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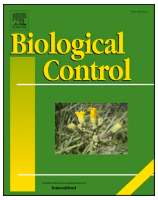

Identifying insect predators using camera traps reveal unexpected predator communities in oilseed rape fields

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HIGHLIGHTS

- Camera traps are used to identify predators of pollen beetles and brassica pod midge larvae.
- An important diversity of predators of oilseed rape pest larvae was identified.
- Carabidae and Staphylinidae larvae are important predators of these pest larvae.
- Oilseed rape pest larvae susceptibility period match predator activity.

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ABSTRACT

Cameras are common tools for ecologists studying species abundance, richness, and interactions. They are mainly used to study large animals but are increasingly used to study invertebrates. Camera traps could be a powerful tool to identify and quantify the natural enemies, such as predators, of specific agricultural pests. This knowledge can then be applied to adapt farming practices to favour the predators identified and improve conservation biocontrol.

Here, cameras were used to identify predators of two insect pests of oilseed rape (*Brassica napus*): the pollen beetle (*Brassicogethes aeneus*) and the brassica pod midge (*Dasineura brassicae*). These insects are spring pests of oilseed rape and are both susceptible to predation by ground-dwelling arthropods during their development cycle. The objectives of this study were to 1) identify the predators of the pest species, and 2) investigate the hypothesis that the diel activity periods of the predators match the timing of pest larval presence on the ground. Field observations were conducted in two locations over two consecutive years in the UK.

In contrast to previous reports, our data collected using cameras showed that larval stages of predatory beetles are responsible for most of the predation events and that adult stages were not frequently observed feeding on the prey. Our data also showed that the traditional method, using pitfall traps, failed to detect the presence of large numbers of beetle larvae. Interestingly, the pests dropped to the ground and were therefore most susceptible to predation at the time when predators were most active.

These results give new insight on the predators of the two most important spring pests of oilseed rape in Europe. This knowledge can be used by practitioners to develop framing practices targeted on enhancing the abundance of the larval stages of these beneficial arthropods to better control the pests in a more sustainable way.

1. Introduction

Biocontrol of insect pests by invertebrate predators is a key component of pest regulation in agrosystems (Symondson et al., 2002). Predators can achieve a high rate of control, especially in semi-controlled environments (i.e., glasshouse) where farmers can release

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predators and maintain them near the crop (Collier and Van Steenwyk, 2004). In open environments, a range of habitat management and diversification techniques are frequently implemented to support large populations of the natural enemies of crop pests in what is often referred to as conservation biocontrol (Symondson et al., 2002; Begg et al., 2017). However, predator populations are variable and difficult to maintain in the long term which lowers the efficacy of conservation biocontrol and limit its adoption by farmers (Collier and Van Steenwyk, 2004). Knowledge of the ecology of the natural enemies involved in biocontrol of target pests is surprisingly limited and constrains the development of farming practices that optimise biocontrol services by both farmers and researchers.

The optimisation of biocontrol services by adoption of measures having a positive effect on natural enemies could help insect pest management and reduce farmer's dependence on pesticides (Begg et al., 2017). To optimise the predation service, the identification of a pest's natural enemies and the quantification of the services provided by different species is essential. Predation services are usually quantified by leaving sentinel prey on predation cards that are then placed in the field (Lövei and Ferrante, 2017). After a period of exposure, cards are checked, and the number of prey remaining is recorded. This method is easy to implement and reliable (Meyer et al., 2015; Lövei and Ferrante, 2017; Boetzl et al., 2020). However, it does not allow for the identification of the predators.

Predator identification, i.e., the species responsible for observed predation events, is commonly done using one of four methods. A common method is to study the spatio-temporal relationship between the abundance of the pest and predators (Bryan and Wratten, 1984; Williams et al., 2010). This method is relatively simple to implement, as is based on common sampling techniques, but the relationships established are not direct proof of an interaction between species. A second method is the analysis of predator gut content. In this case, predators are sampled in the field, and the content of their gut is analysed to identify prey by visual observation or DNA-metabarcoding (Symondson, 2002; Birkhofer et al., 2017). This method can demonstrate predation for certain species, but is technically challenging to implement, as prey fragments can be difficult to identify visually and molecular methods cannot fully rule out contamination from environmental DNA (Cuff et al., 2022). The third method is to use feeding tests under controlled conditions where a predator is placed in an arena in the presence of potential prey and the predation events, or rates, are recorded (Mauchline et al., 2004; El-Danasoury et al., 2017). This type of experiment gives information about the acceptability of the target prey and the predator preference to certain prey when offered in a choice test. Results of these tests must be carefully interpreted because they are conducted in conditions that are very different to that which occurs in the field. It is important to highlight that with these three methods (spatio-temporal relationship, analysis of gut content, feeding test), the predator species are selected by the researchers conducting the experiment. Such *a priori* selection can limit the range of predator species identified and thus bias the results of the study. The last method is to identify predators by observing predation events in the field. This can be done by visual observation, but it is highly time consuming, and observers cannot be in multiple locations simultaneously thereby limiting comparisons (Birkhofer et al., 2017). However, cameras can be used to observe predation. They are increasingly used in ecology to study species distribution, abundance, and behaviour (Delisle et al., 2021). Following technical developments over the last 20 years, cheap and robust cameras able to record the activity of small animals, such as insects, are now commercially available, or can be designed for a reasonable price (Droissart et al., 2021). Cameras are being used to study plant-flower visitor interactions (Bjerge et al., 2022; Alison et al., 2022; Nagai et al., 2022) and can be used to identify insect predators by observing sentinel prey and recording predation events (Grieshop et al., 2012; Zou et al., 2017; Hemerik et al., 2018; Pickett et al., 2022; Seimandi-Corda et al., 2024). This method has the benefit of being less biased than other methods described above because cameras can be set in the field and record a broad range of interactions between predators and their prey in the absence of humans (Birkhofer et al., 2017). These different methods can be combined and the complementarity between predator centred methods (spatio-temporal relationship, analysis of gut content, feeding test) and prey centred methods (observations) can give a better understanding of the trophic network in a community. Prey centred methods can be used to identify the diversity of predators of a particular prey and these predators can then be the focus of predator centred studies informing about the diversity of alternative prey.

Oilseed rape (OSR; *Brassica napus*) is the most important oilseed crop in Europe (FAOSTAT, 2022). The seeds of this plant are used to produce oil for human consumption, biofuel, and animal feed (Hebinger, 2013). Winter OSR is also appreciated by farmers as a break crop in the cereal rotation. It is usually sown at the end of the summer and harvested the following summer. During this long cycle, the plant is attacked by multiple insect pests (Williams, 2010). These pests are becoming increasingly difficult to manage because of the development of resistance to insecticides, in particular, pyrethroids, and the ban on neonicotinoid seed treatments (Zheng et al., 2020; Andert et al., 2021; Ortega-Ramos et al., 2022). Here, we focus on the two main spring pests of the OSR in Europe: the pollen beetle, *Brassicogethes aeneus* (Coleoptera: Nitidulidae), and the brassica pod midge, *Dasineura brassicae* (Diptera: Cecidomyiidae). The pollen beetle is the main target of spring insecticide sprays in Europe (Richardson, 2008). Adults of this insect attack flower buds early in the spring to feed on pollen, leading to bud abscission and reduced yields. The brassica pod midge infests the crop later, and adults lay eggs in the OSR pods. Larvae of this insects develop in the pods eating the seeds and cause up to 80% yield losses (Hausmann, 2021). These two pests both develop in the OSR canopy. Larvae of the pollen beetle develop in the buds and flowers, and larvae of the brassica pod midge develop in the pods. At the end of their developmental cycle, the larvae drop to the ground where they bury themselves and pupate in the soil before emerging as adults (Williams, 2010). When larvae of pollen beetles and brassica pod midges drop to the ground, they are particularly vulnerable to predation from ground dwelling arthropods. Previous studies have shown that predation on the ground can kill 16–27 % of the pollen beetle larvae (Büchi, 2002). However, no data on brassica pod midge predation are available. Understanding which species predate these pests would facilitate the development of farming practices that support those predators in the field, helping to maintain pest populations at a low level, and reducing the need for insecticides.

Predators of the pollen beetle and brassica pod midge larvae are not well known (Williams et al., 2010). Previous studies mainly conducted in the UK and Germany identified some carabid beetles as predators of the two pests using spatio-temporal correlations (Warner et al., 2000, 2008; Büchs and Felsman, 2006), gut content analysis (Piper and Williams 2004; Schlein and Büchs 2006) or feeding tests (Schlein et al., 2006; Williams et al., 2010) (Table S1). DNA analysis conducted in Sweden also demonstrated that two spider species (*Pardosa* spp. and *Theridion impressum*) eat pollen beetle larvae (Öberg et al., 2011). However, our understanding of the relative importance of the different predator species is limited.

We aimed to determine the identity, importance and periodicity of predators associated with the pollen beetle and the brassica pod midge using cameras. We also investigated the timing of larval drop to the ground relative to predator activity.

2. Materials and methods

2.1. Study site

The experiment was carried out over two years (2021 and 2022). In 2021 the trapping was conducted on a 22-ha commercial OSR field in Harpenden, Hertfordshire, UK. Cameras were placed in two locations close to the field edges. One edge was adjacent to a grass strip, and another was adjacent to a hedgerow to increase the potential diversity of predators spilling over from semi-natural habitats. However, we did not aim to compare the differences in predator community between the two edges. The two camera locations were 200 m apart on different sides of the field. In 2022 the study site was located about 3 km from the previous location in a 9-ha OSR field on Rothamsted farm. Similarly, cameras were placed in two locations, along a field edge adjacent to a hedgerow and another edge adjacent to a grass strip. Again, these locations were 200 m apart. In both years/fields OSR was sown in autumn (2020 and 2021, for 2021 and 2022 studies, respectively), with standard conventional agricultural practices for the region, however no insecticide was applied to the crop over the seasons.

2.2. *Camera set-up and sampling location*

Along each edge, five cameras were placed in a 40 m long transect with each camera located 2 m from the crop border to maximise the chances of capturing interactions between the prey and predators coming from the adjacent habitats (Fig. S1). Commercially available camera traps (Wingscapes, WCT-00126) with a short-range focus and a white light flash were used. Each camera was installed on a tripod 30 cm from the ground and directed toward the ground (Fig. S2). Cameras were programmed to take pictures every minute with the flashlight activated at night. A cover was placed over some of the LED cells to reduce the intensity of the flashlight. A preliminary experiment comparing the number of invertebrates observed on cards with pictures taken every minute and every 30 s showed that one picture per minute gave reliable estimation of the number and diversity of visitors (Fig. S3).

2.3. *Predation cards*

A predation card with 10 larvae of pollen beetles or brassica pod midges was installed under each of the cameras depending on the sampling session. Larvae were collected from OSR flowering inflorescences (pollen beetles) or pods (brassica pod midges). Plant material containing insects was brought from the field (Rothamsted farm) to the lab and kept refrigerated until use (8 C, 30 % humidity). Plant material was then dissected to collect the larvae. For the pollen beetle, only second instars were used. Larvae were then glued (3M Spray Mount ^{TM}) on a piece of sandpaper (5 × 7 cm) immediately before being placed in the field directly under each camera (at 15:00 each day). Predation cards were fixed in place to the ground using metal pegs (Fig. S2) and were left for 24 h.

2.4. *Pitfall-trapping*

A pitfall trap (diameter = 6 cm) was placed one metre from each camera, alternating between the left or right side of the equipment (Fig. S1). Traps were filled to 4 cm with water and a drop of unscented detergent to break water surface tension and were protected from the rain by a cover suspended c.5cm from the ground. They were run concurrently with the camera traps and emptied after 24 h in the field at the same time as predation cards were monitored. Trap catch was placed in alcohol for preservation until catches were identified.

2.5. *Sampling sessions*

Cameras, predation cards and pitfall traps were placed in the field at the same time (usually around 15:00 every day) for 24 h. Sampling started when mature larvae were found in the flowers (pollen beetles) or pods (brassica pod midge) and stopped when herbicide was applied to the crop to desiccate the plants before harvest. Because pollen beetle and brassica pod midge develop in OSR plants at different growth stages, it was not possible to conduct sampling sessions with the two species simultaneously. In 2021, sampling was conducted between the end of May and mid-July with a total of six sampling sessions for pollen beetle larvae (27/5/2021–17/6/21) followed by eight sessions for pod midge larvae (29/6/21–15/7/21). In 2022, sampling was conducted between the end of April and the end of June with eleven sessions for pollen beetle larvae (24/4/2022–26/5/2022) followed by fifteen sessions for brassica pod midge larvae (30/5/22–29/6/2022). The difference in sampling periods between both years is due to the difference in crop phenology between years.

2.6. *Diel rhythm of larval drop*

To identify when pest larvae drop to the ground and are susceptible to predation, automatically rotating pan traps modified from a commercial cat feeder (PetSafe, PFD11-13707) were placed on the ground under the OSR canopy in 2022. These devices comprised 5 bowls (70 cm^2) each of which were filled with water and a drop of detergent. The bowls were programmed to rotate at specific times of the day allowing the collection of insects dropping from the canopy during five different phases of a 24-hour period: night (23:20–04:10), dawn (04:10–09:00), morning (09:00–13:50), afternoon (13:50–18:30), and dusk (18:30–23:20). Sunrise and sunset during the sampling period occurred between 04:47–05:18 and 20:39–21:44, respectively, depending on the date. Five rotative traps were placed in the OSR crop adjacent to the cameras located beside the grass margin only, at 4 and 6 m from the crop edge, distant from the cameras and pitfall traps to avoid sampling larval drop due to disturbance of the canopy when camera traps were checked (Fig. S1). Sampling was conducted between 10/5/22 and 17/5/22 for pollen beetle larvae and between 16/6/22 and 24/6/22 for brassica pod midge larvae. The content of the bowls was checked every day, the number of pollen beetle and brassica pod midge larvae counted, and the catch of the traps removed and water replaced.

2.7. *Invertebrate identification from pictures and pitfall traps*

Arthropods collected in pitfall traps were identified to the lowest taxonomical level possible. Focus was on ground-dwelling taxa known to be predators such as Arachnida (including Araneae, Opiliones and Acari), Carabidae, Staphylinidae, Formicidae and Forficulidae. Adult Araneae were identified to the family level. Most of the adult Carabidae, Staphylinidae and Formicidae were identified to the genus or species level. Carabidae and Staphylinidae larvae were identified using the key by Luff and Larsson (1993).

Images from cameras were screened manually and on each picture any invertebrates observed on the card were recorded as visitors and identified. Visitors were identified to the lowest taxonomical level possible but because of the limited quality of the images it was difficult to identify some of the groups. Arachnida were split between Linyphiidae, Lycosidae, Opiliones, Acari, and unidentified Arachnida. Adult Carabidae were identified to the genus level for most observations except *Anchomenus dorsalis*, *Brachinus crepitans*, *Demetrias atricapillus*, and *Poecilus cupreus*, which were easily identifiable at the species level. Smaller individuals of Carabidae such as *Bembidion* sp. and *Trechus* sp. could not be separated clearly and were grouped in a taxon called “small carabids”. Staphylinidae and Formicidae were identified to the family level and the rest of the taxa were identified at the Order level or higher. When the visitors were observed actively foraging on the prey on an image, they were recorded as ‘predating’.

2.8. *Data analyses*

From the pitfall traps, the number of adult Carabidae, adult Staphylinidae, larval Carabidae and Staphylinidae, Arachnida, Formicidae, and Forficulidae were pooled for each sample. To test if some predator taxa were more common than others, a generalised linear mixed model (GLMM) with a Poisson distributed error term was built for each year (2021 and 2022) and each prey species (pollen beetle, brassica pod midge). These models explained the number of individuals of each taxa in a pitfall trap by the taxa, the sampling date, and a unique identifier per pitfall trap location as a random factor. Because the residuals of these models tend to be problematic (not normally distributed and with heteroscedasticity), zero-inflated GLMMs were used instead. The error distribution followed a generalised Poisson distribution for all models except the data collected during the pollen beetle sampling in 2022 where a negative binomial distribution was used (Table S2). Significant differences in abundance between taxa and sampling dates were then tested using a Wald χ^2 test and if significant differences were found between taxa, pairwise comparisons on Estimated Marginal Means (EMM) were used to test differences in abundance among taxa.

Because visitors can stay on the cards for a long time, the number of pictures with visitors was not a reliable estimation of their abundance. Instead, we chose to record the number of “visitation events” as the continuous presence of a taxon on the card on consecutive pictures. It happens that individuals enter and leave the card on multiple occasions. So not to overestimate the number of visitation events, a gap without the individual recorded of up to two minutes (here two pictures) was tolerated in the same visitation event. If the visitor observed was recorded as feeding on the sentinel prey in one of the pictures, the visitation event was considered as a “predation event”. To test the difference in the number of visitation events and predation events per taxa, the same models as for the data from the pitfall traps were used and tested in the same way (Table S2).

The number of pollen beetles or brassica pod midges per trap in the rotative automatic traps was analysed using a linear mixed model because data followed a normal distribution. The models explained the total number of larvae per bowl collected over the sampling period (7 days for the pollen beetles and 8 days for the brassica pod midge) by the time of the day (night, dawn, morning, afternoon, and dusk) and the individual rotative trap as random factor. The differences in the number of larvae per time of the day were analysed using a Wald χ^2 test, and if significant differences were found, pairwise comparisons on EMM were used to test differences in abundance between times of the day. Separate analyses were run for the pollen beetles and the brassica pod midge larvae. Timing of predator activity was analysed by keeping only images with taxa previously identified as predators. The number of pictures with predators per time of the day was summed per camera-day and analysed using a GLMM with a negative binomial error distribution. The model explained the number of observations by the period of the day and the sampling date. The location was included as random factor. Wald χ^2 test and if significant differences were found, pairwise comparisons on EMM were performed.

All the statistics performed were conducted using R 4.2.1 (R Core Team 2022). The R-packages *car* (Fox et al., 2013), *emmeans* (Lenth, 2018), *glmmTMB* (Brooks et al., 2017), *lme4* (Bates et al., 2014), *multcomp* (Hothorn et al., 2016) were used, and model residuals were checked using *DHARMa* (Hartig and Hartig, 2021).

3. Results

On multiple occasions, the cameras used in the experiments ran out of battery power or had the predation card out of the picture frame and consequently were not used in the data analysis. In 2021, out of the 60 camera-days collected with pollen beetle larvae, 24 were analysed. For the pod midge larvae, 42 camera-days out of the 80 collected were used. In 2022, 71 camera-days were analysed out of the 110 collected with pollen beetle larvae, and 102 out of 150 with pod midge larvae were used. One camera-day with pollen beetle larvae in 2022 was removed because of the unusual numbers of ants observed (202 visitation sequences, including some predation events) to avoid bias in the results. This was probably due to the presence of an ant colony in the vicinity of the card. Because of the large number of pictures with slugs passing on the predation cards it was not possible to record all the slugs and they are not included in the analysis. Some of them were observed feeding on the preys but their foraging behaviour seems to indicate that the slugs were mainly feeding on the glue covering the predation cards.

3.1. Abundance of predators found in pitfall traps and observed visiting predation cards with cameras

Diverse groups of ground-dwelling predators were collected in the pitfall traps (Table S3). Over the two years, individuals from 10 Araneae families were found, as well as Acari and Opiliones. Adult specimens from 14 Carabidae genus and 13 Staphylinidae genus were found. Ants found in pitfall traps belonged to two genera (*Lasius* and *Myrmica*). Some Forficulidae (*Forficula auricularia* only) were also found in 2022 only. Significant differences in the number of individuals per taxa were found in both years (2021 pollen beetle: $\chi^2_4 = 82.64$, $p < 0.001$; 2021 brassica pod midge: $\chi^2_4 = 507.39$, $p < 0.001$; 2022 pollen beetle: $\chi^2_4 = 81.54$, $p < 0.001$; 2022 brassica pod midge: $\chi^2_5 = 499.1$, $p < 0.001$). In both years, most of the predators collected were Arachnida, or adult Carabidae and Staphylinidae (Fig. 1). A few larvae of Carabidae and Staphylinidae were also found as well as some Formicidae and Forficulidae. In both years, the numbers of Arachnidae strongly increased at the time of the sampling brassica pod midge larvae, and significant differences in abundance were found between sampling dates (2021 pollen beetle: $\chi^2_5 = 23.51$, $p < 0.001$; 2021 brassica pod midge: $\chi^2_4 = 91.75$, $p < 0.001$; 2022 pollen beetle: $\chi^2_{10} = 55.47$, $p < 0.001$; 2022 brassica pod midge: $\chi^2_{14} = 124.26$, $p < 0.001$).

Arachnida, Carabidae, Staphylinidae, and unidentified predatory larvae (probably Carabidae and Staphylinidae) were the most common taxa observed with cameras visiting the cards (Fig. 1). The frequency of their observations varied between years and prey type considered. Significant differences in the number of visitation events were found between taxa in most datasets (2021 pollen beetle: $\chi^2_4 = 8.82$, $p = 0.066$; 2021 brassica pod midge: $\chi^2_4 = 507.39$, $p < 0.001$; 2022 pollen beetle: $\chi^2_5 = 48.75$, $p < 0.001$; 2022 brassica pod midge: $\chi^2_5 = 1026.45$, $p < 0.001$). However, the number of visitors to pollen beetle larvae predation cards in the first year was not significantly different according to the Wald χ^2 but significant differences were observed between Carabidae and Formicidae in pairwise comparisons. Significant differences in the number of visitation events were found between sampling sessions in most of the models (2021 pollen beetle: $\chi^2_5 = 17.38$, $p = 0.004$; 2021 brassica pod midge: $\chi^2_7 = 9.06$, $p = 0.248$; 2022 pollen beetle: $\chi^2_{10} = 38.07$, $p < 0.001$; 2022 brassica pod midge: $\chi^2_{14} = 251.03$, $p < 0.001$).

3.2. Identification of pollen beetle and brassica pod midge larvae predators

A total of 1,623 pictures and 162 sequences with invertebrates feeding on the sentinel prey were collected on the pollen beetle larvae in 2021 and 1,165 pictures and 44 sequences on the brassica pod midge larvae the same year. In 2022, 15,560 pictures and 348 sequences were observed for the pollen beetles and 7,470 pictures and 511 sequences for the brassica pod midges.

Significant differences in the number of predation events were observed between taxa in both years and prey species (2021 pollen beetle: $\chi^2_5 = 17.04$, $p = 0.004$; 2021 brassica pod midge: $\chi^2_5 = 6800$, $p < 0.001$; 2022 pollen beetle: $\chi^2_5 = 81.07$, $p < 0.001$; 2022 brassica pod midge: $\chi^2_5 = 285.37$, $p < 0.001$). A significant effect of the sampling date was also observed in both years for both prey species except in 2022 with pollen beetle larvae sessions (2021 pollen beetle: $\chi^2_5 = 19.44$, $p = 0.002$; 2021 brassica pod midge: $\chi^2_7 = 1598$, $p < 0.001$; 2022 pollen beetle: $\chi^2_{10} = 10.02$, $p = 0.439$; 2022 brassica pod midge: $\chi^2_7 = 114.89$, $p < 0.001$). In 2021 the main predators of pollen beetle larvae were unidentified predatory larvae, Carabidae and Staphylinidae, “Other” groups. The main predators of the pod midge larvae the same year were unknown predatory larvae and Arachnids. In 2022 for both prey types the main predator group was unknown predatory larvae (Fig. 2, Table S3).

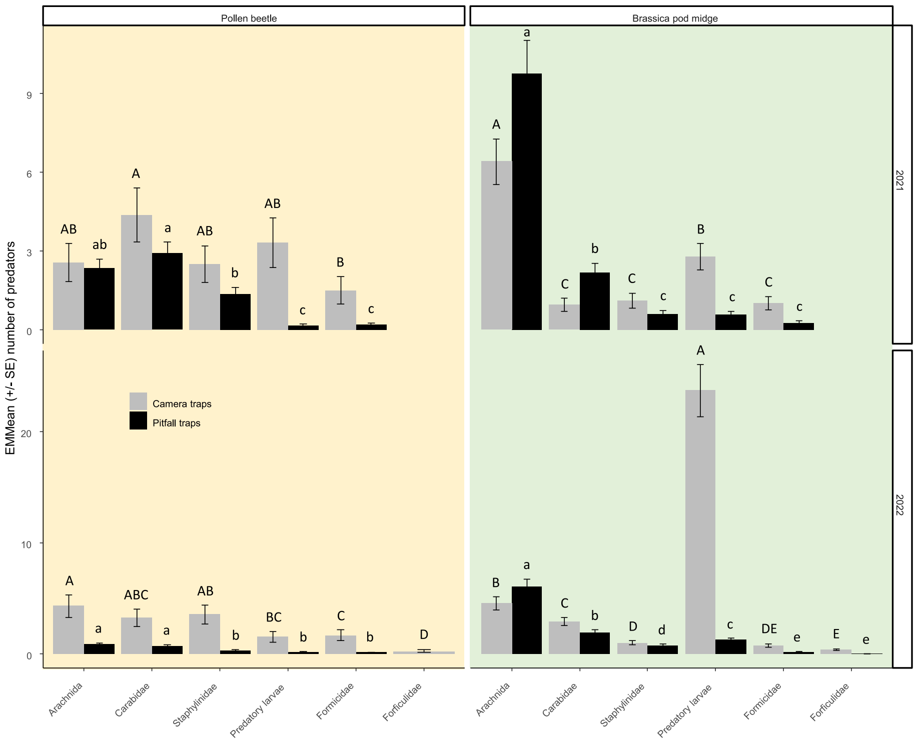

Fig. 1. EMMean (± SE) number of visitation events (set of consecutive images with a predator observed on the card) per camera-day observed with cameras on the predation cards (grey bars) and the number of predators collected in pitfall traps (black bars) in 2021 (top) and 2022 (bottom) when larvae of pollen beetle (*Brassicogethes aeneus*, left) and brassica pod midge (*Dasineura brassicae*, right) were used as sentinel prey. Individuals in the different groups are adults except in the "Predatory larvae" category. Note that separate axis ranges are used for the two years sampled. Significant differences between taxa for each year and prey type are represented by capital letters for the number of visitation events and lower-case letters for abundance in pitfall traps.

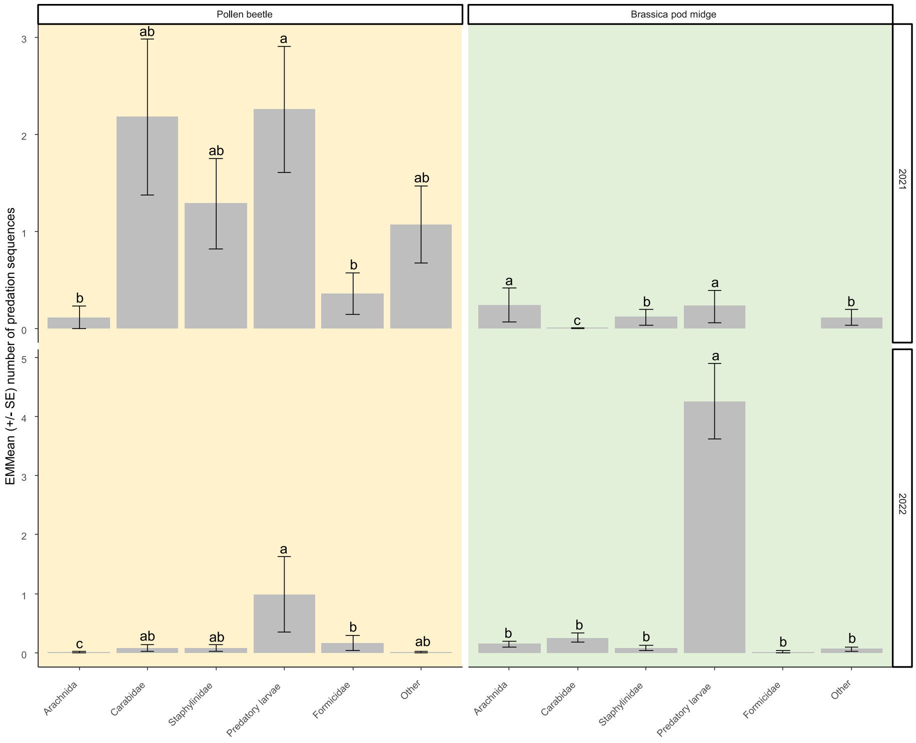

Fig. 2. EMMean (± SE) number of predation events (set of consecutive images with a predator present on the card and observed feeding on the prey at least once) per camera-day carried out by different taxa observed feeding on sentinel prey: either larvae of pollen beetle (*Brassicogethes aeneus*, left) or brassica pod midge (*Dasineura brassicae*, right) in OSR fields recorded using cameras in summer 2021 and 2022. Different letters indicate statistical differences between taxa. 'Other' taxa include Aves, Coleoptera (*Coccinella septempunctata*), Forficulidae, Diptera, and Rodentia. Individuals in the different groups are adults except in the "predatory larvae" category. Letters indicate groups that are significantly different.

It was possible to identify some genus and species of adult Carabidae. In 2021, the main adult Carabidae observed feeding on the sentinel prey were small unidentified Carabidae (probably *Bembidion* sp. and *Trechus* sp. based on pitfall trap catches). The rest of the adult Carabidae observed feeding were: *Anchomenus doralis*, *Harpalus* sp., *Amara* sp., and *Poecilus cupreus* (Table S4). In 2022, most of the predation by Carabidae was also done by small unidentified Carabidae followed by *Nebria* sp., *Harpalus* sp., *Anchomenus doralis, Amara* sp., and *Brachinus crepitans* (Table S4). Arachnida observed feeding in both years include Acari, Opiliones and Linyphiidae. Occasional predation from Forficulidae, *Coccinella septempunctata*, Syrphid larvae, birds (*Prunella modularis* and *Parus major*) and rodents (probably *Myodes glareolus* and *Apodemus sylvaticus*) were also observed and are pooled in the "Other" category (Table S3, Fig. 3).

Fig. 3, Examples of pictures (with magnification of the predators on the right side) collected by camera traps in oilseed rape fields with predation events observed on pollen beetle (*Brassicogethes aeneus*) larvae. Red arrows indicate the location of the predator on the picture. High resolution pictures are available in Supporting Materials (Fig. S4-9) as well as animated sequences of the predation events (see Supporting Materials). a) Carabidae (*Nebria brevicolis*), b) Arachnida (Opilione), c) Staphylinidae, d) predatory larvae (probably Carabidae or Staphylinidae), e) Formicidae, f) Forficulidae.

3.3. *Synchrony between predator activity and larval drop*

Because some of the rotatory pan traps failed, data from 8 and 9 traps out of 10 were used for the pollen beetle and brassica pod midge larvae, respectively. Significant differences between the numbers of larvae dropping at different times of the day were observed for both pollen beetle larvae ($\chi^2_4 = 28.75$, $p < 0.001$) and brassica pod midge larvae ($\chi^2_4 = 21.53$, $p < 0.001$). Significantly more pollen beetle larvae dropped at dusk than any other time of the day (Fig. 4a). No differences between the other times of the day were observed. Significantly more brassica pod midge larvae dropped at dawn than at dusk, or morning, or afternoon (Fig. 4b). Night-time had an intermediary position, with higher numbers being caught but not significantly different from the other times of the day.

Significant differences in predator activity were found when pollen beetle larvae ($\chi^2_4 = 20.22$, $p < 0.001$) were used as sentinel prey. The same was observed when brassica pod midge larvae were used ($\chi^2_4 = 450.48$, $p < 0.001$). Differences in predator activity between sampling dates were also found (pollen beetles: $\chi^2_{10} = 119.39$, $p < 0.001$; brassica pod midges: $\chi^2_{14} = 228.08$, $p < 0.001$). Significantly more predators were active at night than in the morning or the afternoon, but high levels of activity were also observed at dusk and dawn when pollen beetle larvae were used (Fig. 4c). The same pattern was observed when brassica pod midge larvae were used but the differences between times of the day were more marked (Fig. 4d). A similar pattern activity was observed with the data collected in 2021 where high predator activity occurred at night and dawn followed by moderate activity at dusk, and very low activity in the morning and the afternoon (Fig. S10a and b). Differences in activity pattern also existed between taxa with most predators having greater activity during the dark phase of test period and some having a diurnal rhythm of activity, such as *Coccinella septempunctata* and birds (Fig. S11).

4. Discussion

The present study provides a first view of the predator community of critical spring pests of oilseed rape (OSR) in Europe. By using a combination of cameras and pitfall traps around sentinel prey we were able to go beyond the traditional indirect methods for assessing predation on key agricultural pests.

We first characterised the predator community present in OSR fields that were associated with two pests of OSR, the pollen beetle and the brassica pod midge, both of which finish their development on the plants and become susceptible to predation by ground predators. Using pitfall traps and camera traps, a community dominated by Arachnida, and predatory beetles (Staphylinidae and Carabidae) was found. Small Carabidae, such as *Bembidion* sp. and *Trechus* sp., and larvae of predatory beetles were observed very rarely using pitfall taps but were commonly observed on pictures from camera traps (see Fig. 1 for the larvae and Fig. S12 for small Carabidae). This indicates that pitfall traps do not always give a complete nor reliable picture of the predators present in the field (Chiverton 1984; Kotze et al., 2011; Jowett et al., 2021).

Using cameras and sentinel prey placed on the ground, predation events of the OSR pests were studied. The most common predators identified were the larval stages of predatory beetles. This result was consistent over the two years sampled, and for both pests studied. Adult Carabidae, Staphylinidae, Formicidae and Arachnida (mainly Acari) were also observed predating on the prey. Most of the predation by adult

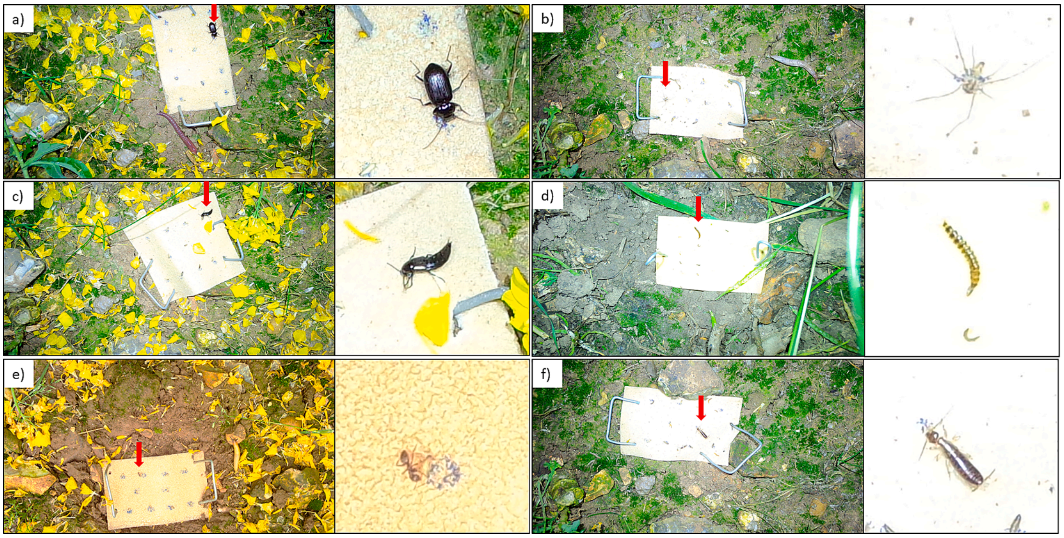

Fig. 3. Example of pictures (with magnification of the predators on the right side) collected by camera traps in OSR fields with predation events observed on pollen beetle larvae. Red arrows indicate the location of the predator on the picture. High resolution pictures are available in Supporting materials (Fig. S4-9) as well as animated sequences of the predation events (see Supporting Materials). a) Carabidae (*Nebria brevicolis*), b) Arachnida (Opilione), c) Staphylinidae, d) predatory larvae (probably Carabidae or Staphylinidae), e) Formicidae, f) Forficulidae.

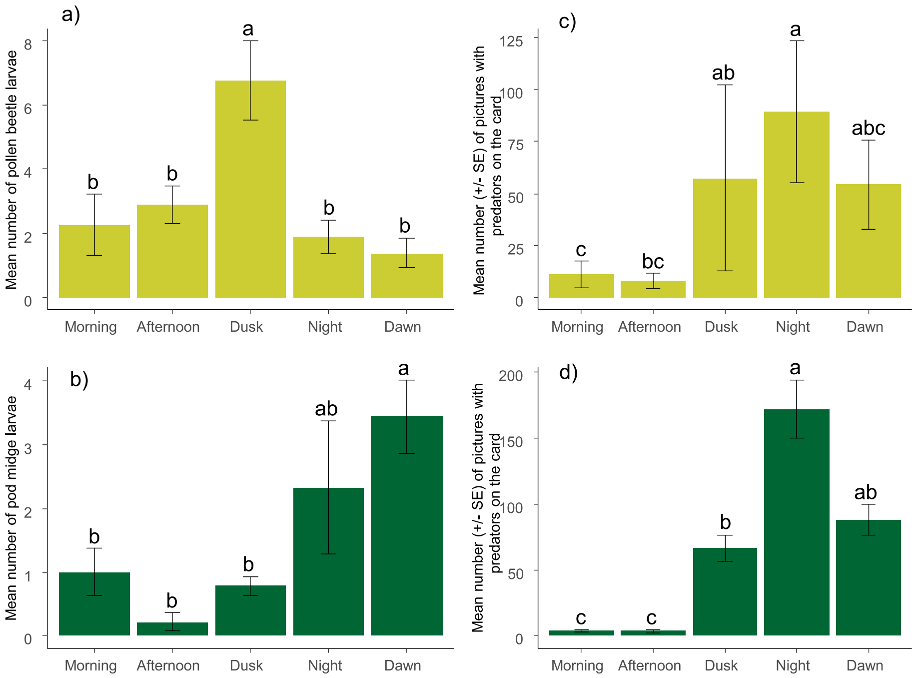

Fig. 4. Mean (±SE) number of larvae of pollen beetle (*Brassicogethes aneus*) (a) and brassica pod midge (*Dasineura brassicae*) (b) collected in water traps placed under the oilseed rape canopy at different times over a 24 h period. Mean (± SE) number of pictures with a predator observed on the predation card at different times of the day. Predation cards contain c) pollen beetle larvae or d) brassica pod midge larvae. Data collected in 2022. Different letters indicate significant differences between times of the day.

Carabidae was done by small species such as *Bembidion* sp. and *Trechus* sp. Formicidae were mainly observed feeding on the pollen beetle larvae. A lower level of predation and a reduced diversity of predators was observed on pod midge larvae than pollen beetle larvae even if the abundance of predators did not change between the two sampling periods. This might be explained because brassica pod midge larvae are much smaller than the larvae of pollen beetles (2 mm against 3–4 mm, respectively) and so might be less attractive for predators. Occasional predation events from opportunistic predators such as birds, rodents, earwigs, and syrphid larvae were also observed. Previous studies identifying predators of the spring pests focus almost exclusively on Carabidae (Table S1 based on Williams et al., 2010; Öberg, Cassel-Lundhagen, and Ekbom 2011; Gagnon 2017). In these studies, predation by some species such as *Amara* sp., *Nebria* sp., *Anchomenus dorsalis*, *Harpalus* sp., *Poecilus curpreus*, or *Bembidion* sp. has been shown and was confirmed in the present study. However, the above studies did not observe predatory larvae being important predators. Additionally, predation by species not previously recorded was observed such as *Brachinus crepitans*, Acari, Opiliones and Linyphiidae, which give a much more diverse picture of the known predator communities.

The larval stages of Carabidae and Staphylinidae are understudied due to difficulty of trapping and identification (Kotze et al., 2011; Jowett et al., 2021), however, due to their high abundance and comparative need for constant nutrition for growth, they potentially eat more biomass of crop pests than adults (Thomas et al., 2009). Moreover, even if adults of some species are primarily granivorous, larvae are predominantly carnivorous, requiring protein for growth (Luff 1974; Luff and Larsson 1993; Saska 2005). Predatory larvae are assumed to be mainly active belowground, but they can move from their usual niche if environmental conditions are unsuitable or resources inadequate (Betz 1992; Traugott 1998). For example, carabid larvae have been observed foraging in the centre of lettuce heads in crop areas (Suenaga and Hamamura 1998). The current study demonstrates for the first time the extent of this foraging activity, which may have been underestimated in previous studies due to their low capture rate in pitfall traps (Jowett et al., 2021). The current study spans two years and multiple sample points. Though activity of predatory larvae varied temporally, it was still notably dominant over time, suggesting that in this system, larval behaviour is not based on unsuitable soil conditions or resource availability. Larvae, with their greater demand for protein rich nutrition, density dependence, and reduced dispersal activity compared with adults (Luff 1974; Luff and Larsson 1993) may respond better to local resources than adults. Gardarin et al., (2023) studying predation of sentinel prey in different arable crops in France, including OSR, did not report predation of sentinel prey by predatory larvae in contrast to the current study. Interestingly, the authors also reported few small carabids on sentinel prey cards, contrary to findings in the present study. Predatory larvae were had to identify from camera traps and were rarely caught in pitfall traps but molecular identification (e.g.(Raupach et al., 2010)) of catches from subterranean traps (Jowett et al., 2021) could be a promising avenue for further research.

When larvae of OSR pests drop from the plant canopy to the ground to pupate, their window of susceptibility to ground-dwelling predators is short. Controlled condition experiments showed that pollen beetles and brassica pod midge larvae bury themselves in just a few minutes (Warner 2001; Gagnon 2017). If predators are not synchronised with the timing of larval drop, they will consequently miss the opportunity to feed on the larvae. The present study showed that pollen beetle larvae drop mainly at dusk (18:30–23:20), and brassica pod midge larvae drop mainly between night and dawn (23:20–09:00). These observations are in line with previous results showing that most brassica pod midge larvae drop from the canopy to the ground between 22:00 and 04:00 (Warner 2001). The majority of predators identified from camera traps in the present study were active between dusk and dawn (18:30–09:00) which is in line with observations from other studies on Carabidae and Staphylinidae (Luff 1978; Kennedy et al., 1986; Warner 2001). These observations suggest that predator activity is high at the time of larval drop and predators observed in this experiment could feed on the larvae before they bury themselves.

Differences in the predator communities were found between the two sampling seasons. Acari, for example, were more abundant in 2021 than in 2022, and no Forficulidae were found in 2021. This result highlights that the predator community can change depending on the sampling location and year. The present study with only two fields sampled over two years does not aim to give a full overview of the predators of the two pests studied. By expanding the scale of sampling, it will be possible to get a better picture of the predator community of the two pests studied and to predict the biological control potential of a community. With this knowledge, it will be possible to better understand how surrounding landscape and management practices affect predator communities and in return biocontrol services. However, using cameras is expensive both in term of equipment (around 170 GB£ for the camera, tripod, batteries, and SD card) and data processing (screening of about 350,000 pictures took several months of work) and it is challenging to deploy them at a large scale. Development of low-cost cameras (e. g., Chui, Wahab, and Leonhardt 2023) and deep learning algorithms able to automatically detect and identify animals in field conditions (Bjerge et al., 2023) would greatly improve the broader applicability of the cameras and help to realise their potential in designing landscape that support predator communities and optimise the potential of conservation biocontrol.

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CRediT authorship contribution statement

Gaëtan Seimandi-Corda: Writing – review & editing, Writing – original draft, Supervision, Investigation, Data curation, Conceptualization. **Thomas Hood:** Investigation. **Matthew Hampson:** Investigation. **Todd Jenkins:** Investigation. **Daniel Blumgart:** Investigation. **Jamie Hall:** Investigation. **Kelly Jowett:** Writing – original draft, Investigation. **Toke Thomas Høye:** Writing – review & editing, Project administration, Funding acquisition. **Samantha M. Cook:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

SMC and **TTH** acquired the funding, administrated the project and acquired resources. **GSC** and **SMC** conceived the experiments and supervised the investigation. **GSC, TH, MH, TJ, DB,** and **JH** conducted the investigation. **GSC** curated the data, conducted the analysis, and produced the visualisation. **GSC** and **KJ** produced the original draft and **GSC, SMC** and **TTH** reviewed and edited the manuscript. All authors read and approved the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2024.105636.

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