

Are birds in agricultural habitats attracted to plant volatiles?

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Abstract

Birds' ability to fly allows them to track resource abundance and relocate themselves to areas with more resources. It has been a longstanding belief that they forage mainly through visual cues due to their relatively small olfactory bulbs. However, a growing body of results show that birds use olfaction for communication, when choosing nesting material and detecting predators. Insectivorous birds can during foraging use herbivore-induced plant volatiles to identify infected trees, and have a preference for olfactory cues over visual cues. Induced plant volatiles are released during herbivorous attack as an indirect defense, attracting predatory arthropods and birds which are natural enemies of the herbivores. Birds, however, act also as top predator, meaning they prey on intermediate predators, thus releasing pest from suppression by predatory arthropods. The possibility that these birds use herbivore-induced plant volatiles to localize predatory arthropods have not yet been investigated, which is the aim of this study. We tested the attraction of birds to a common volatile compound, methyl salicylate (MeSa), and evaluated the importance of visual and olfactory cues in a three-way choice experiment in crop fields. Birds could choose between MeSa, neutral odor and no odor in three experimental setups: visible food, invisible food and artificial prey. Overall visits to all setups showed a slight preference for MeSa, with no difference between visible or hidden food. There was however a preference for visual cues when MeSa was presented without any food, next to a dish with odorless artificial prey. We observed that only certain species approached the experiment, mainly corvids and thrushes, thus our conclusions are limited to these taxa. Our results suggest that olfaction might be important for birds foraging in farmland habitats and could also influence the role of birds as biological pest control agents.

Keywords: insectivorous birds, avian olfaction, foraging, herbivore-induced volatiles, pest control

Sammanfattning

Fåglarnas förmåga att flyga gör det möjligt för dem att spåra resursöverflöd och förflytta sig till områden med mer resurser och det har varit en långvarig uppfattning att de födosöker huvudsakligen genom visuella signaler på grund av deras relativt små luktlober. En växande mängd resultat visar emellertid att fåglar använder kemiska signaler i kommunikation, när de väljer häckningsmaterial och för att upptäcka rovdjur. Insektsätande fåglar kan under födosök använda herbivorinducerade, kemiska växtsignaler för att identifiera infekterade träd och föredrar olfaktoriska signaler över visuella signaler. Inducerade växtämnen släpps under herbivorangrepp som ett indirekt försvar, vilket lockar rovdjur och fåglar som är naturliga fiender till växtätarna. Fåglar lever dock också som topprovdjur, vilket innebär att de jagar rovdjursinsekter och därigenom frigör skadedjur från undertryck av dessa. Möjligheten att dessa fåglar använder herbivorinducerade växtsignaler för att lokalisera rovdjursinsekter är ännu inte undersökt, vilket är syftet med denna studie. Vi testade fåglars attraktion till en vanlig förening i växtsignaler, metylsalicylat (MeSA), och utvärderade betydelsen av visuella och olfaktoriska signaler i ett experiment med trevägsval i fält. Fåglarna kunde välja mellan MeSA, neutral lukt, och ingen lukt i tre experimentuppställningar: synlig mat, osynlig mat, och artificiellt byte. Övergripande besök på alla uppställningar visade en liten preferens för MeSA, utan skillnad mellan synlig eller dold mat. Det var dock en preferens för visuella signaler när MeSA presenterades utan byte, bredvid en skål med luktlöst artificiellt byte. Vi observerade att endast vissa arter närmade sig experimentet, främst korvider och trossar, så våra slutsatser är begränsade till dessa taxa. Våra resultat tyder på att luktsinnet kan vara viktigt för fåglar som födosöker i jordbruksmiljöer och kan också påverka fåglarnas roll inom biologisk skadedjursbekämpning.

Nyckelord: insektsätande fåglar, luktsinne, födosök, inducerade kemiska signaler, skadedjurskontroll

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Introduction

Birds belong to the class of tetrapods with the largest number of living species, which live and breed on all continents. Their ability to migrate across continents provides a link between separated geographic areas, and flight at a more local scale allows them to track resource abundance and relocate themselves to areas with more resources (Whelan et al., 2016a). They forage in terrestrial, aquatic and aerial environments as carnivores, herbivores, nectarivores, frugivores and scavengers, which makes them effective providers of many ecosystem services, e.g. nectarivores provide pollination, frugivores play a role as seed dispersers, predators regulate trophic networks and scavengers provide sanitation and limit spread of disease (Whelan et al., 2016b).

Many birds feed on insects, fish, plants, small mammals or other birds. Foraging strategies among these birds have been presumed to mainly rely on visual cues. But how do birds detect small or hidden prey in thick forests, big open fields or oceans? Though the awareness of birds' olfactory capacities has been around since 1789, and then brought into attention again in 1911 by R.M. Strong (Wenzel, 2007), there has been a longstanding reluctance to "credit birds, as a group, with an acute sense of smell" (Clark & Mason, 1987). The part of birds' brain responsible for the sense of smell, i.e. the olfactory bulb, has increased in size through the evolution of birds from dinosaurs, which suggests that olfaction has played a significant role with a selective advantage (Zelenitsky et al., 2011). Using olfactory cues during foraging enhances birds' chances of finding their prey, since wind can carry odors over long distances and reveal those hidden from site.

Insectivorous bird species feed on small prey often hidden in a lot of vegetation, but it has been shown that birds are able to detect which trees are attacked by herbivores, even when the herbivores and damage by herbivory is veiled (Mäntylä et al., 2008). The mechanism underlying the attraction was later unveiled by Amo et al. (2013), which showed that birds, like predatory arthropods (Dicke 2003, James 2005), can use herbivore-induced plant volatiles to sniff out their prey. This suggests that there is a positive relationship between bird presence

and foraging activity, and plant fitness, because birds can reduce the number herbivorous pest insects feeding on plants. Several studies have found birds reduce herbivory and plant damage on trees and shrubs (Mäntylä et al. 2011, Boesing et al. 2017). However, as a group, birds function at every trophic level (the position in a food chain) (Fig.1) except first level (primary producer) and as decomposers (Whelan et al., 2016b). This means that some birds play a role as top predator at the fourth trophic level and prey on predatory arthropods, and it is possible that they also use plant volatiles to locate their prey. This creates a trophic cascade which could lead to negative consequences for the plants and could reduce ecosystem services provided by predatory arthropods in agricultural crops (Whelan et al., 2016b; Martin et al., 2013).

Background

The olfactory foraging cue hypothesis

A prevalent impression, despite extensive research, is that birds don't have a real sense of smell. It's a strong belief that all birds have relatively small olfactory bulbs, however, in reality bulb size varies from very large to extremely small (Bang & Cobb, 1968) and size alone appears to have little relation to olfactory acuity (Wenzel, 2007). Some bird species, like European starlings (*Sturnus vulgaris*), have small olfactory bulbs but are able to detect and discriminate plant volatiles (Gwinner & Berger, 2008), which show that bulb size alone does not determine olfactory acuity.

The importance of chemical cues when choosing nesting material has been tested with both captive starlings (Clark & Mason, 1987) and free-ranging blue tits (Petit et al., 2002), suggesting that olfactory cues are more reliable information about plants condition (i.e. freshness and pest occurrence). Amo et al. (2008) tested birds' abilities to recognize olfactory cues and assess predation risk by adding mustelid scent to nest-boxes with nestlings. The result suggested that birds are able to detect the scent of predators and they show antipredator behaviour in which they delay their entry to the nest in order to assess the situation. An early experiment testing navigation in birds found that the olfactory sense plays a major role in homing pigeons. Pigeons were released from an unfamiliar area and those with surgically damaged olfactory nerves never returned (Papi et al., 1971; also see review by Gagliardo, 2013). Similarly, seabirds that forage out in the open ocean use olfactory cues to localize prey (Nevitt et al., 2008). Nevitt et al. confirmed their predictions that seabirds should facilitate their search by flying crosswind, followed by upwind, zigzag flight upon encountering prey scent, in a study with free-ranging wandering albatrosses.

The olfactory foraging cue hypothesis states that birds use their sense of smell in their foraging strategy (Koski et al., 2015). Recent studies have provided evidence that birds use herbivore-induced plant volatiles to detect herbivorous prey. Results from a two-way choice experiment with Great tits, *Parus major*, suggests that these birds use plant volatiles as olfactory foraging cues (Amo et al., 2013). The birds in this study paid significantly more visits to infested trees than control uninfested trees, even when all visual cues were removed. They also found a preference for olfactory cues over visual cues, which could be because visual cues such as leaf damage remains even after herbivores left and thus is not an accurate signal for the presence of herbivores. Yang et al. (2015) tested the relative importance of visual and olfactory cues in the Oriental honey buzzard using a series of two-choice experiments. Their results suggest that olfaction and vision are both used to identify food at close distances. This may be true in many cases, as olfactory clues can travel long distances and be used as orientation towards preys, but as the prey becomes visual sight is needed for capture and the distinction between the prey and the rock next to it.

Volatile organic compounds

When under attack by herbivorous arthropods, plants respond with an induced production of volatile organic compounds released in and around the wounds of feeding sites. This can serve as a direct defense affecting the herbivores by inhibiting feeding behaviour, decreasing digestibility or intoxicating the herbivore (Chen, 2008), or as an indirect defense attracting the natural enemies of the herbivores, such as parasitoid and predatory arthropods (Mumm & Dicke, 2010), but also insectivorous birds (Amo et al., 2013). The composition of herbivore-induced plant volatiles (HIPVs) varies depending on type of damage, and herbivore species (Maffei, 2010).

From evolutionary perspective, it is reasonable to suppose that defensive plant volatiles evolved primary as a direct defense, attempting to intoxicate attackers. However, as a positive side effect, predators and parasitoid started to eavesdrop on volatiles induced by arthropod herbivores in order to locate their preys. The ability to smell and distinguish different plant volatiles should have a selective advantage for vertebrate and arthropod predators, since volatiles are a reliable source of information about the presence and identity of herbivores (Koski et al., 2015) and the third trophic level predators that hunts the herbivores. HIPV blends may consist of 200 different compounds (Dicke and Van Loon, 2000), and it is not fully understood how the combinations affect the behavioural response of parasitoid, hyperparasitoid and predatory arthropods and birds at third and fourth trophic level (Mumm & Dicke, 2010). One type of HIPV-compound, methyl salicylate (MeSA), has been shown to activate plants defense genes (He et al., 2006), and has been identified as a common compound in at least 10 plant species infected with different herbivores (Van den Boom et al., 2004; de Boer & Dicke,

2004). The effect of MeSA on natural enemies has been tested in the field, using sticky card traps to estimate the abundance of predatory arthropods (Mallinger et al., 2011). The total number of adult enemies caught was significantly higher in treated plots compared to untreated plots. The same study also found that aphids were more abundant in untreated plots compared to treated plots, which could be a result of increased predation or, as other studies have shown, that MeSA also works as a repellent to several aphid species if applied early in the spring (Ninkovic et al., 2003; Lösel et al., 1996).

Application of HIPVs for pest control

There's an increasing interest of potentially use plant volatiles for pest control (Kaplan, 2012), as the volatiles would attract natural enemies of herbivores, however, there are some problems that needs to be considered. As Zhu and Park (2005) points out, application of plant volatiles for biological control faces the concern of "how to recruit predaceous insects into natural or damaged fields and synchronize their presence with the targeted pest". The use of volatiles deals with three main issues: (1) increased attraction of parasitoids/predators does not equal increased parasitism/predation rates on herbivores, (2) parasitized herbivore can grow larger and consume more, and (3) HIPV can be detected and used by herbivores, hyperparasitoids and fourth trophic level predators (see review by Heil, 2014). Another problem that comes into question is if volatiles are used on crops that are not infested with herbivores, then parasitoids and predators at third trophic level will learn to avoid those plants with artificially produced volatile blends (Heil, 2014). Due to the complexity of trophic interactions, it might be better to step down a level and focus on the direct effects of HIPVs on the herbivores, since there is evidence of HIPVs repelling pests.

Effects of bird predation on pest control

Using HIPVs to attract natural enemies for biological control, may face restrictions due to fourth trophic level enemies (such as birds), that exploits plant volatiles to locate parasitoid and predatory arthropods (Martin et al., 2013). Though it has been shown that vertebrate insectivores can suppress the abundance of both predatory and herbivorous arthropods, and help reduce plant damage (Mooney et al., 2010), results from a meta-analysis of studies with exclusion experiments, show that plants suffer more leaf damage and mortality, and lose more biomass when inside bird exclosures (Mäntylä et al., 2011). The presence of birds may have different effect depending on landscape complexity. A recent exclusion experiment found an increase of pest densities and herbivore rates from simple, intensely cultivated landscapes to complex landscapes containing large amounts of natural or seminatural habitat, except in treatments excluding birds, and pest control potential in complex landscapes was reduced from 37% to

12% when birds were present (Martin et al., 2013). The increased pressure of herbivores in complex landscapes is an example of the mesopredator release hypothesis (Fig.1), where the suppression on herbivores is released due to the negative interactions occurring between birds and predatory arthropods.

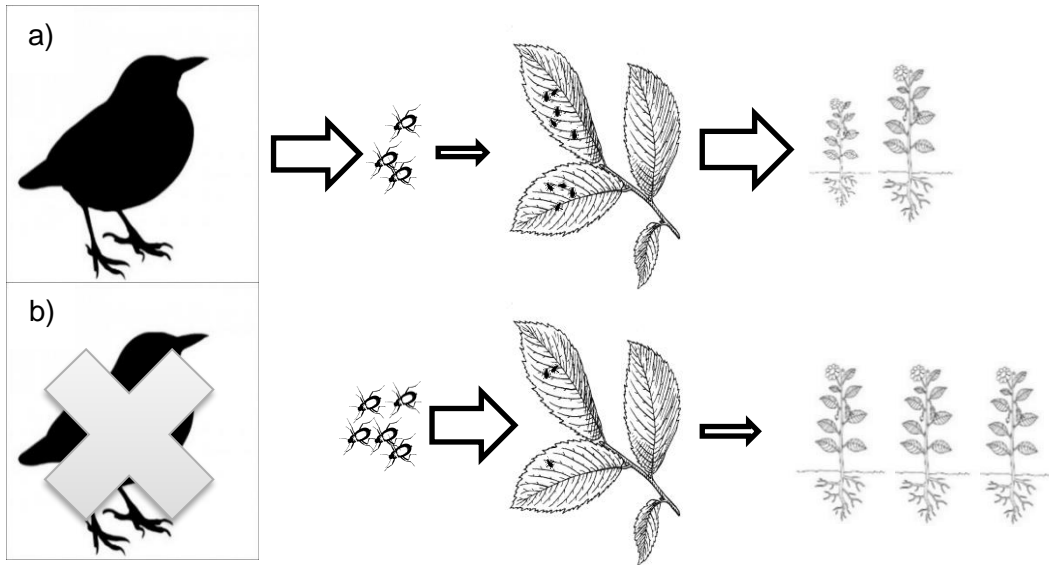


Figure 1. Mesopredator release hypothesis. a) top predator (birds) suppress the mesopredator population thus releasing pest population from suppression and as a result plants suffer more damage. b) when birds are excluded, the mesopredators are released from suppression and pest population is suppressed by mesopredators and plants suffer less damage.

Aims and objectives

To my knowledge, there haven't been any studies that investigated the foraging strategy of fourth trophic level insectivorous birds in agricultural landscapes. Birds of fourth trophic level could potentially negatively influence plant fitness, according to mesopredator release hypothesis. If these birds can also use plant volatiles, this would mean that they can efficiently locate predatory arthropods and reduce their beneficial effects to agricultural ecosystems.

The aim of this study is to investigate if farmland birds are attracted to herbivore-induced plant volatiles, which may suggest that they use olfaction to locate arthropod prey, which would support the olfactory foraging cue hypothesis. I also aim to evaluate the relative importance of olfactory cues in the presence and absence of visual cues, in order to improve understanding on how different senses are used by birds to locate their prey at short distances. To examine whether birds are attracted to volatile compounds I used an artificially produced compound, methyl salicylate (MeSA), in a three-way choice experiment in agricultural fields. I tested the preference for olfactory or visual cues by recording which treatment they visited first. I hypothesize that the majority of birds will pay their first visit to Petri dishes treated with MeSA, thus indicating an attraction for the smell. I expected birds to choose MeSA treated dishes first to a larger extent when the food was hidden, and to a lesser extent when food was visible in all dishes, because visual cues might take over in such situation if vision is the dominant foraging sense. Further, the relative importance of vision and olfaction would be revealed when visual and olfactory cues were presented separately. The results of this study will increase our understanding of birds foraging strategies and provide additional understanding of trophic interactions in agricultural landscapes.

Materials & Methods

Study sites

The experiment was carried out between the beginning of May and beginning of August in 2017, at Lövsta Research centre (59°49'N, 17°48'E) Svista (59°56'N, 17°35'E) and Viksta (60° 6'E, 17°36'E) in Uppland, Sweden. The study landscapes were dominated by organic farming with cereals and cattle grazing, with small forest patches. I selected areas with either forest edge, open field or both. Additional data from previous experiment carried out during July in 2016 at Lövsta Research centre was added to this study. The experimental setup and study landscape in 2016 was the same as in this study.

Experimental setup

Initially, nine experimental plots were installed with a minimum of 100 meters apart. Each plot was set-up with a wildlife camera and three Petri dishes, placed in a triangle with 2 meters to one another (fig.2). I used three types of setups to test birds' preference for odour and visual cues (fig.3). Six of the plots were arranged with dead field crickets and sawdust in each dish, one dish treated with MeSA wax pellets, one with positive control (lemon oil), and one without smell. To test the importance of visual clues, crickets were either visible or hidden in sawdust. First, visible prey was used by placing the crickets above the sawdust, in order to increase the probability of birds finding and approaching the experiment, and when the birds had discovered these, the prey were hidden by placing new crickets under the sawdust for another day or two. To further evaluate the importance of visual and olfactory cues, I arranged the other three dishes without crickets since crickets may give off a scent. These Petri dishes had one with MeSA wax pellets and sawdust, one with plastic spiders on sawdust, and one with only sawdust. The cameras were moved to new locations 2-3 days after

birds had discovered them to minimize the risk that birds learned the location and same individuals revisited the plots frequently.

Volatiles

MeSA wax pellets were produced at the ecology department at the Swedish University of Agricultural Sciences in Uppsala. Pellets release their smell at a stable rate for up to 2 weeks (Ninkovic et al. 2003), but were replaced sooner if for example it had been raining or dishes been moved by animals or wind. Lemon oil was added when smell became faint, after rain or if dish had been moved. Crickets were euthanized by cooling them down in the fridge and when asleep put in freezer for at least 24 hours and only taken out just before use. This assures freshness and prevents decaying. If crickets were not eaten after 3-4 days, they were replaced with new.

Bird monitoring

The cameras (Scout Guard 880 and Scout Guard 550) were installed with a clear view of all three dishes, and became activated and recorded for 15 seconds when birds came within limits of the infrared photo sensor. I analyzed the videos and recorded the first dish inspected by each individual. I set the following criteria

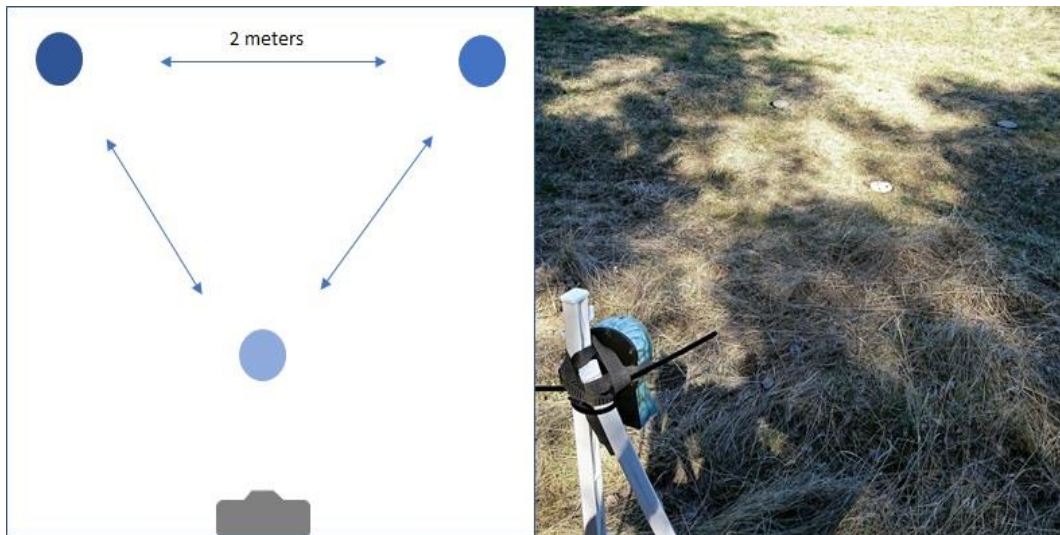


Figure 2. Experimental setup of plots. Each plot was set-up with a camera and three Petri dishes, placed in a triangle with 2 meters to one another.

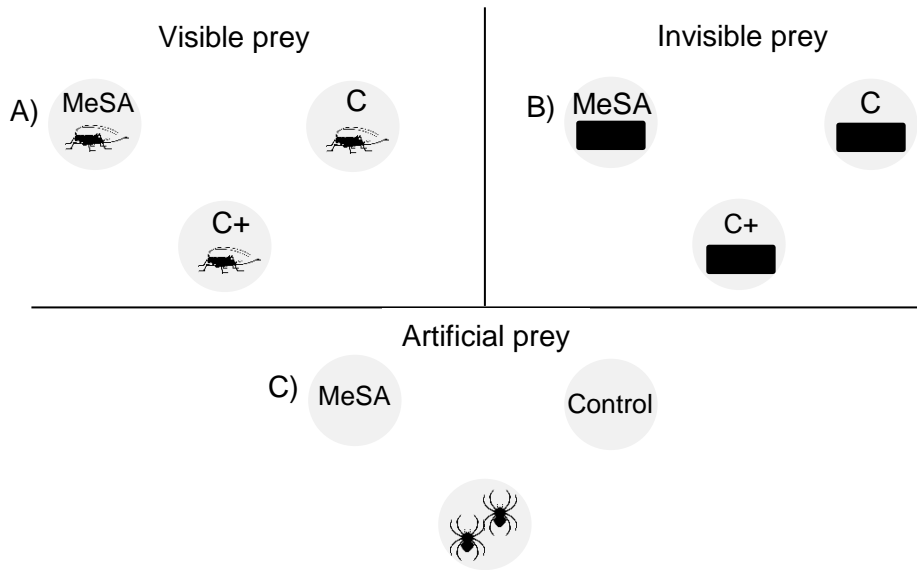


Figure 3. I used three types of setups to test birds' preference for odor and visual cues. A) Two dishes treated with smell, MeSA and lemon oil (positive control), third dish had no olfactory treatment. Visual crickets in all dishes. B) Same olfactory setup as A, but crickets are hidden in sawdust. C) One dish treated only with olfactory cue, MeSA. One dish had only visual cue (plastic spider). Control had neither smell or visual cue.

for a “choice” to be recorded: bird standing in front of dish with beak crossing threshold of the dish edge, or tilting head as to inspect dish, or picking in dish to get the bait, or walking over the dish or past the dish close enough to touch it (fig.4). Reset time was set on 40 minutes, which means that any visiting bird of the same species within this time frame was assumed to be the same individual.

Statistical analyses

Statistical analysis was performed with R (R Core Team 2016) using Generalized Linear Mixed Models (GLM) with “lme4” package (Bates et al., 2017). I combined the data collected during this study with previously collected data from summer 2016, to increase the sample size. These data were collected from the same study landscape, but only in a setup with invisible prey. First choice was analyzed using generalized linear model following a binomial distribution, with odor treatment as explanatory factor. One row of data for each dish in a setup was created for each bird individual and the first choice was given a value of =1, while the other two values of =0. Then I used a random individual effect to control for the non-independence of dishes within same setup, and an additional random effect

for each camera location, because there is a larger probability of same bird individuals to visit the location several times. I tested two models – one with only treatment as explanatory factor and one with an interaction between treatment and setup in order to see if birds' preference changed depending on availability of visual cues.



Figure 4. Criteria for a “choice” to be recorded: Bird standing in front of dish with beak crossing threshold of the dish edge, or tilting head as to inspect dish, or picking in dish to get the bait, or walking over the dish or past the dish close enough to touch it.

Results

Plots in “open field” had more visits from birds if there were some bushes or small trees in/between fields. Recordings occurred day and night, but most visits took place during the day. Several individuals spend time visiting all dishes, but only the first visit of each individual was used for the analysis. A total of 11 different species from 65 individuals were recorded (fig.5).

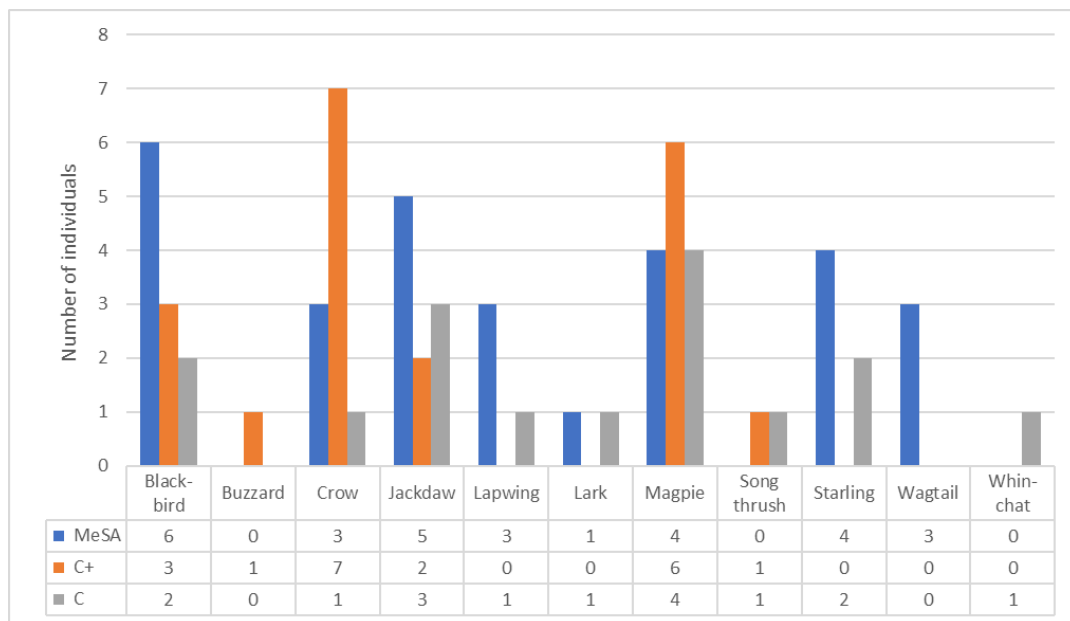


Figure 5. Number of individuals per species for each treatment.

The Generalized Linear Model (GLM) showed significant preference for MeSA when only using treatment as explanatory factor ($p < 0.02$) (table 1). However, when considering the interaction between treatment and setup, there's a tendency towards preference for spiders (visual cue without odor) ($p < 0.07$) (table 2). Data showed that for all setups combined 44% of the birds paid the first visit to MeSA treated dishes, 31% paid first visit to positive control (neutral smell/odorless visual cues), and 25% to negative control (no smell and/or no visual cues). There was no difference between the two setups with crickets (visible vs. invisible food), which both show a preference for MeSA, but there was a preference for visual cues in the third setup with plastic spiders (fig.6).

Table 1. Results from the Generalized Linear Model (binomial with logit link) with only treatment as factor. Sample size $n=65$, reference category = C.

Coefficients:	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1,1192	0,2879	-3,887	0,000101	***
treatmentC+	0,3083	0,3939	0,783	0,433769	
treatmentMe	0,903	0,381	2,37	0,017786	*

Table 2. Results from the Generalized Linear Model with treatment*setup interaction. Sample size $n=65$, reference category = C.

Coefficients:	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1,02E+00	3,89E-01	-2,6280	0,008580	**
Treatment C+	2,90E-15	5,50E-01	0,0000	1,000000	
Treatment MeSA	9,04E-01	5,19E-01	1,7420	0,081480	.
Setup Spiders	-4,82E-01	8,73E-01	-0,5530	0,580560	
Setup Visible	-7,70E-02	6,46E-01	-0,1190	0,905220	
C+*Spiders	2,06E+00	1,14E+00	1,8060	0,070970	.
MeSA*Spiders	-9,04E-01	1,22E+00	-0,7400	0,459220	
C+*Visible	-2,88E-01	9,39E-01	-0,3060	0,759280	
MeSA*Visible	3,95E-01	8,59E-01	0,4600	0,645280	

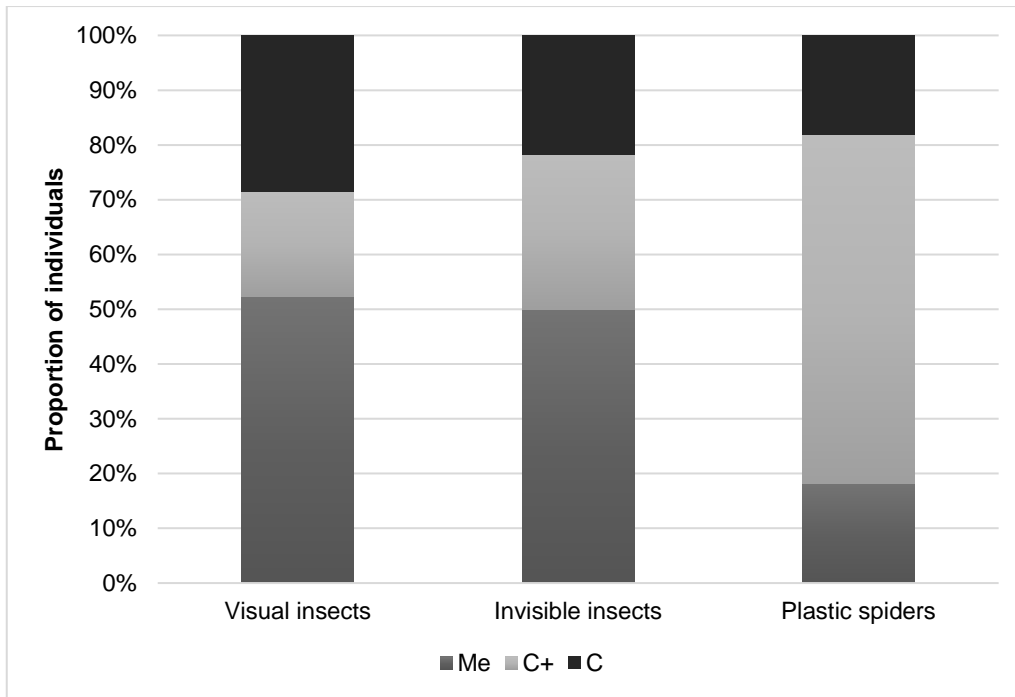


Figure 6. Proportion of bird individuals approaching MeSa, control and positive control treatments as their first choice in the three experimental setups.

Discussion

The aim of this study was to investigate the foraging strategy of birds in agricultural landscapes. Results show that birds orientate towards plant volatiles when visual cues are equal, but switch to visual cues when olfactory and visual cues are separated. The attraction towards MeSA imply that olfaction indeed plays an important role in birds' foraging strategy, and that birds are able to identify and localize volatiles under natural conditions with many other odors present and the elements of the weather. Other studies have been performed in the lab and have not been able to draw such conclusions. This study was carried out in an agricultural cropland, which is dominated by bird species which have not been studied before in this aspect. Species that showed a preference for MeSA are likely to feed on predatory arthropods, so the effects of bird foraging activity might be negative in some ecosystems. All birds feeding on insects, not only specialist insectivores can use plant volatiles to find their prey, which means that this ability is more widespread than previous studies suggest.

In their study, Amo et al. (2013) found a strong preference for olfactory cues, based on the frequency of visits to each treatment. There was however no preference in first visits. In line with their study I offered olfactory and visual cues alone or in combination, but I only recorded first visits. Contrary to their results, I found a preference for visual cues when offered separately from olfactory cues. This could be explained as birds use olfactory cues to localize areas with higher volatile rate, which means more herbivores and thus an attractive spot for predatory arthropods. Similar to how seabirds find prey in open ocean (Nevitt 2008), when farmland birds detect the spot with strongest volatile smell, it is probable that they circulate it to be able to visualize their prey. Another explanation is that fourth trophic level birds search for arthropods moving around in the field, and thus does not need to find the infested plant but the area which is attracting the predatory arthropods. As the Oriental Honey buzzard orientated towards the smell of pollen even when visual cues were equal (Young et al., 2015), birds in my experiment could choose between crickets on all dishes but only one smelling like MeSA. Their preference for MeSA might indicate that they perceive/expect a

higher prey abundance, despite equal visual cues. When MeSA dish did not contain visual cues, but the next dish contained odorless visual prey (plastic spiders), visual cues became more important.

Performing experiments in the field may face some limitations. In comparison to a controlled environment with captive birds, it is not possible to know for sure that the birds in this study are different individuals. The risk of counting one individual twice was thus reduced using a reset time limit of 40 minutes and by moving cameras to new locations every couple of days. Also, since visual cues are equal (all dishes have food) this means that birds do not learn to associate MeSA with food and so the effect should diminish over time and make findings weaker, not stronger.

Though MeSA has shown to attract arthropods in the field (Mallinger et al., 2011), the presence of aphids in that study means other volatile compounds were active as well. It would be interesting to recreate this experiment in our study in a more standardized and controlled setup, implementing the same method as Amo et al. (2013), i.e. using crops infected with herbivores to get a natural blend of volatile compounds and compare the attraction for the natural blend with artificially produced MeSA. A possible positive outcome of using methyl salicylate is that it induces a volatile response in surrounding plants (Dahlin et al. 2015), so the vegetation around the dish with MeSA should produce a broader odor spectrum, which would contribute to the experimental odor cue.

Contrary to earlier statements, olfaction plays a bigger role in birds' life than we could imagine. Visual cues may also be misleading since for instance leaf damage of herbivores remain for a long time after the herbivores have left (Amo et al., 2013; Mäntylä et al., 2008). Farmland birds that forage in big agricultural fields have to deal with prey hidden in vegetation, so there's a great advantage if they can somehow smell their prey. Following the scent of HIPVs to find arthropods is a strategy that could significantly reduce time spent foraging. Previous studies have focused on the beneficial effects on plants of bird predation on herbivores, but this study shows that birds at a fourth trophic level also exploit plant volatiles to localize prey, which is known to create a trophic cascade which reduces suppression of herbivores.

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