Social Learning in Noncolonial Insects?

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Summary

Social-information use has generated great interest lately and has been shown to have important implications for the ecology and evolution of species [1–6]. Learning about predators or predation risk from others may provide low-cost life-saving information and would be expected to have adaptive payoffs in any species where conspecifics are observable and behave differently under predation risk. Yet, social learning and social-information use in general have been largely restricted to vertebrates ([1–3, 5, 7–9], but see [10–16]). Here, we show that crickets adapt their predator-avoidance behavior after having observed the behavior of knowledgeable others and maintain these behavioral changes lastingly after demonstrators are gone. These results point toward social learning, a contingency never shown before in noncolonial insects. We show that these long-lasting changes cannot instead be attributed to long re-emergence times, long-lasting effects of alarm pheromones, or residual odor cues. Our findings imply that social learning is likely much more phylogenetically widespread than currently acknowledged and that reliance on social information is determined by ecological rather than taxonomic constrains [17, 18], and they question the generally held assumption that social learning is restricted to large-brained animals assumed to possess superior cognitive abilities.

Results and Discussion

Socially acquired information has many adaptive consequences: it enables naive individuals to learn where, when, what, or how to eat; with whom to mate; whom to fight; where to migrate; and which predators to avoid and how (see [1–4] for reviews); and it may even affect biological evolution through cultural evolution [5]. Likewise, social learning has potential implications for the ecology and evolution of species. Indeed, by enhancing population persistence in new environments through learning about new food, predators, or habitat features, social learning may affect species range and distribution, expose species to new selection pressures, and potentially allow for evolutionary change to occur in the new environment (see [6]).

The literature, however, suggests that social learning,

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and even mere collection of social information not involving learning, occurs in a limited range of taxa. Indeed, although instances of social learning have been reported in gastropoda, cephalopoda, and crustaceans [10], it has been most studied and most widely demonstrated in vertebrates [1, 3, 7–9]. Social learning or processes akin to it have also been reported in colonial insects (bees [11], bumblebees [12, 13], termites [14], ants [15, 16]), but to the best of our knowledge, never in noncolonial insects.

Irrespective of their social structure, insects have proven to be plastic in behavior, to present evolved learning abilities [19–22], and to be affected in their behavior by social influences [12, 23, 24]. Social learning might thus extend to noncolonial insects as well. In fact, given the numerous benefits of social learning and the wide range of situations it applies to, species where conspecifics have the opportunity to observe each other's behavior and whose behavior is informative about some aspect of the world (e.g., food, mates, predators) are potential social learners. If social learning extends to noncolonial insects, this will have important repercussions for our understanding of the cognitive abilities underlying this process and will question the generally held assumption that social learning is restricted to large-brained animals assumed to possess superior cognitive abilities.

Individuals rely generally on personally acquired information but use social learning when asocial learning would be too costly [4]. This principle should generalize to all animals, including invertebrates. Thus, an obvious situation favorable to the use of social learning and social information in general is the context of predation, where the costs of acquiring personal information range from injury to death. We here aim at determining the occurrence of social learning by noncolonial insects in a predation context.

Wood crickets (*Nemobius sylvestris*, Bosc 1792) are particularly well suited to test whether noncolonial insects use congeners' behavior to assess current levels of danger and adapt their own level of predator-avoidance behavior accordingly. Juveniles respond behaviorally to the presence of wolf spiders (*Pardosa* spp.) [25], in particular by hiding under leaves more (O.D., J.C., and I.C., unpublished data). Such a behavioral change, and possibly other concomitant changes, may constitute a source of information to nearby congeners about the current level of danger. Moreover, natural densities of crickets and spiders (see the Supplemental Data available with this article online) are such that crickets are more likely to acquire social information about the presence of predators through encounters with conspecifics than to acquire personal information through direct encounters with predators. Irrespective of their efficiency at detecting and escaping predation attacks, prey should always try to interrupt a predation sequence at the earliest possible stage [26]. Learning from others about nearby danger may allow prey to avoid encounter with and thereby detection by predators.
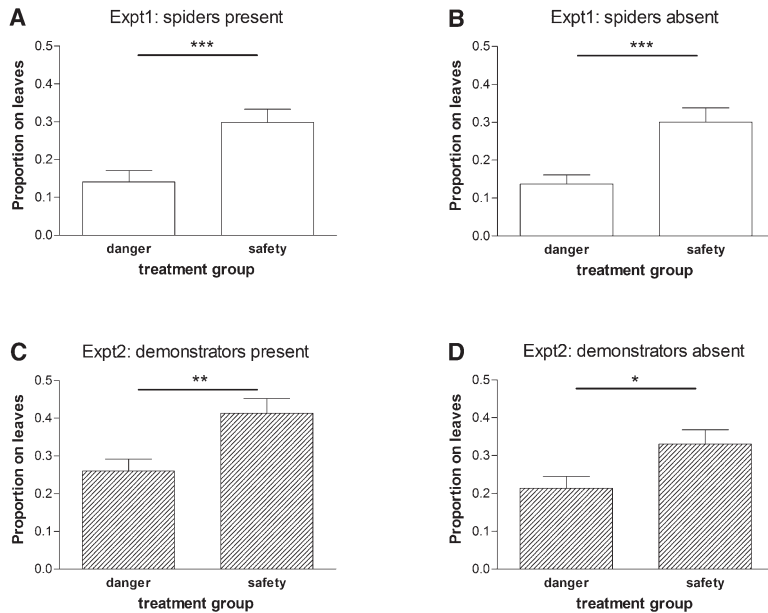
Figure 1. Acquisition and Social Transmission of Predator-Avoidance Behavior

Experiment 1: Mean (+SEM standard error of the mean) proportion of demonstrators seen at the surface of leaves in the "danger" and "safety" group (A) when spiders are physically present in the "danger" group boxes and (B) 6 hr after both treatment groups had been transferred in boxes devoid of spiders. Experiment 2: Mean (+SEM) proportion of observers seen at the surface of leaves in the "danger" and "safety" treatment (C) when demonstrators are still present and (D) 24 hr after demonstrators had been removed. *** p < 0.005, ** p < 0.01, * p < 0.05

We thus monitored crickets' hiding behavior in a "danger" versus a "safety" treatment (Figure S1 and further details in Supplemental Data). All experiments were conducted in the laboratory with wild-caught crickets and spiders. In the first experiment, we were interested in the behavior of subjects that had direct experience with the treatments, whereas in the second experiment we focused on subjects that experienced the treatments only indirectly, through conspecifics behavior. Because the subjects of Experiment 1 acted as demonstrators to the subjects in Experiment 2, we hereafter refer to the former subjects as "demonstrators" and to the latter as "observers." In Experiment 1, 48 groups of ten demonstrators spent 2 days in boxes that contained either three spiders or no predator. On the morning of day 3, groups of demonstrators were transferred to new boxes that never contained spiders, and they were joined by 5 observers. After 6 hr, demonstrators were removed and observers remained in their boxes for an extra 24 hr (Experiment 2). Visibility was measured in each cage as the proportion of subjects of a given category (demonstrator or observer) that were seen at the surface of leaves during 30 s scans relative to the total number of subjects of that category. Note that visibility at the surface of leaves was used here as an operational measure of crickets' antipredatory behavior, but by no means do we imply that this is how naive crickets assess nearby danger. For Experiment 1, demonstrators' visibility was measured after 2 days in a dangerous or safe environment and after 6 hr spent in new boxes. For Experiment 2, observers' visibility was measured after 6 hr spent with the demonstrators and 24 hr after demonstrators were removed.

After two days, demonstrators were found to hide under leaves significantly more in an environment containing spiders ("danger") than in a predator-free ("safety") environment (Mann-Whitney test: Z = –3.16, n = 24, p = 0.0015; Figure 1A). In addition, this difference in hiding

propensity was maintained 6 hr after crickets were transferred to new cages devoid of spiders or any spider cue (Z = –3.17, n = 24, p = 0.0015; Figure 1B). This reflects the difficulty of prey to assess a lowering of predation risk [27] and supports the prediction that animals should overestimate risk [28, 29]. Prey should thus benefit from maintaining predator-avoidance behavior for a period following their last encounter with a predator. This maintenance of hiding behavior also sets the conditions for a social transfer of information regarding nearby danger to naive, newly arrived crickets (observers).

Indeed, observers were seen in lower proportions at the surface of leaves when housed with demonstrators from the danger treatment than from the safety treatment (Z = –2.73, n = 30, p = 0.0063; Figure 1C). Clearly, by altering their own levels of hiding, observers acted as though their perception of nearby danger had been altered socially, likely through the observation of demonstrators' behavior.

Moreover, 24 hr after demonstrators were removed, subjects still showed a higher propensity to hide when they had been previously housed with demonstrators from the danger treatment than from the safety treatment (Z= –2.25, n = 30, p = 0.025; Figure 1D), suggesting the possibility that social learning had occurred.

A series of controls was conducted to test for alternative, simpler, interpretations. A first control determined whether the 24 hr retention of predator-avoidance behavior in observers could be explained by long re-emergence times [27] rather than learning. For that, we monitored the visibility of seven groups of ten crickets both before and after their litter has been artificially disturbed by the experimenter's hand (Control 1, see Supplemental Data for further details). We found that crickets' visibility decreased immediately after artificial perturbation of the litter by the experimenter (Figure 2), at levels comparable to those shown by crickets housed
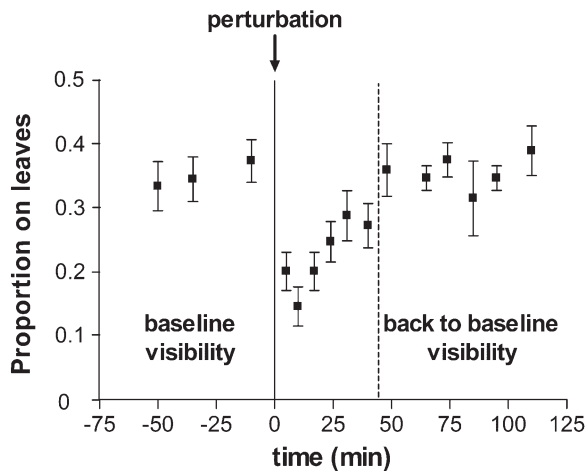
Figure 2. Re-emergence Times of Crickets

Mean (±SEM) proportion of individuals seen at the surface of leaves before and after an artificial perturbation (indicated by an arrow) of the litter by the experimenter. The vertical full line separates the data before (baseline levels) and after perturbation. The vertical dashed line indicates the point at which subjects' visibility first returned to baseline levels. Bonferroni post-hoc comparisons test shows that the mean visibility 45 min after perturbation does not differ from the initial baseline visibility levels, but that the mean visibility noted during the 45 min following perturbation differs from those in both the previous and the following periods.

Figure 3. No Effect of Residual Odor Cues on Crickets' Behavior

Mean (+SEM) proportion of individuals seen at the surface of leaves after 24 hr spent in cages containing either cues left by safe crickets ("past safety"), cues left by spiders and by crickets scared and/or preyed upon ("past danger"), or cues left by live spiders ("current danger"). Lowercase letters above bars indicate differences between means based on Bonferroni post-hoc comparisons test, $\alpha < 0.03$.

with live spiders (Figure 1A). Those crickets, however, returned to baseline levels of visibility within 45 min after perturbation (repeated-measures ANOVA: $F_{2,12}$ = 22.15, p < 0.001; Figure 2). Note that the increased hiding following artificial perturbation lasted only for 45 min, whereas it lasted at least 24 hr for observers of Experiment 2, thereby dismissing long re-emergence times as an alternative explanation to learning. The threat perceived by observers in Experiment 2 was thus much greater than that perceived by subjects in Control 1. The information conveyed by demonstrators in the danger treatment could therefore not be merely indicative of microhabitat preferences (i.e., position in the litter) and must rather have been indicative of danger to observers.

It is unlikely that residual odor cues played a significant role in the lasting behavioral change noted in observers; naive observers in Experiment 2 were placed in an environment that did not, and never had, contained spiders. Besides, most alarm pheromones in insects are short lived and active only over a close range, thereby allowing for normal activity to resume once the threat has passed [30, 31]. Crickets' alarm pheromones, if any are indeed released, are thus unlikely to be effective 24 hr after release. Nonetheless, we ensured this was not the case in another experiment (Control 2), by providing subjects with cues indicative of "past safety," "past danger," or "current danger" (Figure S2 and further details in Supplemental Data). For that, crickets and/or spiders were held in cages for 48 hr. We assumed that any odor cues left by crickets alone were indicative of past safety, whereas any odor cues left by both crickets and spiders were indicative
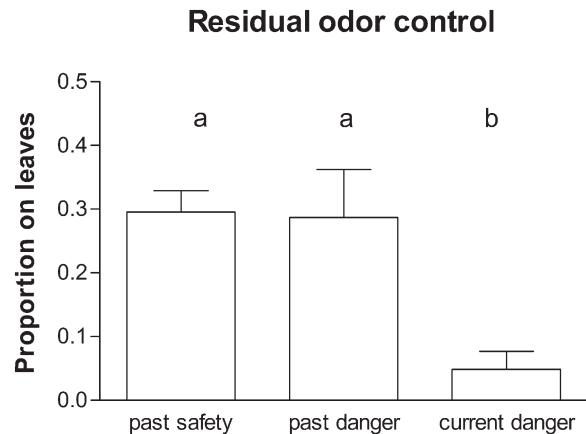
of past danger. Crickets and spiders were then removed and replaced by crickets naive of the state of the environment. The current-danger treatment was similar to the past-danger treatment except that in the former, three live spiders remained present when naive crickets were added in. The proportion of naive crickets seen at the surface of leaves was noted after 24 hr in those treatments. We found that freshly caught juvenile crickets strongly decreased their visibility in response to the presence of spiders (current danger) but not to odor cues potentially left either by safe crickets (past safety) or by both spiders and conspecifics subject to stress and predation (past danger), ($F_{2,9}$ = 7.13, p = 0.014; Figure 3).

We also ensured that the long-lasting hiding in observers was not the expression of a simple negative taxic response triggered by alarm pheromones alone (Control 3). For that, we subdivided cages with a partition that allowed for pheromone exchange between the two compartments, but not for physical or visual contact (Figure S3 and further details in Supplemental Data). After spending 15 hr in an environment containing either three spiders or no predator, ten demonstrators were transferred into one compartment while ten naive observers were transferred into the other. After 6 hr during which observers and demonstrators shared the same air, we found no difference in observers' visibility in the danger (mean ± SEM = 0.21 ± 0.04) or the safety treatment (0.19 ± 0.02; Mann-Whitney test: Z = −0.22, p = 0.843).

Those controls confirm that predation-avoidance response in Experiment 2 (Figure 1D) could not have been triggered, let alone lastingly maintained, by spider cues (Control 2) or by putative cricket alarm pheromones alone, whether fresh (Control 3) or 24 hr old (Control 2). Hiding response hence requires either direct encounters with live spiders (Experiment 1, Control

2) or encounters with individuals that just had contact with spiders (Experiment 2). Although we cannot strictly rule out the possibility that a hiding response is elicited by a combination of odor cues and behavior of scared conspecifics, our results strongly suggest that indirect information about spider presence will efficiently trigger a hiding response only if others' behavior indicates so.

Conclusions

Our study provides supporting evidence for social learning in noncolonial insects as well as original evidence for the use of social cues indicative of danger by insects in general. Our results are also reminiscent of informational cascades that predict that individuals should copy the predator-avoidance behavior (e.g., fleeing, hiding) of others, irrespective of their own personal information regarding danger, especially if several others are observed engaging in the same predator-avoidance behavior [2, 32]. Copying others' predator-avoidance behavior blindly may appear costly in the absence of actual threat, yet it may be the optimal solution; the benefit of avoiding predation often largely exceeds the cost of forgoing sustenance activities.

Social learning in a predatory context is commonly regarded as the learning of a specific cue allowing identification of a new predator identity [9], habitat type [33], or local escape route [34] but usually not of nearby danger. Social learning, however, is classically defined as "learning about the environment […] through conspecific observation" [35] and refers to "any incidence in which individuals acquire new behavior or information about their environment via observation of, or interaction with, other animals or their products" [3]. According to those definitions, social learning may thus also serve to update one's own estimate of the state of the world, such as the current level of predation, and may be interpreted in those terms, provided it leads to a lasting change in behavior [36]. We argue that our findings in Experiment 2 may be a first case of social learning in noncolonial insects and review the supporting evidence.

First, the fact that observers maintained their predator-avoidance behavior after demonstrators were removed dismisses an interpretation in simple terms of social facilitation. Social facilitation occurs when the mere presence of others simultaneously showing a behavior is sufficient to trigger it in nearby observers [37]. Second, the retention time of modified behavior we observed (24 hr) was at least 4-fold the time that was necessary for it to spread (6 hr or less), making a social-contagion interpretation unlikely; in social contagion, a given behavior spreads automatically and easily, and often as quickly it decays, whereas behavior patterns modified by social learning are more robust and durable [38]. Third, the 24 hr delay after which a difference in behavior was still detectable matches or exceeds those commonly reported in the social-learning literature (e.g., minutes [39, 40]; 1 hr [41]; 15–16 hr [42]; 24 hr [40]). Lastly, although the precise mechanisms at play remain to be determined, visual contact and observation of others' behavior appear to be a key component of the social-information transfer described here. For all these reasons, we argue that our results are consistent with classical definitions of social learning. Moreover, given our various controls to assess alternative, simpler interpretations for the long-lasting behavioral changes reported, an explanation involving social learning is so far the most parsimonious.

Rather than being indicative of high cognitive abilities, social learning may be a relatively simple solution used by a wide range of animal species. In the case of wood crickets, social learning in a predation context is probably favored by the need to acquire highly risky yet beneficial information at low costs, the possibility to acquire that information through the conspicuous predator-avoidance behavior of conspecifics, and the opportunity to do so provided by the high densities at which the species occurs. Crickets' high densities make conspecific encounters, and thus the transfer of information, highly probable (see Supplemental Data). It follows that the decisive factor favoring social learning in insects may not be coloniality, as suggested by the comparison between colonial and solitary bees [43, 44], but more simply the opportunity to interact with organisms sharing similar ecological needs and constrains [13]. For prey to benefit from social information about nearby danger, encounter rates with potential demonstrators must be higher than with predators. It follows that social learning in a predation context should be favored in species occurring at high local densities in areas of the species range where prey overcome predators in numbers.

Although the view of a stereotyped insect behavior is no longer prevailing, it remains that the domain of social learning and information transfer in general is heavily biased toward vertebrates ([1, 4, 5, 7, 8]; but see [6, 10]). It is interesting to note that this domain has largely ignored insects, a taxon that represents the vast majority of animal species. Our results indicate that social learning may be more phylogenetically widespread than commonly thought and thus that the taxonomic bias apparent in the literature is unjustified. Furthermore, our findings further support the view [17, 18] that social learning is conditioned upon ecological rather than taxonomic determinants.

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