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Socially Influenced Behaviour and Learning in Locusts

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Abstract

As a part of our research on the evolution of social learning in insects, we examined socially influenced behaviour and social learning in desert locust (*Schistocerca gregaria*) nymphs and adults. In the nymphs, the only positive effect we documented was an increased tendency to feed while in the company of another locust than alone. The adults, on the other hand, showed significant preference for joining others (local enhancement) in both the contexts of feeding and egg laying. Neither nymphs nor adults, however, showed social learning. Our preliminary analyses pointed to locusts as a likely insect that might possess social learning. Our research, when taken together with research on phase-shifts and swarm/marching behaviour of gregarious locusts, suggests that the behavioural dynamics of gregarious locusts may make local enhancement but not social learning beneficial. The possible difference we documented between the nymphs and adults could enable us to further explore the proximate and ultimate mechanisms that underlie socially influenced behaviour.

Introduction

Social learning, defined as learning from others, has been studied primarily in a few vertebrate taxa and social bees (von Frisch 1967; Heyes & Galef 1996; Leadbeater & Chittka 2007; Kendal et al. 2009). We know little, however, about the prevalence, evolutionary biology and neurogenetic mechanisms of social learning. Dukas (2010) identified key life-history traits that would promote the evolution of social learning. These include parental care, overlapping generations and a social structure that allows for frequent interactions among conspecifics. These characteristics provide opportunities for inexperienced individuals to learn from experienced ones. Based on this premise, Dukas and colleagues (Dukas & Simpson 2009; Sarin & Dukas 2009) chose two established insect model systems, fruit flies (*Drosophila melanogaster*) and migratory locusts (*Locusta migratoria*) for examining social learning. While we documented social learning in the context of egg-laying substrate in fruit flies (Sarin & Dukas 2009), we failed to document social learning about food in migratory locusts (Dukas & Simpson 2009). In fruit flies (*D. melanogaster*), social learning in the context of egg-laying substrates has also been documented by F. Mery (unpubl. data), who has also reported social learning in the context of mate choice (Mery et al. 2009). Neither Auld et al. (2009) nor R. Dukas (unpubl. data), however, observed mate choice copying in either *D. melanogaster* or two other fruit fly species (*D. seratta* and *D. pseudoobscura*).

Our failure to document social learning in migratory locusts (Dukas & Simpson 2009) represents data from a single population of a single species in the context of food and thus should not lead one to conclude that locusts (family Acrididae, order Orthoptera) do not show social learning. Research on locusts has documented some social interactions involving the synchronization of movement, feeding and egg laying in the gregarious form (reviewed in Pener & Simpson 2009). Thus, even if further research indicates no social learning in locusts, additional information on socially influenced behaviour in locusts may help us understand the evolution of social learning. Locusts are an especially attractive

group for research on incipient social learning, because they have both solitary and gregarious phases. This means that one can examine the mechanisms underlying socially influenced behaviour through a within-species comparison between the solitary and gregarious forms (see Anstey et al. 2009; Ott & Rogers 2010).

Animals are subjected to a variety of social influences that could affect their propensity to either perform or learn a given task (Thorpe 1963; Galef 1976; Whiten & Ham 1992; Galef & Giraldeau 2001). We distinguish here among three classes of social influences. First, social support merely means that subjects are more likely to perform a task when in the presence of others than when alone. This phenomenon is well known in a variety of species that live in groups [e.g. shoaling fish (Ryer & Olla 1992)] and most often reflects subjects' stress when separated from their group (Whiten & Ham 1992). Second, social facilitation and local enhancement mean that subjects' behaviour is affected by either the specific behaviour or the exact location of others. Specifically, social facilitation implies that subjects are more likely to perform a specific behaviour when others perform it than when others do not, and local enhancement means that subjects are more likely to visit a site frequented by others than a site of equal quality that is not used by others. Finally, social learning involves cases where an individual (observer) acquires new information through interaction with either another individual (model) or cues left by that individual. The new information learned may include individuals other than the model, other biotic entities (e.g. prey, predators or competitors) or physical factors (e.g. shelter or nutrients). Of the three categories of socially influenced behaviour just described, only the last one (social learning) explicitly involves learning.

To broaden our knowledge of social effects on behaviour in locusts, we extended our analyses to another key model species from the same family (Acrididae), the desert locust (*Schistocerca gregaria*). In addition to testing for individual and social learning in fifth-instar nymphs as Dukas & Simpson (2009) did with migratory locusts (*L. migratoria*), we expanded the scope of this work to (1) search for evidence of possible evolutionary precursors to social learning (e.g. local enhancement), (2) investigate multiple life stages, (3) account for possible confounding/masking effects of synthetic diet and (4) investigate multiple behavioural contexts (i.e. feeding and egg laying).

General Methods

In all the experiments, we used either newly moulted fifth-instar nymphs or sexually mature adult females taken from a gregarious laboratory population of desert locusts (*S. gregaria*) and fed on wheat seedlings and wheat germ in 46 × 29 × 30 cm plastic containers under a 14:10 light/dark cycle. Incandescent light bulbs above the containers allowed the locusts to thermoregulate at their preferred temperature between 30 and 40°C. In addition to wheat seedlings, we used in the experiments two novel food types. The synthetic diet was based on the recipe in Simpson & Abisgold (1985). To create two novel diets, we mixed the synthetic food powder with either 2% by weight cinnamon or 2% by weight cumin. Preliminary experiments showed no significant difference in the proportion of time the nymphs spent feeding on the cinnamon and cumin-flavoured food (binomial test, $p = 0.845$, $N = 26$). Although nymphs willingly consumed the synthetic diet, many adult locusts avoided it. Hence, we used in some of the experiments novel plant diets consisting of thin slices of carrot (*Daucus carota*) and cabbage (*Brassica oleracea*).

All the experiments involved removing locusts from the colony for a day of habituation followed by training and testing. During the habituation period, the nymphs fed on a plain synthetic diet, and the adults fed on wheat seedlings. Unless otherwise stated, we used 16 × 12 × 10 cm (length × width × height) clear plastic cages with wire-screen covers for training and testing. The boxes contained a water dish and a perch next to an incandescent light bulb, which provided heat. In the experiments involving either a food dish or models located at one side of the cage during training, we randomized the location of models and food dishes within each cage (either left or right), which consistently had no significant effects on food preference. For brevity, we do not discuss location further. All the behavioural recordings during the tests were conducted by an observer blind to locust experience. Because all experiments but one (social support) involved choices between two options, the data were not normally distributed, and we thus used non-parametric statistics.

Individual Learning

Locusts show excellent individual learning (Bernays 1995; Dukas & Bernays 2000; Behmer et al. 2005), so we began by verifying that locusts from our population can show robust individual learning in our experimental settings.

Methods

Nymphs

On day 1, we placed the nymphs in pairs inside the cages, where they fed on plain synthetic diet for 24 h. The nymphs were placed in pairs to encourage feeding during the training phase (see below). To differentiate between the nymphs, we marked one of the nymphs with a dot of white paint (Dukas & Simpson 2009). On day 2 at 0800 hours, we removed the food from the cages for a 2-h food deprivation period. At 1000 hours, we placed one food dish in each cage for a 2-h training period. Half the nymphs received cinnamon-flavoured food in a green petri dish and the other half received cumin-flavoured food in a brown petri dish. At 1200 hours, we placed each nymph alone in a cage for a 4-h food deprivation period. At 1600 hours, we placed two food dishes inside each cage, one green with cinnamon-flavoured food and the other brown with cumin-flavoured food. The dish locations in the test matched the locations experienced by each nymph, so they could identify the food they experienced by location, colour and flavour. We recorded the time the nymphs spent feeding at each food dish during the 1-h test period. All but two of the 40 nymphs fed during the training period, and all the remainder 38 nymphs fed during the test.

Adults

The protocol was similar to the one used with the nymphs except that we used carrot and cabbage as food and the training phase was shortened to 30 min because the adults fed in much shorter bouts and had the same number of feeding bouts in 30 min as nymphs had in 2 h. All but one of the 40 adults fed during the training period. Of the remainder 39 adults, only 32 individuals fed during the test.

Results

Both the nymphs and adults showed a significant preference for the novel food they experienced in the training period (Mann–Whitney U-test: U_{38} = 47.5, $p < 0.005$ and $U_{32} = 187$, $p < 0.05$ for the nymphs and adults, respectively; Fig. 1a).

Social Support

Our incidental observations suggested that locusts fed more readily while in the presence of others than alone. We thus quantitatively characterized the influence of conspecific presence on feeding via a controlled experiment.

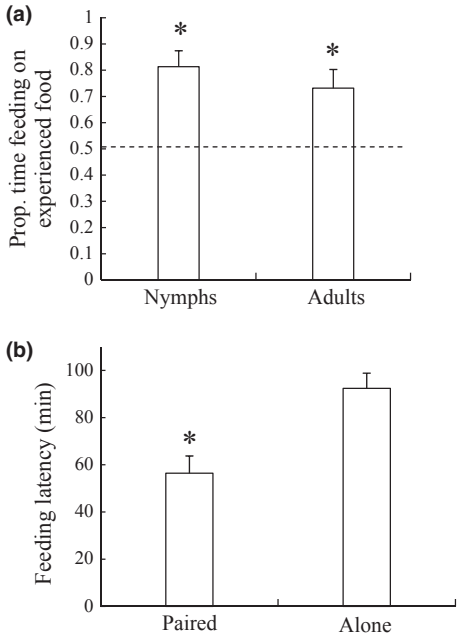

Fig. 1: (a) *Individual learning*. The average (+1 SE) proportion of time locusts spent feeding on the food they previously experienced (n_{nymphs} = 38, n_{adults} = 32). The nymphs were trained on either cinnamon- or cumin-flavoured synthetic food and the adults were trained on either cabbage or carrot. The stars indicate $p < 0.05$ and the broken line shows the expected random choice. (b) *Social support*. The average (+1 SE) feeding latency of nymphs that were either paired with another nymph or placed alone in the cage (n = 59).

Methods

The general protocol was similar to that mentioned above except that there was no training. Rather, we placed focal nymphs of the solitary treatment one per cage and focals of the social treatment each with another nymph marked with a white dot. All the cages contained a novel cinnamon-flavoured food, and we recorded the feeding latencies of the focals (N = 59) for up to 2 h.

Results

The feeding latency was significantly shorter for focals in the social than solitary condition (ANOVA: $F_{1,57} = 13.5$, $p < 0.005$; Fig. 1b).

Local Enhancement

Our next step was to examine stronger social influences on behaviour involving a simple tendency to

join others, a preference to feed with others and a propensity to lay eggs next to others. Previous experiments on local enhancement in *S. gregaria* have been inconclusive. Roessingh et al. (1993) suggested that gregarious nymphs tend to join others while Sword (2003) found no such preference. The literature on egg laying, while also inconsistent (Pener & Simpson 2009), suggests that gregarious females prefer to lay eggs next to either other females or egg pods (Norris 1963; Saini et al. 1995).

Methods

Nymphs

We conducted three experiments testing nymphs' preference to join others under three scenarios. The first experiment involved no food, the second included synthetic food and the third had wheat seedlings. In the first experiment (no food), we used 35 × 23 × 14 cm clear plastic boxes with wire-screen chambers at each far edge. Marked lines divided the centre chamber into three equal sections. Incandescent light bulbs at both edges provided heat, so we expected the focals to move from their initial centre position to one of the wire-screen edges (Fig. 2a). We introduced five models into one of the chambers and kept the other chamber empty. Half the cages had models on the right and the other half on the left. After a 10-min habituation period, we introduced one focal inside a vial into the centre of each cage. We allowed the focals to habituate for 2 min and then removed the vials' lids. For the following 20 min, we recorded each focal's location and later calculated the proportion of time each focal spent in the section of the cage close to the models over the time spent in the two sections adjacent to the screen chambers (Fig. 2a).

In the second experiment (synthetic food), the set-up was similar to the one in Fig. 2b, with each cage having two wire screen chambers at the two far corners. Each cage had two 35-mm petri dishes containing plain synthetic food with one half of each dish inside and the other half outside each screen enclosure. We placed one model inside one of the screen enclosures in each cage, alternating between sides. After a 10-min habituation period, we placed one focal in the main area of each cage. We then recorded the focals' feeding durations at each dish for 1 h. The third experiment (wheat seedlings) was similar to the second (synthetic food) except that we

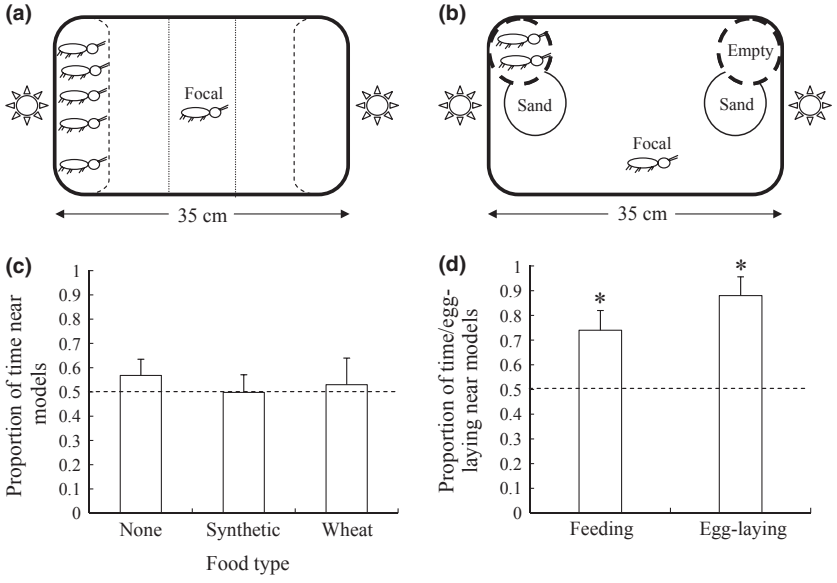

Fig. 2: *Local enhancement*. (a) The set-up of the experiment involving no food. Each cage had heat lamps (☼) on each side, screen enclosures (broken lines) at each edge, and the central sector was divided by a marker (dotted lines) into three sections of equal sizes. (b) The set-up for the experiments involving food and egg laying. Each cage had heat lamps (☼) on each side and enclosures (broken lines) and sand cups (continuous lines) at each edge. (c) The average (+1 SE) proportion of time nymphs spent either next to models in the experiment with no food (left bar, n = 35) or feeding from the food located next to the models in the experiments with synthetic food (middle bar, n = 39) and wheat (right bar, n = 21). (d) The average (+1 SE) proportion of time adults spent feeding near the models (left bar, n = 26), and the average (+1 SE) proportion of egg pods laid inside the egg cup closer to the models' enclosure (right bar, n = 18). The broken lines in (c) and (d) show the expected random choice.

used two models inside each screen enclosure and wheat seedlings as food.

Adults

We conducted two experiments to assess the influence of local enhancement on feeding and egg laying by sexually mature adults. The feeding experiment was similar to the third nymph experiment (wheat seedlings). The general set-up for the egg-laying experiment was similar to that for food (Fig. 2b). Each cage contained two sand cups 8 cm in diameter and 10 cm deep with their tops levelled with the cage floor. The sterilized sand contained 15 ml water per 100 g sand (Saini et al. 1995). We used young, sexually mature females with no prior egg-laying experience as focals and older mature females as models. Both models and focals fed on wheat seedlings during the experiment. We placed two models inside one of the enclosures in each cage. The models were adjacent to one of the sand cups but had no access to the sand (Fig. 2b). We then added a single-focal female to each cage. After 4 d, we counted the egg pods in the cups. Our preliminary experiments indicated that females did not lay more than one egg pod during a 4-d period.

Results

Nymphs

In the first experiment (no food), the focal nymphs did not show a significant preference for the side of the cage that contained the models (Wilcoxon signed-ranks test: $Z_{35} = -1.3$, $p = 0.2$; Fig. 2c). Neither did the focals touch the wire screen next to the models first (0.57 near vs. 0.43 far; binomial test, $p = 0.5$). In the second and third experiments (synthetic food and wheat seedlings respectively), the focals showed no significant preference for feeding near the models over away from the models (Wilcoxon signed-ranks test: $Z_{39} = -0.06$, $p = 0.9$ and $Z_{21} = -0.4$, $p = 0.7$ for synthetic food and wheat seedlings, respectively; Fig. 2c).

Adults

In the feeding experiment, the adults preferred to feed on the wheat clump near the models (Wilcoxon signed-ranks text: $Z_{26} = -2.462$, $p < 0.05$; Fig. 2d). In the egg-laying experiment, the adults preferred to lay egg pods in the sand cup next to the models (binomial test, $p < 0.005$, $n = 18$; Fig. 2d).

Social Learning

Methods

Nymphs

We conducted two experiments with the nymphs, one involving direct interactions with models who had previously fed on novel food and the other consisting of focals observing models feeding beyond a screen. In the first experiment, we collected the models on day 1, marked each with a white dot on the thorax and placed half in a large cage containing cinnamon-flavoured synthetic food and the other half in a large cage containing cumin-flavoured synthetic food. On day 2, we collected the focals and placed them in a large cage containing synthetic food and water. On day 3, we moved the focals in pairs into small boxes with plain food and water for 24 h. On day 4 at 0800 hours, we removed the food from the focals' cages for a 2-h food deprivation period. We then dusted each of the models who had fed on cinnamon-flavoured food with a small amount of cinnamon and dusted each of the models who had fed on cumin-flavoured food with a small amount of cumin. This was carried out to enhance the odours released by the models, which were indeed perceptible to us. At 1000 hours, we placed each focal in a cage with two models who had previously fed on either cinnamon- or cumin-flavoured food. We allowed the focals and models to interact for two hours without the presence of any food. At 1200 hours, we removed the focals and placed them in new cages for the test phase. Each cage contained one dish of cinnamon-flavoured food and one dish of cumin-flavoured food. We recorded the focals' feeding behaviour for 1 h.

The other experiment involved focals observing models feeding beyond a screen. Here, we split each cage lengthwise into two sections using a wire screen. The half closer to the incandescent light bulb contained two models and either a green dish with cinnamon-flavoured synthetic food or a brown dish with cumin-flavoured synthetic food. After 10 min of model habituation, we placed a focal nymph in the other section of each cage. All models fed within 30 min. In most cages, the focals perched on the screen separating them from the models and food. At the end of the 30-min observation period, we transferred the focals into the test cages and allowed them to habituate for 30 min. We then added the green, cinnamon and brown, cumin-flavoured food dishes while preserving the locations of the food dishes observed during the observation phase and watched the focals for 1 h.

Adults

The focals in this experiment were sexually mature adult females, and the models were older adult females. The experiment involved the focals observing the models via a wire screen, and the protocol was similar to the experiment with nymphs except that we used carrot and cabbage as the novel foods.

Results

Nymphs

The nymphs did not prefer the novel food consumed by the models over the other novel food in either the experiment with perfumed models ($\bar{x} \pm$ SE proportion of preference for models' food: 0.58 ± 0.11; Mann–Whitney U-test: $U_{38} = 152$, $p = 0.3$) or the experiment involving models feeding beyond a screen ($\bar{x} \pm$ SE proportion of preference for models' food: 0.48 ± 0.1; Mann–Whitney U-test: $U_{19} = 49$, $p = 0.6$).

Adults

The adults did not prefer the novel food consumed by the models over the other novel food ($\bar{x} \pm$ SE proportion of preference for models' food: 0.56 ± 0.08; Mann–Whitney U-test: $U_{32} = 101$, $p = 0.3$).

Discussion

In agreement with the previous locust studies (reviewed in Bernays 1993, 1995), our desert locusts (*S. gregaria*) showed robust individual learning (Fig. 1a) in the general set-up we also used for examining socially influenced behaviours and social learning. Perhaps as expected from gregarious individuals (Whiten & Ham 1992), the desert locusts showed social support as indicated by the fact that they were faster to feed when in a social than solitary setting (Fig. 1b). Our examinations of local enhancement, however, produced two surprising outcomes. First, contrary to intuition and in spite of repeated attempts using distinct protocols, gregarious fifth-instar nymphs showed neither a tendency to join a group of other nymphs nor a preference to feed next to other nymphs (Fig. 2c). Our results expand on previous studies that examined the tendency of gregarious desert locust nymphs (*S. gregaria*) to join others because, in addition to examining focals' tendencies to join others, we also looked at their propensities to feed with others. While our data agree with that of Sword (2003), they contradict the conclusion of Roessingh et al. (1993) that gregarious desert locust (*S. gregaria*) nymphs prefer to join others. We cannot explain the discrepancy. Our other surprising result was that, unlike the nymphs, the adults did show a robust, consistent tendency to both feed and lay eggs next to others (Fig. 2d). While our data indicating local enhancement of egg laying substantiate previous observations (Norris 1963; Saini et al. 1995), the results indicating local enhancement in the context of feeding is, as far as we know, novel.

Our final noteworthy result was that, using another locust species, we extended the results of Dukas & Simpson (2009) indicating no social learning about food in either nymph or adult locusts. Missing from our report here is a test of social learning in the context of egg laying. The reason for this is that our extensive preliminary experiments indicated that it would be difficult to produce a convincing test given that locusts lay only a single-egg pod every few days and that it was hard to control the timing of that egg-pod laying. Although two sets of negative data obtained in two distinct locust species and two laboratories are more convincing than a single data point, one is always more tempted to question negative than positive results even though positive results deserve equal scrutiny (Ioannidis 2005). It is thus worthwhile to discuss the utility of reporting our second set of data indicating no social learning in locusts.

First, to truly understand the evolution of and mechanisms underlying social learning, we must thoroughly examine species that might end up showing no social learning. This is analogous to insights gained from either solitary or primitively social species in research on the evolution of social behaviour in insects (Wilson 1971; Michener 1974; Costa 2006). Second, we have expanded the scope of our research programme to encompass a larger variety of socially influenced behaviours and have succeeded in documenting local enhancement in adult locusts in the contexts of both food and egg laying. If further research substantiates our results indicating local enhancement in the adults but not nymphs, these behavioural data can pave the way for a within-species comparison of the mechanisms underlying the distinct socially influenced behaviour in the nymphs and adults. Indeed, it is already established that solitary and gregarious locusts (*S. gregaria*) show substantial differences in brain size and anatomy (Ott & Rogers 2010) and that serotonin is a key mediator of the transformation from the solitary to gregarious phases (Anstey et al. 2009). Hence,

one can apply techniques similar to those of Rogers and colleagues (Anstey et al. 2009; Ott & Rogers 2010) for studying the neurobiological differences between the nymphs and adults. Furthermore, in mice, recent research has identified neuronal circuits mediating social learning (Munger et al. 2010). Finally, on the methodological side, one can always explain away negative data as indicating experimenters' failure to either properly maintain their subjects or produce a proper protocol. Our way of addressing this important issue is to convince ourselves and others that, using the same laboratory settings and general protocol, we can also obtain positive data. Indeed, we have documented significant individual learning in both nymphs and adults, social support in the nymphs and local enhancement in the adults (Figs 1 and 2).

Socially Influenced Behaviour in Locusts

In spite of extensive research, the social structure of locusts is not fully understood. It appears, however, that favourable conditions such as rainfall and vegetation lead to a dramatic increase in locust population density and a switch from the solitary to gregarious phases, which is accompanied by the locusts' increased tolerance to each other (Uvarov 1977; Simpson et al. 1999; Sword 2003; Pener & Simpson 2009). That is, a focal locust in a crowded aggregation may focus on exercising a tight balancing act of staying within the aggregation owing to reduced predation risk (Sword et al. 2005) and keeping some distance from potentially cannibalistic conspecifics (Bazazi et al. 2008). In such a setting of crowded conspecifics, social learning may be futile. First, a focal would almost certainly be surrounded by numerous others, and, second, local cues may be irrelevant owing to the continuous swarm movement. We should note, however, that according to our scenario, we would expect both nymphs and adults to show local enhancement, so the lack of local enhancement in the nymphs remains unexplained. A promising next step to clarifying this issue would be to test local enhancement in nymphs and adults in the field.

The Evolution of Social Learning

Until recently, the two major approaches in research on social learning have been the characterization of social learning categories (Zentall & Galef 1988; Heyes & Galef 1996) and an examination of the trade-offs that determine the use of individual vs. social learning in a few vertebrate model systems that show robust social learning (Laland 2004; Galef 2009; Kendal et al. 2009). Hence, we still know little about the evolution of social learning. Perhaps not surprisingly, much of the research on social learning has focused on the species most likely to show it, which are mostly vertebrates with parental care (mammals and birds) and animals that live in groups (schooling fish and social hymenoptera). Our focus on non-eusocial insects, however, can help us understand incipient social learning. Our current assumption, which requires critical tests, is that most insects do not show social learning as defined in the introduction. If this is true, we can think of three non-mutually exclusive paths leading to social learning in insects.

The first route to social learning involves prolonged parental care, which, although rare, does exist in some insects (Costa 2006). Parental care is probably the premier trait that has facilitated the evolution of social learning because it involves inexperienced individuals interacting closely with experienced kin. This means that the observer offspring can benefit from information gleaned from their parents, which is likely to be highly relevant (Dukas 2010). The second route to social learning involves insects that typically live in groups and thus tend to join conspecifics. Joining models at a given location, or local enhancement, may or may not lead to acquiring new information from the models. Intriguingly, our data for desert locust (*S. gregaria*) indicated local enhancement in the adults but not nymphs (Fig. 2) and lack of social learning in the adults even though they showed local enhancement. We should note that local enhancement can have powerful effects on behaviour that we do not categorize as social learning. That is, focals showing local enhancement may, for example, encounter and feed on novel food that they would later prefer. However, if focals that are placed and feed on novel food alone also later prefer that food, we would attribute the food preference following local enhancement to individual learning or even habituation rather than to social learning (Sarin & Dukas 2009).

Finally, the third route to social learning could involve insects that gain from joining conspecifics. Examples include bark beetles (e.g. *Dendroctonus* and *Ips* spp) and some species of fruit flies (*Drosophila* spp), in which individuals release and are attracted to an aggregation pheromone and have a higher fitness in a group than alone (Prokopy & Roitberg 2001; Wertheim et al. 2005). As in the second route, the observers joining models may or may not show

social learning. Here, however, one can envision that joiners would learn to associate conspecifics by some relevant salient cue such as the smell of food or egg-laying substrate. Thus, a critical test would document that focals prefer an odour experienced with certain conspecifics over an odour experienced alone, that is, social learning (Sarin & Dukas 2009), but the ultimate explanation is attraction to conspecifics rather than attributing a higher value to food others have chosen. Our analysis of the routes leading to social learning can help us understand the lack of social learning in locusts documented here and elsewhere (Dukas & Simpson 2009).

In sum, our broadened analysis of socially influenced behaviour in locusts has revealed no social learning in either nymphs or adults, local enhancement in the contexts of both food and egg laying in the adults and social support in the nymphs. The intriguing possible within-species difference between the nymphs and adults may help us reveal proximate and ultimate mechanisms affecting the ontogeny and evolution of social learning.

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Literature Cited

Anstey, M. L., Rogers, S. M., Ott, S. R., Burrows, M. & Simpson, S. J. 2009: Serotonin mediates behavioral gregarization underlying swarm formation in desert locusts. Science **323**, 627—630.

Auld, H. L., Punzalan, D., Godin, J. -G. J. & Rundle, H. D. 2009: Do female fruit flies (*Drosophila serrata*) copy the mate choice of others? Behav. Process. **82**, 78—80.

Bazazi, S., Buhl, J., Hale, J. J., Anstey, M. L., Sword, G. A., Simpson, S. J. & Couzin, I. D. 2008: Collective motion and cannibalism in locust migratory bands. Curr. Biol. **18**, 735—739.

Behmer, S. T., Belt, C. E. & Shapiro, M. S. 2005: Variable rewards and discrimination ability in an insect herbivore: what and how does a hungry locust learn? J. Exp. Biol. **208**, 3463—3473.

Bernays, E. A. 1993: Aversion learning and feeding. In: Insect Learning (Papaj, D. R. & Lewis, A. C., eds). Chapman and Hall, New York, pp. 1—17.

Bernays, E. A. 1995: Effects of experience on feeding. In: Regulatory Mechanisms in Insect Feeding (Chapman, R. F. & de Boer, G., eds). Chapman & Hall, New York, pp. 279—306.

Costa, J. T. 2006: The Other Insect Societies. Harvard Univ. Press, Cambridge, MA.

Dukas, R. 2010: Insect social learning. In: Encyclopedia of Animal Behavior (Breed, M. & Moore, J., eds). Academic Press, Oxford, pp. 176—179.

Dukas, R. & Bernays, E. A. 2000: Learning improves growth rate in grasshoppers. Proc. Natl Acad. Sci. U. S. A. **97**, 2637—2640.

Dukas, R. & Simpson, S. J. 2009: Locust show rapid individual learning but no social learning about food. Anim. Behav. **78**, 307—311.

von Frisch, K. 1967: The Dance Language and Orientation of Bees. Harvard Univ. Press, Cambridge, MA.

Galef, B. G. 1976: Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. Adv. Study Behav. **6**, 77—100.

Galef, B. G. 2009: Strategies for social learning: Testing predictions from formal theory. Adv. Study Behav. **39**, 117—151.

Galef, B. G. & Giraldeau, L. A. 2001: Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim. Behav. **61**, 3—15.

Heyes, C. M. & Galef, B. G. 1996: Social Learning in Animals. Academic Press, San Diego.

Ioannidis, J. P. A. 2005: Why most published research findings are false. PLoS Med. **2**, e124.

Kendal, R. L., Coolen, I. & Laland, K. N. 2009: Adaptive trade-offs in the use of social and personal information. In: Cognitive Ecology II (R., D. & Ratcliffe, J., eds). Univ. of Chicago Press, Chicago, pp. 249—271.

Laland, K. N. 2004: Social learning strategies. Learn. Behav. **32**, 4—14.

Leadbeater, E. & Chittka, L. 2007: Social learning in insects – from miniature brains to consensus building. Curr. Biol. **17**, R703—R713.

Mery, F., Varela, S. A. M., Danchin, É., Blanchet, S., Parejo, D., Coolen, I. & Wagner, R. H. 2009: Public versus personal information for mate copying in an invertebrate. Curr. Biol. **19**, 730—734.

Michener, C. D. 1974: The Social Behavior of the Bees. Harvard Univ. Press, Cambridge, MA.

Munger, S. D., Leinders-Zufall, T., McDougall, L. M., Cockerham, R. E., Schmid, A., Wandernoth, P., Wennemuth, G., Biel, M., Zufall, F. & Kelliher, K. R. 2010: An olfactory subsystem that detects carbon disulfide and mediates food-related social learning. Curr. Biol. **20**, 1438—1444.

Norris, M. J. 1963: Laboratory experiments on gregarious behaviour in ovipositing females of the desert locust, (*Schistocerca gregaria*; (Forsk.)). Entomol. Exp. Appl. **6**, 279—303.

Ott, S. R. & Rogers, S. M. 2010: Gregarious desert locusts have substantially larger brains with altered proportions compared with the solitarious phase. Proc. R Soc. B Biol. Sci. **277**, 3087—3096.

Pener, M. P. & Simpson, S. J. 2009: Locust phase polyphenism: an update. Adv. Insect Physiol. **36**, 1—272.

Prokopy, R. J. & Roitberg, B. D. 2001: Joining and avoidance behavior in nonsocial insects. Annu. Rev. Entomol. **46**, 631—665.

Roessingh, P., Simpson, S. J. & James, S. 1993: Analysis of phase-related changes in behaviour of desert locust nymphs. Proc. R Soc. B Biol. Sci. **252**, 43—49.

Ryer, C. H. & Olla, B. L. 1992: Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. Anim. Behav. **44**, 69—74.

Saini, R. K., Rai, M. M., Hassanali, A., Wawiye, J. & Odongo, H. 1995: Semiochemicals from froth of egg pods attract ovipositing female *Schistocerca gregaria*. J. Insect Physiol. **41**, 711—716.

Sarin, S. & Dukas, R. 2009: Social learning about egg laying substrates in fruit flies. Proc. R. Soc. Lond. B Biol. Sci. **276**, 4323—4328.

Simpson, S. J. & Abisgold, J. D. 1985: Compensation by locusts for changes in dietary nutrients – behavioral mechanisms. Physiol. Ent. **10**, 443—452.

Simpson, S. J., McCaffery, A. R. & Hagele, B. F. 1999: A behavioural analysis of phase change in the desert locust. Biol. Rev. **74**, 461—480.

Sword, G. A. 2003: To be or not to be a locust? A comparative analysis of behavioral phase change in nymphs of *Schistocerca americana* and *S. gregaria* J. Insect Physiol. **49**, 709—717.

Sword, G. A., Lorch, P. D. & Gwynne, D. T. 2005: Migratory bands give crickets protection. Nature **433**, 703.

Thorpe, W. 1963: Learning and Instinct in Animals. Methuen and Co, London.

Uvarov, B. P. 1977: Grasshoppers and Locusts. Anti-Locust Research Centre, London.

Wertheim, B., van Baalen, E. -J. A., Dicke, M. & Vet, L. E. M. 2005: Pheromone-mediated aggregation in nonsocial arthropods: an evolutionary ecological perspective. Annu. Rev. Entomol. **50**, 321—346.

Whiten, A. & Ham, R. 1992: On the nature and evolution of imitation in the animal kingdom – reappraisal of a century of research. Adv. Study Behav. **21**, 239—283.

Wilson, E. O. 1971: The Insect Societies. Harvard Univ. Press, Cambridge, MA.

Zentall, T. R. & Galef, B. G. 1988: Social Learning: Psychological and Biological Perspectives. Erlbaum, Hillsdale, NJ.