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# **REVIEW ARTICLE**

Agricultural and Forest Entomology

Royal Entomologi Society

Understanding insect predator-prey interactions using camera trapping: A review of current research and perspectives

# Comprendre les interactions prédateurs-proies chez les insectes à l'aide de pièges caméra: un état de l'art des recherches et perspectives

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# Abstract

- 1. Cameras are increasingly used by ecologists to study species distribution and interactions. They are mainly used to study large animals such as mammals but can also be used to record small invertebrates, including insects.
- Camera traps, capturing images within a specified field of view, can be used for biomonitoring and investigating insect-related interactions, such as predation. Understanding predation on insect prey has direct implications for agriculture and conservation biology, enabling predator species identification and quantification of biological control.
- 3. This review examines 28 studies published between 1988 and March 2024 focusing on the use of cameras to monitor insect predator-prey interactions, predominantly targeting agricultural pests. Studies varied in recording equipment used and tended to be spatially and temporally limited, making results difficult to generalise at larger scale.
- 4. We provide an overview of equipment options, camera settings, the merits of video versus picture recording, night-time imaging strategies, trigger mechanisms, equipment costs, and strategies for managing theft and vandalism. Additionally, we discuss avenues for improving image processing efficiency, including enhancing predator identification through artificial intelligence methods. Challenges related to limitations in the taxonomic levels of predator identification are also addressed.
- 5. Finally, we offer guidelines for researchers interested in using camera technology and propose future perspectives on their use in insect conservation and biocontrol efforts.

#### KEYWORDS

biocontrol, hunting camera, predation, sentinel prey, surveillance camera

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# INTRODUCTION

The use of camera traps, defined as cameras specifically designed to capture images of animals, is becoming more and more common in ecology, especially in conservation biology, for biomonitoring of terrestrial vertebrates and to study their interactions (Delisle et al., 2021; Wearn & Glover-Kapfer, 2019). Cameras are used to study species distribution, abundance, diversity, behaviour and interactions such as predation (Caravaggi et al., 2017; Delisle et al., 2021; Smith et al., 2020). Cameras are currently mainly used to study relatively large animals such as mammals, birds and herpetofauna (Agha et al., 2018; Delisle et al., 2021). Their increase in popularity (from about 40 studies published per year in the early 2000s to more than 900 in 2022 based on the keywords 'camera trap\*' and 'trail camera' in Web of Science-2 February 2024) can be explained by their reliability, the fact that they are easy to use and that they are noninvasive. Furthermore, as they can be used largely in the absence of a human operator, they also have the advantage that they can be run continuously for long periods, can be used at unsociable hours of the day (i.e., night), and in some situations where it may be unsafe for a human operator to remain for long periods. The cost efficiency of cameras over other sampling methods, such as pitfall traps, has been demonstrated for several groups, such as squamates and small mammals (Adams et al., 2017; Bondi et al., 2010; Welbourne et al., 2020).

However, camera traps are less used to study smaller animals, and in particular arthropods, despite their ecological importance. Due to their diversity and abundance, arthropods are critical to ecosystem functioning and they support multiple services such as pollination, biological control and organic matter recycling that are essential for human life (Crespo-Pérez et al., 2020). Where camera traps have been used, it is often to estimate insect pest abundance. Several camerabased systems have been developed to alert farmers of the presence of insect pests in their fields (reviewed by Preti et al., 2021). These systems are usually made of a physical trap to capture insects (designed according to the pest species of interest), which is often baited (with, e.g., pheromones) to maximise the catches and reduce variation and non-target bycatch. They are equipped with cameras taking images of the content of the trap which are then processed by a remote operator to identify and count individuals or are automatically processed via image analysis algorithms (Diller et al., 2023; Li et al., 2021; Preti et al., 2021). To a lesser extent cameras are also used to study insect plant-pollinator (Alison et al., 2022; Bjerge et al., 2022; Pegoraro et al., 2020) or predator-prey interactions-the focus of this review.

The study of predation on insect prey can have important applications in agricultural research regarding predators and their role in biological control of insect pests, but also in conservation science to identify the predators of endangered insect species to better protect them, or the contrary; to identify the predators of an invasive species for biological control. Multiple methods have been used to study insect predator-prey interactions and identify predator species. Camera trapping can provide important contextual information absent in other methods and has several advantages over more traditional

measures of predation. Often, the identity of a potential predator is inferred from the spatio-temporal correlation between the abundance or activity-density of potential predators, estimated using standard sampling methods such as plant scouting, pitfall traps, or sticky traps, and the degree of the prey reduction (Park & Obrycki, 2004; Pearce & Zalucki, 2006; Williams et al., 2010). These methods provide useful information, but they are purely correlative and do not directly document interaction between the two species, that is, it cannot be certain that predators collected by sampling contribute to the predation observed or the extent to which they contribute. It is also possible to quantify predation service using live prey or artificial prey (dummies) as sentinels exposed to predators in the environment. Their disappearance, or damage occasioned by predators are recorded to estimate the predation service (Birkhofer et al., 2017; Lövei & Ferrante, 2017). However although observations on dummy prev can help to distinguish between predation by birds, lizards, rodents or Coleoptera they do not reliably inform on the identity of the predator (Howe et al., 2009; Low et al., 2014). Methods to directly identify predation include the analysis of gut content by visual identification of prev fragments or use of herbivore DNA primers or DNA meta-barcoding of the predator (Birkhofer et al., 2017). However, identification of prey based on fragments retrieved from the gut is very time-consuming and can be very difficult even for experienced taxonomists (Lövei & Ferrante, 2017), and DNA-based methods are very sensitive and results can easily be misinterpreted. As an example, if a carabid beetle has eaten a spider, which has eaten an aphid, aphid DNA found in the beetle, may be erroneously attributed to direct predation of the beetle on the aphid; also samples can be easily contaminated (Cuff et al., 2023). More importantly, these methods are predator-centred and inform us about the identity of the prey of a predator, but not about the identity and relative importance of predators of a certain prey. The use of cameras could overcome these problems as it is possible to directly observe predation in the field, without observer bias, and can also be done in real time to inform on diurnal activity and phenology that cannot be gained without continuous observation.

A systematic literature review of the scientific literature database Web of Science (2024) using the keywords: (camera OR video OR photo OR photography) AND (insect OR arthropod) AND (predation OR predator\*), complemented by articles cited in the references of these articles or grey literature known by the authors, yielded 28 studies (Table S1). This number is low compared with what has been done to study insect pest abundance (141 between 1980 and 2022 using the keywords from Preti et al. (2021)). This is not surprising as the economic interest in the development of tools to monitor insect pests is greater than the interest in predators. However, with increased interest in integrated pest management and calls for insecticide reduction, a better understanding of predator-prey interactions is vital to inform management practices that support conservation biocontrol and can stimulate further interest in predation. Here we review the methods used to study predator-prey interactions involving insect prey with cameras. Based on the information collected and knowledge available in other research areas where the use of cameras is more

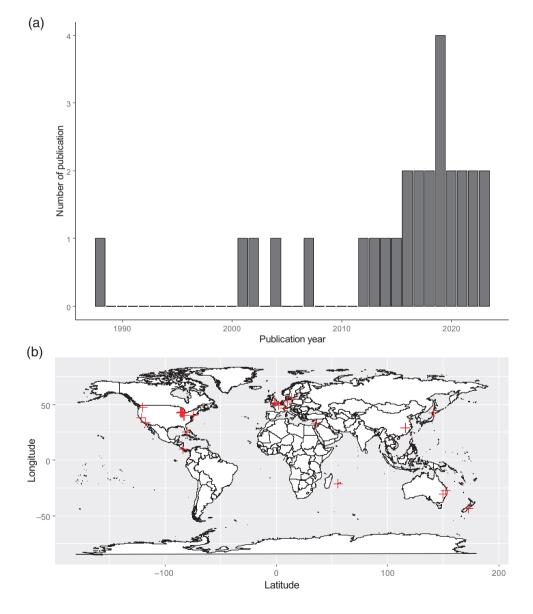
common, such as wildlife research, the different equipment and data processing options are discussed. We aim to provide guidelines for researchers to use this method to explore new horizons.

# GENERAL TRENDS IN THE USE OF CAMERA TRAPS

We identified 28 studies using cameras to record predation of insects published between 1988 and March 2024 (Table S1). The first study was published in 1988 and studied the predation of aphids by carabid species in wheat fields (Halsall & Wratten, 1988) and remained the only example until 2001 when another paper was published on aphidophagous predation of parasitized and unparasitized aphids in sugar

beet (Meyhofer, 2001); this was the first of only four in a decade. After 2012, papers using cameras started to be published on a more regular basis (annually) with multiple papers being published per year since 2016 (Figure 1a); 17 of the 28 studies identified were published after this date, and there is a trend towards an increase in the number of published articles in the last 5 years. This can probably be explained by the development of digital cameras and a reduction in the price of the equipment making this method more affordable. A similar trend is observed for publications involving the use of cameras to monitor insect pests over the same period (Preti et al., 2021).

Most of the studies involving the use of cameras to monitor insect predation were conducted in North America (12) and only a few have been conducted in the other continents: six in Europe, four in Oceania, four in Asia, one in Africa, and one in Central America; no



**FIGURE 1** (a) Number of publications on the use of cameras to study predation of insect prey per year from 1988 to March 2024. (b) Location of the experiments published (indicated by red crosses). Multiple experiments were sometimes conducted at the same location explaining why there are less locations marked than studies published.

publications have yet detailed studies in South America or Antarctica (Figure 1b).

A large majority of the articles identified focus on biocontrol applied to agriculture (24), and only a few studies were designed for conservation purposes (4). The insects used as sentinel prey were exclusively herbivores, even for studies with a conservation purpose. Different developmental stages (eggs, larvae and adults) were used in the experiments depending on the interest of the researchers (Table S1). For studies with a conservation purpose, the sentinel prey used was the arthropod of focus in the study (Table S1), but in studies relating to biocontrol, it was either the specific subject insect of the study (22), a commercially available insect ('model insect') (6), or even dummies made of plasticine (1). The camera was usually focused on the plant with prey either attached to a leaf, stem or trunk (16), placed on the ground (11), or attached to a pole (3), depending on the ecology of the prey and predators of interest. In eight studies, more than one prey type were used, showing a strong focus of the studies on interactions with a specific insect prey.

For most studies, data presented in articles were collected from only a few locations (min = 1, median = 2.5, max = 16). The number of cameras used for these experiments was usually low, varying between 1 and 60 with a median of eight cameras used simultaneously. Cameras were usually left in the field for a few days although in some studies cameras were left for up to several months or even a whole year (min = 1 day, median = 8 days, max = 365 days).

Images were mainly recorded using surveillance cameras, that is, cameras designed for home security purposes, modified to record arthropod activity (18), but commercially available hunting cameras, that is, camera traps specifically designed to collect game pictures, were also frequently used (6), and digital cameras (2) or 'homemade' cameras (2) are also reported. These cameras were usually powered only with batteries (20), however other sources of energy such as solar panels (2), generators (1), or connection to the electric grid (1) were also reported. These cameras were set up to record videos (18) more often than photos (10). For cameras not recording continuous videos, the recording was time-lapse triggered, with a duration between 2 s and 5 min (8), or with motion detection when predation of insect prey by large animals was studied (e.g., birds, bats and other mammals) (2). Interestingly, most of the studies used infrared (IR) sensitive cameras (22), the others used cameras to capture photos with white flashlight (4) or use of a red light (1). In all the studies, reviewed pictures or videos were checked manually to record predation events and identify the predators involved.

The way experiments were conducted in these studies was in line with research using insect sentinel prey without cameras in terms of preparation of the sentinel prey. The only major difference was that the designs of the experiments using cameras were less wellreplicated both spatially and temporally than experiments using only sentinel prey. Studies estimating biocontrol services are usually conducted over several seasons, at multiple locations with multiple replicates per location (e.g., Beaumelle et al., 2021; Denan et al., 2020). However, with camera trapping experiments availability of cameras is usually low which limits the number of replicates. Studies using cameras to understand insect predation are therefore often limited in the way data are collected, based on their experimental design and the equipment used. In the following sections, we review the equipment options and potential data processing methods that can be used to mitigate these constraints.

# CHOICE OF EQUIPMENT

Variation in the choice of equipment between the studies reviewed partly depends on the biological system studied and the environmental context, but is also strongly dependent on the skills and knowledge available in the research teams. Consequently, it is important to explore what are the pros and cons of the different types of equipment and their options, as well as the costs associated, to facilitate the best choice for the use of cameras in future research.

#### Type of cameras

In the studies reviewed, the main type of cameras used were surveillance cameras designed for security purposes (Figure 2b,e). These consist of one camera, or a set of cameras all connected to a video recording system. The cameras need to be connected to a power source (usually 12 V batteries) and the recording system must be connected to a storage unit with high capacity, such as a hard drive, to store videos. They are designed to record videos and are usually IR sensitive and need to be supplemented by extra IR light to record pictures at night. The cameras are weather protected and adapted to record video outdoors, but they are designed to be placed close to buildings so researchers must adapt the rest of the equipment (i.e., recorder, storage systems and batteries) for outdoor activity. It is a common practice to place this equipment in waterproof plastic boxes to store the batteries, recording and storage systems (Grieshop et al., 2012; Kistner et al., 2017). The oldest publications probably used surveillance cameras because they were the only commercial option available, but the use of this type of equipment is losing appeal as it is more costly than other options.

Commercially available hunting camera traps are also used by researchers. They are all-in-one devices containing a camera, a computer, a battery, and a storage unit, all enclosed in a waterproof box (Figure 2c). These cameras can be set up to take pictures, series of pictures, or videos, and the devices are usually coupled with a passive thermal IR sensor. They are designed to be used outdoors and are very common in wildlife research (Glover-Kapfer et al., 2019). They are usually designed to record pictures of large mammals as their main market is North American hunters (Meek & Pittet, 2012). Tschumi et al. (2018) first used this type of camera to study vertebrate predators of *Tenebrio molitor* (L. 1758) larvae in cereal crops. However, these cameras have several features that are problematic for insect monitoring. Pictures are usually triggered by animal movement via the passive thermal IR sensor, with the camera focus adapted to take pictures of large objects several metres away from the lens, which is not



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**FIGURE 2** Examples of cameras used in four of the studies reviewed. (a) Seimandi-Corda et al., 2022, (b) Hemerik et al., 2018, (c) Tresson et al., 2022, (d) Gardarin et al., 2023, (e) Myers et al., 2020 and (f) Kistner et al., 2017.

suitable for capturing images of small ectothermic predators like arthropods. Some large arthropods have been reported to trigger thermal IR sensors, but these are exceptions of special groups such as Odonata and large moths (Houlihan et al., 2019; Johnson & Raguso, 2016). However, some camera trap models can take pictures at close range (e.g., Windscape TimelapseCam or Bushnell NaureView) or lenses can be added to the objective of the camera to reduce the focal distance. Recently a new IR sensor combined with a platform placed under the camera has been reported to effectively trigger the camera when arthropod passes through its beam (Hobbs & Brehme, 2017).

'Homemade' camera traps are becoming increasingly popular among ecologists following the commercialisation of low-cost computers such as Raspberry Pi (Jolles, 2021) (Figure 2d,f). These computers are very simple single-board computers comprising a central processing unit, a graphics processing unit, memory, and power input. Other elements such as cameras, screens, or lights can then be added to the computer to create a bespoke camera trap. These systems are open source and can easily be programmed for desired purposes. This makes these options cheap, versatile and adaptable for specific research purposes. They have been used to study predation of citrus psyllid pests in orchards (Kistner et al., 2017) and hemipteran and coleopteran pests in arable and semi-natural habitats (Gardarin et al., 2023).

Digital cameras are widely available and have been used to investigate predation by both vertebrates and insects on insect prey (Tresson et al., 2019, 2022). Smartphones can also be used to study predation on insects and both devices are expensive. Although none of the studies reviewed used smartphones, the authors are aware of an ongoing research project on biological control of generalist predators in arable fields using second hand smartphones to reduce the cost of the equipment (RMT BioReg, 2023). Like hunting camera traps, commercial digital cameras and smartphones are all-in-one devices (including a camera, battery, computer, and storage). Most devices commercialised nowadays have cameras with high resolutions able to focus on close range objects, and time-lapse image capture can be set. However, IR light is usually not available and a white flash needs to be activated to record pictures at night. Other issues with these devices are that they are not completely waterproof and need to be protected from humidity, and they are also costly.

# CAMERA SETTINGS

# Video or picture recording

When using cameras researchers can decide to use video or photographic picture recording. With videos it is easier to see a predation event, and multiple still images of a predator can be taken which facilitates later identification. However, video recording uses more energy and systems recording video need power from the grid, generators or 12 V batteries. Videos also generate a large quantity of data which is more difficult to store on an SD card and often needs to be stored on a hard drive. The quantity of data is also a problem during the data processing as it takes more time to process videos than photos (Grieshop et al., 2012). Pictures, or series of pictures, are more energy efficient and can be more easily stored (Schenk & Bacher, 2002). Devices recording only pictures can consequently be cheaper and smaller than those recording video. However, predators and behaviours can be missed, and this might explain why video recording is usually favoured by researchers.

# Night lighting

A significant proportion of predation events on insect prey occur at night (Brust et al., 1986; Seifert et al., 2016; Tomita, 2021), and so it is important to choose an appropriate way to capture quality images at night. Some studies indicate that constant white light or flashes affect the behaviour of some predators (Allema et al., 2012; Griffiths et al., 1985), but these studies have been conducted using only two species as models (the carabid beetles Anchomenus dorsalis (Pontoppidan, 1763) and Pterostichus melanarius (Illiger, 1798)). White light could also attract species that might not otherwise be active in the area and bias observations. Most surveillance cameras and camera traps are designed to switch on IR light at night but how the light quality affects arthropod behaviour, in particular predation, is not well established. It is important to note that pictures recorded with IR light are black and white and that the absence of colour can then pose problems during image processing to correctly identify predator species (e.g., Orpet et al., 2019).

# Camera trigger

When videos are not constantly recording, it is important to decide how image capture from cameras can be triggered. As previously noted, most commercial camera traps are equipped with passive IR sensors detecting heat movements; these sensors can be used when vertebrate predators of insects are studied (Kolkert et al., 2021; Nagari & Charter, 2023; Tschumi et al., 2018), but they are not very efficient to detect predatory arthropods which are ectotherms. Software developed to detect changes in the pixel recorded by a camera exists, and their source codes are publicly available (Droissart et al., 2021; Tresson et al., 2022). Such pieces of software are currently used as a post-collection method to identify pictures with potential animal movement, but they could also be used to trigger cameras. Their robustness in detecting movement needs to be tested at larger scale before being implemented in devices to trigger cameras. Even if these detection methods could be a useful approach in the future, time-lapse triggering at intervals of a minute or more has been shown to be effective. Several studies showed that predators often spend several minutes feeding on their prey (e.g., Gardarin et al., 2023; Meyhofer, 2001) and continuous recording of the predation event may be unnecessary. Time-lapse triggering was used with success in different studies to record predation on insects by multiple types of predators including small mammals, birds, and diverse arthropod taxa (Gardarin et al., 2023; Nagy et al., 2020; Pickett et al., 2022; Seimandi-Corda et al., 2022; Tomita, 2021; Tresson et al., 2022).

#### Cost of the equipment

The cost of the equipment is recognised as a major constraint for the use of camera traps in ecology (Glover-Kapfer et al., 2019). Camera prices have dropped significantly over the last 20 years, but even if the equipment is cheaper now than in the past, it remains more expensive than standard insect traps. Set-ups comprising a surveil-lance camera can cost several thousand US\$ (Clayborn & Clayborn, 2019; Meyhofer, 2001), but hunting camera traps are much cheaper options with prices ranging from 100 to 200 US\$ for the cheapest devices (Wearn & Glover-Kapfer, 2019). The cost can be further reduced with the development of homemade cameras containing only essential features costing from 16 US\$ to 100 US\$ (Chui et al., 2023; Droissart et al., 2021). Most of the studies reviewed used a very limited number of cameras and the robustness of the data collected would greatly benefit from an increase in replication by adopting cheaper camera options.

# Theft and vandalism mitigation

The price of the equipment itself is a constraint and is probably the main target to reduce the cost of an experiment, but polls conducted in the community of camera hunters also reported that theft and vandalism cause major losses (Glover-Kapfer et al., 2019; Meek et al., 2019). This loss is not limited to the camera which is damaged or stolen but includes the batteries, SD cards, and the invaluable data collected. Consequently, the risks of theft and vandalism need to be mitigated. These issues are often considered by researchers when setting up their experiments, but they do not often report how they dealt with this problem. Although insurance is an option, these problems can be reduced by operating within unpopulated areas, away from public footpaths, or in fenced private or institutional properties. It is also possible to physically protect the camera using cables, chains, or locked security boxes. However, even when these protections are implemented, thefts have still been reported with thieves using heavy equipment to remove the protections, even when far from human

settlements (Meek et al., 2019). Polls indicate that physical protection tends not to be cost effective (Meek et al., 2019), so solutions based on camouflage or hiding cameras in natural features such as logs, bushes or in tall crops are often favoured. Finally, it is also possible to communicate with people by placing signs on the cameras with personal messages explaining the purpose of the scientific study or threatening the potential offender. Research has shown the first option is more efficient to reduce the risks than the latter (Clarin et al., 2014). Engaging with local communities is also a way to mitigate these problems. The different users of the studied environment, for example, farmers, hunters and hikers could be contacted directly or via local organisations relevant to the local situation. People can therefore be made aware of the research carried out and could even help researchers in setting up the cameras, collecting the data and participating in the data processing.

# INCREASING THE EFFICIENCY OF IMAGE ANALYSIS

Once pictures are collected, they need to be screened to record predation events. Image analysis is a highly time-consuming step, which is currently limiting the use of cameras in ecology. Ways to relieve this bottleneck would clearly facilitate the use of cameras for improving understanding of insect predation. The only method directly mentioned in the studies reviewed is to increase the speed of the video or picture scrolling and to adjust the set-up used to screen the pictures by watching different videos simultaneously on multiple screens (Grieshop et al., 2012; Orpet et al., 2019). These methods can increase the speed of the data extraction but are still highly time-consuming and cannot be adopted for large-scale studies. Moreover, the increase in the video speed or the multiplication of focus points can affect the capacity of the observer to accurately detect objects. Different methods to reduce the time spent on image analysis by decreasing the quantity of data to analyse or by automatic identification of the target species will be explored in the following two sections. Some of these methods are still in development but are easy to implement for people with a minimal computing skill.

#### Reduce the quantity of images

The first option to reduce the time spent processing images is to reduce the quantity of images collected. This can be achieved by switching from video to photographic picture recording, or by changing the frequency of camera triggering. However, these parameters are dependent on researchers' questions and cannot always be modified. When cameras are motion-triggered, it is also possible to improve the placement of the camera to avoid the movement of vegetation, cloud and sunlight in the background, which can trigger the IR sensors.

If the quantity of pictures taken cannot be reduced, there is still the option of using post-collection processing methods. When

screening pictures or video collected for ecological research purposes, most of the images are 'empty', without target animals (Willi et al., 2019). Automatically identifying 'empty' pictures and separating these from images containing the target(s) would greatly improve data processing by allowing the researcher to focus their attention on the images with animals to identify. Empty images can be detected using background subtraction methods, where series of pictures are compared to find significant differences between frames (Tresson et al., 2022; Wei et al., 2020; Yousif et al., 2019). This method is particularly useful when data are recorded in videos or short series of pictures but can be difficult to implement if the time lapse between two images is long and/or differences between frames are obvious. This can be the case at sunset and sunrise where shadows are moving fast and can rapidly change from one picture to another and unfortunately. these periods are when predators tend to be more active. Movement of vegetation or fog in the background can also affect this method, and the location and positioning of the camera are critical if this method is to be used (Wei et al., 2020). Deep learning algorithms can also be trained to identify empty images (Norouzzadeh et al., 2018; Tabak et al., 2019; Willi et al., 2019; Yang et al., 2021). These algorithms learn features of pictures by iteratively training on data without the need for manual feature extraction (Høye et al., 2021). Deep learning is becoming increasingly popular among ecologists and is used for ecological modelling (Bourhis et al., 2023), to identify animals based on sounds (Stowell et al., 2019), images (Norouzzadeh et al., 2018) or optical sensors (Kirkeby et al., 2021). Removing empty images using deep learning seems efficient, but very large numbers of pictures need to be classified as empty (or not empty) to train these algorithms, and this is not always practical. Previous work where this method was used studied large mammals (Ahumada et al., 2020) and it is not clear how efficient the method would be when the target is a small arthropod. If such methods are planned to be used, pictures need to be taken with a background as constant and homogeneous as possible, to clearly see with contrast the target predator on the image.

### Improve insect identification

Another option to facilitate image analysis is to automatically identify predators in video footage or on pictures. Before 2016 most of the automatic animal identifications were based on feature extraction where the relevant image features, such as shape, colour pattern, or size, were chosen for a specific class of animal and then algorithms were developed to extract those (Schneider et al., 2020). With the increase in computing capacity, deep learning algorithms have been recently developed. As detailed in the previous section, this method does not need manual feature extraction but needs a large training set (several hundreds or thousands, if not millions, of pictures depending on the use case) with images of the different species identified. Deep learning algorithms have successfully been used to identify animals, mainly mammals, observed on images from camera traps (Norouzzadeh et al., 2018; Tabak et al., 2019). These algorithms are also commonly used to automatically identify insect pest species from

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Two main constraints arise from deep learning approaches. The first is that a large training set needs to be built. Citizen science has been successfully used to help researchers annotate pictures from camera traps targeting mammals (Willi et al., 2019), and platforms, such as Zooniverse (www.zooniverse.org), host researcher projects on their site and invite members of the public to make annotations. This kind of approach can be biased towards charismatic species, and it could be more difficult to implement for arthropods, not only because they are generally less charismatic, but also because they can be more difficult to identify by people without strong taxonomical skills. Recently, platforms collecting annotated pictures of plants and animals have opened and are used to build smartphone applications to identify living organisms (Joly et al., 2016; Mesaglio & Callaghan, 2021). The training set of these platforms is built with images collected using various devices in different environments and with different angles and could be used to improve the automatic identification in various studies. These platforms could also be directly used to identify insect predator species on images. Furthermore, funding bodies increasingly require that data generated during research projects are openly accessible and stored for the long term according to the FAIR principles (Findability, Accessibility, Interoperability, and Reusability) (Wilkinson et al., 2016). This applies to pictures collected during research projects. Image repositories exist for live science (Hartley et al., 2022) with some designed for camera trap studies (Ahumada et al., 2020; Casear et al., 2019). These repositories could be used as large training sets for the development of identification algorithms, but they do not yet contain enough images of arthropods for this purpose.

The second constraint with deep learning approaches is that most of training sets are imbalanced. This is not surprising as most living communities comprise a few dominant species and a lot of rarer species (Avolio et al., 2019). Collecting data from these communities leads to imbalanced datasets that can bias species identification. To address this issue, it is possible to artificially balance the dataset by oversampling, repeating the sampling of rare classes, or on the contrary to under-sample the dataset, by reducing the number of training images collected of common species to match the numbers of the rarer ones. The issue with these methods is that it can decrease the performances of the model (Kellenberger et al., 2018). Splitting deep learning algorithms between object detection and classification seems to improve classification in imbalanced datasets and has been tested to identify ground-dwelling arthropods (Tresson et al., 2021). Data augmentation by automatic generation of images of rare classes (Klasen et al., 2022) or specifically collecting images of known species, in controlled conditions set-ups or from museum collections (Robillard

et al., 2023), can also be a way to create a more balanced datasets

# Level of identification

and overcome this problem.

Another challenge related to the identification of predators is the level of taxonomic identification achievable with the use of cameras. Studies on mammals and birds can usually identify individuals at species level or even at the individual level (Ferreira et al., 2020; Schneider et al., 2019). In the studies reviewed that focus on large vertebrate predators of insects, identification was successful at the species level (e.g., Tomita, 2021; Tresson et al., 2022; Tschumi et al., 2018). However, due to black and white images from IR cameras, even the identification of vertebrates was not always possible (Kolkert et al., 2021). For the studies reviewed here that focussed on arthropod predators, the identification is often done at the level of the Order or the Family. In some cases, more precise identification is possible if the diversity present for a particular group is limited, or if the species is clearly identifiable (e.g., Gardarin et al., 2023; Myers et al., 2020; Seimandi-Corda et al., 2022). This difference in the level of identification achieved between large animals and arthropods is because criteria to identify large animals and mammals are more easily spotted on images than those of small animals. However, the level of the Order or Family for arthropods is often enough to be informative as most of the studies using conventional sampling methods tend to group individuals at this level, but limits the development of more targeted approaches to support specific biocontrol agents or protected rare species from specific predators (Smith & Gardiner, 2013).

An increase in the image resolution with pictures taken at shorter range could facilitate identification. However, dissection and a microscope are sometimes needed to identify individuals at species level which is not possible with camera images. When individuals cannot be dissociated at the species level, data collected by the cameras can be combined with other types of data to elucidate the identification. For example, the location or habitat where the insect was seen and the time of year; knowledge on the host-plant relationships of arthropods and their phenology, distribution and relative abundance can be applied to improve the probability of correct identification. It is also possible to imply identification from identified individuals trapped using standard methods (e.g., pitfall traps for ground-dwelling predators) at the same time as camera traps are running (Gardarin et al., 2023; Seimandi-Corda et al., 2022).

# USER GUIDELINES

The 28 studies reviewed here show that researchers using cameras to monitor insect predation used a diversity of set-ups to record these interactions. This reflects the diversity of the predation interactions, but general guidelines can be provided to help people develop their own methodology. The camera equipment used will depend on the ecology of the prey and their potential predators. As an example, the size of the predators and the duration of the predation event can affect the way a camera set-up is designed. Motion-triggered cameras could be used if vertebrate predators are considered, while video recording or time-lapse trigger cameras are better for invertebrate predators. Similarly, if predation events last several minutes, timelapse cameras might be better adapted but if predation events are fast, video recording will be more suitable. If night-time recording is planned, lighting needs careful thought depending on the level of taxonomic identification required.

Cameras should be focussed on the appropriate area to record the target prey in a set-up as close as possible to the natural habitat of the target predators or prev; be this on the ground or on plants. When prey is placed on the plant, special attention needs to be paid to avoid movement of the vegetation which may result in blurry images of predators which will be difficult to identify. Information about the ecology of the predators can be retrieved from the literature and can be complemented with preliminary tests to identify the most common predators, the duration and frequency of the predation events (e.g., Orpet et al., 2019; Woltz & Landis, 2014) information which is rarely available in the literature. Taking into account these ecological considerations will allow the design of the ideal camera setup. The choice of the most suitable camera set-up will be driven by a trade-off between the quality of the set-up and its cost, as it is often not possible to design a cheap device that is able to record everything with low maintenance, and with data that are easy to process. Where to draw the line in this trade-off depends on what ecologists consider critical, as this field of research is not yet well established. The development of new methods of image processing, such as deep learning, could change this trade-off by strongly reducing the cost associated with image processing, but the application of this method is still in its infancy in ecology and is limited to large-scale studies.

# PERSPECTIVES

Cameras are a powerful tool for the study of insect predation. The majority of the studies that we reviewed used the technique to identify the major natural enemy communities of certain target insect prey. Camera traps are able to go beyond circumstantial linkages between the presence of predators in the habitat and removal of prey to unambiguously determine the taxa involved in predation. Target prey included species of conservation interest such as endangered swallowtail butterflies to improve reintroduction efforts (Clayborn & Clayborn, 2019); native coccinellids which were hypothesised to be threatened by the introduced coccinellid Harmonia axyridis (Pallas, 1773) (Smith & Gardiner, 2013); and Cassida rubiginosa (Müller, 1776) larvae, a biocontrol agent for weeds which was monitored to assess the potential for successful establishment (Schenk & Bacher, 2002). Most studies aimed to better understand the natural enemy community of certain crop pests (e.g., Frank et al., 2007; Salamanca et al., 2019; Walton & Grieshop, 2016). Several studies uncovered unexpected predation events, such as the importance of paper wasps as predators of shield bugs (Schenk & Bacher, 2002), egg predation by

collembolas (Pickett et al., 2022), and predation by 'herbivores' including grasshoppers and slugs (Grieshop et al., 2012). Several studies highlighted the underestimation of vertebrates as predators, finding frogs, birds and small mammals as major predators of insects (Hemerik et al., 2018; Tresson et al., 2022; Tschumi et al., 2018; Zou et al., 2017); taxa which may go unnoticed by traditional methods centred on the predator such as pitfall trapping. The continued use of camera trapping will undoubtedly reveal many more previously unknown interactions and help to quantify the relative importance of different species as predators.

Cameras have the advantage that they can operate under standardised conditions over long periods of time, including night, facilitating data acquisition which would otherwise be extremely labour intensive if done by eye (Pfannenstiel & Yeargan, 2002). Cameras have enabled the understanding of the importance of night-active predators such as earwigs and spiders (Opiliones and Araneae) (Myers et al., 2020; Petersen & Megan Woltz, 2015), determination of the diel/seasonal predation periodicity of individual predators (e.g., Seimandi-Corda et al., 2022; Tomita, 2021), and demonstration that predator communities differ widely between night and day (e.g., Kolkert et al., 2021; Petersen & Megan Woltz, 2015). Furthermore, cameras allow for observation of commensal (Merfield et al., 2004) or antagonistic (Orpet et al., 2019) interactions and determination of live attacks from scavenging visits (Grieshop et al., 2012) which may help to fully explain field data. Other important behaviours revealed include prey handling and residence times (Meyhofer, 2001; Orpet et al., 2019) which help to guantify predation and enable the creation of predation indices (Merfield et al., 2004). The groundbreaking work of Halsall and Wratten (1988) showed that camera traps supported previous assumptions made from pitfall experiments which suggested increased activity-density of Bembidion carabid beetles in response to high aphid densities (Bryan & Wratten, 1984); the camera traps sowed increased entries of carabids into areas of high than low aphid density and a higher proportion of time spent feeding, demonstrating density-dependent predation activity in response to high aphid infestation in cereal fields.

Although the work of Halsall and Wratten (1988) supported assumptions made using pitfall traps, several studies have compared the predator community derived from pitfall trapping and camera trapping, with most finding significant differences between them (Grieshop et al., 2012; Nagy et al., 2020; Phillips & Gardiner, 2016; Salamanca et al., 2019), indicating that predicting predation from pitfall-trapping methods is not as robust as the use of cameras. However, in some studies cameras missed small predators such as Anthocorids due to their small size (Woltz & Landis, 2014) or similar-looking predators could not be identified to an acceptable precision due to insufficient camera resolution (Orpet et al., 2019). In this case, the concurrent use of cameras with traps like pitfall and sticky traps from which all potential predators are identified could help. Moreover, not all predation interactions can be studied using cameras. Cryptic species living in soil, dung, or plant tissues pose challenges for camerabased studies, necessitating the use of alternative methods like DNA metabarcoding (Bonato et al., 2021) or bioacoustics (Robinson

et al., 2023) to help investigate these interactions effectively. The fusion of multiple biomonitoring methods is ideally needed for a comprehensive understanding of the predation of insects in the field and holds great promise for future advancements.

It is difficult to present a large number of prey in a sentinel prey set-up for camera trapping. Gut content analysis (Birkhofer et al., 2017) can help to explain the diet and prey preferences of particular species of predators once they have been identified as key predators via camera trapping. Gut analysis through DNA metabarcoding using a large number of individuals from a wide spatial area helps to overcome the spatial limitations of camera trapping. The poor spatial field of view of cameras coupled with a lack of spatio-temporal replication in the studies is a strong limitation to camera trapping and hampers the generalisation of researchers' observations. Future technical advancements must prioritise addressing this issue, with a focus on further reducing equipment costs and improving image processing. Progress in artificial intelligence, such as deep learning, will improve target detection and the development of automatic species identification (Suresh et al., 2024). Developments in this area will also allow some level of automatic filtering (e.g., removing 'empty' images) and identification, with existing solutions already available for larger animals (Ahumada et al., 2020; Casear et al., 2019; Rigoudy et al., 2023).

The development of camera trap systems suitable for the study of small invertebrates at a larger scale will open new research perspectives. Predicting predation services at a specific location is challenging due to multiple factors interacting together and our limited knowledge of predators' ecology. This challenge can be mitigated using cameras with good spatio-temporal replication allowing to account for the variability in environmental factors, such as crop management practices and landscape features, and enabling understanding of how these factors affect the predator community, and what level of predation is achieved for each species. Hunting camera traps often contain a thermometer, and information on some meteorological conditions (overcast, sunshine, hail, or snow) can be inferred from pictures and inform about microclimates (Alison et al., 2024; Hofmeester et al., 2020) at the same time interactions are recorded. Meteorological conditions affect predator activity-density (Frank & Bramböck, 2016) and nutritional needs (Walker et al., 2020) and consequently can have an impact on trophic interactions. Combining observations from cameras and microclimatic data can enhance predictions of predation services. Cameras also show the date and time on images allowing a greater understanding of the phenology and periodicity of predation events as previously described. This could help inform management decision such as the timing of insecticide applications in agricultural contexts.

# CONCLUSION

With fast-paced technical developments, cameras are becoming increasingly common tools used by ecologists. Cameras are good at collecting temporally rich, quantitative data on predation, such as the frequency of observed species feeding on insect prey or the quantity

of prey consumed by individual predators, and can give other contextual information such as the timing of predation. Therefore, they can help us to better understand predator-prey interactions for arthropods and better help us to protect endangered species and predict pest regulation services provided by beneficial species. Here we identified 28 studies using this method with a high diversity of equipment, set-ups, and applications. We are still far from the availability of tools that are cheap and easily used, but this goal is within reach. With an increasing number of research projects and publications in the future, a more standardised methodology will emerge. This standardisation will streamline the use of these tools, particularly for people with no experience in their use, thus democratising their application within the scientific community. Furthermore, the integration of camera traps with other sensors, such as meteorological devices and bioacoustics, along with complementary methods like DNAmetabarcoding, promises to open new frontiers in ecological research. These interdisciplinary approaches hold exciting potential for uncovering new insights into ecosystem functioning.

# AUTHOR CONTRIBUTIONS

Gaëtan Seimandi-Corda: Conceptualization; data curation; investigation; visualization; writing – original draft; writing – review and editing. Thomas Hood: Writing – original draft. Samantha M. Cook: Conceptualization; funding acquisition; project administration; resources; supervision; writing – review and editing.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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# SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1.** Summary of details from publications on the use of cameratrapping to study predation on insect prey.

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