Effect of Scotch broom, *Cytisus scoparius*, pod size and patch density on *Exapion fuscirostre* (Coleoptera, Apionidae) seed weevil oviposition

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Abstract   *Cytisus scoparius* (L) Link (Fabaceae) is a broom species of European origin introduced both accidentally and as an ornamental plant to Australia, New Zealand and America, where it is classified as a noxious invasive species. One of its main seed predators is *Exapion (Exapion) fuscirostre* (Fabricius), a weevil with a Palearctic distribution and which has been introduced to United States and New Zealand as a biological control agent. Factors influencing the insect's choice of oviposition location are crucial for the plant's reproductive success. We examined *E. fuscirostre* oviposition on the host plant, *C. scoparius*, in the European Mediterranean region. We analysed the effect of pod size, seed abortion rate and host plant patch density on seed infestation rate. Oviposition was greater in patches with low-medium plant densities. Oviposition was also negatively related with seed abortion rate per pod and the rate of infestation by other seed-eating insects. Pod dimensions, particularly width, were positively related with *E. fuscirostre* oviposition.

Key words   biological control, insect–seed interrelationship, oviposition preference, plant density, pod size.

INTRODUCTION

Oviposition patterns exhibited by seed weevils are related to several factors that determine the recognition and selection of appropriate laying sites in potential host plant species. Some of the factors serve as cues to ovipositing females that indicate the suitability of these plants as a trophic resource for their larval stage, feeding and living inside the seeds until that growth stage is complete. These factors have been widely studied to explain the survival and breeding mechanisms of seed eaters and also to explain the strategies used by host plants to ensure and increase their dispersal capacity (Janzen 1969, 1971; Center & Johnson 1974; Fox *et al*. 1994).

The dispersal methods used by host plants lead some predispersive predator insects such as Curculionoidea and Bruchinae to develop a clear specificity in their host plants. In the case of Fabaceae, there is an insect–plant synchronisation of biological cycles in which the end of the larval growth stage coincides with the pod dehiscence, the point when the seeds are ejected to some distance from the plant, and with them, the mature larvae or recently formed imagos (as in the case of the *Pachytichius* and *Exapion* genera, respectively) (Parnell 1966; Sanz 1994; Barat *et al*. 2007). Their occupation of the seed until its ejection at maturity explains the strategies used by insects to consume resources and at the same time avoid inter-

specific competition with other predispersive predator insects growing in certain parts of the seed (Sanz & Gurrea 2000; Messina & Karren 2003).

The number and size of clutches (number of eggs per clutch) indicates the breeding potential of the insect species and defines the infestation level in the host plant. Patch density or distance between host plants (independently of their quality) is an important factor that influences the ovipositing female's choice of clutch location and size. Optimal patch acceptance and clutch size both depend on travel cost between patches. According to the travel-cost hypothesis, when patches are scarce, travel costs are high because the female invests more energy in searching for a suitable egg-laying site, thus increasing the predation risk and leading ovipositing females to lay fewer and larger clutches (Heard 1998; Shea *et al*. 2000; Takahashi 2007; Heard & Remer 2008).

Fruit size and number of seeds per fruit also determine the insect's choice of an egg-laying site. A significant positive relationship has been found between pod length and the number of bruchid eggs (Chrysomelidae: Bruchinae) laid in them in North Carolina *Cytisus scoparius* populations (Redmon *et al*. 2000). The number of eggs also increases with the number of seeds per pod, but it is a less reliable indicator than pod length (Redmon *et al*. 2000).

The use of seeds by seed-eater insects also depends on the number of available viable seeds. Aborted seeds have been found to reduce predation on viable seeds as a strategic response by the plant to avoid predispersive predation and

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increase the plant's dispersal capacity (Traveset 1993; Fuentes & Schupp 1998; Bonal *et al.* 2007).

Information about factors affecting oviposition of seed predators can be incorporated into insect–plant host population models with potential implications for biological control of invasive plants. *C. scoparius* seed production is higher in areas such as the United States, New Zealand and Australia, where it is an invasive plant, than in its European area of origin (Rees & Paynter 1997; Sheppard & Hosking 2000; Sheppard *et al.* 2002). Paynter *et al.* (2010) recently investigated seed production in New Zealand and found that it was not as high as previously supposed and that seed set was strongly correlated with pollinator visitation rate.

Ongoing control research is searching for and introducing seed-eaters such as *Exapion fuscirostre*, *Bruchidius villosus* (Fabricius 1792), the stem-miner *Leucoptera spartifoliella* (Hubner 1813) and the sap-sucker *Arytainilla spartiofila* Foster 1848, as biological control agents (Syrett *et al.* 1999; Paynter *et al.* 2010), and assessing their effectiveness as a predispersal predators. The infestation levels of *C. scoparius* pods by *E. fuscirostre* in the native distribution areas are rather low (between 9 and 20%, Sanz 1994). Nevertheless, reported infestation rates are higher where *E. fuscirostre* has been used as a biocontrol agent (perhaps because the beetles experience enemy release or reduced competition with other pod-infesting species). For example, Scotch broom seeds have been reduced by 60% in California because of *E. fuscirostre* (Coombs & Markin 2004). Furthermore, the finding that low-density broom patches have higher infestation rates than high-density patches may also have relevance to integrating biocontrol with other control methods if, e.g., treating large broom patches with herbicide results in the low-density regrowth being more heavily attacked by biocontrol agents (e.g. Paynter & Flanagan 2004).

The present paper analyses the factors that determine the infestation rate of the legume *C. scoparius* by *E. fuscirostre*, a common seed eater specific to Fabaceae species in south-western Europe, used widely as a biological control agent on this invasive plant in other locations. These factors are analysed using a new approach that also relates resource density-dependent factors to others that are density-independent. The specific aims are: (1) to define the influence of host plant density on the pod infestation rate in the context of localities with different environmental characteristics; and (2) to ascertain whether pod infestation rate depends on seed size and the seed abortion rate.

MATERIALS AND METHODS

Plant characteristics

Scotch broom (*C. scoparius*) is a densely branched medium shrub (1–2 m in its native area), with attractive yellow flowers (16–25 mm) that bloom between February and July, depending on the locality. This plant mainly grows on acidic soils, in scrubland accompanying oak, beech and pine woodlands up to 2000 m. It is found in clearings on deep, fresh soil in a large part of western Asia and in Europe across to the Canary Islands, including the entire Iberian Peninsula with the exception of provinces with predominantly limestone soils (López 2007). It has been accidentally introduced to North and South America, Australia, Hawaii and New Zealand as an ornamental plant (Sheppard *et al.* 2002; Palmer *et al.* 2010).

Scotch broom is dispersed by seeds that fall roughly 2 m from the parent plant and may be dispersed more widely by other dispersive factors and agents such as ants (Rees & Paynter 1997). Its ballistic seed dispersal mechanism permits a high-potential establishment of new individuals despite its low seed density (Malo 2004).

E. fuscirostre characteristics

E. fuscirostre has a Palaeartic distribution. The adults are found in species (Fabaceae: Leguminosae) of the genera *Genista*, *Cytisus*, *Ulex* and *Echinospartum*. The soft, oval eggs have a whitish colour and yellow traces, measuring 0.62–0.71 mm in width and 0.27–0.29 mm in length (Parnell 1966). They are laid beside a seed in *C. scoparius*, *C. oromediterraneus* and *C. multiflorus* legumes (Sanz & Gurrea 1999). Larvae develop in a single seed, preferably in the upper part (Sanz & Gurrea 2000). After emerging, the larva enters the top of the seed through the micropore and starts to feed on the cotyledons until it reaches the third larval stage. In this state, it also consumes the chorion, the rest of the upper section of the seed and part of the adjacent seeds in order to build the chamber for the pupa. The larva then generates a cementing layer using a mixture of faecal deposits and saliva, after which it enters the prepupal and finally the pupal stage. Pupation takes place in the seed until dehiscence, when the new adults hatch (Parnell 1966).

E. fuscirostre adults can be found throughout the year. In winter, they are in a relatively inactive state beneath shrubs, on shoots or among leaves. Adults start to emerge from hibernation in early spring to feed on these leaves and shoots. Their numbers increase until May and peak in June, coinciding with broom flower and pod production, when the females oviposit alongside the seeds of these young pods. The oviposition process begins when the female moves across the pod surface in search of a bulge produced by a seed. It then starts to open a hole with its face beside the seed through which it inserts its ovipositor to lay a single egg. When the ovipositor is retracted, it secretes a transparent fluid that quickly hardens and closes the hole (Parnell 1966).

In July and August, the population declines because of adult death following oviposition. At the end of summer and in October, the number of individuals increases slightly once again when they emerge from their larval state. These individuals spend their winter hibernation period on the ground beside the host plant (Sanz & Gurrea 2000).

Sampling area

Sampling was conducted in three zones (approximately 6016 ha) on the southern flanks of the Sierra de Guadarrama

Table 1 Study location UTM coordinates

Location	Density	Zone	X	Y
La Barranca	Low	30T	414784	4510123
	Medium	30T	416047	4511172
	High	30T	415944	4511362
Mataelpino	Low	30T	419496	4508122
	Medium	30T	419207	4508903
	High	30T	419411	4508086
Cerceda	Low	30T	430236	4504270
	Medium	30T	424549	4504214
	High	30T	431254	4504308

(Madrid, Spain) in June 2009, coinciding with the plant fruiting peak, after the seed weevil oviposition (Table 1).

The study area is in the transition zone between the meso- and supra-Mediterranean bioclimatic zones, where the predominant vegetation formations are *Quercus ilex* subsp. *ballota* and *Q. pyrenaica* woodlands, as well as mixtures of these species. *C. scoparius* broomfields are the first substitution stage for both formations (Costa Tenorio *et al.* 1997), when the level of degradation is not high and the soil depth is suitable for their growth. The study area, heavily altered by long-term human usage, is now a *dehesa* (open woodland) with low-density livestock grazing, facilitating the spread of broom thickets. The climate is characteristically Mediterranean, with a relatively mild summer drought and lower winter temperatures than the characteristic Mediterranean range, because of its proximity to the Sierra de Guadarrama. The mean annual temperature is 12.7°C, and the total annual rainfall is 725 mm.

Sampling design

Three levels of plant density were considered in the choice of *C. scoparius* patches in the study areas. Because density is hard to estimate in *C. scoparius* populations because of its growth form, these three levels were defined on the basis of percentage cover: low (<20%); medium (40–80%); and high (>80%). Three 50 m×50 m plots per plant density level were defined, separated by at least 100 m.

Five plants were chosen at random in each plot, and ten pods were collected from each one. A total of 450 pods were collected and then lab-dried.

Each pod was measured for length, width and number of seeds ('viable', aborted and infested), considering well-developed seeds, whether or not they were infested, as 'viable', and undeveloped or malformed seed as aborted. We also recorded the numbers of *E. fuscirostre* eggs, larvae and pupae per seed, as well as the pre-imagines of other curculionid species and parasitoid insects identified at the order level. For each pod, we calculated the number of seeds infested by *E. fuscirostre* and the number of seeds infested by other insects (considered jointly), in order to define an indicator of the potential influence of competition for an oviposition niche.

Data analysis

The rate of seed infestation by *E. fuscirostre* per pod was analysed using a general linear model, assuming a binomial error and a logit link function (Crawley 1993). The dependent variable was the number of seeds infested by *E. fuscirostre* per pod, whereas the binomial denominator was the number of seeds per pod. The explanatory variables were: geographical location of the host plant (block factor with three levels), density (fixed factor with three levels), the individual plant as a nested factor (plant (density (location))), and as co-variables, pod length and width, abortion rate per pod (number of aborted seeds divided by total seeds), and rate of infestation by other parasitic insects (number of seeds infested by Bruchidae, *E. compactum*, *Pachytychius sparsutus* and other orders, divided by total seeds in the pod). The SPSS 15.0 (Statistical Package for the Social Sciences) statistical package was used for all the statistical analysis.

RESULTS

We analysed a total of 5468 seeds from 450 pods (see Table 2 for abundance of *E. fuscirostre* eggs, larvae and pupae). Pre-imaginal states of other Curculionoidea species, including *E. compactum*, *E. putoni*, *P. sparsutus* and Bruchinae, and other insect orders, such as Lepidoptera, Diptera, Hemiptera, Thysanoptera and Himenoptera parasitoids, were also found in smaller proportions.

The best-fitted model for *E. fuscirostre* infestation rate was highly significant (chi-squared = 301.7, $P < 0.0001$). It included the three experimental design factors – density, location and plant – as significant variables (Table 3). Density showed a negative relationship with infestation rate (Fig. 1). Infestation was also affected negatively by the abortion rate (regression coefficient: −2.14, $P < 0.001$) and the rate of infestation by other insects (regression coefficient: −6.25, $P < 0.001$). The only pod dimension that entered the model was width, which related positively to the *E. fuscirostre* infestation rate (regression coefficient: 0.18, $P < 0.013$).

DISCUSSION

C. scoparius density influences the rate of seed infestation by the seed weevil *E. fuscirostre*. The highest levels of infestation always match medium/low plant densities, whereas the lowest levels match high densities (Fig. 1, Table 2). The travel-cost hypothesis could explain the higher infestation incidence at medium and low host plant densities. In species with mobile adults but sedentary larvae, the optimal allocation of total fecundity depends on the result of the trade-off between the cost of sib competition in large clutches and the travel costs of distributing many small clutches (risk of searching for patches and travelling between them). When less resources are available, as in the case of low densities, female oviposition is concentrated in the locality's few plants, and hence in their

Table 2 Number of preimaginal states found in *Exapion fuscirostre* pods and seeds, and infestation percentages (*n* = 450 pods and 5468 seeds)

Location	Density	Eggs	Larvae	Pupae	Total	% infested pods	% infested seeds	% seed infested by other insects
La Barranca	Low	35	8	0	43	42	6.5	4.3
	Medium	33	5	0	38	40	5.9	4.1
	High	21	6	0	27	30	3.8	1.7
Mataelpino	Low	0	49	0	49	34	7.1	1.6
	Medium	0	31	0	31	28	5.4	3.0
	High	0	24	0	24	26	3.5	2.2
Cerceda	Low	2	46	0	48	54	6.7	1.7
	Medium	0	35	6	41	56	7.9	2.9
	High	0	22	7	29	42	4.5	2.0

Table 3 Results of the logistic binary model for rate of seed infestation by *Exapion fuscirostre* per *Cytisus scoparius* pod

	Wald chi-squared	df	*P*-values
Intersection	36.2	1	<0.001
Plant density	158.1	2	<0.001
Location	359.7	2	<0.001
Plant (plant density location)	162.0	38	<0.001
Abortion rate	30.0	1	<0.001

Statistically significant values for *P* < 0.05. Abortion rate: rate of pod seed abortion. Infestation by others: infestation rate by other insects. Width: pod width.

pods, resulting in a higher infestation rate (Heard 1998; Heard & Remer 2008). While the travel-cost hypothesis could explain the observed pattern of attack, other alternative hypotheses should be considered. Plant nutrient quality is affected by plant density, which in turn affects insect performance. For example, Fagan *et al*. (2004) reported that insect herbivory on *Lupinus lepidus* exhibited striking spatial structure for over a decade, with inverse density-dependent damage patterns that were linked to plant nutrient chemistry.

This initial approach to the effect of plant density on infestation levels highlights the importance of this factor and the advisability of future studies along density gradients using real density values instead of cover, which is used in the present study as a surrogate for density.

Contrary to our initial hypothesis, the block factor (geographical location) was highly significant in explaining *E. fuscirostre* infestation rates per pod, despite the locations being relatively close to each other. The relevant factors are unclear because the relationships are complex and influence both *C. scoparius* and *E. fuscirostre*, with variables such as altitude, temperature and soil also playing a role. Both the plant and the parasite are characteristically supra-Mediterranean species (Sanz 1994; Costa Tenorio *et al*. 1997). Sanz (1994) notes that *E. fuscirostre* appears in different bioclimatic zones, but it is most abundant in the supra-Mediterranean level. Barat *et al*. (2007) have found differing rates of *E. ulicis* (Forster 1771) infestation in *Ulex europaeus L*. seeds at sea level and at inland continental locations.

Our results show that the host plant location factor must be considered in similar studies. In this specific case, a larger number of locations must be studied in order to reach conclusions about the underlying causes of this factor. These results show a considerable variation between locations in the infestation rate, which may be caused by differences in soil quality, land use, and small-scale temperature and rainfall regimes caused by altitudinal differences, and topographical variables such as slope and derivative effects such as sunlight intensity. None of these factors are plant density-dependent, but they have a considerable impact on the size of the host plant population and its space-time dynamics (Sale & Tolimieri 2000).

Another possible interpretation is that the location effect may only be stochastic, and infestation rates may vary between years, as it is often the case in host/parasite relationships (Ehrlén 1996). Infestation rates vary heavily between plants possibly because of different plant physiology conditions that are probably related to genetic variations in defence, resulting in different energy expended by each plant in its defence against seed weevils (Janzen 1981), the most heavily affected individuals being those that invest least in their defence. Differences between plants may also be caused by microhabitat differences that influence the growth of individual plants.

The seed abortion rate is also closely related to the rate of pod and seed infestation, and is more explanatory than pod width in the final model, as females in the study area chose pods with a smaller proportion of aborted seeds. This may be related to the mechanism used by females to choose the oviposition site. Females can select an ideal site by feeling the pods with their feet and antennae, halting when they find seeds that are 'more suitable' for their larvae (Parnell 1966), i.e. they can discriminate between a gap left by an aborted seed and one occupied by a healthy seed. By this means, a low proportion of abortions in pods might enable females to spend more energy on ovipositioning, as otherwise they must spend more time searching for suitable host sites in more pods. A vitally important factor for seed weevils is the presence of healthy seed in the pod, given that each larva grows inside a single seed (Parnell 1966). Additionally, larvae have very low mobility inside the pod, and if the egg is laid in an incorrect location, the larva will most probably die if it cannot find a seed to feed on in the immediate environs. This relationship has also been found in other predispersive insects (Östergård *et al*. 2007), confirming that fruit and seed abortion is a selective factor for
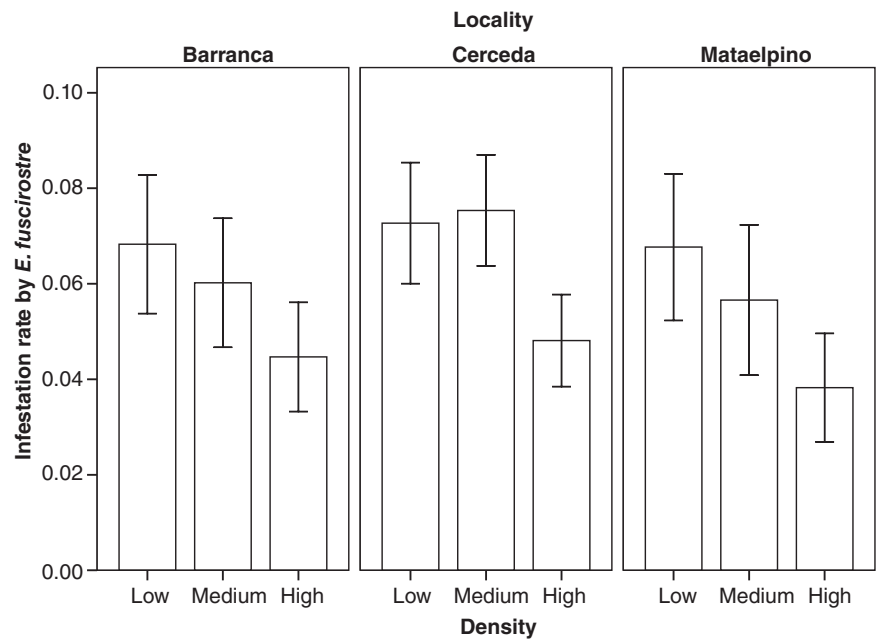
Fig. 1. Differences in the rate of seed infestation by *Exapion fuscirostre* according to location and density of host plant. Bars represent mean ± SD.

ovipositioning in predispersive insects and is a strategy used by plants to ensure the dispersal of viable seeds.

The presence of other non-parasitoid inquilines in seeds also helps to explain the incidence of *E. fuscirostre* (Table 3). If a seed is occupied prior to ovipositioning, the female finds it more difficult to lay on it. Thus, if the number of seeds occupied by other inquilines increases, a smaller number of seeds will be occupied by *E. fuscirostre*. However, competitive relationships are complex and are not merely a race to oviposit; different predispersive predator species use different times and strategies for ovipositioning (Messina 1991; Sanz & Gurrea 2000), and in some cases, the larvae themselves have to fight for survival when confronted by undesired competitors or parasitoids even within the seeds.

In our analysis, pod width was found to have a more significant effect than length on seed infestation, as initially, females choose wider pods to lay their eggs. However, other studies conclude that pod length rather than width carries more weight in explaining infestation (Parnell 1966; Redmon *et al.* 2000). According to Parnell (1966), pods that open earlier during dehiscence have a greater incidence of *E. fuscirostre* and are also longer. Although the model selection retained pod width instead of length (Table 3), width and length were substantially collinear ($r = 0.56$, $n = 45$, $P < 0.0001$), reducing our confidence in which variable is more likely to be a causal driver. The real effect of pod dimensions may be also camouflaged by other habitat-related aspects such as density and location, which carry more weight in the model. Seed size may play a more decisive role in seed infestation (Janzen 1969), represented indirectly by pod width.

General conclusions

Patches of *C. scoparius* with differing densities in areas with similar climatic and geographical features were used to analyse the role of patch density and pod size as factors in the choice of ovipositioning locations by *E. fuscirostre* and its influence on plant dispersal.

1   Our results show that there is a significant, previously undetected effect of plant density on the pod infestation rate, with a greater incidence at low and/or medium densities of the host plant.
2   These results show that abortion rate and rate of infestation by other insects are more important variables than pod size for the assessment of *E. fuscirostre* as a pre-dispersive seed predator.
3   Geographical location and other factors that are independent of plant density are complex factors to take into account, as they participate in the expression of these variables. A thorough analysis of these factors requires more detailed studies to define and quantify the variables that are interrelated with geographical location.

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