

Research



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Animal behaviour

A larval aggregation pheromone as foraging cue for insectivorous birds

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Although birds have traditionally been considered anosmic, increasing evidence indicates that olfaction plays an important role in the foraging behaviours of insectivorous birds. Recent studies have shown that birds can exploit herbivore-induced plant volatiles and sexual pheromones of adult insects to locate their prey. Many insectivorous birds prey on immature insects, providing relevant ecosystem services as pest regulators in natural and agricultural ecosystems. We asked whether birds could rely on chemical cues emitted by the immature stages of insects to prey on them. To address this question, we performed field experiments to evaluate if insectivorous birds can detect the aggregation pheromone produced by the larvae of the carpenter worm, *Chilecomadia valdiviana*. Groups of five artificial larvae were placed in branches of 72 adult trees in a remnant fragment of a sclerophyllous forest in central Chile. Each grouping of larvae contained a rubber septum loaded with either larval pheromone as treatment or solvent alone as control. We found that the number of larvae damaged by bird pecks was significantly higher in groups with dispensers containing the larval extract than in control groups. Our results show that birds can rely on immature insect-derived chemical cues used for larvae aggregation to prey on them.

1. Introduction

Communication through chemical signals is considered the most ancient form of communication among currently living organisms [1]. From bacteria to animals, chemical cues mediate intra- and interspecific interactions between organisms, allowing them to find food or choose their mate while avoiding noxious conditions, predators and pathogens [2–5]. Olfaction is the main sensory system by which animals perceive chemical cues, and its role in the ecology of animals has been extensively documented across species [6].

Birds have traditionally been considered anosmic (i.e. having little or no sense of smell) and dependent on visual and acoustic signals to guide their behaviour. However, since Bang [7] documented the first anatomical study of avian olfactory function, evidence has accumulated supporting the role of olfaction in the behavioural ecology of birds. Olfaction was initially documented for its role in foraging, navigation and partner-specific recognition in seabirds [8–12]. For instance, penguins and Procellariiformes locate their prey through volatile cues produced by phytoplankton when grazed by zooplankton [8,13]. Since those early studies on seabirds, the use of olfaction by birds has been widely documented across taxonomic levels, mediating a broad range of behaviours, including food searching [14,15], mate choice [16–18], kin recognition [19,20], nest localization [21] and predator avoidance [22,23].

Insectivorous birds have also been documented to rely on olfaction to locate their prey. It has been shown that herbivore-induced plant volatiles can guide birds to prey on the insects inducing the emissions of those volatiles [24–26]. Furthermore, a recent study revealed that birds could exploit the pheromones of adult insects to locate their prey. Saavedra & Amo [27] showed that artificial caterpillars in the proximity to dispensers releasing the pheromone of adult females of the winter moth, *Operophtera brumata*, showed more signs of avian predation than controls. Considering that many bird species prey on immature stages of insects and the relevance of this behaviour in pest control [28], we asked whether insectivorous birds can exploit chemical signals emitted by the larvae they prey on.

The larvae of some lepidopteran species use pheromones to form aggregations [29]. For instance, trail pheromones mediate group foraging in *Malacosoma americanum* and *Thaumetopoea pityocampa* [30]. Another example is the larvae of the carpenter worm, *Chilecomadia valdiviana* (Lepidoptera: Cossidae), which produce an abundant volatile secretion that is attractive to conspecifics and that consists of saturated and unsaturated straight-chain acetates and alcohols with (Z)-5,13-tetradecadienyl acetate as its main component [31,32]. *Chilecomadia valdiviana* (Philippi) is a moth native to Chile and Argentina. In this species, the eggs are laid in groups of 30–50 at the branch attachment, in small cracks in the trunk or big branches, or beneath the bark. After hatching, the larvae cluster at the site, boring into the wood, where they feed and remain until the end of their larval development, pupating in individual galleries [33]. However, eventually it is possible to observe larvae at the base of trunks and on branches. The larvae of this species feed on the wood of native and cultivated species of trees and bushes [34,35], with an important impact on fruits and wood production [36]. Larvae vary in colour from pink to dark-orange and grow up to 50 mm in length. Based on the increasing evidence that birds use olfaction to locate their prey and considering that the larvae of *C. valdiviana* produce high amounts (up to 10% of the body weight) of secretions, which have a strong characteristic smell to the human nose, we hypothesized that birds could use the larval secretion of *C. valdiviana* as an olfactory cue to locate and prey on the larvae. To test this hypothesis, we performed a field experiment using pheromone-releasing dispensers and artificial larvae, aiming to disentangle the role of chemical cues in the predation of *C. valdiviana* larvae by birds.

2. Methods

The study was conducted within the distribution range of *C. valdiviana*, in an area of ca 20 ha (32°53' S, 71°10' W) of southern aspect in the foothills of the coastal mountain range of the La Campana-Peñuelas Biosphere Reserve in central Chile. The vegetation type is characterized by evergreen sclerophyllous matorral [37], dominated by the endemic tree species *Crytocarya alba* (Lauraceae), *Peumus boldus*, (Monimiaceae) and *Schinus molle* (Anacardiaceae), and the shrub *Retanilla trinervia* (Rhamnaceae). The canopy of these trees represents the habitat of insectivorous birds from different families (see electronic supplementary material, table S1). Among these bird species, the striped woodpecker (electronic supplementary material, figure S1), the Chilean flicker, the thorn-tailed rayadito and the white-throated tree-runner feed mainly on xylophagous larvae

or insects present on trunks and branches [38]. Although Chilean forest insectivorous birds have been classified in different habitat-use guilds such as large-tree users, vertical-profile generalists, understorey species and shrub-users, among others [39], an opportunistic foraging strategy has been documented [40]. Thus, insectivorous birds exploit resources actively on different substrates (electronic supplementary material, table S1).

Larvae of *C. valdiviana* were obtained from local fishing supply stores in Valparaíso and were identified according to Olivares & Angulo [35]. Hexane extracts from larvae were obtained as described earlier [31]. Briefly, homogenized larvae of all instars were stirred with hexane overnight. After filtration, drying over MgSO₄, and evaporation of the solvent, the resulting extract was used for preparation of the lures. Dispensers were prepared by loading white rubber septa (Sigma-Aldrich, St Louis, MO, USA, catalogue no. Z553905) with 100 µl of a solution containing 1 mg of pure larval extract in hexane (treatment) or with 100 µl of hexane only (control). Based on Saavedra & Amo [27], who used commercially available pheromone dispensers, we used a dose of 1 mg of the larval extract per lure, which is in the range of most commercial pheromone lures used in monitoring for other lepidopterans [36,41].

We carried out a sentinel experiment using artificial larvae as target. For this experiment, artificial larvae ($n = 360$) of approximately the size of a fifth instar larva (length 2.7–3.5 cm) were made with a combination of brown, pink and orange non-toxic plasticine to resemble the natural colour variation of the *C. valdiviana* larva. A total of 177 orange and 183 pink artificial larvae were used for the experiments. The similarity in colour appearance of natural and artificial larvae for birds was evaluated by representing their colours in the avian tetrahedral colour space [42] (see electronic supplementary material, methods and figure S2).

At the experimental site, 72 adult trees from seven different species were randomly chosen, separated from each other by a distance of 49.6 ± 15 m (mean \pm s.d.), according to field conditions. Distance between trees was defined based on information available about the foraging range of the Austral thrush, a common native medium-sized bird (weight ca 90 g) that inhabits the area [43,44]. Selected distances were similar to those used by Saavedra & Amo [27] for great tit (*Parus major*) and blue tit (*Cyanistes caeruleus*) and were aimed to maximize the chance that different individuals attempt foraging on the larvae models. All trees were georeferenced using a Garmin e-Trex GPS. At each selected tree, five artificial larvae (with the orange and pink morphs arranged randomly) were glued to the tree with cyanoacrylate and disposed in groups on the principal branch (ca 1.5 m height above ground) to increase the probability of detecting bird damage in the larvae. In half of the selected trees ($n = 36$), a dispenser loaded with pheromone was placed near the artificial larvae (see electronic supplementary material, figure S3), while the other trees ($n = 36$) were used as a control, where dispensers were treated with solvent only. The dispensers were fixed with a pin to the tree branch (electronic supplementary material, figure S3). The fieldwork was set up in the Austral spring in mid-October 2019 to guarantee the absence of *C. valdiviana* larvae, which could interfere with the experiment with the presence of their pheromones in the environment [34]. Artificial larvae were monitored after two weeks, recording two response variables: (i) the number of trees with at least one larva with damage by birds, such as peck marks, and (ii) the number of larvae with damage at each tree (following [27]). Any damage not attributable to birds was not considered, e.g. damage inflicted by rodents leave clear signs of their incisor teeth on the artificial larvae [44,45].

We used a generalized linear model (GLM) to evaluate the effect of *C. valdiviana* pheromone treatments on the number of trees with at least one larva with damage by birds. A binomial distribution was assumed for this response variable. To evaluate

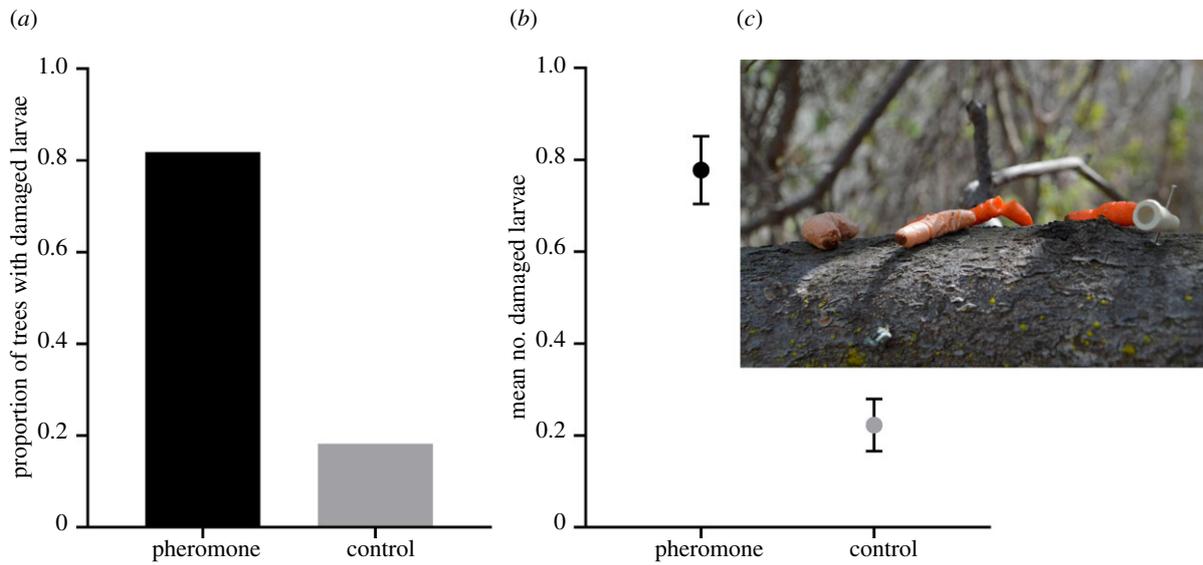


Figure 1. (a) Proportion of trees with damaged larvae, (b) mean number of damaged larvae in trees with pheromone dispenser and control (error bars in (b) indicate one standard error of the mean), and (c) example of larvae damaged by bird pecks.



Figure 2. Records of birds pecking artificial larvae. (a) The thorn-tailed rayadito, (b) the Patagonian tyrant, and (c) the Austral blackbird.

the effect of *C. valdiviana* pheromone treatments on the number of larvae with damage at each tree, we used a generalized linear mixed model (GLMM), including treatment as fixed factor and tree species as random factor. For this response variable a Poisson distribution was assumed. Additionally, we discarded spatial autocorrelation of the response variable for each experimental treatment using a Mantel test, considering the spatial location of each tree in the study area (Mantel test = -0.07 , $p = 0.84$). Statistical analyses were conducted using the statistical software R v. 4.0.0 [46], using the packages *lme4* [47] and *ade4* [48]. Finally, we installed a camera trap (Bushnell Trophy cam HD) to confirm that birds were responsible for the damage to the larvae and to know which species of insectivorous birds pecked the artificial larvae in our sentinel experiment.

3. Results

We found that artificial caterpillars close to pheromone-emitting dispensers showed significantly more signs of attacks from birds than the control group with unbaited dispensers. From the total number of trees with at least one damaged larva ($n = 22$), 82% ($n = 18$) had dispensers loaded with larval pheromone, while 18% ($n = 4$) had control dispensers (GLM: $Z = 3.32$, $p = 0.000901$; figure 1a). The number of larvae showing signs of predation was significantly higher in groups with pheromone-treated dispensers (mean \pm s.e. = 0.78 ± 0.07) compared with the control groups (mean \pm

s.e. = 0.22 ± 0.05 , GLMM: $Z = 3.172$, $p = 0.00151$, figure 1b), independent of the colour morph (e.g. 19 and 17 damaged larvae from the orange and pink morphs, respectively). In this context, colour variation did not affect the behaviour of birds (see electronic supplementary material, figures S2 and S4).

Based on the photographic records extracted from the trap camera, only birds were recorded to be responsible for the observed damage. The thorn-tailed rayadito (figure 2a), the Patagonian tyrant (figure 2b) and the Austral blackbird (figure 2c) were recorded as the main insectivorous birds that pecked the artificial larvae in our sentinel experiment (figure 2).

4. Discussion

Our results show that insectivorous birds responded positively to the larval aggregation pheromone of the carpenter worm, *C. valdiviana*. The number of trees with at least one artificial larva damaged by bird pecks was more than four times higher in trees with dispensers loaded with pheromones (82%) than with control dispensers (18%). Furthermore, artificial larvae near dispensers with the aggregation pheromone had proportionally more bird pecks than larvae near the control dispenser. These results support previous findings showing that insectivorous birds can use chemical cues to locate and consume their prey

[8,9,11,25,27,49,50]. Considering that many birds prey on immature stages of insects, the capacity to perceive chemical cues emitted by insect larvae would be of great ecological relevance in birds' foraging strategies. To the best of our knowledge, our results provide the first evidence that birds perceive chemical cues emitted by insect larvae and that they can exploit those cues to prey on insects.

The larva of *C. valdiviana* is a polyphagous woodborer native to Argentina and Chile, which mainly feeds on the xylem without killing the tree. The larvae make a single transverse tunnel to the heartwood, turn longitudinally ascending and remain in the tunnel until the pupa stage. Their damage to the tree is almost imperceptible, making it difficult for insectivorous birds to detect the larvae visually. Previous studies suggest that insectivorous birds, such as woodpeckers, use cryptic visual cues to detect woodborer larvae [51,52]. Our results indicate that woodpeckers can also rely on chemical cues emitted by the larvae to detect them. The use of larval aggregation pheromones would reduce woodpeckers' energy expenditure in pecking trees and increase their chances of detecting more prey owing to the increase in the concentration of pheromones in the local environment [29,53].

Many evolutionary advantages have been suggested as to why animals live in groups [54–58], including the selfish herd hypothesis, in which gregarious behaviour diminishes the individual risk of being attacked [59]. It has been proposed that by forming aggregations, insect larvae would increase their foraging efficiency, growth rate and survivorship (see [57,58,60]). According to our results, living in groups would also have detrimental effects, given that the aggregation of larvae would increase the concentration of pheromones in their immediate surroundings, making them more detectable by birds.

While only a few studies have addressed the aggregation behaviours of lepidopteran larvae, the chemical cues mediating such behaviours have received even less attention [61,62]. In addition to studies on *C. valdiviana*, compounds eliciting aggregation have been identified for the larvae of the greater wax moth, *Galleria mellonella* [63], and the codling moth, *Cydia pomonella* [64]. Experiments using real and artificial larvae of the codling moth, a major pest in apple crops, revealed that birds prey on real larvae significantly more than plasticine models [65]. These results are in line with ours in that visual cues alone do not induce larvae predation rates as high as when combined with chemical cues. The

increasing amount of evidence supporting the role of olfaction in birds' foraging behaviours, together with the extensive knowledge on chemical communication among insects, suggest that the use of chemical cues in the predation of insect larvae by birds might be a widespread phenomenon.

Herbivorous insects are considered one of the main pests in agriculture. Insectivorous birds play an important ecological role in controlling herbivores in natural and agricultural ecosystems [28,66]. For instance, woodpeckers (Picidae) were shown to regulate the population of bark beetles (Curculionidae) in coniferous forest landscapes [67]. Moreover, different studies have demonstrated that insectivorous birds use herbivore-induced plant volatiles as olfactory cues to locate their prey in agricultural ecosystems [25,49]. Within this context, the capacity of birds to detect insect-derived chemical cues, such as sexual or aggregation pheromones, may present an opportunity for the regulation of insect populations in human-modified landscapes. Further studies are needed to understand the mechanisms by which birds perceive insect-derived chemical cues and the impact of avian olfaction on larval predation.

Ethics. This research complies with ethical guidelines by the Pontificia Universidad Católica de Valparaíso under approval no. BIOEUCV-BA 331-2020.

Data accessibility. Original data and code associated with this manuscript are available in the Figshare repository <https://doi.org/10.6084/m9.figshare.15173706.v1> [68] and in the electronic supplementary material.

Authors' contributions. P.D.-S., J.T.-G., J.B. and J.L.C.-D. conceived and designed the study. P.D.-S. and J.T.-G. conducted fieldwork and data acquisition. P.D.-S., J.M.-H. and J.L.C.-D. analysed the data. P.D.-S., J.T.-G., J.M.-H., J.B. and J.L.C.-D. wrote the manuscript. P.D.-S., J.M.-H., J.B. and J.L.C.-D. edited the manuscript. All the authors approved the final version of the manuscript and agreed to be held accountable for all aspects of the work.

Competing interests. We declare we have no competing interests.

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