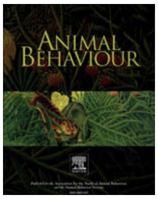
Animal Behaviour 78 (2009) 307–311

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe



Locusts show rapid individual learning but no social learning about food

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ARTICLE INFO

Article history:
Received 9 January 2009
Initial acceptance 12 March 2009
Final acceptance 8 May 2009
Published online 11 June 2009
MS. number: A09-00023R

Keywords:
foraging
locust
Locusta migratoria
social learning
sociality

Socially influenced learning is important because it can drive the spread of novel behaviours among individuals within and between generations. While work on a few vertebrates suggests the conditions favouring the use of social over individual learning, we know little about the evolution of social learning. As a part of an ongoing examination of the evolutionary roots of social learning in insects, we tested for social learning in locusts, *Locusta migratoria*. Locusts showed rapid individual learning, preferring a diet they ate for a single meal of only 20 min over another diet of equal nutritional quality. Locusts, however, did not show stronger preference for novel food that they had previously consumed while in the presence of a conspecific experienced with that food. Furthermore, focal locusts did not learn about novel food from (1) experienced conspecifics that were observable through a screen, (2) interactions with conspecifics that had previously fed on and gave off odours from novel food and (3) cannibalizing conspecifics that had recently fed on novel food. Whereas our results extend previous work indicating excellent individual learning in locusts, they provide no evidence for socially influenced learning in a species that, in its gregarious form, has the opportunity for social learning and could benefit from such an ability.

Social learning, defined as learning from other individuals, is evolutionarily important because it enables the spread of novel behaviours within and between generations. Animals can gain from social learning because it may be faster than individual learning, could save the fitness costs of errors associated with inexperience or enable learning of otherwise inaccessible information (Galef 1976). Whereas humans and some other vertebrates rely extensively on social learning (Heyes & Galef 1996), the current published data do not indicate whether most animals possess the ability to learn from others. Specifically, among insects, well replicated data that indicate social learning exist only for social Hymenoptera (Leadbeater & Chittka 2007; Dukas 2008, in press a).

A variety of studies have examined the ecological settings favouring social over individual learning (Boyd & Richerson 1985; Galef & Giraldeau 2001; Laland 2004; Kendal et al., in press). We still, however, know little about the evolution of social learning. Some life history traits can promote the evolution of social learning. First, social learning is perhaps most likely to evolve when related, closely interacting individuals differ strongly in their knowledge, such as in the case of young, inexperienced individuals that are being cared for by their experienced parents. Second, social learning may also evolve when inexperienced individuals can gain relevant information from unrelated, experienced ones. This may occur in animals with overlapping generations, in which members of younger, inexperienced generations can acquire relevant information from older, more experienced individuals. Finally, social learning is more likely to evolve if individuals interact often with each other. In short, one would expect social learning to be most prevalent in species with parental care, occur to a lesser extent in species with overlapping generations that have frequent social interactions among related or unrelated individuals, and to be least common in solitary, nonaggregating species with nonoverlapping generations (Dukas, in press a).

Social learning has been mostly studied in animals with parental care, shoaling fish and social Hymenoptera. In these animal categories, there are frequent interactions among related individuals with distinct levels of experience. It is possible, however, that social learning occurs in a variety of other species, but it has not yet been closely examined. Promising taxa for examining the evolutionary roots of social learning are insects with overlapping generations that occur in large groups. Among such taxa, locusts (family Acrididae) appear especially attractive because individuals of the gregarious form tend to join and synchronize feeding behaviour with conspecifics (Roessingh et al. 1993; Simpson et al. 1999; Despland & Simpson 2006; Simpson & Sword 2008) and they possess robust individual learning (Bernays 1995; Raubenheimer & Tucker 1997; Behmer et al. 2005). Thus, one can readily envision a variety of

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doi:10.1016/j.anbehav.2009.05.004

scenarios under which inexperienced locusts would join more experienced conspecifics that provide relevant information, either by feeding on a novel food plant, or by giving off odours from a novel food plant on which they have previously fed. Because plant species and parts available to locusts in the field vary in the quantity and quality of essential nutrients and damaging secondary compounds (Simpson & Raubenheimer 2000; Behmer et al. 2002), it is conceivable that locusts could increase growth rate and fitness by quickly obtaining reliable information about novel food from others.

To test for social learning in a nonsocial insect, we conducted a series of experiments with the gregarious form of *Locusta migratoria*, which has served as a central model system in research on insect feeding and learning (Simpson & Raubenheimer 2000). Our general prediction was that inexperienced locusts would show a stronger preference for a novel food associated with an experienced conspecific than for a novel food presented alone.

GENERAL METHODS

We used newly moulted fifth-instar locusts (*L. migratoria*) reared at high density and fed on wheat germ and wheat seedlings under a 14:10 h light:dark cycle with lights on at 0700 hours. We transferred the necessary numbers of locusts into clear plastic cages measuring 30 × 20 × 20 cm (length × width × height) housed at a constant room temperature of 30 °C. The newly moulted focal locusts spent at least 1 day habituating to the laboratory setting and, except for experiment 1, consumed wheat germ and wheat. Locusts in experiment 1 fed on unflavoured synthetic food, and locusts used as demonstrators in experiments 2–5 fed on flavoured synthetic food. All locusts always had free access to water. The chemically defined dry, granular food was based on the recipe in Simpson & Abisgold (1985) and contained 21% (weight/weight) protein and 21% digestible carbohydrates, which is near optimal in nutrient composition (Simpson & Raubenheimer 2000).

To generate the two novel diets, we added either 2% by weight cinnamon powder or 2% cocoa powder to the plain synthetic food. Preliminary experiments indicated that the locusts preferred plain over flavoured food (ANOVA $F_{1,18} = 20.5$, $P < 0.001$) regardless of the flavour used ($F_{1,18} = 0.15$, $P = 0.7$), they showed no side preference ($F_{1,18} = 0.3$, $P = 0.6$), and that, given a choice between diets flavoured with cinnamon and cocoa, they showed no statistically significant preference for either flavour ($F_{1,19} = 2.8$, $P = 0.11$).

Each experiment consisted of a training period followed by a test and included two replicates, each starting with 20 focal locusts. For training and testing, we used small and large chambers made of transparent plastic containers and measuring 14 × 8 × 6 cm and 18 × 12 × 6 cm, respectively. White cardboard dividers prevented locusts from seeing other chambers. The chambers always contained water dishes, to allow locusts to regulate their hydration state independently of nutrients, and perches, upon which locusts typically rested between meals. During training, which lasted 2 h in experiments 1, 4 and 5 and 1 h in experiments 2 and 3, we observed locust behaviour continuously. In experiments 1, 2 and 5, in which food was provided in the training phase, we recorded the duration of all feeding bouts into a laptop computer equipped with a custom-made recording program. We then included in the following test only focal locusts that fed for at least 10 s. This time period had previously been shown to be the criterion for initiation of a committed period of feeding (a meal) rather than a food-sampling event (Simpson 1995). In the tests, observers blind to locust experience monitored the insects continuously for 1 h and recorded all feeding bouts. All statistical analyses involved ANOVAs on the arcsine square-root proportions of time spent feeding on a given diet out of the total time spent feeding.

EXPERIMENT 1: INDIVIDUAL LEARNING

Methods

In this baseline experiment, we tested whether locusts would show significant learning after a relatively short experience with novel food. On day 1, we placed locusts individually in cages and provided each with unflavoured diet. At 0700 hours on day 2, we eliminated the locusts that had not fed and removed the food from the remainder locust cages. At 0900 hours (by which time the locusts would have missed an average of two meals relative to ad libitum-fed insects; Simpson 1995), we transferred each locust to its own small chamber containing water and a single food dish. Half of the locusts received cinnamon-flavoured food and the other half received cocoa-flavoured food. All but one of the 34 locusts fed during the 2 h training period for an average duration of 22 ± 2 min (mean ± SE) for the cinnamon group ($N = 16$) and 18.3 ± 1.8 min (mean ± SE) for the cocoa group ($N = 17$). Feeding duration did not differ between groups ($F_{1,31} = 2$, $P = 0.17$). At 1100 hours, we transferred all locusts but the single unfed one to large chambers containing only water for a 4 h food deprivation period. The remaining locust fed 1 h later, was then subjected to 3 h starvation, and was included in the test. At 1500 hours, we placed each locust alone inside a large chamber holding one cinnamon- and one cocoa-flavoured food dish, placed at random at the opposite corners of the container furthest from the perch. Observers blind to the test locusts' dietary experience recorded feeding behaviour for 1 h.

Results

The focal locusts showed moderate, statistically significant preference for the food that they had consumed during training ($F_{1,32} = 4.5$, $P = 0.04$; Fig. 1).

EXPERIMENT 2: FEEDING WITH OR WITHOUT A DEMONSTRATOR

Methods

This experiment simulated a realistic scenario in which locusts inexperienced with a given food either approach it alone or join experienced conspecifics at that food. We predicted that locusts that feed on a novel food together with a conspecific would later

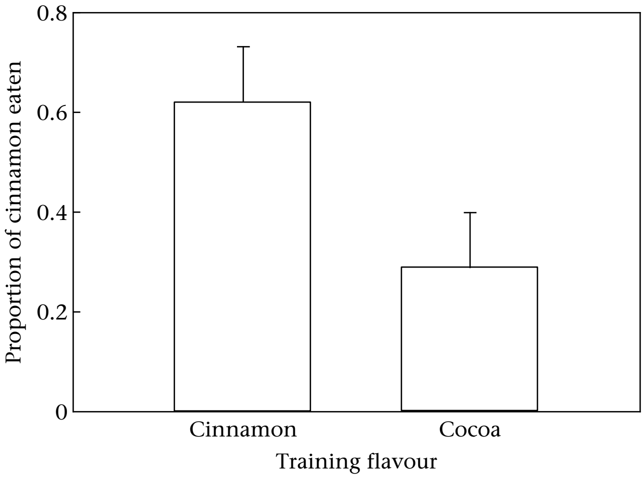

Figure 1. Mean + SE proportion of cinnamon-flavoured food eaten by focal locusts ($N = 34$) in the test after feeding on either cinnamon- or cocoa-flavoured food during training.