperature for July and August was very similar to the average monthly temperature for July and August in the previous year, while the total precipitation was

about 40% higher in July and about 20% lower in August (Table 1). Thus, the July temperature and precipitation were close to the long-term temperature and precipitation average for this month, whereas August was generally much warmer and drier. In 2018, the average monthly temperature for July and August was



Fig. 6. Representative damage (feeding holes and edge feeding) to petals of the white mustard flowers caused by rose flea beetle (RFB) feeding

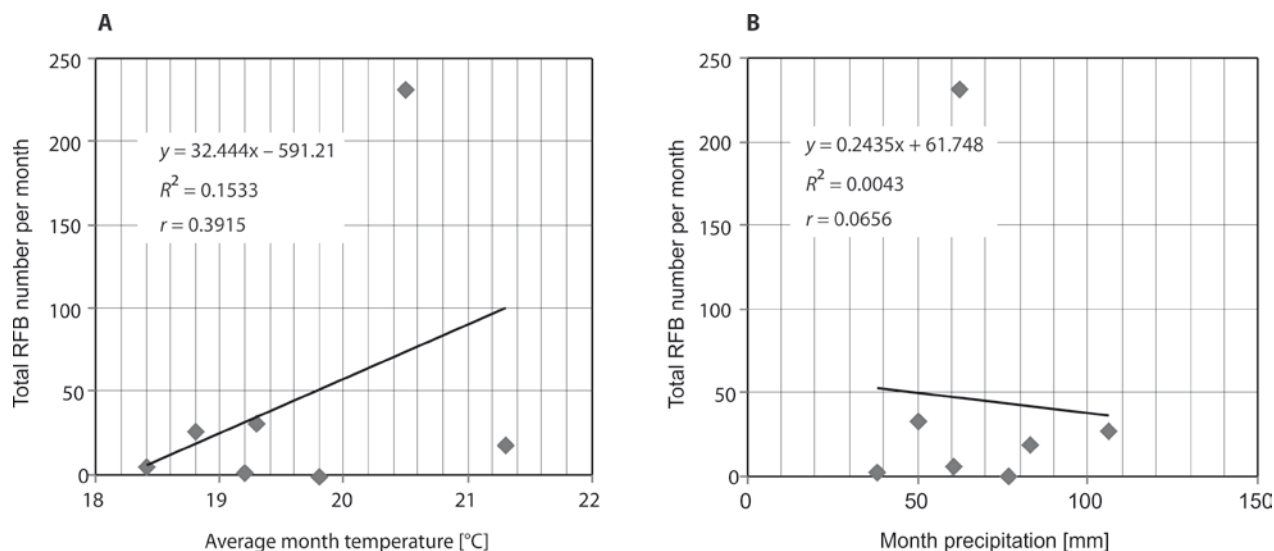
the highest since 2016, while the total precipitation was at the level of the long-term average and was similar to the total precipitation in these months in 2016. In 2018 the weather conditions should have facilitated the RFB development. Indeed, the beetle occurred in the greatest numbers, but contrary to our expectations, we found no evidence of any significant correlation neither between the number of the RFB captured per month and the average monthly temperature ($N = 7$; $r = 0.3915$; $P_{\text{(one-tailed)}} = 0.1925$), nor between the number of the RFB captured per month and the total monthly precipitation ($N = 7$; $r = 0.0656$; $P_{\text{(one-tailed)}} = 0.4445$) over the examined period of the study (Figs. 7A–B).

Discussion

Here, we reported on the establishment of a RFB population in a new geographical region far away from its native environment, thus contributing to knowledge about the RFB host plant selection and colonization in a new environment. The results of our study clearly show that 4 years after the first RFB individual had been identified on oregano (Kozłowski and

Legutowska 2014), the beetle was not only still present in the area, but it had reproduced and the abundance of its population had increased exponentially. The beetles showed preference for the strongly fragrant and nectar-rich medicinal/aromatic plant species of the Lamiaceae and Brassicaceae families. Additionally, within and between the seasons, the RFB females relocated between plants, choosing those which bloomed abundantly and vividly.

Current literature data indicates that the first phase of an invasion of a foreign species is its arrival, and it usually vanishes without intervention (Lodge *et al.* 2016; Roderick and Navajas 2017). This can occur due to the lack of an appropriate site to live in (e.g. host plants). It can also be due to the inability to overcome the so-called 'Allee effect' occurring when an arriving population is subjected to adverse factors related to small numbers, which results in a failure to locate mates, inbreeding or cooperative feeding (Raffa and Berryman 1983; Jerde and Lewis 2007; Liebhold and Tobin 2008). Based on our results, we cannot exclude the possibility that already in 2012, when the single RFB male was found on oregano, there was a very small number of beetles in the area which was able to reproduce. Thus, they were not able to create a new population on this new site. On the other hand, it is



Figs. 7A–B. Correlation between rose flea beetle (RFB) total abundance and climatic variables – monthly temperature (A) and total precipitation (B) over the three seasons of study

also possible that the appearance of the beetles in the area during the years following the first introduction could have been related to recurring RFB migrations from the beetle-infested ornamental plants newly imported to the gardening centre situated close to the experimental plots. It has been documented that recurring introductions of alien insects to Europe are related to the considerable increase of international plant trade (Kenis *et al.* 2007; Roques *et al.* 2009; Kenis and Branco 2010; Rabitch 2010). Nevertheless, the beetles detected in 2016 first settled on Baikal skullcap flowers which they later abandoned after blossoming and migrated to *Monarda* spp., at that point in full flowering stage. Our next results (2017) also showed that when the only plant species available in the area were those of the Lamiaceae family, hyssop and *Monarda* were the most attractive for the RFB. However, those species were not equally attractive to the beetle at the same time, since plant attractiveness varied depending on the flower developmental stage: the number of the RFB peaked on each plant species when its flowers were fully developed.

Usually, insect visitors are attracted by the combination of floral stimuli (e.g. colour, fragrance, nectar, pollen, shape etc.). To our knowledge there is no literature data on the floral stimuli responsible for the selection of certain plant species by the RFB. It is well known that flowers release a diverse range of multifunctional volatile organic compounds (VOCs), mainly terpenoids (Dudareva *et al.* 2004; Unsicker *et al.* 2009; Schiestl 2010). VOCs can interact with neighbouring plants, attract pollinators, repel or attract arthropod herbivores and their natural enemies. The results of our study in 2018 provide evidence that

the RFB could relocate between plants of two families (Lamiaceae and Brassicaceae) at the stage of full flowering i.e. from hyssop, *Monarda*, and oregano to the highly nectariferous white mustard. For reasons yet unknown, this *Brassica* species promoted the RFB aggregation. Presumably, the beetles were more preferentially attracted to the stronger floral cues of the white mustard plants growing in a large patch than to the cues of the Lamiaceae plants growing nearby in smaller patches. This assumption requires further study. The question also arises as to whether the RFB will be able to inhabit *Brassica* species of economic importance such as rape, and disperse over long distances, or not. On the other hand, since only moderate flower damage was the result of RFB feeding on the medicinal/aromatic plants examined here, it needs to be determined if the abundant population of RFB detected on white mustard flowers could threaten the host plant performance or, conversely, the host plant could somehow benefit from the presence of the beetles, for instance as pollinators.

We found no significant relationship between the RFB abundance and the climatic variables (monthly temperature or total precipitation) over the three seasons of the study. However, we cannot exclude the possibility that the higher RFB density in 2018 was related to the greater number of warm days per month and its lower density in 2017 was related to the greater number of cold days per month. Other environmental variables (the presence of predators and/or competitors, host-plant resistance, environmental heterogeneity and micro-conditions etc.) unexamined here could also affect the RFB development rate and its final density.

Summing up, it seems likely that the accessibility of highly suitable host plants at full flowering stage, and not climatic variables affect the RFB abundance and distribution. However, an indirect effect of the climatic variables on the suitability of the host plants should not be excluded. Moreover, the complexity of the plant species distribution, wind speed or even direction probably may affect the RFB sensitivity to plant odours (attractant/repellent volatiles). Further study is needed to learn if the exponential increase of the RFB after some period of lag time (here between 2012 and 2016) can be maintained as it is suggested.

There is more and more evidence that an invasive population, if established in a new site, can increase its abundance (often exponentially), then spread, and finally impact the environment (Sakai *et al.* 2001; Mehta *et al.* 2007; Liebhold and Tobin 2008; Liebhold *et al.* 2016; Lodge *et al.* 2016). However, the ways the RFB multiplies and establishes itself in new sites can vary. For example, in Tuscany, Italy in large plant nurseries the RFB multiplied in numbers over the two following years causing only a little damage to flowers of different botanical families (Del Bene and Conti 2009). In France and Russia (Sochi), the RFB was recorded in a few sites but only in one location (Varenes-lès-Macon) in higher numbers, especially on garden grown roses with brightly coloured flowers (Vincent and Doguet 2011; Bieńkowski and Orlova-Bienkowskaja 2018a). In Montenegro, flowers and leaves of some citrus species, ornamentals and strawberries were damaged by the RFB but the beetle's population did not increase dramatically (Radonjić and Hrnčić 2017).

We have no plausible explanation for the strongly female biased sex ratio (SR) observed on the flowering plants in our study. The predomination of physogastric individuals in the female pool raises further questions. In Chrysomelidae, SR can be accounted to genetics (Gomez-Zurita *et al.* 2006), male killing microorganisms (Chang *et al.* 1991), conditions of larval development (Weiss *et al.* 1985) or differences in displacement between breeding sites and feeding resources. The RFB larvae develop in roots of many plants but adults perform supplementary feeding on flowers or sometimes on leaves of plants other than the host plants of their larvae (Del Bene and Conti 2009). Flea beetles (Alticinae) usually perform larval and adult feeding, as well as mate on the same host plant (Bartlet *et al.* 2001; Aslan and Gök 2006). The RFB is different in this respect. It is both polyphagous in larval and adult stages, and prone to changing host and/or food plants for adult supplementary feeding, mating and oviposition which take place in the soil in the vicinity of the prospective larval host plant. Del Bene and Conti (2009) reported

mating on flowers over an extended period of the season ("number of weeks"). Each year, we started our research mainly in the middle of May or June and did not observe any pairing episodes, neither in the field, nor in the laboratory. However, males in low numbers were continuously present on flowers. We have no plausible explanation of this male sexual indifference. Since we did not observe the beetles at the onset of their activity, it could be that pairing activity on flowers had ceased before our research started and a considerable number of males may have died. Some pairing may also occur around places of oviposition later in the season, but this supposition should be verified by separate observations.

Conclusions

Here, we report on the establishment of the invasive RFB population in a new geographical region (central Poland) far away from its native environment (Asia), thus contributing to knowledge about host plant selection and colonization by the exotic pest in a temperate climate. The results of our 3-year study cast new light on the behaviour and short distance spreading of RFB in new areas. The abundance of RFB extended exponentially on those medicinal/aromatic Lamiaceae, Brassicaceae and Asteraceae plant species which flourished abundantly and vividly. Among the examined plant species, the RFB preferred white mustard, hyssop and *Monarda* spp. The general sex ratio of the RFB was strongly female biased. In the pool of females, physogastric females predominated. This research should be of interest to readers assessing RFB behaviour as well as its risk as an agricultural pest. Furthermore, our data should encourage further study concerning beetle biology and reproductive tactics, larval host plant preference and the progression of damage since the present knowledge in this aspect is still fragmentary.

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