



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

Reuven Dukas^{a,b,*}, Stephen J. Simpson^{b,1}^aAnimal Behaviour Group, Department of Psychology, Neuroscience & Behaviour, McMaster University^bSchool of Biological Sciences, The University of Sydney

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.

© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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

* Correspondence: R. Dukas, Animal Behaviour Group, Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada.

E-mail address: dukas@mcmaster.ca (R. Dukas).

¹ S. J. Simpson, School of Biological Sciences, The University of Sydney, Heydon-Laurence Building, A08, NSW 2006, Australia.

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 $30 \times 20 \times 20$ cm (length \times width \times 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 $14 \times 8 \times 6$ cm and $18 \times 12 \times 6$ 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 \pm SE) for the cinnamon group ($N = 16$) and 18.3 ± 1.8 min (mean \pm 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

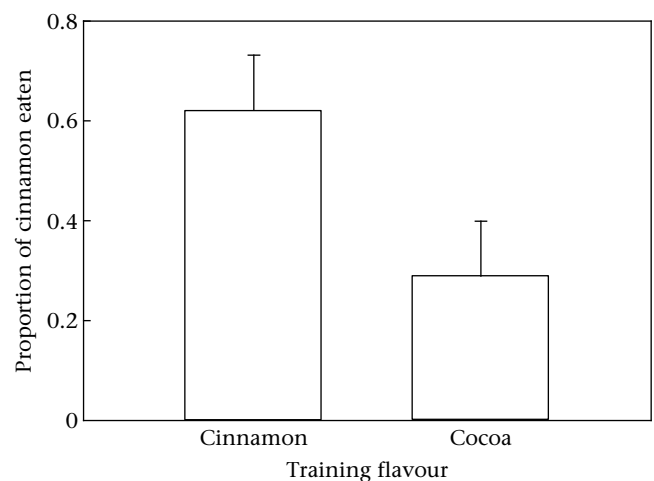


Figure 1. Mean \pm SE proportion of cinnamon-flavoured food eaten by focal locusts ($N = 34$) in the test after feeding on either cinnamon- or cocoa-flavoured food during training.

show a stronger preference for that food over another novel food of equal quality than would locusts that initially feed alone on that food.

On day 1, we placed newly moulted fifth-instar nymphs (the models) inside two large cages containing water and food dishes. The models in one cage fed on cinnamon-flavoured food placed next to a 6×6 cm brown card, and the models in the other cage fed on cocoa-flavoured food placed next to a 6×6 cm green card. The coloured cards served as visual stimuli supplementing the olfactory and flavour cues (Dukas & Bernays 2000). On day 2, we placed newly moulted fifth-instar nymphs (the focals) inside a large cage with wheat germ and wheat seedlings. Hence, focals were younger (less experienced) than models by approximately 20% of the active feeding period of the fifth stadium. On day 3, we removed the food from all the cages before lights on at 0700 hours. Before 0900 hours, we marked the demonstrators' thoraxes with a white correction fluid and prepared small chambers, each containing a single food dish next to a 4×4 cm card placed at one corner. At 0900 hours, we placed (1) a focal locust in each of five small chambers containing cinnamon-flavoured powder on the right side and marked with a brown card, (2) a focal locust in each of five small chambers containing cocoa-flavoured powder on the left side and marked with a green card, (3) a focal locust and a cinnamon-fed demonstrator in each of five small chambers containing cinnamon-flavoured powder on the right side and marked with a brown card and (4) a focal locust and a cocoa-fed demonstrator in each of five small chambers containing cocoa-flavoured powder on the left side and marked with a green card. In short, half the locusts could feed on a novel food alone and the other half could feed on a novel food together with an older demonstrator that had already fed on that food for 2 days. The focal locusts fed during the training for an average duration of 18.7 ± 3 min (mean \pm SE) for the alone group ($N = 12$) and 16.6 ± 2.2 min (mean \pm SE) for the social group ($N = 11$). Feeding duration did not differ between groups ($F_{1,21} = 0.3$, $P = 0.6$). At the end of training, we transferred the focals individually into large chambers containing only water for a 4 h deprivation period.

At 1500 hours, we started the test, in which each focal locust was placed in a large chamber with a cinnamon-flavoured food dish marked with a brown card and placed on the right side, and a cocoa-flavoured food dish marked with a green card and placed on the left side. Observers who were blind to locust treatment recorded all feeding bouts for 1 h.

Results

The focal locusts that experienced novel food together with a demonstrator did not subsequently show a stronger preference for that food than the focals that experienced the novel food alone ($F_{1,19} = 0.4$, $P = 0.52$). Regardless of social experience, however, the locusts showed a significant preference for the food that they had consumed during the training phase ($F_{1,19} = 5.5$, $P < 0.05$; Fig. 2).

EXPERIMENT 3: DEMONSTRATORS FEEDING BEYOND A SCREEN

Methods

Experiment 2 revealed no additional effect of demonstrators on the strength of food preference by focal locusts that had fed on a novel food. We thus switched to examining types of social learning that do not involve actual feeding on novel food.

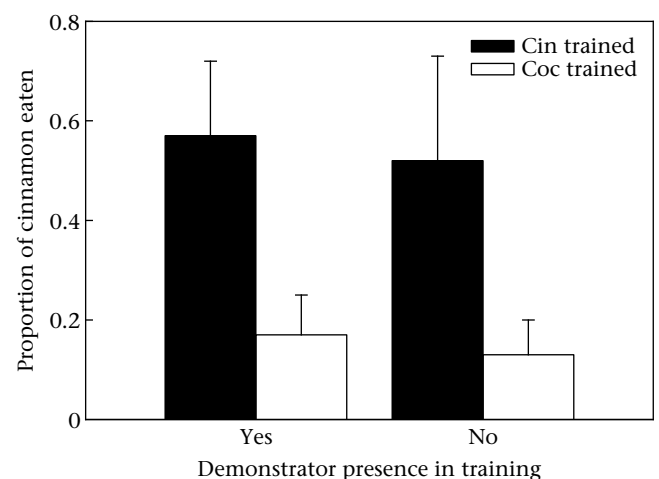


Figure 2. Mean \pm SE proportion of cinnamon-flavoured food eaten by focal locusts ($N = 23$) in the test. During training, the focals fed on either cinnamon- or cocoa-flavoured food in either the presence or the absence of conspecifics experienced with feeding on that food.

Because the general protocol for experiment 3 was similar to that of experiment 2, we focus here on the specific features of this experiment. We equipped the small chambers with small pieces of standard insect screen (7 threads per cm), dividing each chamber into one-third and two-thirds, consisting of a small observation cell and a large demonstration cell, respectively. All the demonstration cells contained a coloured food dish next to a coloured card. The cinnamon-flavoured food was associated with brown colour and the cocoa-flavoured food was associated with green colour. At 0900 hours, we placed one focal locust in each observation cell of all chambers and two demonstrators in the demonstration cell of half of the chambers of each food type. That is, half of the focal locusts could only observe and smell a novel diet through the screen, whereas the other half could observe and smell two demonstrators feeding on a novel diet. At 1000 hours, we moved the focal locusts into test chambers and recorded their feeding as in experiment 2. We included in the analysis the 31 focal locusts that fed during the test.

Results

The focal locusts did not show a preference for the food consumed by demonstrators beyond a screen over a food presented alone beyond a screen. The proportion of cinnamon diet consumed was 0.12 ± 0.12 versus 0.23 ± 0.15 for the locusts in the cinnamon diet treatment with demonstrators versus alone, and 0.39 ± 0.18 versus 0.13 ± 0.13 for the locusts in the cocoa diet treatment with demonstrators versus alone (social treatment: $F_{1,28} = 0.4$, $P = 0.5$; food type: $F_{1,28} = 0.4$, $P = 0.5$; social treatment*food type interaction: $F_{1,28} = 1.7$, $P = 0.2$).

EXPERIMENT 4: INTERACTIONS WITH PREVIOUSLY FED DEMONSTRATORS

Methods

Because we found no evidence that locusts attended to information provided beyond a screen, we next examined whether residual odours on demonstrators influenced the locusts' choice of novel foods. This protocol simulates a common scenario of focal locusts joining conspecifics in a marching band (Simpson & Sword

2008) in which some locusts carry residual odours from plants they have fed on previously. Here we placed one focal locust in each small chamber. Half of the chambers contained two demonstrators that had fed on cinnamon-flavoured diet for 2 days and the other half contained two demonstrators that had fed on cocoa-flavoured diet for 2 days. We could readily smell the food flavourings on the demonstrators while handling them. We recorded numerous interactions between focals and demonstrators during the 2 h training period. Such interactions included perching closer than one body width from each other and contacts between the observers' heads and demonstrators' bodies. We then transferred the focals to test chambers and examined their food preference.

Results

Focal locusts that spent 2 h in a small cage with demonstrators that had fed on a novel food did not prefer the demonstrators' food over another novel food. The mean \pm SE proportion of time spent feeding on the cinnamon diet was 0.17 ± 0.10 and 0.29 ± 0.18 for the locusts interacting with the cinnamon- and cocoa-fed demonstrators, respectively ($F_{1,18} = 0.3$, $P = 0.6$).

EXPERIMENT 5: SOCIAL LEARNING VIA CANNIBALISM

Methods

Locusts and other mass migrating Orthoptera often cannibalize conspecifics (Simpson et al. 2006; Bazazi et al. 2008). Because our previous experiments indicated that the locusts readily learned about novel food through feeding but not via indirect cues, we wished to test whether locusts can learn about novel food from consuming a conspecific that had previously fed on that food. Here half of the focal locusts were placed in a training chamber containing a recently killed demonstrator that had fed on cinnamon-flavoured diet for 2 days and the other half had the opportunity to eat a demonstrator that had fed on cocoa-flavoured diet for 2 days. About half (18/40) of the observers fed on demonstrators for a mean \pm SE duration of 11.5 ± 1.7 min during the 2 h training period and only they were tested after a 4 h starvation period. The test was similar to that of experiment 1.

Results

Focal locusts that cannibalized demonstrators that had fed on novel food did not prefer the demonstrators' food over another novel food. The mean \pm SE proportion of time spent feeding on the cinnamon diet was 0.24 ± 0.16 and 0.27 ± 0.14 for the locusts cannibalizing cinnamon- and cocoa-fed demonstrators, respectively ($F_{1,17} = 0.01$, $P = 0.9$).

DISCUSSION

The results indicating quick learning after feeding for only about 20 min on novel food (Figs 1, 2) extend previous data showing robust learning in locusts after longer practice (Simpson & White 1990; Bernays 1995; Raubenheimer & Tucker 1997; Dukas & Bernays 2000; Behmer et al. 2005). However, all of our attempts to document socially influenced learning about food have failed. Experiment 2 indicated that, although locusts rapidly learn to prefer a novel food that they have consumed, the presence of a conspecific already experienced with this food does not increase preference for that food. Although one might argue that social learning could not elevate the preference scores above the moderate value of about 0.7, similar experiments with locusts indicate that they can have preference scores approaching 1 (Dukas

& Bernays 2000). Experiments 3–5 showed that focal locusts did not rely on three types of social cues that could help them choose between novel diets. In experiment 3, the opportunity to observe experienced conspecifics feeding on novel food did not influence locusts' subsequent diet choices. In experiment 4, close interactions with experienced conspecifics that had previously fed on and gave off odours from novel food did not lead locusts to prefer that food. Finally, in experiment 5, cannibalizing locusts that had recently consumed a novel diet did not influence locusts' subsequent food choices, even though cannibalism provides an important organizing force sustaining cohesive mass movement in bands of locusts and other Orthoptera (Simpson et al. 2006; Bazazi et al. 2008).

Because our protocols indicated robust individual learning but no socially influenced learning even within a single experiment (Fig. 2), we conclude that gregarious-phase *L. migratoria* probably do not use social learning to inform food choices. We should note that, relying on the literature on vertebrate social learning (Laland 2004; Kendal et al., in press), we designed protocols to maximize our likelihood of finding social learning in locusts. First, we used inexperienced and mildly food-deprived individuals, which should be most receptive to social cues about novel food. Second, our demonstrators were older, experienced individuals that were either mildly deprived before receiving free access to the novel food (experiments 2, 3) or well fed and giving off odours from a novel food during the experience phase (experiments 4, 5). Such individuals should be the best source of socially acquired information. Whereas one can always envision other protocols that could theoretically provide positive evidence for social learning, we think we have tried some of the most promising methods available. We should note, however, that our strict, although sensible, standards for identifying social learning required that focal individuals had to show a stronger preference for a food type either when they experienced it with models than when they experienced it alone, or when they sensed that the models had fed on it than when they sensed the food alone. These standards imply that we do not consider local enhancement as social learning. In local enhancement, focals are attracted to models at food that they subsequently prefer. Focals that feed on that food alone, however, might show a similar preference to that food. That is, we wished to examine whether individuals assign a higher value to novel food consumed by conspecifics than to another novel food of equal quality. Given that gregarious locusts are strongly attracted by conspecifics and synchronize bouts of activity and feeding behaviour when in groups (Roessingh et al. 1993; Simpson et al. 1999; Despland & Simpson 2006; Simpson & Sword 2008), local enhancement may affect patterns of food choice in locust groups.

While we have a growing understanding of the evolution of individual learning (Dukas, in press b) and the settings thought to favour social over individual learning (Galef & Giraldeau 2001; Laland 2004; Kendal et al., in press), we know little about the evolution of social learning. One can argue that the distinction between individual and social learning is artificial because either translate into learning by the individual. However, research on a few vertebrates has clearly documented that subjects can decide based on their circumstances to rely either on their own trial and error learning or information gained from others (Galef et al. 2008; Webster & Laland 2008; Kendal et al., in press). Moreover, it is likely that there are many species that do not obtain some relevant information from conspecifics. There may even be many solitary animals that do not possess the necessary cognitive machinery that enables individuals to attend to and learn from some relevant cues provided by others.

In summary, although our theoretical considerations suggested that locusts would be a likely species to show social learning, we

could readily document rapid individual learning based on feeding on novel diet but no socially influenced learning based on food cues from others.

Acknowledgments

We thank Lauren Dukas, Tim Dodgson and Naz Soran for assistance, Fiona Clissold for advice, and Lauren Dukas, Dave Stephens and two anonymous referees for illuminating comments on the manuscript. This study was supported by the Natural Sciences and Engineering Research Council of Canada, a University of Sydney International Research Fellowship to R.D. and an Australian Research Council Federation Fellowship to S.J.S.

References

- 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. *Current Biology*, **18**, 735–739.
- Behmer, S. T., Simpson, S. J. & Raubenheimer, D. 2002. Herbivore foraging in chemically heterogeneous environments: nutrients and secondary metabolites. *Ecology*, **83**, 2489–2501.
- 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? *Journal of Experimental Biology*, **208**, 3463–3473.
- Bernays, E. A. 1995. Effects of experience on feeding. In: *Regulatory Mechanisms in Insect Feeding* (Ed. by R. F. Chapman & G. de Boer), pp. 279–306. New York: Chapman & Hall.
- Boyd, R. & Richerson, P. J. 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.
- Despland, E. & Simpson, S. J. 2006. Resource distribution mediates synchronization of physiological rhythms in locust groups. *Proceedings of the Royal Society, B*, **273**, 1517–1522.
- Dukas, R. 2008. Evolutionary biology of insect learning. *Annual Review of Entomology*, **53**, 145–160.
- Dukas, R. In press a. Social learning in insects. In: *Encyclopedia of Animal Behavior* (Ed. by M. Breed & J. Moore). San Diego: Elsevier.
- Dukas, R. In press b. Learning: mechanisms, ecology and evolution. In: *Cognitive Ecology II* (Ed. by R. Dukas & J. Ratcliffe). Chicago: University of Chicago Press.
- Dukas, R. & Bernays, E. A. 2000. Learning improves growth rate in grasshoppers. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 2637–2640.
- Galef, B. G., Jr. 1976. Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. *Advances in the Study of Behavior*, **6**, 77–100.
- Galef, B. G., Jr & Giraldeau, L.-A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, **61**, 3–15.
- Galef, B. G., Jr, Dudley, K. E. & Whiskin, E. E. 2008. Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. *Animal Behaviour*, **75**, 631–637.
- Heyes, C. M. & Galef, B. G., Jr. 1996. *Social Learning in Animals*. San Diego: Academic Press.
- Kendal, R. L., Coolen, I. & Laland, K. N. In press. Adaptive trade-offs in the use of social and personal information. In: *Cognitive Ecology II* (Ed. R. Dukas & J. Ratcliffe). Chicago: University of Chicago Press.
- Laland, K. N. 2004. Social learning strategies. *Learning & Behavior*, **32**, 4–14.
- Leadbeater, E. & Chittka, L. 2007. Social learning in insects: from miniature brains to consensus building. *Current Biology*, **17**, R703–R713.
- Raubenheimer, D. & Tucker, D. 1997. Associative learning by locusts: pairing of visual cues with consumption of protein and carbohydrate. *Animal Behaviour*, **54**, 1449–1459.
- Roessingh, P., Simpson, S. J. & James, S. 1993. Analysis of phase-related changes in behaviour of desert locust nymphs. *Proceedings of the Royal Society, B*, **252**, 43–49.
- Simpson, S. J. 1995. Regulatory mechanisms in insect feeding. In: *Regulatory Mechanisms in Insect Feeding* (Ed. by R. F. Chapman & G. de Boer), pp. 137–156. New York: Chapman & Hall.
- Simpson, S. J. & Abisgold, J. D. 1985. Compensation by locusts for changes in dietary nutrients: behavioral mechanisms. *Physiological Entomology*, **10**, 443–452.
- Simpson, S. J. & Raubenheimer, D. 2000. The hungry locust. *Advances in the Study of Behavior*, **29**, 1–44.
- Simpson, S. J. & Sword, G. A. 2008. Locusts. *Current Biology*, **18**, R364–R366.
- Simpson, S. J. & White, P. R. 1990. Associative learning and locust feeding: evidence for a 'learned hunger' for protein. *Animal Behaviour*, **40**, 506–513.
- Simpson, S. J., McCaffery, A. R. & Hagele, B. F. 1999. A behavioural analysis of phase change in the desert locust. *Biological Reviews of the Cambridge Philosophical Society*, **74**, 461–480.
- Simpson, S. J., Sword, G. A., Lorch, P. D. & Couzin, I. D. 2006. Cannibal crickets on a forced march for protein and salt. *Proceedings of the National Academy of Sciences, U.S.A.*, **103**, 4152–4156.
- Webster, M. M. & Laland, K. N. 2008. Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proceedings of the Royal Society, B*, **275**, 2869–2876.