



## Research

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# Speed and accuracy in nest-mate recognition: a hover wasp prioritizes face recognition over colony odour cues to minimize intrusion by outsiders

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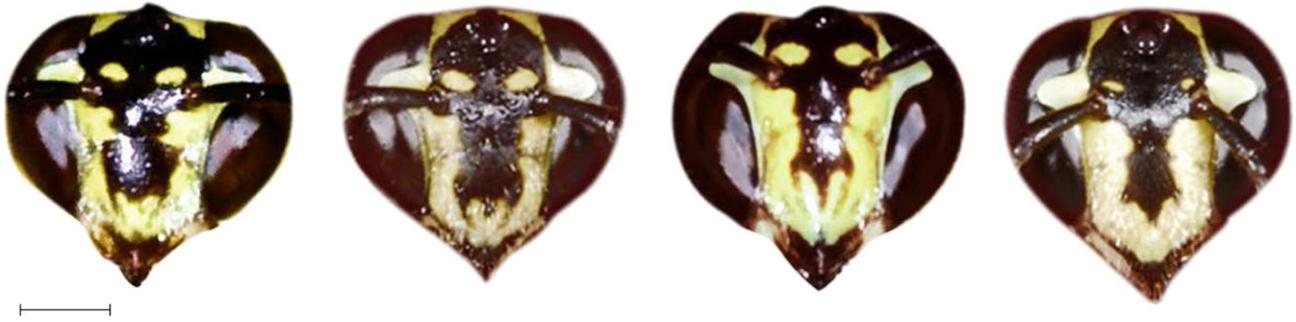
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Social insects have evolved sophisticated recognition systems enabling them to accept nest-mates but reject alien conspecifics. In the social wasp, *Liostenogaster flavolineata* (Stenogastrinae), individuals differ in their cuticular hydrocarbon profiles according to colony membership; each female also possesses a unique (visual) facial pattern. This species represents a unique model to understand how vision and olfaction are integrated and the extent to which wasps prioritize one channel over the other to discriminate aliens and nest-mates. *Liostenogaster flavolineata* females are able to discriminate between alien and nest-mate females using facial patterns or chemical cues in isolation. However, the two sensory modalities are not equally efficient in the discrimination of 'friend' from 'foe'. Visual cues induce an increased number of erroneous attacks on nest-mates (false alarms), but such attacks are quickly aborted and never result in serious injury. Odour cues, presented in isolation, result in an increased number of misses: erroneous acceptances of outsiders. Interestingly, wasps take the relative efficiencies of the two sensory modalities into account when making rapid decisions about colony membership of an individual: chemical profiles are entirely ignored when the visual and chemical stimuli are presented together. Thus, wasps adopt a strategy to 'err on the safe side' by memorizing individual faces to recognize colony members, and disregarding odour cues to minimize the risk of intrusion from colony outsiders.

## 1. Introduction

The recognition of group members is an essential capability for many animals living in societies [1–3]. In many species, this requires a simple ingroup–outgroup discrimination, while other animals use individual recognition to recognize neighbours, relatives or individuals in dominance rank orders [2,3]. In eusocial insects, shrimps and mole rats, where cooperation is a main driver of ecological success [1,4], efficient communication and recognition abilities are required for almost all social behaviours. In particular, the ability of an individual to recognize its colony mates (i.e. nest-mate recognition) is crucial to prevent outsiders from exploiting colony resources [5]. Indeed, eusocial organisms and particularly insects have evolved recognition systems enabling them to behave altruistically towards nest-mates and to reject alien conspecifics [6].

Chemical communication plays a major role in social insects' recognition systems [7]. Cuticular hydrocarbons (hereafter CHCs) together with pheromones are assumed to regulate almost all social interactions, implying the chemical senses as the predominant channels of communication in insect societies [6,8]. In the last two decades, however, visual communication abilities have been discovered in two subfamilies of social wasps [9–13]. A pioneering experiment demonstrated that males of the stenogastrinae wasp *Parischnogaster mellyi* use a visual status badge during flying duels for winning a perch in aerial



**Figure 1.** *Liostenogaster flavolineata* females' portraits representing some examples of different facial patterns present in the species. The bar indicates 1 mm in length. (Online version in colour.)

leks [14]. It was since found that visual communication plays a key role in the social interactions between colony members and indeed, a facial badge of status has been shown to convey information on the agonistic qualities in foundresses of the North American population of *Polistes dominula* and to regulate dominance hierarchies in the stenogastrinae wasp *Liostenogaster vechtii* [10,11], but see [15,16]. *Polistes fuscatus* wasps are more aggressive to individuals with unfamiliar appearances landing on the nest [9] and they are able to remember the individual identity of partners after one week of interactions with several other wasps [17]. Visual communication seems to be developed to the extent that specialized face learning is associated with individual recognition ability in *P. fuscatus* [18].

In this regard, the ability to discriminate nest-mates using chemical odours or visual features are not just distinct sensory channels, but fundamentally different cognitive systems based on different information processing mechanisms of recognition cues. Processing of chemical cues appears to be decentralized, requiring at its basic level, nothing more than habituation at the antennal lobe level—elementary type of behavioural plasticity mediated by neuro-modulation—or sensory adaptation [19]. Even if some form of long-term memory is involved, a wasp only has to memorize one odour or a pattern of molecules [19]. Conversely, since there is no known single visual cue by which all members of a colony can be identified, visual recognition requires specific memories not just of one defining feature, but of all the individual faces of one's colony. So far, many studies on chemical and visual communication in social wasps have been done, but no information exists about the relationship between them. Recognition processes in different sensory modalities might have a different efficiency in terms of speed and accuracy and the resulting output might depend on the sensory mode involved. A particular sensory modality might allow rapid decisions at the expense of accuracy, whereas another might allow the obtaining of high-quality information while increasing sampling time. For example, when an animal must make a rapid decision, such as when an outsider suddenly approaches the nest, there is a risk of low decision accuracy [20–24]. Depending on the ecological context, an animal guarding a nest entrance might rely more on a sensory mode than on another to maximize efficiency. So far, it is evident that trade-offs exist between decision speed and accuracy in many ecologically relevant tasks (reviewed in [25]) but no information is available on the guarding behaviour of social insect at the nest entrance. The study of multimodal sensory cues and speed and accuracy in the nest-mate recognition process deserves more attention.

The primitively eusocial wasp *Liostenogaster flavolineata* builds mud comb nests with up to more than 100 cells,

sometimes in huge aggregations of approximately 10–150 nests in close proximity [26]. Social groups are relatively small (rarely up to 10 females). Bridge & Field [27] reported the existence of a queue for dominance based on gerontocracy (dominance order and access to reproduction is age-based: in a nest a subordinate inherits dominance only when all her older relatives have disappeared). Newly emerged females may become helpers on natal nests or disperse and join other colonies where they have higher probability to jump the queue for reproduction and to monopolize reproduction (reviewed in [26]). Individuals differ in CHCs profiles according to their colony membership and each female also has a unique facial marking [11,28] (figure 1). Both chemical and visual channels mediate nest-mate recognition, and wasps presenting unfamiliar odours or faces are rejected aggressively from the nests [11,28,29]. *Liostenogaster flavolineata* represents a unique opportunity to understand how these senses are combined and to which extent wasps prioritize one channel over the other to discriminate aliens and nest-mates. We explore the speed and the accuracy of visual and chemical channels in recognizing individuals' colony membership, and explore how wasps integrate these sensory modalities to minimize the risk of colony intrusion by outsiders.

## 2. Material and methods

### (a) Sample collection and preparation of lures

The experiments were carried out in the field on one nest cluster of *L. flavolineata* located at Bukit Fraser (1000 m.a.s.l.; 03°42.774' N—101°46.319' E) in the Pahang State of Peninsular Malaysia, always on sunny days between 10.00 and 17.00 local time. Overall, 50 colonies of *L. flavolineata* with a total of 233 females (mean:  $4.6 \pm 1.6$  females per colony, range: 2–8) were used for behavioural tests. The day before the trials, a non-dominant female (foraging female according to Cervo *et al.* [29]) was collected from each experimental colony (first experiment  $n = 20$ ; second experiment  $n = 30$ ) that had at least three wasps. The same day an equivalent number of alien females ( $n = 50$ ) were also collected from a different cluster of nests located at 20 km apart as the crow flies and on the other side of the mountain (3°38'0" N—101°42'0" E) to ensure individuals had not previously interacted with tested colonies. Each wasp was killed by freezing and then rinsed in 1 ml of pentane for 24 h in order to eliminate all cuticular lipids (epicuticular hydrocarbons and CHCs). Pentane extracts were then dried at room temperature (approx. 26°C), re-suspended in 200  $\mu$ l of pentane and split in two aliquots of 100  $\mu$ l each. Aliquots were then placed, by means of a micropipette, on pre-washed wasps (head and thorax) or square pieces of clean filter paper (5 mm

side length) depending on the experiment (see below). The aliquots were applied on lures 15 min before presentations in order to ensure the evaporation of the solvent.

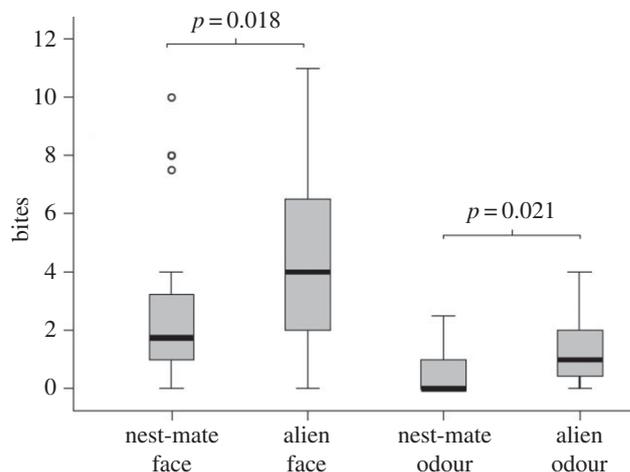
In order to test whether a visual stimulus alone or a chemical stimulus alone was able to allow the resident wasps to discriminate between alien and nest-mate females, we presented, in a first assay, four stimuli to 30 colonies: a nest-mate visual stimulus (nest-mate wasp deprived of its CHCs), alien visual stimulus (alien wasp deprived of its CHCs), a nest-mate chemical stimulus (filter paper drenched with a full aliquot of a nest-mate CHCs extract) and an alien chemical stimulus (filter paper drenched with a full aliquot of an alien CHCs extract). A preliminary assay had shown that resident wasps do not react to a piece of filter paper applied with the solvent only (Friedman test,  $\chi^2_2 = 20.77$ ,  $p = 0.0001$ ,  $n = 30$  colonies; *post hoc* test (Wilcoxon Monte-Carlo Exact test), solvent–alien odour:  $n = 30$ ,  $Z = -3.79$ ,  $p = 0.0001$ ; solvent–nest-mate odour:  $n = 30$ ,  $Z = -2.39$ ,  $p = 0.017$ ). The same set of presentations plus two controls—nest-mate and alien females (washed wasp re-coated with its own CHCs extract)—were used to evaluate speed and accuracy of responses elicited by either faces or odours.

To understand whether one stimulus prevails over the other in the nest-mate recognition context, we conducted a second assay in which we presented four stimulus combinations to 20 colonies: a full nest-mate stimulus (nest-mate washed wasp re-coated with its own CHCs extract), a full alien stimulus (alien washed wasp re-coated with its own CHCs extract) and two crossed lures (nest-mate washed wasp reapplied with an alien CHCs extract and an alien washed wasp reapplied with a nest-mate CHCs extract). The removal of CHCs is a standard protocol and gas chromatography-mass spectrometry (GC-MS) analyses demonstrated that washed insects had no CHCs left on their cuticle [30]. Moreover, preliminary GC-MS analyses and behavioural tests have shown that this protocol does not alter the quality of the extracted CHCs as well as the response to these stimuli presented on pieces of paper [31].

## (b) Behavioural assays

In both assays, the stimuli were presented to the resident females at approximately 1 h intervals. To control for order effects, the stimuli were presented in a random sequence. During the experiments, we held the lure approximately 1 cm away from the nest for 30 s. Our video recordings (see the electronic supplementary material S1) showed that wasps are able to reach the lures when presented at this distance, which allows resident wasps to easily reach, antennate or bite the lure (the wasps' average ( $n = 5$ ) body length is approx.  $17.9 \pm 0.4$  mm, hind leg length is approx.  $10.9 \pm 0.1$  mm and antennae length is approx.  $5.5 \pm 0.1$  mm). The fact that resident females could easily assess the scent of lures from the very first instant of the presentation rules out the possibility that holding a wasp 1 cm away from the nest leads to an initial over-reliance of vision (possible from 1 cm away) on chemoreception (which in the case of CHCs require contact). We used dead surrogates for intruders owing to logistical constraints, but our results can be extended to live interactions, since the use of live and dead wasps in *Stenogastrinae* gives similar results in nest-mate recognition tests [28,29]. This methodology represents a standard procedure used in recognition tests in both *Polistinae* and *Stenogastrinae* [11,28,32].

In order to avoid excessive disturbance, wasps of experimental colonies were not marked. The number of responses presented by all colony members was normalized for the number of females on the nest [11]. The aggressive reaction of resident females considered were the bites towards the stimulus. The speed of the reaction was calculated as the latency between the start of the presentation and the first evident reaction toward the lure made by resident females. Accuracy in recognition was calculated classifying the reaction of each experimental colony



**Figure 2.** Comparison between the average number of bites directed by resident females towards a nest-mate visual stimulus (nest-mate wasp deprived of its CHCs), alien visual stimulus (alien wasp deprived of its CHCs), a nest-mate chemical stimulus (nest-mate CHCs extract applied on a square piece of filter paper) and an alien chemical stimulus (alien CHCs extract applied on a square piece of filter paper). Box plots show medians, 25th and 75th percentiles.

as correct (i.e. attacking an alien or being peaceful to a nest-mate) or incorrect (i.e. attacking a nest-mate or being peaceful to outsiders) based on the presence or absence of aggressive behaviour (i.e. resident females biting the presented lure). To evaluate how nest aggression varied over time, we also counted and compared the number of aggressive reactions every 10 s. The tester was blind to the stimulus presented (i.e. whether it was a nest-mate or non-nest-mate; a third person chose the stimulus and prepared it for the presentation). All the experiments were videotaped and the videos were later analysed with a blind procedure in which the watcher did not know the nature of the stimulus presented (alien versus nest-mate). When the data were not normally distributed and homogeneity of variances could not be assumed, they were analysed with a non-parametric test (i.e. Friedman and Wilcoxon signed-rank test), so that, for each colony, we compared the reactions towards the different presented stimuli. All analyses were performed using the statistical program SPSS v. 19.0 for Windows.

## 3. Results

When resident females of *L. flavolineata* ( $n = 30$  colonies; experiment 1) were presented with CHC extracts or faces belonging to nest-mates and alien females, the alien cues invariably sparked significantly more aggressiveness (Friedman test,  $\chi^2_3 = 31.83$ ,  $p = 0.0001$ ,  $n = 30$  colonies; *post hoc* test (Wilcoxon Monte-Carlo Exact test), visual stimuli:  $n = 30$ ,  $Z = -2.21$ ,  $p = 0.018$ ; chemical stimuli:  $n = 30$ ,  $Z = -2.31$ ,  $p = 0.021$ ; figure 2). Real wasps received more aggression than pieces of paper with smell regardless of whether the stimuli were alien or not (Wilcoxon Monte-Carlo Exact test; nest-mates:  $n = 30$ ,  $Z = -3.61$ ,  $p = 0.001$ ; aliens:  $n = 30$ ,  $Z = -3.97$ ,  $p = 0.001$ ). These results indicate that the residents of the tested colonies were alarmed by a stimuli which was unfamiliar owing to its visual component (face) and its odour.

Visual cues, when presented without odour cues, caused erroneous responses in the 31% of cases (46% of which were false alarms). Chemical cues alone caused erroneous responses in the 45% of cases (66% of which were erroneous acceptances of outsiders).

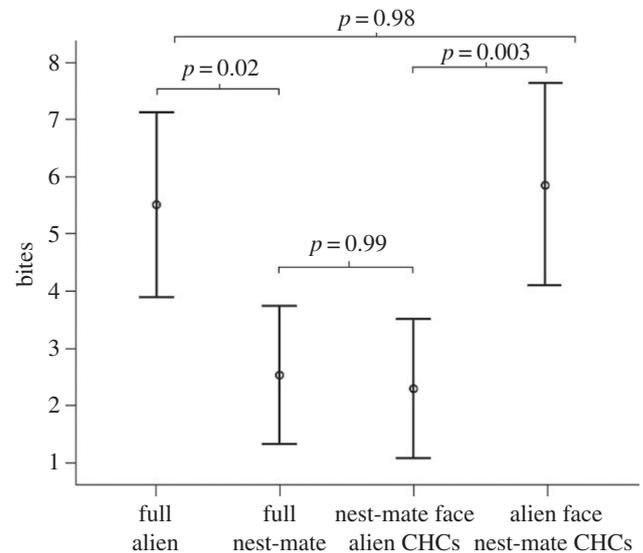
The costs of false alarms just resulted in a brief scuffle with the lure and the aggressiveness rapidly decreased over the presentation (experiment 1) when resident wasps could rely on both visual and chemical cues together (Friedman test, number of aggressive reactions every 10 s over 30 s presentation,  $n = 21$ ,  $\chi^2_2 = 8.8$ ,  $p = 0.012$ ; Wilcoxon *post hoc* test: 1st 10 s versus 2nd 10 s,  $Z = -1.39$ ,  $p = 0.18$ , 2nd versus 3rd,  $Z = -1.46$ ,  $p = 0.16$ ; 1st versus 3rd,  $Z = -2.14$ ,  $p = 0.02$ ; see the electronic supplementary material, figure S1). The same trend, even if not statistically significant, occurred when resident wasps had access to only visual cues (Friedman test,  $n = 15$ ,  $\chi^2_2 = 3.56$ ,  $p = 0.16$ ; see the electronic supplementary material, figure S1) suggesting that odours might have a role in fine-tuning the recognition process. By contrast, the level of aggressiveness towards alien wasps remained high and stable over all the 30 seconds of presentation (Friedman test, number of aggressive reactions every 10 s,  $n = 24$ ,  $\chi^2_2 = 0.17$ ,  $p = 0.93$ ; see the electronic supplementary material, figure S1).

Overall, in our dataset, colonies responding faster to intruders did not commit an increased number of mistakes, suggesting that there is no speed-accuracy trade-off in nest-mate recognition (Spearman correlation—visual cues:  $\rho = 0.12$ ,  $n = 60$ ,  $p = 0.82$ ; chemical cues:  $\rho = -0.26$ ,  $n = 60$ ,  $p = 0.11$ ; visual and chemical cues together:  $\rho = 0.073$ ,  $n = 60$ ,  $p = 0.59$ ).

When resident females ( $n = 20$  colonies, experiment 2) were allowed to use visual and chemical stimuli to evaluate the presented lures, chemical cues were not used by the wasps to discriminate between alien and nest-mate females (one-way ANOVA,  $F_3 = 7.18$ ,  $n = 20$ ,  $p = 0.0001$ ; figure 3). Indeed, the difference existing in the aggression level directed towards a full alien and a full nest-mate lure (i.e. washed wasp reapplied with its own CHCs extract) was equal to that existing between the ‘crossed’ lures (i.e. washed nest-mate reapplied with alien CHCs extract and vice versa), (Tukey HSD *post hoc* test,  $n = 20$ , full–full: mean difference = 3.03,  $p = 0.02$ ; cross–cross: mean difference = -3.50,  $p = 0.003$ ; figure 3). More importantly, the aggression level directed towards a full alien female was very similar to that directed towards a ‘crossed’ lure displaying an alien face but with a nest-mate odour (Tukey HSD *post hoc* test,  $n = 20$ ,  $p = 0.98$ ; figure 3). Similarly, the aggression level directed towards a full nest-mate female was very similar to that directed towards a ‘crossed’ lure displaying a nest-mate face but with an alien odour (Tukey HSD *post hoc* test,  $n = 20$ ,  $p = 0.99$ ; figure 3). Furthermore, over the 30 s presentation, ‘crossed’ lures displaying an alien face triggered a constantly higher aggressiveness than ‘crossed’ lures displaying a familiar face (Friedman test, number of aggressive reactions every 10 s over 30 s presentation, nest-mate face–alien CHCs:  $n = 20$ ,  $\chi^2_2 = 0.001$ ,  $p = 0.99$ ; nest-mate CHCs–alien face:  $n = 20$ ,  $\chi^2_2 = 2.21$ ,  $p = 0.34$ ; see the electronic supplementary material, figure S2). These findings indicate that resident wasps regulate the level of aggression on the basis of the opponent’s faces regardless of their CHCs.

## 4. Discussion

A number of vertebrate species are well known for memorizing and identifying familiar individuals using a variety of sensory modalities [33–35]. Multimodal recognition of conspecific



**Figure 3.** Average number of bites shown by resident females reacting towards a full alien and a full nest-mate lure (alien and nest-mate washed wasp reapplied with own CHCs extract, respectively), and two crossed lures (a nest-mate washed wasp reapplied with alien CHCs extract and an alien washed wasp reapplied with alien CHCs extract).

group members has been demonstrated in crows (*Corvus macrorhynchos*), which recognize group members using visual and vocal signals [36] and various mammals such as dogs [37], horses [38] and non-human primates [39,40]. For example, ring-tailed lemurs (*Lemur catta*) are capable of individual recognition through olfactory–auditory matching [41]. Rhesus monkeys (*Macaca mulatta*) [39,40] can recognize familiar conspecifics by matching the identity information in vocal signals to the identity information in visual signals.

The study of multisensory integration, and in particular, the exploration of hierarchies of visual and chemical cues, already has a long history in flower-visiting insects [42–45] and other animals [46,47]. Conversely, the venerable study of nest-mate recognition in social insects, has, for many decades, focused almost exclusively on chemical cues [8], perhaps because to many scholars, insect colonies appeared too populous, individuals too indistinguishable and insect visual learning abilities too limited for vision to play a role in individual and nest-mate recognition. In the last two decades, however, visual communication abilities have been discovered in two subfamilies of social wasps and the use of individual facial features in nest-mate identification is now well established [9–13].

All the preceding studies on nest-mate recognition in insects have focused on either vision or olfaction in isolation and have never, to our knowledge explored how those sensory modalities are integrated. Our results show that *L. flavolineata* wasps are able to assault and reject alien conspecifics appearing unfamiliar owing to their individual facial markings or their chemical odour [11,28,29], raising the question of how these cues are integrated. The benefit of using both senses to discriminate conspecifics may be to improve accuracy in decision-making [48], and to increase robustness in the face of changing environmental conditions [49]. For example, in dim light, perceptual certainty of vision might be reduced, increasing the value of chemosensory cues, as has been shown for flower-visiting bees [50].

Wasps guarding at their nest might likewise shift reliance to chemical cues under decreased light levels at dusk, on cloudy days or when facial diversity of the individuals in the population is too low. Similarly, they might attach higher priority to visual stimuli in environments where olfactory stimuli are 'noisy' or 'homogeneous'.

Our observations demonstrate a strong prioritization of vision in nest membership classification via face recognition early in an encounter and only a later usage of olfactory cues, suggesting that time plays a key role in cue prioritization. A previous study [28] showed that alien wasps deprived of their CHCs and dabbed with those of nest-mates were treated less aggressively than those with their own CHCs; the authors concluding that only CHCs were used to recognize alien females. However, in that study, lures were presented for extended periods, probably giving the resident wasps more opportunity to integrate chemical information during the encounters. Using higher resolution observations (i.e. considering data normalized for number of wasps on the nest, and the level of aggression of each single colony instead of just the frequency of colonies accepting the presented lures), we demonstrate that visual information is clearly important (see also [11]). We found that when resident females are allowed to use visual and chemical stimuli together for short periods, the latter were not considered by the wasps to evaluate the lures. Indeed, the aggression level directed towards an alien lure was very similar to that directed towards a 'crossed' lure displaying an alien face and a nest-mate odour. Similarly, a nest-mate lure and a 'crossed' lure displaying a familiar face combined with an alien odour received the same peaceful treatment. Thus, when the encounter is relatively brief, as is typically the case in natural conditions, resident wasps regulate the level of aggression on the basis of opponents' faces regardless of their CHCs. Conversely, it appears that when lures are presented for extended periods (more than 30 s), chemosensory cues gain the upper hand in nest-mate recognition [28].

A selective attention process might explain the predominance of one sensory modality over the other, as observed here. Multisensory stimuli are thought to influence attention via both stimulus-driven and goal-related processes (reviewed in [45]) and top down attention-like processes are well researched in visual search bees [51,52]. Resident wasps might choose the most clearly displayed cue, avoiding division of attention between two forms of input, and thus responding more accurately and more swiftly to the opponent. Although no studies exist on the abilities of wasps integrating information from more than one modality or dealing with multiple cues, it is known that other Hymenoptera (i.e. pollinating bees) can at least in principle juggle multiple tasks, albeit coping most efficiently when they face only one task at a time [53,54].

Most likely, vision is prioritized over olfaction because it allows recognition of individuals from a distance (while chemosensory assessment mediated by CHCs requires contact). It remains to be explored with certainty whether visual cues are better at discriminating among individuals than chemical ones. It might be that, in wasps patrolling their nests to repel intruders, visual information is prioritized simply because of the need to make a rapid decision. Indeed, even though resident wasps can assess the scent of lures by antennating their cuticle from the very first instant of the presentation, they base their reaction solely on visual

information. CHCs are used only later to enhance accuracy by fine-tuning the recognition process over more lasting encounters between residents and outsiders. Indeed, our results show that erroneous attacks on nest-mates are quickly aborted during the course of the presentation if wasps can also rely on CHCs cues. CHCs are heavy compounds, requiring an antennal contact between wasps to allow information flow [55,56] and, since chemosensory assessment mediated by CHCs is not possible from a distance, it probably delays recognition. By contrast, the ability to visually recognize approaching females as aliens allows residents to assume an alarm posture and to deter conspecifics without making contact with them. Furthermore, alien females often approach nests with explorative flights and hover in front of the colonies [57], which could favour visual recognition by guards. As *L. flavolineata* nests form large aggregations and individuals have a tendency to shift between different nests to join them and gain reproduction benefits, colonies in clusters experience continuous landing attempts by alien individuals [58], raising the costs of nest defence.

Even if speedy responses do not come at the expense of accuracy, suggesting that in *L. flavolineata* there is no speed-accuracy trade-off in nest-mate recognition, the two sensory modalities do not have the same accuracy. Relying on facial cues allows a more accurate response towards intruders but induces an increased number of erroneous attacks on nest-mates. Relying on odour cues (when presented in isolation in our tests) results not only in a better accuracy in responding to nest-mates but also in an increased number of erroneous acceptances of outsiders. Social insect colonies involve significant investments in time and resources that need to be defended from non-nest-mate exploiters, suggesting that being peaceful to outsiders has potentially a higher cost than false alarms. Although we did not quantify the costs of aggression, our results showed that erroneous attacks on nest-mates are quickly aborted, suggesting the negligible cost of a false alarm that in nature would not result in serious injury.

In conclusion, we show that *L. flavolineata* adopts a strategy to 'err on the safe side' by memorizing faces to recognize colony members, and disregarding odour cues to minimize the risk of intrusion from colony outsiders. Our findings have important implications for the understanding of multisensory integration in decision-making in animal recognition systems. Different components of the multimodal recognition cues may affect speed and accuracy in decision processes. These components might in some cases trade-off against each other [20,59] and the prioritization of one modality over others might allow animals to better balance between speed and accuracy at different times of the decision-making process. Any cooperative group, from social insects and shrimps to mole rats and other vertebrates faces the challenge of preventing outsiders from exploiting colony resources. The accuracy and speed of various sensory processes will affect the way in which animals prioritize them while optimizing colony defence.

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