SOCIALLY INFLUENCED BEHAVIOUR AND LEARNING IN LOCUSTS

SOCIALLY INFLUENCED BEHAVIOUR AND LEARNING IN THE CONTEXT OF FOOD CHOICE AND EGG-LAYING SITES IN *SCHISTOCERCA GREGARIA*

By

YAARA LANCET, B.Sc.

A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree
Master of Science

McMaster University

MASTER OF SCIENCE (2011)	McMaster University
Psychology, Neuroscience, & Behaviour	Hamilton, Ontario

TITLE: Socially influenced behaviour and learning in the context of food choice and egg-laying sites in *Schistocerca gregaria*

AUTHOR: Yaara Lancet, B.Sc. (Hebrew University of Jerusalem)

SUPERVISOR: Reuven Dukas, Ph.D.

NUMBER OF PAGES: vi, 51

Abstract

Social learning, defined as learning from other individuals, has been well studied in vertebrates and social insect species. In order to promote further understanding of the evolution of social learning, I tested a non-social insect for social learning and socially influenced behaviour. The desert locust (*Schistocerca gregaria)* is a gregarious insect which has the opportunity for social learning and can benefit from such ability. Locusts showed rapid individual learning, preferring a diet they have experienced over another of equal nutritional quality. Adult locusts also showed socially influenced behaviour, preferring to eat and lay eggs in the vicinity of other locusts over doing so alone. Fifth instar locusts did not show the same socially influenced behaviours. Neither adult nor nymphs showed social learning after interacting with previously fed models or after observing models feed through a screen. These results provide evidence for socially influenced behaviour in locusts and for a difference in social behaviour between nymphs and adults. Further research utilizing locusts as a model system may help us gain a better understanding of the evolution of social learning.

Acknowledgments

First and foremost, I would like to thank my supervisor, Reuven Dukas, for his endless support and wisdom and his continuing guidance and patience. I would also like to thank my supervisory committee, Jeff Galef and Jim Quinn, for providing their invaluable knowledge, time and experience. I would like to express special gratitude to Lauren Dukas, for her never-ending encouragement, advice and friendship. Thank you to all my lab members who have helped me during the past two years; Zac Durisko for his chats and encouraging opinions, Lana Petchenova and Dominika Tomczyk for all the hours they've put in and for always being there for a friendly locust-room chat, Corrine Seeley, for always helping me see that things are not as bad as they seem. I would like to thank my fellow graduate and undergraduate students and the department staff for always being there. A special thanks goes to my very special friend, Erez Zukerman, for sharing all the good and bad moments, and to Lilach Lancet, for always listening and reminding me there is something other than this.

Table of Contents

List of Figures

INTRODUCTION

General rationale

A previous attempt by Dukas & Simpson (2009) found no evidence for social learning about food in the migratory locust (*Locusta migratoria*). It did, however, find individual learning about food to exist in locusts. In order to enhance the understanding of the evolution of social learning, I decided to examine another species from the same family, the desert locust (*Schistocerca gregaria*). While Dukas & Simpson (2009) tested only for the presence of social learning about food, I assessed a broader range of socially influenced behaviours, such as social support and local enhancement (see definitions below). I tested locusts in the context of egg-laying in addition to the context of food, and therefore used adults in addition to 5th instar nymphs. Below I provide introductory material which further expands on this rationale as well as an overview of the experiments I conducted.

Social learning and socially facilitated behaviour

Social learning, defined as learning from other individuals or cues left by them, is an important mechanism that can affect decision making. The affected decisions are various and include mate choice (Dugatkin, 1992; Galef & White, 1998), predator avoidance (Griffin, 2004) and foraging preferences (Galef & Giraldeau, 2001). It also enables the spread of novel information and behaviours across and within generations. Specifically in the context of food, social learning of what to eat has been well studied in rats and other rodents (Galef & Stein, 1985; Valsecchi & Galef, 1989). After interacting with models who have previously fed on a novel food, rats developed a preference for the novel food they have smelled on the models' breath (Galef & Wigmore, 1983).

Much has been speculated about the cost efficiency of social learning vs. asocial learning, and whether this method of learning is in the best interest of the individual (Boyd & Richerson, 1988; Kendal et al., 2005; Laland, 2004). By learning from others, animals risk the acquisition of wrong information, but may also avoid the costs of errors made due to inexperience, and gain access to information that may be otherwise inaccessible. This is especially important for young or naïve individuals (Galef & Laland, 2005). Although not much is known about the evolutionary aspect of social learning, Dukas (2010) suggests that social learning is much more likely to evolve in species with certain life history traits; it is most likely to occur in species with parental care, will appear to less extent in species with overlapping generations and will rarely evolve in solitary species that do not exhibit these two traits. Leadbeater & Chittka (2007) suggest that social learning occurs mostly when novel information needs to be evaluated, and is less likely to occur if the individual already has some experience with the matter at hand. It is also suggested that social learning only occurs when a certain balance is in place, in which social learning is rarer than individual learning, thus preserving the reliability of the models (Kendal et al., 2005).

Social influences on behaviour are numerous and are defined in many ways (Galef, 1976; Whiten & Ham, 1992). For the purposes of this study, I use the definitions described in Shettleworth (2010) which are as follows: *Social learning* is the reproduction of a behaviour, in part or in full, by a focal, following the performance of this behaviour by a model. To be considered learning, the focal should perform the new behaviour at a later time and away from the direct influence of the model. In *Social facilitation,* individuals are more likely to perform a behaviour when in the company of others who are performing it. Whiten & Ham (1992) call this *contagion*, and it is differentiated from *social support* which is the increased likelihood of an individual to learn a similar act or behaviour because of the effect of the presence of conspecifics. *Local enhancement* is the increased likelihood of a focal visiting a place where other individuals are present.

Social learning in insects

Social learning has been studied mainly in vertebrates, and many examples have been shown in mammals, birds and fish (Heyes & Galef, 1996). In insects, studies have been limited mostly to social insects, especially social hymenoptera (Leadbeater & Chittka, 2007; Nieh, 2004). Social insects are defined as insect species that share resources and reproduce cooperatively. The most known phenomenon in this field, and in the insect world in general, is the honeybee waggle dance in which successful foragers deliver information about the location and quality of flower patches to other foragers in the hive (Von Frisch, 1967). Other examples include recruitment behaviour in stingless bees (Nieh, 2004) and stop signals in honeybees, which relay information about dangers and low-quality patches to other bees (Nieh, 2010). The study in non-social insects has been much more limited. Evidence for social learning have been found in wood crickets (*Nemobius sylvestris*) and suggest that the crickets can use social information about predators and change predator-avoidance behaviours accordingly (Coolen et al., 2005). Fruit flies have been shown to exhibit social learning in mate choice and egg-laying site choice. Sarin & Dukas (2009) suggest that female fruit flies that experience a novel food substrate with mated females and their eggs will later prefer this novel food over a novel food they experienced alone. When experiencing a novel food with virgin females or aggregation pheromone, females did not show the same effect. A different study suggests that female fruit flies use social information when choosing mates and will prefer to mate with males they have observed mating with other females (Mery et al., 2009).

In locusts, attempts have been made to find social learning in different species. An experiment by Dukas & Simpson (2009) which tested the migratory locust *(Locusta migratoria)* found no evidence of social learning in the context of food choice. The locusts did not exhibit social learning after interacting with, observing or eating conspecifics who have previously consumed a novel food.

Locusts remain an attractive model for social learning because they are known to feed together (Roessingh et al., 1993; Simpson et al., 1999) and lay eggs in the same spots (Norris, 1963; Saini et al., 1995). They also show robust individual learning (Dukas & Simpson, 2009; Raubenheimer & Tucker, 1997) and are a gregarious species in which both nymphs and adults aggregate in groups with overlapping generations and numerous social interactions. This places them high on the list of non-social insects that stand to gain from socially influenced learning (Dukas, 2010).

Individual learning in locusts

In the past, it has been suggested that insects rely mostly on innate behaviours because of their relatively simple brains and short generation times. Research in the past few decades, however, suggests that many insects exhibit learning behaviours in various life scenarios such as feeding, sexual behaviour and predator avoidance (Dukas, 2008). Locusts, specifically, have shown a robust ability to learn new information using various cues. It has been suggested that locusts can learn to associate cues such as color and spatial location with food quality and quantity (Behmer et al., 2005; Raubenheimer & Tucker, 1997). Behmer and colleagues (2005) tested desert locusts using a Y-maze protocol. Each arm of the Y-maze was associated with a positive or negative reward, as well as with a color or an odour. Locusts learned to associate color and odour with the positive reward, and continued to do so even when the association was reversed, i.e., they chose the "wrong" arm of the maze which they previously learned was associated with the positive reward. Raubenheimer & Tucker (1997) conducted a series of tests which suggest that locusts can learn to associate color with a diet that contains a specific macronutrient. In the test, protein or carbohydrate deficient locusts, which were trained to associate different diets with different colors, significantly preferred the color which was previously paired with the macronutrient they were currently lacking. Locusts also learn to prefer known foods over novel foods (Dukas & Simpson, 2009). In this experiment, locusts that were given a choice between two diets significantly preferred the one they had already experienced over the one which was completely novel.

Locusts as a model system for social behavior

Social insects are defined as insect species that share resources and reproduce cooperatively. Locusts are not a social insect, but they form large aggregations or swarms. When population densities are high, locusts undergo a striking phase change and turn from a solitary and inconspicuous grasshopper into a highly gregarious form.

This phase change produces vast differences in morphology, behaviour and physiology (Pener, 1991; Uvarov, 1966). Gregarious locusts exhibit synchronized feeding behaviours (Roessingh et al., 1993; Simpson et al., 1999) and egg-laying behaviours (Norris, 1963; Saini et al., 1995) and show marked behavioural differences between the solitarious and the gregarious phase; these include differences in food preferences, activity levels, attraction level to conspecifics and egg-laying preferences (Bashir et al., 2000; Despland & Simpson, 2005; Sword, 2003).

The swarms and bands travel together over great distances and eat many of the plants in their path. The locusts' environment is rich with different kinds of food plants, many of which contain secondary compounds that are either beneficial or harmful (Behmer et al., 2002; Simpson & Raubenheimer, 2000). Diet choices made by locusts and grasshoppers have been shown to directly affect growth and fitness (Dukas & Bernays, 2000; Toye, 1973) and it is therefore conceivable that locusts would use social information to determine which plants to feed on.

There are many speculations as to what drives huge locust swarms forward over such great distances. In addition to the ongoing search for food, it has been suggested that social interactions such as cannibalism are a key factor in the band's movement (Bazazi et al., 2008). Locust bands may be driven forward by a constant need to escape from being eaten, which becomes less imminent when the band reaches a food rich area and stops.

Egg-laying site choice may also be influenced by social interactions. Bashir and colleagues (2000) suggest that female locusts, gregarious or solitary, prefer to lay eggs in the vicinity of other females and eggs. This is suggested to affect the behavioural phase state of the hatchlings and brings on a strong predisposition for gregarization by females (Bashir et al., 2000; McCaffery et al., 1998).

Feeding and egg-laying in locusts

Locusts are polyphagous and feed on many different plant species as well as on conspecifics. The gregarious form, being yellow and conspicuous, use aposematism as a defense mechanism and will feed on plants containing toxic secondary compounds (Despland & Simpson, 2005). A locust will feed on as much as its own weight in a day and the swarm travels over many kilometers to find food, so locusts need to balance multiple and changing nutritional needs with a constantly changing environment (Simpson & Raubenheimer, 2000; Simpson & Abisgold, 1985)

Females lay eggs in moist sand, usually away from plants, and can lay up to 80 eggs in one egg pod. The egg pod is coated for protection and is plugged on its top with froth. This froth has been shown to contain volatiles that attract other females to the egg-laying site and can also affect the behavioural phase state of the hatchlings (McCaffery et al., 1998; Saini et al., 1995). When ready to oviposit, the female probes the sand and then extends her abdomen and burrows about 10cm into the sand to lay the eggs. Gregarious and solitary females have different site preferences – solitary females prefer sand patches close to plants while gregarious females prefer to lay eggs away from plants (Bashir et al., 2000). All females seem to prefer their hatchlings to be gregarious and therefore solitary females are also attracted to lay eggs near gregarious egg pods (Bashir et al., 2000).

Overview

To learn more about social learning and socially influenced behaviours in a non-social insect, I conducted a series of experiments with the desert locust, which tested the social influences on the locusts' choices of diet and egg-laying sites. I conducted the first set of food-related experiments on 5th instars. In this first set, I determined whether my locust population can learn to prefer a novel food they have previously experienced. I then went on to test whether locusts approach a novel food faster when in the presence of conspecifics. The next set of experiments dealt with the effect of local enhancement on the locusts' choices of perching and feeding locations. In the last set of food choice experiments, I tested locusts for social learning; either by interactions with previously fed models or by observing models feed on a novel food. Finally, I used adult female locusts to test whether the females are more likely to lay eggs in the vicinity of other locusts than alone. Having found local enhancement in adult females in this context, I went on to test adult females in my food-related experiments as well, in order to see if this social influence exists in adults only in the context of eggs or in the context of food as well. My general prediction was that locusts would use socially acquired information when choosing between novel foods and egg-laying sites. Specific predictions are given in the rationale part of each experiment.

GENERAL METHODS

I used a population of desert locusts (*Schistocerca gregaria*) that have been bred for several generations in our lab at McMaster. Locusts were reared in 46x29x30cm plastic boxes under a 14:10 light:dark cycle (lights on at 0800h) and were fed on wheat seedlings and wheat germ. High population densities maintained the locusts in the gregarious form (Pener, 1991).

The data were analyzed in SPSS using non-parametric statistics (Mann-Whitney U test, paired-samples Wilcoxon signed ranks test and binomial tests). In chapter 2, a one-way ANOVA was used.

Individual learning

Rationale

Locusts are known to show individual learning (Dukas & Simpson, 2009). When allowed to feed on a novel food for a short time, locusts will later prefer to feed on that food over another novel food. In order to test whether this exists in our own population, using our own protocols, I conducted two individual learning experiments. In these experiments, the locusts could rely on several cues when learning: odour, color, location and the feeding itself. I predicted that locusts would show a significant preference to the food they have already experienced over a completely novel food.

Experiment 1: Individual learning of nymphs with flavoured powders

Methods

For this experiment, I collected locusts after moulting into fifth instar, at which time they were habituated to the experimental settings while feeding on plain powdered food (14% weight/weight protein, 14% weight/weight carbohydrates) based on the recipe in Simpson & Abisgold (1985). To create two novel diets, I mixed the food with either 2% by weight cinnamon or 2% by weight cumin. Preliminary experiments showed no significant difference in the proportion of time locusts (N=26) spent feeding on cinnamon or cumin flavoured food (binomial test: test value = 0.5, 0.46 cinnamon vs. 0.54 cumin, P=0.845).

I conducted the tests inside 16x12x10cm clear plastic boxes with wire screen covers. I placed each box in front of a lamp that maintained the same light:dark cycle as in the large bins. The boxes included a perch close to the lamp. I used 35mm Petri dishes as food and water dishes. Green dishes always contained cinnamon flavoured food and brown dishes always contained cumin flavoured food. Plain powder and water were presented in clear dishes (Fig. 1).

On day 1, I collected 5th instar nymphs and placed them together in a cage measuring 34x19x14cm and containing plain powder and water. On day 2, I placed the nymphs in pairs inside the test cages, where they fed on plain powder for 24h. The nymphs were placed in pairs in order to encourage feeding during the training phase (see experiment 3). In order to differentiate between the locusts during the test, I marked one of the locusts with whiteout liquid. On day 3 at 0800 hours, I removed the food from the cages for a 2h starvation period. At 1000 hours I placed one food dish in each cage for a 2h training period. Half the locusts received cinnamon flavoured food and the other half received cumin flavoured food. I alternated the dish locations in the cages so that each flavour was placed equally on the left and on the right sides. At 1200 hours I removed the food and separated the locust pairs. I discarded 2 locusts that did not feed during the training period so my final sample size for the test included 38 locusts. I placed each locust alone in a cage for a 4h starvation period. At 1600 hours I placed two food dishes inside each cage, one containing cinnamon flavoured food and the other cumin flavoured food. The dishes' locations in the test were the same as the location in the training. Each locust was tested alone. The locusts' feeding durations at each food dish were recorded for 1h by an observer blind to the locusts' prior food experience.

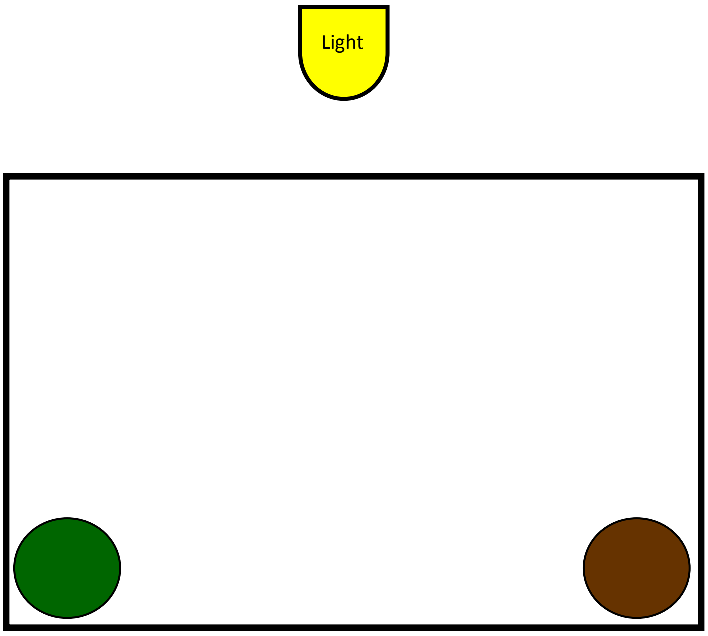

Fig. 1: basic apparatus for experiments 1, 2 and 6.1 – individual and social learning.

Experiment 3 uses similar apparatus, with clear dishes in place of colored ones.

Results

The fifth instar locusts (N=38) showed a significant preference for the novel food they experienced in the training period. The mean proportion of cinnamon eaten was 0.944 for the group trained on cinnamon and 0.304 for the group trained on cumin (Mann-Whitney test: *U*=47.5, N=38, P<0.005; Fig. 2). There was no significant side preference (Mann-Whitney test: *U*=177, P=0.902).

Experiment 2: Individual learning of adults with two plant spp.

Methods

For this experiment, I collected newly sexually mature adult females, at which time they were habituated to experimental settings while feeding on wheat seedlings.

This experiment was similar to experiment 1, except for a few details noted below. I used adult females which were trained and tested on two novel plant spp. – carrot (*Daucus carota sativus*) and cabbage (*Brassica oleracea)*. The two foods were presented in clear dishes. The training phase was shortened to 30 minutes because the adults fed in much shorter bouts and had the same number of feeding bouts in 30 minutes as fifth instars had in 2h. All but one of the 40 locusts fed during the training period**.** Of the remainder 39 locusts, only 32 individuals fed during the test.

Results

The adult locusts (N=32) showed a significant preference for the food they experienced in the training period. The mean proportion of cabbage eaten was 0.706 for the group trained on cabbage and 0.231 for the group trained on carrot (Mann-Whitney test: *U*=187, N=32, P<0.05; Fig. 2). There was no significant side preference (Mann-Whitney test: *U*=110.5, P=0.477).

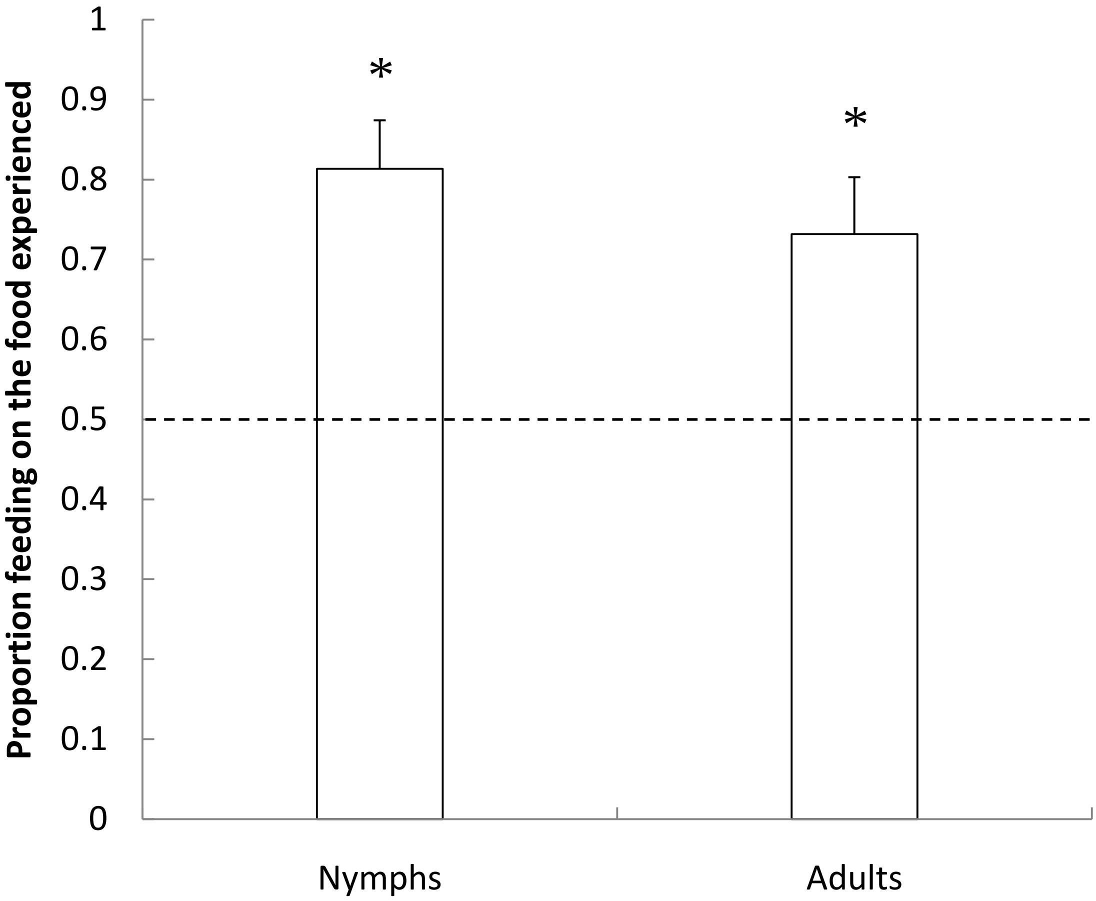

Fig. 2: the mean (+1 SE) proportion of time locusts spent feeding on the food they previously experienced (N_{nymphs} = 38, N_{adults} = 32). In Experiment 1, nymphs were trained on either cinnamon or cumin; in experiment 2, adults were trained on either cabbage or carrot.

Discussion

Experiments 1 and 2 suggested that locusts, both nymphs and adults, prefer a novel food they have previously fed on over a novel food they have never experienced. After a 30min/2h experience period with a novel food, locusts will significantly prefer to feed on the novel food they already know (Fig. 2).

Social influences on feeding propensity

Rationale

In light of the fact that I found individual learning to exist in locusts and in light of the fact that locusts had a greater tendency to eat when placed in pairs (see training phase of chapter 1), I decided to test whether the presence of a conspecific would influence the locusts' feeding behavior. In this experiment I used a social treatment and a solitary treatment. In the social treatment, I observed the focals feeding in the presence of a conspecific; in the solitary treatment I observed the focals feeding alone. I predicted that due to the effect of social support, which can cause reduced fear when in groups, the presence of the conspecific would cause the focal to approach the food and start feeding faster.

Experiment 3: Social influences on feeding latency

Methods

The general methods and apparatus were similar to experiment 1 so I focus here on methods that are specific to this experiment. On day 1, I collected 5th instar nymphs and placed them together in a large cage with plain powder and water. On day 2, I divided the nymphs into two groups, the focals and the influence group. I placed the focals individually into small cages with plain powder and water for 24h. I marked locusts of the influence group with whiteout liquid and kept them in the large cage with plain powder and water. On day 3, I placed on focal and each test cage, and introduced 10 marked locusts into 10 of the focal cages, while 10 focals remained alone. I placed a dish containing cinnamon flavoured food inside each cage, either on the right or left side of the cage. The cinnamon flavoured food was novel to all locusts. I then observed the focal locusts for 2h and recorded their feeding latencies. I tested 30 focals in pairs and 29 focals alone.

Results

The feeding latency in minutes was significantly shorter for focals in the social (N=30) than in the solitary (N=29) condition (ANOVA: $F_{1,57} = 13.512$, $P < 0.005$; Fig. 3).

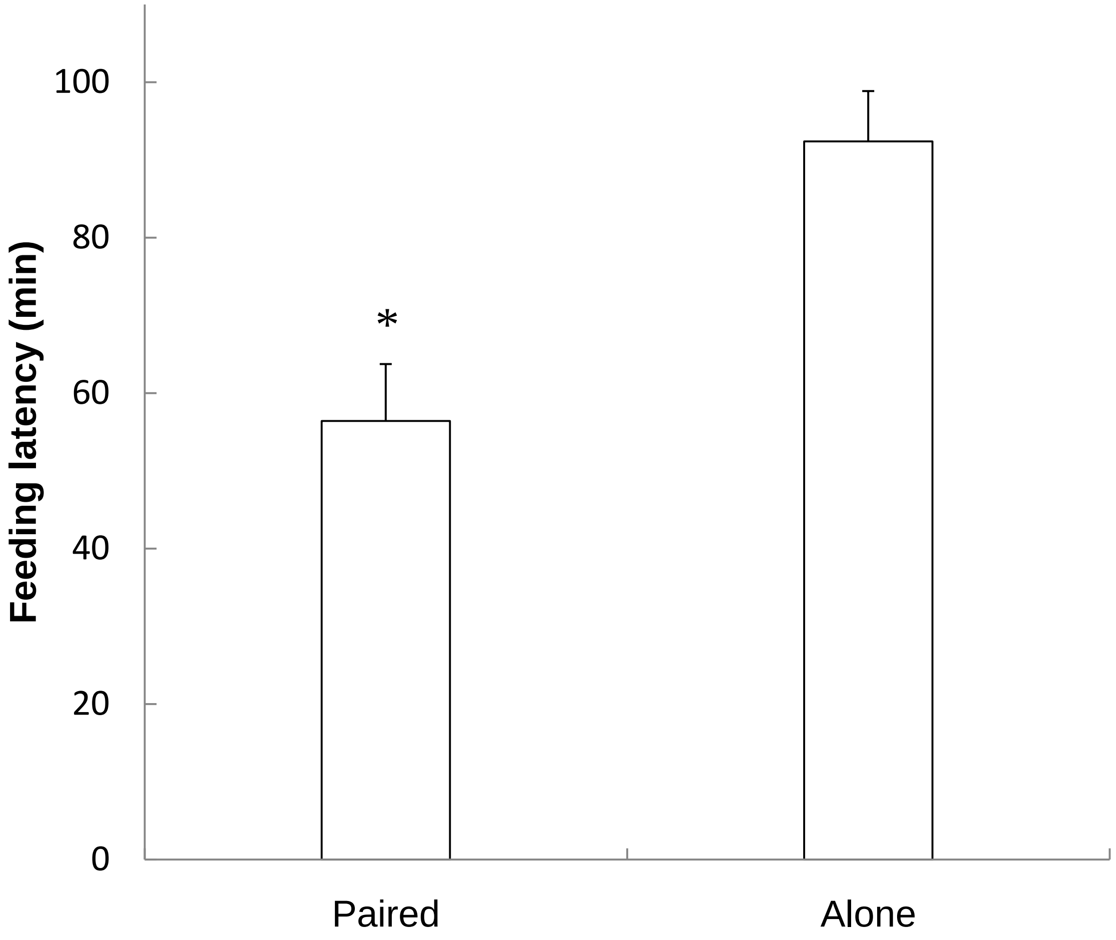

Fig. 3: the mean (+1 SE) of feeding latency for focals that were either paired with another locust (Paired, N=30) or placed alone in the cage (Alone, N=29).

Discussion

Experiment 3 suggested that nymphs' feeding propensity is influenced by conspecifics. When housed with another individual, nymphs will approach the food faster than when housed alone (Fig. 3).

Local enhancement

General Methods

In all local enhancement experiments, with the exception of experiment 5.1, I used 35x23X14cm clear plastic boxes with white plastic covers. I cut a rectangular hole in the middle of each cover, and covered it with wire screen. In experiment 5.1 I used the 16x12x10cm boxes described in chapter 1. For each experiment I created different enclosures inside the cage that held an influence group of locusts. All experiments were conducted while using either powdered food as described in chapter 1 or wheat seedlings.

Experiment 4: The influence of local enhancement on position in a cage

Rationale

In this experiment I tested whether the presence of a group of conspecifics on one side of the cage would influence a locust's choice of perching location inside the cage. This was an attempt to replicate the results of Roessingh and colleagues (1993) which suggested that 5th instar locust nymphs (*Schistocerca gregaria)* were attracted to conspecifics in a cage. I predicted that the locusts would show a preference for the side of the cage that contained the influence group.

Methods

In this experiment, the cages included two wire screen chambers on opposite sides of the cage. I placed the cages between two lamps, thus making the wire screen chambers brighter than the rest of the cage. I covered the middle portion of each cage (the section between the wire screen chambers) with a sheet of parchment paper which I replaced after each run of observation. This area was divided into three portions: right, middle and left (Fig. 4).

On day 1, I collected the models and placed them in a large cage with plain powder and water. On day 2, I collected the focals and placed them in a similar cage with plain powder and water. On day 3, I placed five models inside one of the wire screen chambers in each cage. The chamber containing the models was alternated between the six test boxes so that 3 boxes contained models on the right side and 3 boxes contained models on the left side. After a 10 minutes habituation period, I introduced the focals into the cages in the following manner: I placed each focal in a small circular container, 5cm in diameter and 3cm high, which I then placed in the middle of the test cage. I gave the focals 2 minutes to habituate, after which I removed the lid from the containers and the focals were allowed to climb out. The focals were observed for 20 minutes from the moment the lid was removed and the time spent in each side of the cage (right or left) was recorded, as well as the first side visited during each test.

For each locust, I calculated the proportion of time spent in the side near the influence group out of the total time spent on both sides.

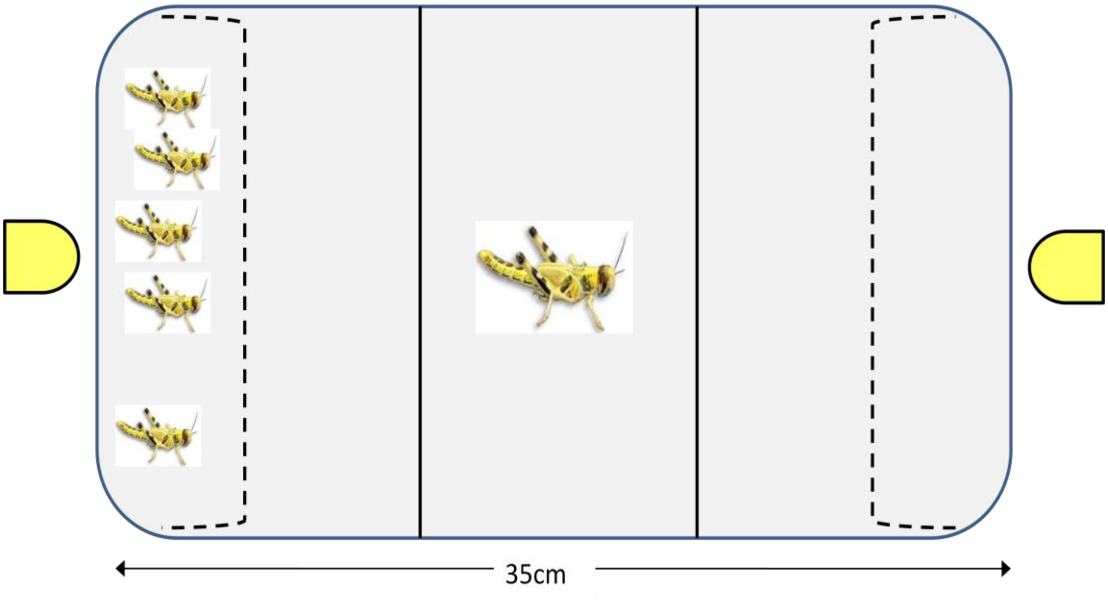

Fig. 4: apparatus for experiment 4. The main area of the cage was divided into three portions. The focal was released in the middle point of the cage and was observed while choosing a perch location. As seen in the figure, one side contained a group of models.

Results

The focal locusts (N=35) did not show a significant preference for the side that contained the models (Wilcoxon signed-ranks test: Z=-1.292, P=0.196; Fig. 6). Neither did the focals touch the side near the models first (binomial test: test value = 0.5, 0.57 near vs. 0.43 far, P=0.5).

Discussion

In experiment 4, the locust nymphs did not prefer to perch at the side of the cage that contained conspecifics. Gregarious nymphs live in large groups, but do not seem to prefer the proximity of conspecifics in the settings of this specific experiment. These results contradict the findings of Roessingh and colleagues (1993), but confirm the findings of Sword (2003).

Experiments 5.1-5.3: Local enhancement and feeding location

Rationale

In this series of experiments, I tested whether the presence of a conspecific would influence a locust's choice of feeding location. Although I did not find attraction to conspecifics without the presence of food, I theorized that, in the presence of food, focals might be more likely to join conspecifics. I predicted that locusts can benefit from local enhancement when choosing a food patch, and therefore locusts would prefer feeding closer to conspecifics over feeding far from them.

5.1 Nymphs and plain powder

Methods

In this experiment, the cages included two wire screen chambers on opposite corners of the cage and I used clear Petri dishes for food (Fig. 5).

On day 1, I collected the models and placed them in a large cage with plain powder and water. On day 2, I collected the focals and placed them in a similar cage with plain powder and water. On day 3, I placed the focals individually into small cages with plain powder and water for 24h. On day 4, I placed one model in one of the wire screen chambers in each cage. I alternated the side that contained the model so that half the cages had a model on the left side and half the cages had a model on the right side. Each screen chamber contained a food dish with plain powder which I placed half inside the chamber and half outside of it, making the dish accessible from both sides of the screen (Fig. 5). After a 10 minutes habituation period, I placed a focal in the main area of each cage. Focals were observed for 1h and the duration of feeding bouts was recorded.

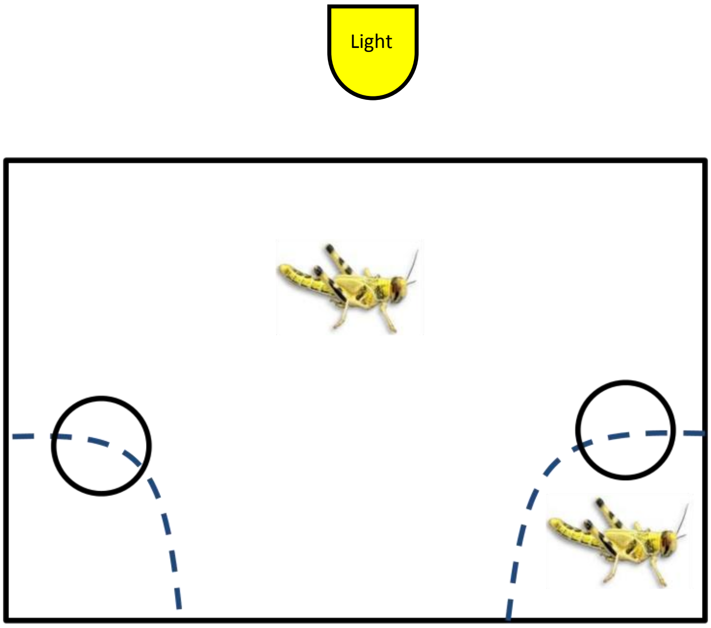

Fig. 5: apparatus for experiment 5.1. A wire screen enclosure was placed in each corner, one of which contained a model. A food dish was placed half inside and half outside each enclosure to allow access from both sides of the wire screen.

Results

The focals (N=39) did not show a significant preference for the food dish near the models over the other food dish (Wilcoxon signed-ranks test: *Z* =-0.059, P=0.953; Fig. 6).

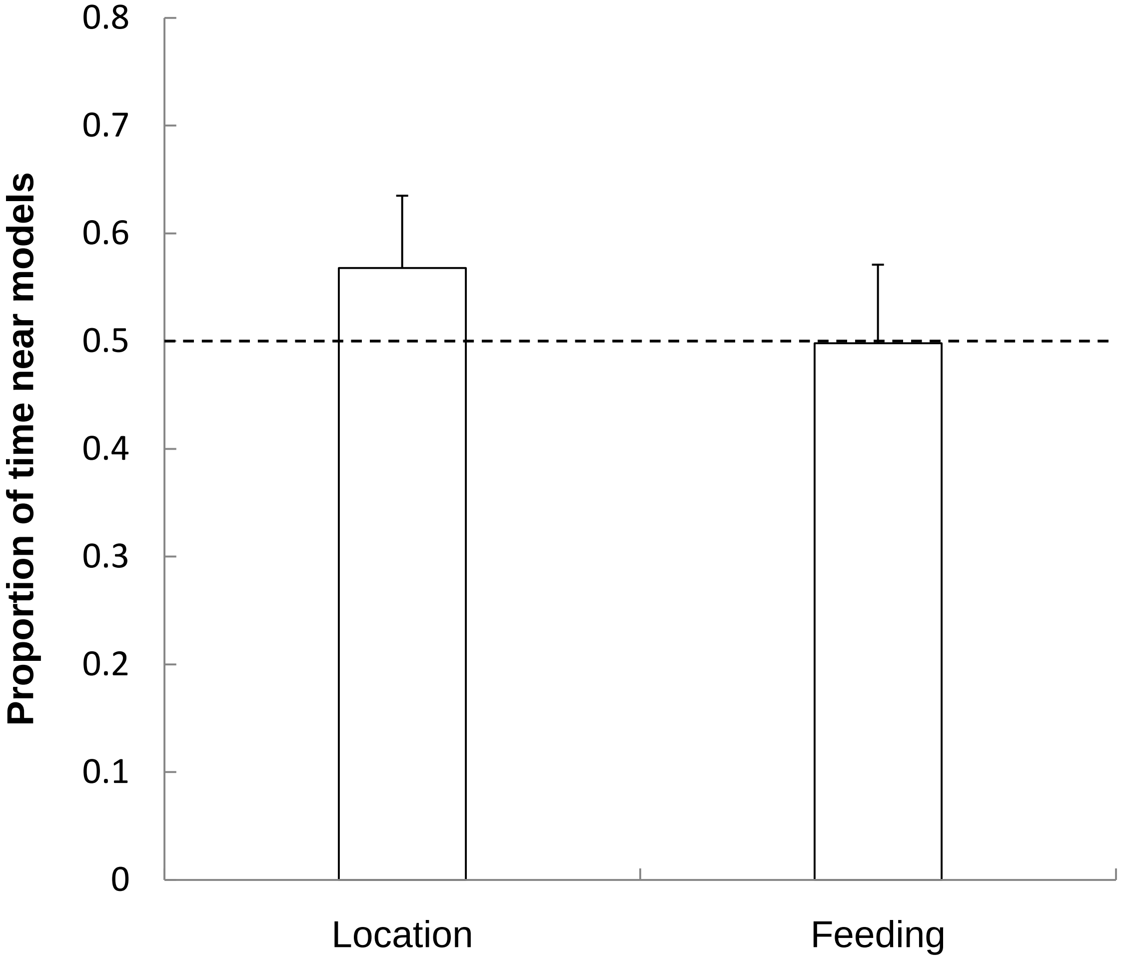

Fig. 6: the mean (+1 SE) proportion of time spent near models by focals (N=35) in experiment 4 (Location) and the proportion of time focals (N=39) spent feeding near the models in experiment 5.1 (Feeding).

5.2 Nymphs and wheat

Methods

In this experiment, I placed two cylindrical enclosures in each side of the cages. The enclosures consisted of cups were 8cm dia. X 10cm clear plastic with a rectangular 4x3cm screened window (Fig. 7).

On day 1, I collected the newly moulted 5th instar models and focals and placed them in separate large cages with wheat seedlings. On day 2 at 0800 hours I divided the focals into groups of 6 and removed the food from the cages for a 2h starvation period. At 0900 hours, I placed two models inside one of the enclosures in each cage. The enclosure containing the models was alternated between the six test boxes so that 3 boxes contained models on the right side and 3 boxes contained models on the left side. I placed a few wheat seedlings at each side of the cage. One clump was close to the models and the other clump was close to the empty enclosure. I ensured that the wheat clumps were as identical as possible in size and amount. At 1000 hours, I introduced the focals into the cages in the same manner described in experiment 4. The focals were observed for 30 minutes from the moment the lid was removed and the time spent feeding on clump of wheat (right or left) was recorded.

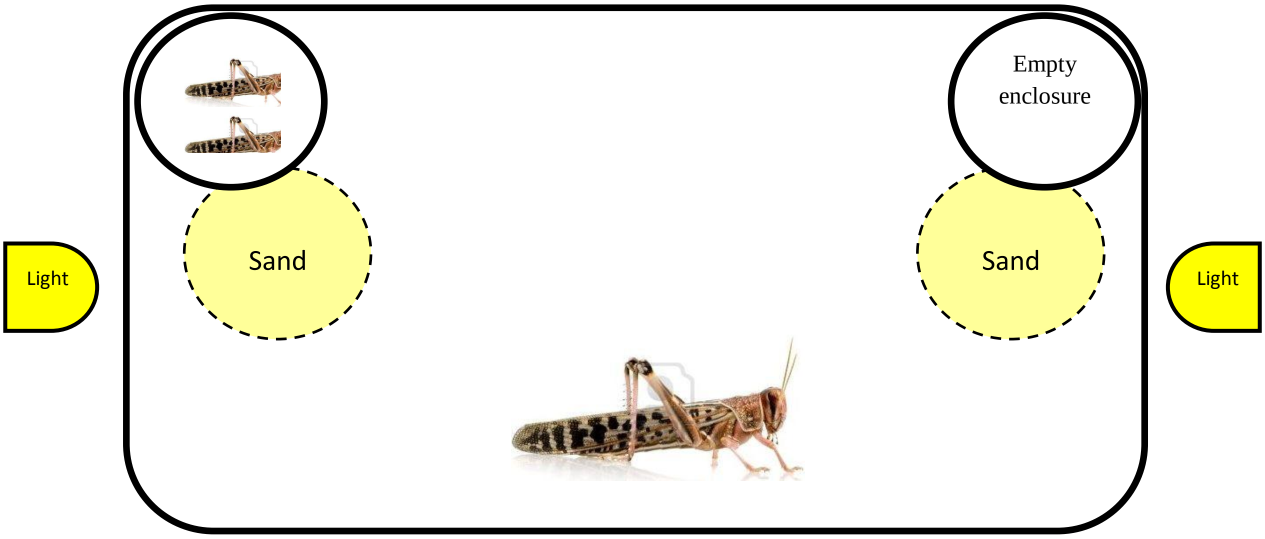

Fig. 7: apparatus for experiments 5.2, 5.3 and 8. The top of the sand cup is level with the floor of the cage. Each enclosure had a small window covered in wire screen and facing toward the sand. For experiments 5.2 and 5.3, a piece of wheat was placed on each sand patch.

Results

The focals (N=21) did not show a significant preference for the wheat clump that was located near the models over the other wheat clump (Wilcoxon signed-ranks text: Z = -0.428, P = 0.669; Fig. 8). Average feeding duration was 11.75 ± 1.1 min (mean ± SE).

5.3 Adult locusts and wheat

Methods

The methods and protocol for this experiment were identical to those described in experiment 5.2, except that I used sexually mature adult females.

Results

The focals (N=26) showed a significant preference for the wheat clump that was located near the models over the other wheat clump (Wilcoxon signed-ranks text: Z= -2.462, $P < 0.05$; Fig. 8). Average feeding duration was 4.2 ± 0.55 min (mean ± SE).

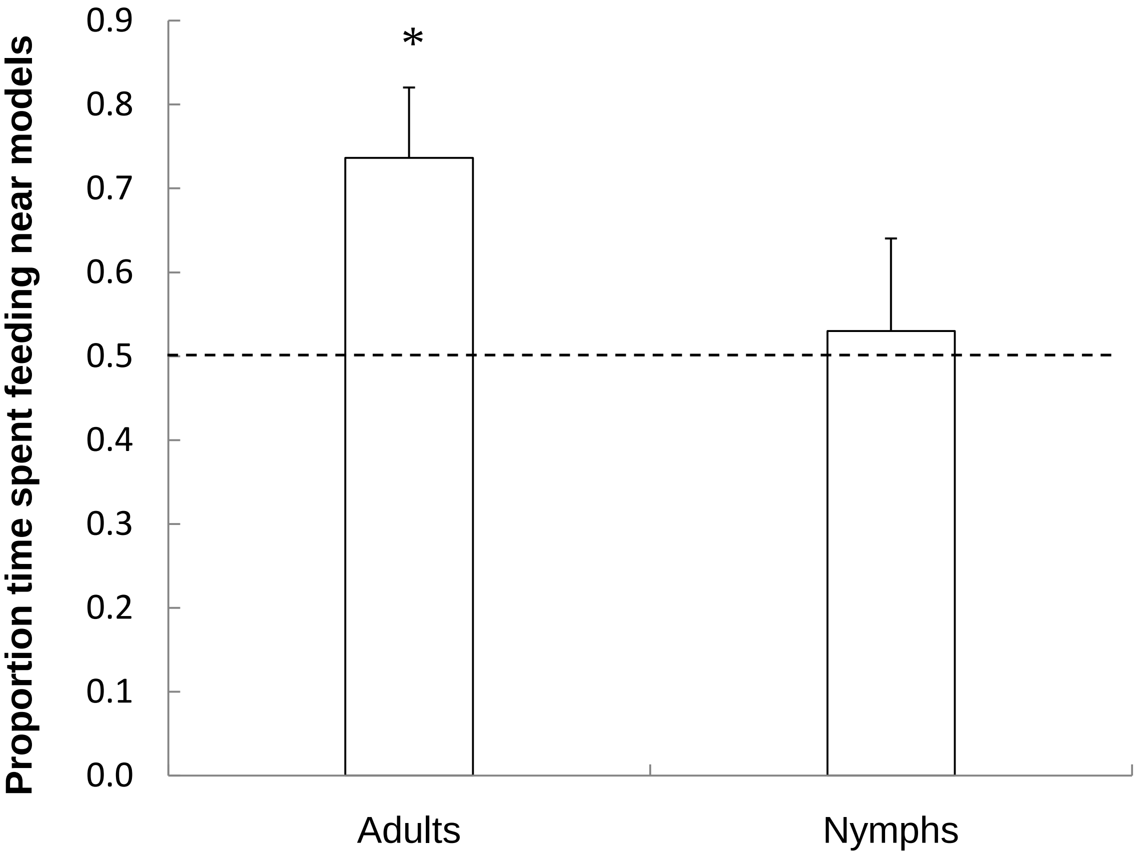

Fig. 8: the mean (+1 SE) proportion of time spent feeding near the models by adults (N=26) or by fifth instar nymphs (N=21).

Discussion

In experiment 5, fifth instar locusts did not show a tendency to feeding close to conspecifics. Hungry nymphs approached food quickly but did not show a side preference for the side that contained models. Adult female locusts did show a tendency to feeding close to conspecifics. After a starvation period, adult females preferred to feed on the wheat patch which was close to conspecifics over the other wheat patch.

Social learning of food preference

Rationale

In these experiments I tested whether locusts would prefer a novel food after interacting with models who previously fed on that food, or after observing models feeding on that food. This was a simulation of a scenario in which locusts or nymphs join older ones in a marching band (Simpson & Sword, 2008) or a swarm. When making a diet choice, inexperienced locusts may rely on the sight of other locusts feeding on a plant or on residual odours of that plant on more experienced locusts. I predicted that locusts would prefer a novel food that was associated with a model over another novel food.

Experiment 6: Social learning with fifth instars and flavoured powder

General Methods

The general methods for these experiments are similar to experiment 1; therefore I will focus on the methods specific for these experiments.

6.1 Interactions with previously fed models

Methods

On day 1, I collected the models and marked them with whiteout liquid. I then separated them into two groups and placed each group in a large cage with either cinnamon or cumin flavoured food and water. On day 2, I collected the focals and placed them in a large cage with plain powder and water. On day 3, I placed the focals in pairs into small boxes with plain powder and water for 24h. On day 4, at 0800 hours, I removed the food from the focals' cage for a 2h starvation period. At 1000 hours I placed each focal in a cage with two models who have previously fed on cinnamon or cumin flavoured food. Before placement in the cages, I enhanced odour cues on the models by dusting them with the relevant raw spice. I allowed the focals and models to interact for two hours without the presence of any food. At 1200 I 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. I alternated the dish location in the cage so that half the cages contained cinnamon on the right and half the cages contained cinnamon of the left. All but 2 of the focals fed during the test phase. An observer blind to the focals' experience recorded their feeding behaviour for 1h.

Results

The locusts (N=38) did not prefer the novel food consumed by the models over the other novel food (Mann-Whitney test: *U*=152, N=38, P=0.337; Fig. 9). There was no significant side preference (Mann-Whitney test: *U*=142.5, P=0.195).

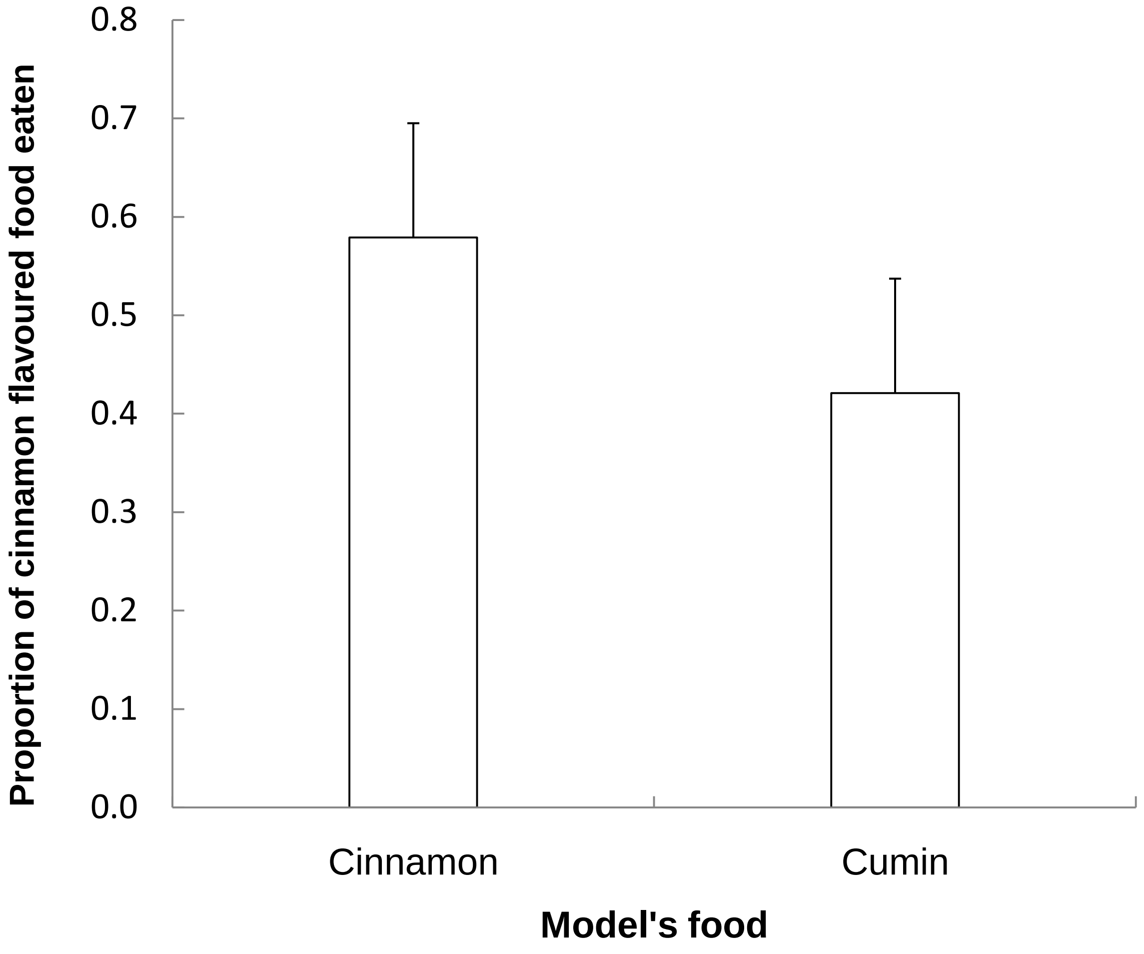

Fig. 9: the mean (+1 SE) proportion of cinnamon flavoured food eaten by locust nymphs (N=38) after interacting with models who have previously fed on either cinnamon or cumin flavoured food.

6.2 Observing models through a screen

Methods

For this experiment, I used the same small cages described in experiment 1, with an added screen which divided the cage into two chambers. The bigger chamber housed the models and the food, and was closer to the light source, and the smaller chamber housed the focals (Fig. 10). Days 1-3 were identical to those in experiment 6.1. On day 4, at 0800 hours, I removed the food from the focals' and models' cages for a 2h starvation period. At 1000 hours I placed two models in each cell, together with one dish of either cinnamon or cumin flavoured food. The location of the dishes was alternated between the cages. After allowing 10 minutes for habituation, I placed one focal in each of the adjacent chambers. I observed the locusts until all the models fed, approximately 15 minutes. In many cases, focals were observed perching on the dividing screen or trying to cross to the other chamber through the top or bottom parts of the screen. When all the models had fed, I transferred the focals individually into the test cages. Focals habituated to the test cages for 30 minutes, at which time I placed two food dishes with cinnamon and cumin flavoured foods in each cage. The location of the dishes was the same as in the training phase. An observer blind to the focals' experience recorded their feeding behaviour for 1h.

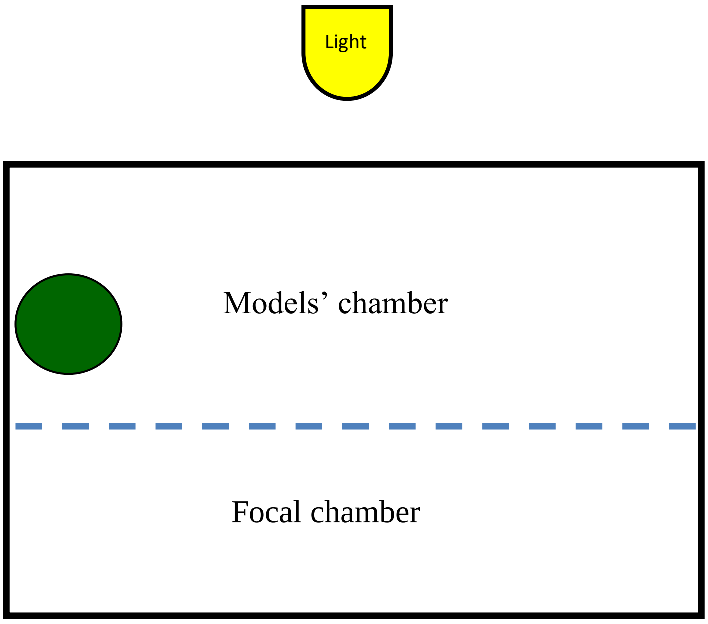

Fig. 10: apparatus for experiments 6.2 and 7. The focal and models were separated by a wire screen. The focals could observe the models feeding on a novel food but did not have access to the food. The novel food was placed either on the right side or the left side of the cage.

Results

The locusts (N=19) did not prefer the novel food consumed by the models over the other novel food (Mann-Whitney test: *U*=49, N=19, P=0.609; Fig. 11). There was no significant side preference (Mann-Whitney test: *U*=37, P=0.418).

Experiment 7: Social learning with adults and two plant spp.

Methods

Methods for this experiment were identical to those of experiment 6.2, except that I used adult females and carrot and cabbage as the novel foods.

Results

The locusts (N=32) did not prefer the novel food consumed by the models over the other novel food (Mann-Whitney test: *U*=101, N=32, P=0.341; Fig. 11). There was no significant side preference (Mann-Whitney test: *U*=91, P=0.129).

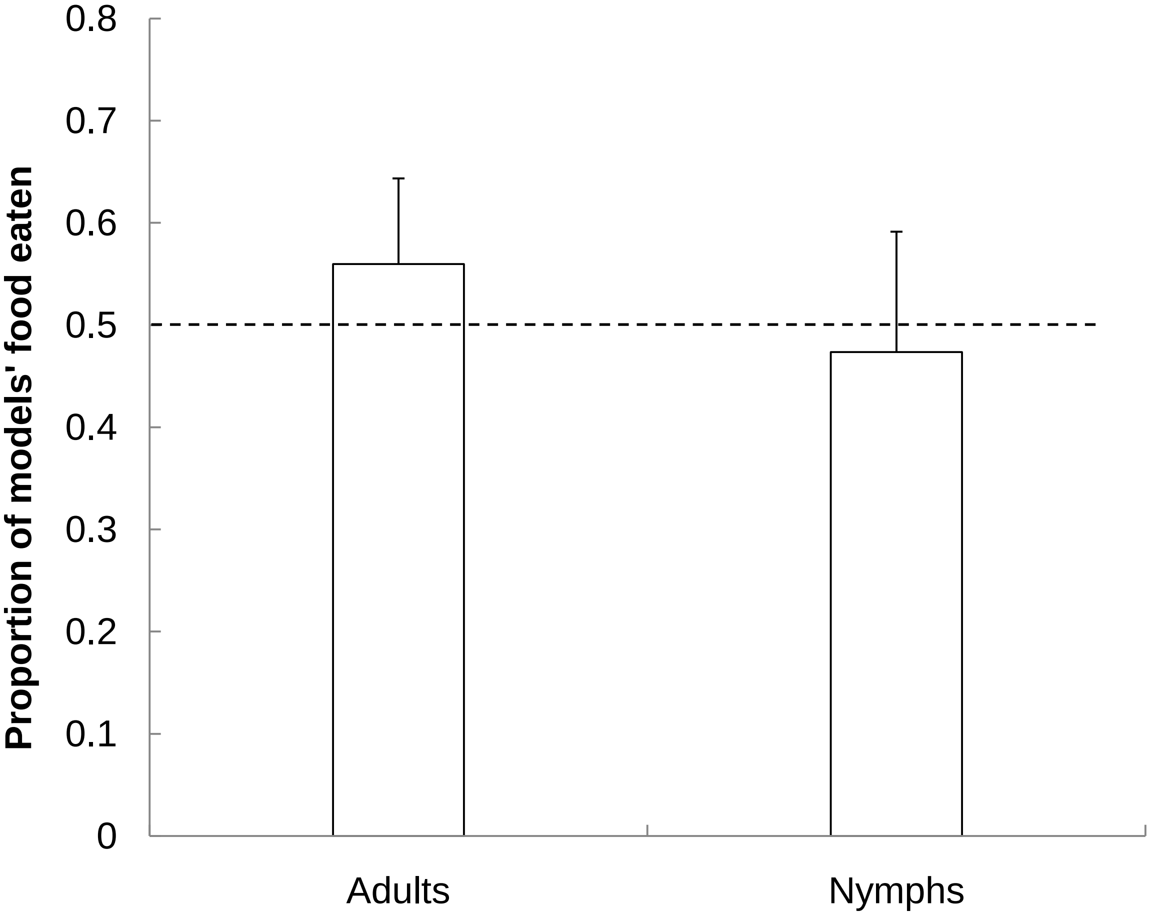

Fig. 11: the mean (+1 SE) proportion of time locusts spent feeding on the food they previously experienced with models (N_{nymphs} = 19, N_{adults} = 32). In Experiment 6.2, nymphs observed models feed on either cinnamon or cumin; in experiment 7, adults observed models feed on either cabbage or carrot.

Discussion

Experiments 6 and 7 suggested that locust nymphs and adults do not exhibit social learning when choosing between two novel diets in these settings. Social learning was not found when focals interacted with previously fed models, or when focals observed other locusts feeding on novel diets through a screen. There was no difference between nymphs and adults, neither of them showed social learning in this context.

Egg-laying

Experiment 8: Influences of local enhancement on egg-laying site choice

Rationale

In these experiments I tested whether female locusts prefer to lay eggs in a sand patch located close to other females over a patch located far from other females. I predicted that females would prefer to lay eggs close to other females.

Methods

I conducted egg-laying experiments in 35x23X14cm clear plastic boxes with wire screen covers. As an egg-laying substrate, I used moist sand. I sterilized the sand and added 15ml of water to each 100g of sand, based on the recipe in (Saini et al., 1995). I placed the sand in clear plastic cups (8cm dia. X 10cm depth) in which females laid eggs during the experiments. Each cage contained two pairs of a sand cup and an adjacent enclosure (as in experiments 5.2-5.3), one pair on each side of the cage (Fig. 7). The models and focals were fed with wheat seedlings throughout the experiments.

I used mature females as models and young, newly mature females as focals. I placed two models inside one of the enclosures in each cage, which restricted their movement and did not allow access to the sand. The focals were free to move around inside the cage and had access to both egg cups. Each cage contained one empty enclosure and one enclosure containing two models. The location of the enclosures with models was alternated between cages.

After an habituation period of 24h in a large cage with wheat seedlings, I placed the focals individually inside the text cages. After 4 days, an observer blind to the focals' experience took out the sand cups and checked each cup for egg pods. Females do not lay more than one egg pod during a period of 4 days.

Results

Females (N=18) showed a significant preference for the cup that was located closer to the models over the cup that was located further away from the models (binomial test: test value = 0.5, 0.89 near vs. 0.11 far, $P < 0.005$; Fig. 12). There was no significant preference for either side of the cage ($P=0.815$)

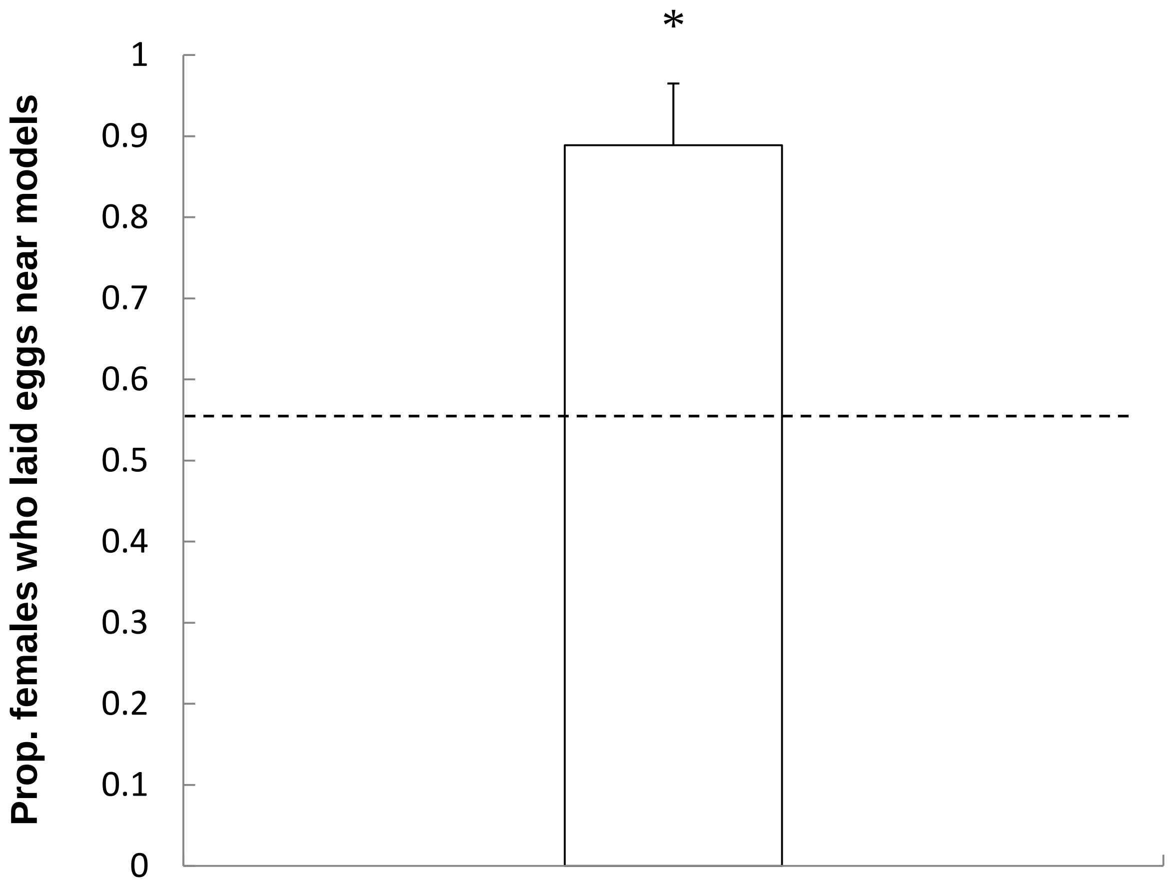

Fig. 12: the mean (+1 SE) proportion of adult females who laid eggs in the egg cup closer to the models' enclosure (N=18).

Discussion

Experiment 8 suggested that adult females are attracted to conspecifics when choosing egg-laying sites. When choosing between an empty sand patch and a sand patch which is close to other females, adult females will prefer to lay eggs closer to other females.

GENRAL DISCUSSION

Major Findings

Individual Learning

In this set of experiments, I managed to replicate the finding of individual learning based on previously experienced food. After a brief experience with a novel food (one meal), both nymphs and adult locusts learned to later prefer this food over another novel food (Fig. 2). This is a replication of the findings of Dukas & Simpson (2009), which showed that migratory locust nymphs learn to prefer food they have already experienced. Other studies have shown locusts to exhibit robust individual learning in the context of food (Behmer et al., 2005; Raubenheimer & Blackshaw, 1994).

Socially Facilitated Behaviour

I found evidence for local enhancement and social support in the context of food choice. I could not replicate the finding of nymphs being attracted to other locusts, either when choosing a perching location or a food patch (Figs 6, 8). I did, however, find that nymphs show a higher propensity to feed when placed in pairs than when placed alone (Fig. 3). Adult locusts, on the other hand, did show local enhancement in the context of food choice and were significantly more attracted to a food patch closer to conspecifics (Fig. 8). It is important to note that protocols and settings for experiments 5.2 and 5.3 were identical except that they were not conducted simultaneously, a fact that suggests a possible difference in the social interactions and preferences of locust nymphs and adults. In the course of these experiments I also found a significant difference in feeding durations between nymphs and adults, suggestive of yet another difference between nymphs' and adults' feeding patterns.

In addition to the findings in the context of food choice, I have also found evidence of local enhancement in the context of choosing an egg-laying site. When given a choice between two sand patches, adult females significantly preferred the patch that was closer to conspecifics (Fig. 12). This may support the findings in Norris (1963) which suggest that females wander around in search of a sand patch, and stop when they encounter conspecifics. In a smaller cage, the sand patch that was farther away from the other females may have been close enough to conspecifics to cause the focal females to stop and lay eggs.

Social learning

I did not find any evidence of socially influenced learning in the context of food choice. Experiments 6 and 7 showed that focal locusts did not rely on two types of social cues when choosing between two novel diets. In experiment 6.1, the focal locust nymphs interacted with previously fed models that emitted strong novel food odours, but this had no effect on the focals' later choice between two novel foods (Fig. 9). In experiments 6.2 and 7, the focal nymphs and adults could observe models feeding on a novel food through a screen which also allowed for the passage of odours, but this also had no effect on the focals' later choice between two novel foods (Fig. 11).

Adaptive Significance

As mentioned earlier, there are several reasons to foresee social learning as adaptive in gregarious locusts. Locusts are migratory and feed on numerous plant species as they travel – a choice which may affect their fitness (Despland & Simpson, 2005; Toye, 1973). With overlapping generations and some individuals in the swarm more naïve than others, locusts stand to benefit from socially influenced learning about food (Dukas, 2010). Given that I found no evidence of social learning in the context of food in locusts (Figs 9, 11), and previous attempts have also failed to find it (Dukas & Simpson, 2009), it may be prudent to consider the adaptive significance of lack of social learning in locusts in this context. Laland (2004) describes several scenarios in which social learning would be more costly and less adaptive than asocial learning. Given that locusts are polyphagous, and can even consume plants containing toxic secondary compounds when necessary (Behmer et al., 2002), asocial learning, or learning by trial and error, might not be a very costly method. Moreover, as locusts travel in huge swarms which are always on the move, possibly even due to cannibalism stress (Bazazi et al., 2008), the question of *who* to learn from might be one that is too costly to consider at too small a time window.

Local enhancement, on the other hand, may be a fitness increasing behaviour for locusts, as it may aid the initial finding of a food patch only by approaching an area in which others are feeding. In this study, I found evidence of local enhancement in adults, but not in 5th instar nymphs (Fig. 8). Given that I found nymphs to feed in much longer bouts than adults, it is possible that young nymphs may need more food than adults and thus show less regard to food choice than adults.

It is important to note that although my protocols have been designed to increase the possibility of finding social learning (young and slightly food-deprived individuals learning from older, more experienced models), it is possible that in a different scenario locusts will show social learning about food.

Future Research

I believe the results of this study provide an avenue for future research about social interactions in locusts. Below I discuss several different avenues of potential research that I think are particularly interesting and pertinent to the locust problem, and also to the understanding of social dynamics in locusts. Numerous differences have been found between the solitary and gregarious phase in locusts. These include differences in feeding behaviour and nutrient regulation (Simpson et al., 2002) and in activity levels (Sword, 2003). Differences have also been found in the learning abilities of different instars in another species of grasshopper, *Melanoplus bivittatus* (Holliday & Holliday, 1995). The differences I found in feeding behaviours and social influences between 5th instar nymphs and adults can help expand this avenue of research and aid in finding more differences in the way nymphs and adults are affected by and use social information. Other areas in which such differences might exist can be explored in order to reach a better understanding of the subject. Such research can focus on the behavioural differences or on the structural differences that might exist between nymphs' and adults' brains. Another interesting angle would be to examine the differences in nutrient regulation between nymphs and adults, which could provide further explanation to the differences in feeding behaviours.

Other future experiments can also examine the possibility of social learning in locusts using different protocols or different contexts. In this study, I replicated results indicating that females prefer to lay eggs close to other females. Females have also been shown to be attracted to egg volatiles in sand and to choose egg-laying sites that will have a gregarizing effect on the hatchlings (Bashir et al., 2000; Torto et al., 1999). Given this evidence, it may be adaptive for females to use socially learned information when choosing egg-laying sites. In my study, I made several attempts to find attraction to sand containing eggs and to develop a protocol that would test for social learning in this context. I could not replicate the findings of attraction to other females' eggs. Examining this possibility further, however, can increase understanding about social interaction in locusts and provide important information about how females choose egg-laying sites.

Contribution

Aside from Dukas & Simpson (2009), I know of no other study that has looked into social influences in the context of food choice in asocial insects. A lot of research has been done on locusts in the context of food, finding robust individual learning, nutrient regulation abilities, and specialized adaptations in the two different phases (Behmer et al., 2005; Despland, 2005; Simpson et al., 2002). Most of these studies were conducted on locust nymphs, and did not look at social influences on food choice. Sarin & Dukas (2009) tested an asocial insect, the fruit fly, for social learning in the context of egg-laying site choice, which in fruit flies is also a food substrate. While this does show a social influence in the context of food, this was not the focus, and a study which focuses only on food has not been done to the best of my knowledge.

This study is also unique for looking at social influences in adult locusts in a context other than egg-laying. Roessingh and colleagues (1993) studied the effect of gregarization on movement, activity and attraction in locusts, but while they did test several developmental stages of nymphs, no tests were done on adults. Other studies which did use adult locusts focused on egg-laying behaviours and preferences (Saini et al., 1995). Social influences were studied in this context, but a comparison to nymphs was obviously impossible.

This study provides a first glimpse into the differences that might exist between the social behaviours of adult and nymph locusts. A study in grasshoppers showed that different instar nymphs have different learning abilities (Holliday & Holliday, 1995). Differences have also been found between the brains of solitary and gregarious locusts (Ott & Rogers, 2010). Differences in the brains of adults and nymphs could provide an explanation for the different social behaviours. Another possible explanation is the existence of different social needs which might be derived from different living conditions and different nutritional needs.

Conclusions

This thesis presents evidence that gregarious locusts do not exhibit social learning in the context of food. Specifically, locusts do not rely on social learning when choosing between two novel diets. I did find evidence for social support and local enhancement, which suggest that locusts are socially influenced by conspecifics when making fitness-affecting choices. I believe that future research into these social interactions may uncover more complex social behaviours and aid to our further understanding of the evolution of social learning.

REFERENCES

Bashir, M. O., Hassanali, A., Rai, M. M., & Saini, R. K. (2000). Changing oviposition preferences of the desert locust, Schistocerca gregaria, suggest a strong species predisposition for gregarization. *Journal of Chemical Ecology*, *26*(7), 1721–1733.

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*(10), 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? *Journal of Experimental Biology*, *208*(18), 3463.

Behmer, S. T., Simpson, S. J., & Raubenheimer, D. (2002). Herbivore foraging in chemically heterogeneous environments: nutrients and secondary metabolites. *Ecology*, *83*(9), 2489–2501.

Boyd, R., & Richerson, P. J. (1988). *Culture and the evolutionary process*. University of Chicago Press.

Coolen, I., Dangles, O., & Casas, J. (2005). Social learning in noncolonial insects? *Current Biology*, *15*(21), 1931–1935.

Despland, E. (2005). Diet breadth and anti-predator strategies in desert locusts and other Orthopterans. *Journal of Orthoptera Research*, *14*(2), 227–233.

Despland, E., & Simpson, S. J. (2005). Food choices of solitarious and gregarious locusts reflect cryptic and aposematic antipredator strategies. *Animal Behaviour*, *69*(2), 471–479.

Dugatkin, L. A. (1992). Sexual selection and imitation: females copy the mate choice of others. *The American Naturalist*, *139*(6), 1384–1389.

Dukas, R. (2008). Evolutionary biology of insect learning. *Annu. Rev. Entomol.*, *53*, 145–160.

Dukas, R. (2010). Social learning in insects. Forthcoming. In: *Encyclopedia of Animal _Behavior* (Ed. by Breed, M. & Moore, J.): Elsevier.

Dukas, R., & Bernays, E. A. (2000). Learning improves growth rate in grasshoppers. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(6), 2637.

Dukas, R., & Simpson, S. J. (2009). Locusts show rapid individual learning but no social learning about food. *Animal Behaviour*, *78*(2), 307–311.

Galef Jr, B. G. (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 Jr, B. G., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *Bioscience*, *55*(6), 489–499.

Galef Jr, B. G., & White, D. J. (1998a). Mate-choice copying in Japanese quail, Coturnix coturnix japonica. *Animal Behaviour*, *55*(3), 545–552.

Galef Jr, B. G., & Wigmore, S. W. (1983b). Transfer of information concerning distant foods: A laboratory investigation of the “information-centre” hypothesis. *Animal Behaviour*, *31*(3), 748–758.

Galef, B. G., & Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, *61*(1), 3–15.

Galef, B. G., & Stein, M. (1985). Demonstrator influence on observer diet preference: Analyses of critical social interactions and olfactory signals. *Learning & behavior*, *13*(1), 31–38.

Griffin, A. S. (2004). Social learning about predators: a review and prospectus. *Learning & Behavior*, *32*(1), 131.

Heyes, C. M., & Galef Jr, B. G. (1996c). *Social learning in animals: The roots of culture.* Academic Press.

Holliday, J. L., & Holliday, N. J. (1995). Changes in learning ability and mechanism during development of grasshopper nymphs, Melanoplus bivittatus. *Physiological Entomology*, *20*(2), 109–116.

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, 333–379.

Laland, K. N. (2004). Social learning strategies. *Learning and Behavior*, *32*(1), 4–14.

Leadbeater, E., & Chittka, L. (2007). Social learning in insects—from miniature brains to consensus building. *Current Biology*, *17*(16), 703–713.

McCaffery, A., Simpson, S., & others. (1998). A gregarizing factor present in the egg pod foam of the desert locust Schistocerca gregaria. *The Journal of experimental biology*, *201*(3), 347.

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. *Current Biology*, *19*(9), 730–734.

Nieh, J. C. (2004). Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). *Apidologie*, *35*, 159–182.

Nieh, J. C. (2010). A Negative Feedback Signal That Is Triggered by Peril Curbs Honey Bee Recruitment. *Current Biology*.

Norris, M. J., & Richards, O. W. (1963). Laboratory experiments on gregarious behaviour in ovipositing females of the desert locust,(Schistocerca gregaria (Forsk.)). *Entomologia Experimentalis et Applicata*, *6*(4), 279–303.

Ott, S. R., & Rogers, S. M. (2010). Gregarious desert locusts have substantially larger brains with altered proportions compared with the solitarious phase. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1697), 3087.

Pener, M. P. (1991). Locust phase polymorphism and its endocrine relations. *Adv. Insect Physiol*, *23*(1), 79.

Raubenheimer, D., & Blackshaw, J. (1994). Locusts learn to associate visual stimuli with drinking. *Journal of Insect Behavior*, *7*(4), 569–575.

Raubenheimer, D., & Tucker, D. (1997). Associative learning by locusts: pairing of visual cues with consumption of protein and carbohydrate. *Animal behaviour*, *54*(6), 1449–1459.

Roessingh, P., Simpson, S. J., & James, S. (1993). Analysis of phase-related changes in behaviour of desert locust nymphs. *Proceedings: Biological Sciences*, *252*(1333), 43–49.

Saini, R. K., Rai, M. M., Hassanali, A., Wawiye, J., & Odongo, H. (1995). Semiochemicals from froth of egg pods attract ovipositing female Schistocerca gregaria. *Journal of Insect Physiology*, *41*(8), 711–716.

Sarin, S., & Dukas, R. (2009). Social learning about egg-laying substrates in fruitflies. *Proceedings of the Royal Society B*.

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*. Oxford University Press, USA.

Simpson, S. J., McCAFFERY, A. R., & HAeGELE, B. F. (1999). A behavioural analysis of phase change in the desert locust. *Biological Reviews*, *74*(04), 461–480.

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*(9), R364–R366.

Simpson, S. J., & Abisgold, J. D. (1985). Compensation by locusts for changes in dietary nutrients: behavioural mechanisms. *Physiological Entomology*, *10*(4), 443–452.

Simpson, S. J., Raubenheimer, D., Behmer, S. T., Whitworth, A., & Wright, G. A. (2002). A comparison of nutritional regulation in solitarious-and gregarious-phase nymphs of the desert locust Schistocerca gregaria. *Journal of Experimental Biology*, *205*(1), 121.

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. *Journal of insect physiology*, *49*(7), 709–717.

Torto, B., Assad, Y. O. H., Njagi, P. G. N., & Hassanali, A. (1999). Evidence for additional pheromonal components mediating oviposition aggregation in Schistocerca gregaria. *Journal of chemical ecology*, *25*(4), 835–845.

TOYE, S. A. (1973). Effects of food on the development of the Desert Locust, Schistocerca gregaria (Forskal). *Journal of Entomology Series A, General Entomology*, *48*(1), 95–102.

Uvarov, S. B. (1966). GRASSHoppers and locusts. *A handbook of general acridology. Volume I. Anatomy, physiology, development, phase polymorphism, introduction to taxonomy.*

Valsecchi, P., & Galef Jr, B. G. (1989d). Social influences on the food preferences of house mice (Mus musculus). *Int J Comp Psychol*, *2*, 245–256.

Von Frisch, K. (1967). The dance language and orientation of bees.

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