

## RESEARCH ARTICLE

Collective selection of food patches in *Drosophila*Mathieu Lihoreau<sup>1,\*,#,¶</sup>, Ireni M. Clarke<sup>1</sup>, Jerome Buhl<sup>1,§</sup>, David J. T. Sumpter<sup>2</sup> and Stephen J. Simpson<sup>1</sup>

## ABSTRACT

The fruit fly *Drosophila melanogaster* has emerged as a model organism for research on social interactions. Although recent studies have described how individuals interact on foods for nutrition and reproduction, the complex dynamics by which groups initially develop and disperse have received little attention. Here we investigated the dynamics of collective foraging decisions by *D. melanogaster* and their variation with group size and composition. Groups of adults and larvae facing a choice between two identical, nutritionally balanced food patches distributed themselves asymmetrically, thereby exploiting one patch more than the other. The speed of the collective decisions increased with group size, as a result of flies joining foods faster. However, smaller groups exhibited more pronounced distribution asymmetries than larger ones. Using computer simulations, we show how these non-linear phenomena can emerge from social attraction towards occupied food patches, whose effects add up or compete depending on group size. Our results open new opportunities for exploring complex dynamics of nutrient selection in simple and genetically tractable groups.

**KEY WORDS:** Aggregation, *Drosophila melanogaster*, Collective behavior, Foraging, Fruit flies, Individual-based model, Social attraction

## INTRODUCTION

Social behavior is widespread and varies across developmental stages, taxonomic groups and ecological contexts (Bourke, 2011). Over recent years, simple model organisms such as the common fruit fly *Drosophila melanogaster* have been increasingly used to explore the physiological bases of social interactions (Dubnau, 2014; Sokolowski, 2010). Although relatively little is known about *D. melanogaster* behavior in nature, adults tend to form temporary aggregations on fermenting fruits, where they feed, mate and oviposit (Reaume and Sokolowski, 2006). Fruits also serve as primary habitat and source of nutrients for the developing larvae (Wertheim et al., 2005), thereby creating considerable potential for social interactions. Laboratory studies in which the composition and size of *D. melanogaster* groups could be manipulated have begun to reveal the rich social repertoire of adults and larvae, highlighting many similarities with socially more complex animals, such as the ability to recognize familiar conspecifics (Lizé et al., 2014), establish dominance relationships (Yurkovic et al., 2006), develop

stable social interaction networks (Schneider et al., 2012) or copy the food and mate choices of more experienced individuals (Battesti et al., 2012, 2015; Mery et al., 2009). However, despite the growing interest in the social biology of *D. melanogaster*, collective dynamics by which groups initially form and disperse on food resources have received little attention (see Prokopy and Roitberg, 2001; Wertheim et al., 2005 and references therein).

Social and competitive interactions can have a crucial impact on the feeding choices and acquisition of nutrients by individuals, ultimately affecting fitness traits such as growth, reproduction and lifespan (Lihoreau et al., 2014, 2015). In gregarious species, these interactions often lead to complex group dynamics such as the collective decision to exploit the same feeding site among several alternatives of various qualities (Conradt and Roper, 2005). Research on arthropod swarms (e.g. midges, Attanasi et al., 2014; acari, Mailleux et al., 2011; ants, Sasaki et al., 2013; bees, Seeley et al., 2012), fish schools (Ward et al., 2011), bird flocks (Ballerini et al., 2008), mammal troops (Strandburg-Peshkin et al., 2015) and human crowds (Moussaïd et al., 2011) shows how consensus decisions are typically reached via mechanisms of quorum sensing and networks of feedback loops that disproportionately amplify or reduce the responses of individuals to social stimuli (Camazine et al., 2001; Couzin, 2009; Sumpter, 2010). Through transfer and collective processing of social information, grouped individuals can make faster and/or more accurate decisions than isolated conspecifics, an emergent property of collective decisions known as ‘swarm intelligence’ (Krause et al., 2010; Sumpter and Pratt, 2009). Ant colonies, for instance, rapidly allocate their workforce towards the richest or the largest source of sucrose when presented with two or more alternatives (Detrain and Deneubourg, 2008).

Although group behaviors have long been known in *D. melanogaster* (Del Solar, 1968), only recently have these dynamics been re-examined within the framework of collective animal behavior, demonstrating how self-organized escape responses can emerge from contact interactions among individuals (Ramdya et al., 2014). This novel approach raises the question of whether flies, just like ants, can collectively decide to exploit selected resources in their environment. Previous studies in *D. melanogaster* have involved situations in which flies were observed aggregating in uniform environments, such as a large food patch (Durisko et al., 2014), or choosing one of several food patches of differing qualities (Bartelt et al., 1985; Durisko and Dukas, 2013; Tinette et al., 2004). Although these observations constitute an important first step, a comprehensive assessment of the mechanisms driving collective foraging decisions requires disentangling the attractive power of food itself from that of conspecifics, or their potential interactive effects. This approach necessitates observing groups in the presence of two or more identical, mutually exclusive options. Only in these experimental conditions, departure from a symmetrical distribution of choices by individuals can demonstrate a collective decision arising solely from social interactions (Amé et al., 2006; Beckers et al., 1990). Comparing the collective

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dynamics in groups of various sizes may then inform about the nature and the strength of the social amplification rules at work (Sumpter and Pratt, 2009; Jeanson et al., 2012).

Here we investigated the dynamics of collective foraging decisions by fruit flies *D. melanogaster* and their variation with group size and composition. We tested groups in binary choices situations between two food patches, equal in both quantity and balance of nutrients. Using different group types, we compared the effects of developmental stage, sex, mating status and group size on the dynamics and magnitude of asymmetrical distributions of individuals on patches, and explored the mechanisms involved with simulations of an individual-based model. We hypothesized that both speed and magnitude of collective decisions would increase with the number of individuals in the group.

MATERIALS AND METHODS

Flies

We cultured fruit flies (*Drosophila melanogaster* Meigen 1830, Canton-S, Bloomington *Drosophila* Stock Center, IN, USA) on a standard yeast-sugar medium at 25°C, 60% humidity, under a 12 h:12 h light:dark cycle (Lee et al., 2008). To obtain experimental individuals, we collected virgin adults within 2 h of eclosion from the pupae and maintained them in groups of 50 (either 50 females, or 25 males with 25 females) in 250 ml bottles with standard food medium. Under these conditions, males and females in the mixed groups could freely copulate. We composed the experimental groups 72 h later with virgin females, mated females or mated males, and food-deprived them in 30 ml vials containing a humidified piece of cotton wool for 12 h. To obtain larvae, we placed mated females in egg-laying bottles containing standard food medium for 2 h. We composed the experimental groups 72 h later with second instar larvae that had emerged from the eggs and food-deprived them in empty 55 mm Petri dishes for 1 h. Compositions, sizes and numbers of experimental groups are detailed in Table 1.

Food patches

We tested adults and larvae with a nutritionally balanced diet made of a 1:2 ratio of protein to carbohydrate at 180 g total nutrients per liter (22.23 g of sucrose, 31.77 g of yeast hydrolysate enzymatic, 3 g of agar in 200 ml of distilled water) (Lee et al., 2008). For testing adults, we set 2 ml of diet in 55 mm Petri dishes. Because aggregated flies typically maintain an average inter-individual

distance of 2.5 mm (Simon et al., 2012), each food patch could hold more than 200 adults. For testing larvae, we set 1.2 ml of diet in 22 mm circular wells cut from an 8 ml layer of agar-gelled water (30 g l<sup>-1</sup>) in an 85 mm Petri dish. Each food patch could hold more than 50 larvae.

Binary choice tests

Each group was given a simultaneous choice between two identical food patches. Adults were tested in 350×260 mm clear plastic arenas containing two food patches 120 mm apart (Fig. S1). For testing larvae, we used 85 mm Petri dishes containing two food patches 30 mm apart (Fig. S2). In both setups, we positioned a webcam (Logitech c250, Fremont, CA, USA) above each food patch. Webcams were programmed with Zone Trigger (Omega Unfold, Quebec, Canada) to record images every minute for 1 h, starting with the introduction of a group into the observation arena. We conducted all tests under far red light (LED bulb 625–630 nm, Rubin-Lacaque, Valdoie, France) to which fruit flies are not sensitive (Heisenberg and Buchner, 1977). All observations were started at 10:00 h (i.e. 2 h after the beginning of the light phase of the photocycle). At the beginning of each test, we released the flies in the arena by opening the lid of the small Petri dish (in the case of larvae) or vial (in the case of adults) in which they were maintained prior to the observations. The number of individuals on foods was monitored every minute using automated image capture and analysis.

Image analysis

We used ImageJ (National Institute of Health, Bethesda, MD, USA) to analyze each of the 46,623 images acquired during the behavioral tests. Dark particles (between 5 and 15 pixels) on the food background were automatically counted as individuals (see details in Fig. S3). From these data, we reconstructed the complete dynamics of patch exploitation by flies, detailing the number of individuals on each food patch at every time step. The raw data are provided in Table S1.

Individual-based model

We developed a model replicating our binary choice test conditions. Based on the experimental results, in the model we assume that each fly performs a search that is partly random, but biased by the position and the number of individuals feeding at each of the patches. The more individuals that are feeding at the patch, the more attractive it is. Social attraction is mediated by long-range chemical communication, for instance, through the perception of the volatile sex pheromone 11-*cis*-vaccenyl acetate (cVA) known to attract flies over distances larger than the maximal dimensions of our observation arena (Wertheim et al., 2005).

We make the simplifying assumption that one individual is released at a time. The first fly lands with equal probability 0.5 on either of the two patches. Subsequent flies then perform a random walk from the release site at the origin (0,0) towards the food sources. In the experimental setup, the distance between the two food patches is *D*=120 and the distance from release site to each food patch is *L*=280 (see experimental setup in Fig. S1). From these we determined *a* to be a unit vector pointing from the release site towards patch A and *b* to be a unit vector pointing to patch B, i.e.:

$$\vec{a} = \frac{1}{L} \left( \frac{D/2}{\sqrt{L^2 - D^2/4}} \right)$$

(1)

Table 1. Composition of the experimental groups

Group composition	Group size	No. of groups	Tests with significant asymmetry (%)
2nd instar larvae	50	80	55.75
Virgin females	50	60	28.89
Mated males	50	90	25.00
Mated females	4	34	29.41
	10	36	38.89
	20	88	32.95
	30	84	46.43
	40	128	46.09
	50	81	51.85
	100	42	61.90
	200	42	30.95

The proportion of tests in which the final distribution of individuals on patches was different from random (sign test with probability 0.5 of choosing either side, *P*<0.05) varied across group types ( $\chi^2=37.06$ , d.f.=10, *P*<0.001).

and

$$\bar{b} = \frac{1}{L} \left( \frac{-D/2}{\sqrt{L^2 - D^2/4}} \right). \quad (2)$$

We assume that the flies are attracted to both sites, with the strength of attraction depending on the number (proportion) of flies that have already gone to that site, as is standard in models of group decision-making (Amé et al., 2006; Beckers et al., 1990). The difference in our case is that we explicitly model movement in space. The mean direction of a foraging fly is determined by the sum of the two attractive forces, i.e.:

$$\bar{v} = A\bar{a} + B\bar{b} = \frac{1}{L} \left( \frac{(A-B)D/2}{(A+B)\sqrt{L^2 - D^2/4}} \right), \quad (3)$$

where the number of individuals already on the two patches are denoted  $A$  and  $B$ . From this, we model the change in position of an individual fly as:

$$\begin{pmatrix} x_{t+1} \\ y_{t+1} \end{pmatrix} = \begin{pmatrix} x_t \\ y_t \end{pmatrix} + \hat{v} + c \begin{pmatrix} e_t \\ 0 \end{pmatrix}, \quad (4)$$

where  $\hat{v}$  is a normalized direction vector, i.e.  $\hat{v} = \bar{v}/\bar{v}$ . The variable  $e_t$  is a normally distributed random number with mean 0 and variance 1 that models unpredictability in the fly's path at time  $t$ . The constant  $c$  is a weighting of the importance of random noise. Larger values of  $c$  imply weaker attraction to the food and greater randomness.

An individual performs this random walk until it is level with the two food patches, i.e.:

$$y_t = \sqrt{L^2 - D^2/4}. \quad (5)$$

We assume that at the end of this random walk the simulated fly goes to the food patch that it is nearest to. So if it arrives at patch A, we set  $A=A+1$ . The next fly then commences its walk. We omit the possibility that flies could leave food patches, as departures were only infrequently observed in our experiments.

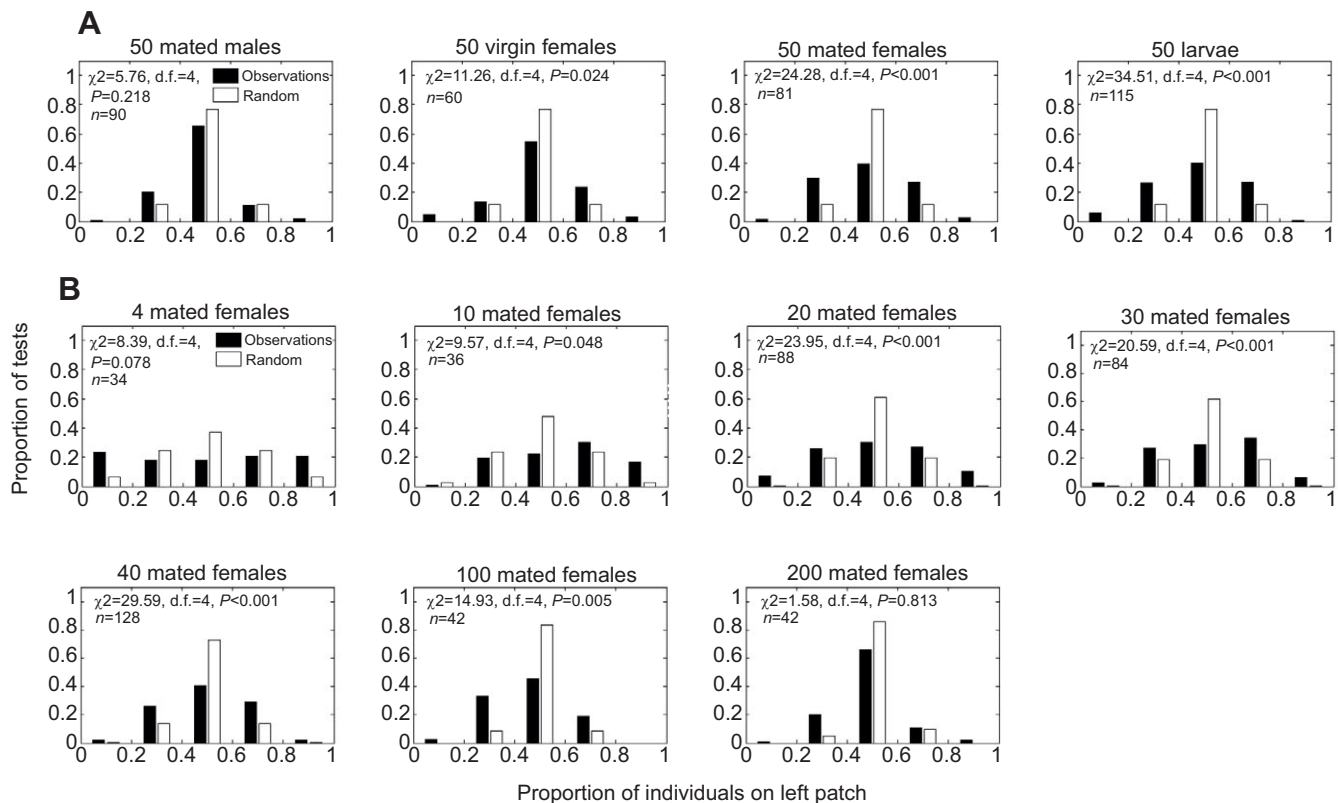
Our model is a variation of a reinforced random walk (Stevens and Othmer, 1997), but the reinforcement only occurs when the individuals have reached the target. All simulations were run in MATLAB R2013b (MathWorks, Natick, MA, USA). The complete code is available on request from the corresponding author.

## RESULTS

### Effects of developmental stage, sex and mating status

First we tested whether fruit flies of different age, sex and mating status make collective foraging decisions. Groups of 50 individuals (larvae, mated females, virgin females or males; see details in Table 1) were given a choice between two identical food patches for 1 h (Figs S1, S2).

On average,  $86.7 \pm 3.7\%$  (mean  $\pm$  s.e.m.,  $n=311$  groups) of individuals per group were found on patches by the end of the observations. This percentage was similar across group types (one-way ANOVA, effect of group type on final % of individuals on foods:  $F_{3,307}=1.11$ ,  $P=0.345$ ). Adults accumulated significantly faster on patches than larvae (one-way ANOVA, effect of group type on time elapsed until 50% of individuals were on foods:



**Fig. 1. Effect of group composition on final choices.** (A) Effect of developmental stage, sex and mating status. (B) Effect of group size. Black bars show the observed frequency distribution of individuals on the left food patch ( $n$  is the number of groups). White bars show the theoretical random distributions (0.5 probability of choosing either patch,  $n=10,000$  runs). Observed and random data were compared using chi-square tests.

$F_{3,307}=14.36$ ,  $P<0.05$ ; Tukey's HSD:  $P<0.05$  for all pairwise comparisons between adults and larvae). Presumably, adults moved much faster by flying or walking across the arena than the crawling larvae. However, virgin females, mated females and males accumulated on patches at similar rates ( $P>0.05$  for all other pairwise comparisons between adult types).

When considering all individuals on foods (population of flies on both patches), we found that the final distributions of individuals on the two patches were different from random in groups of larvae, virgin females and mated females, but not in groups of males (Fig. 1A). To further analyze these aggregative responses, we quantified an aggregation level for each group by comparing the final distribution of individuals on patches to a binomial distribution with a probability 0.5 of choosing either patch using a sign test [function `1-binocdf()` in MATLAB R2013b]. The  $P$ -value gives the probability that the number of individuals on the winner patch (patch containing the largest number of individuals) is obtained by chance (Corder and Foreman, 2014). The lower this probability, the higher the aggregation level in the group. The proportion of tests for which the distribution of individuals on patches was significantly different from random increased from a minimum of 25% in groups of males to a maximum of 55.8% in groups of larvae ( $\chi^2=21.17$ , d.f.=3,  $P<0.001$ ; Table 1). On average, groups of males had lower aggregation levels than groups of females and larvae (Kruskal–Wallis one-way ANOVA, effect of group type on aggregation level:  $\chi^2=24.40$ , d.f.=3,  $P<0.001$ ; Nemenyi *post hoc* test  $P<0.05$  for pairwise comparison between males and all other group types). In all four group types, flies equally chose the left and right patches across tests (sign test with equal probability 0.5 of choosing either side,  $P>0.17$  in all group types), indicating no inherent side preference.

### Effect of group size

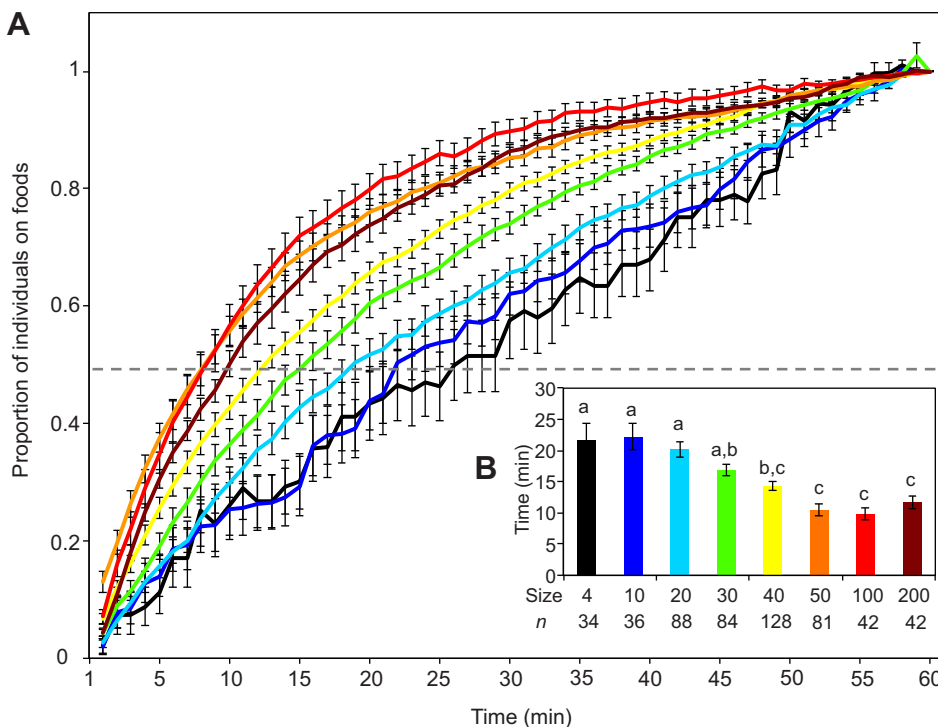
To investigate whether collective dynamics varied with group size, we tested groups of four to 200 mated females in the binary choice situation (see details in Table 1). On average,  $87.3\pm0.4\%$  of

individuals per group (mean $\pm$ s.e.m.,  $n=524$  groups) were on patches by the end of the observations. This percentage was similar for the eight group sizes (one-way ANOVA, effect of group size on final % of individuals on foods:  $F_{7,527}=1.75$ ,  $P=0.095$ ). However, the larger the groups, the faster the flies joined the food patches (Fig. 2A). The speed at which half of the groups settled on foods initially increased with group size until reaching a plateau at approximately  $10.6\pm0.7$  min ( $n=165$  groups) for groups of 50 or more individuals (one-way ANOVA, effect of group size on time elapsed until 50% of individuals were on food:  $F_{6,486}=14.67$ ,  $P<0.001$ ; Fig. 2B).

When considering all individuals on foods (population of flies on both patches), we found that the final distributions of flies were different from random in groups of 10 to 100 individuals, but not in groups of four and 200 (Fig. 1B). The proportion of tests for which the distribution was significantly different from random (sign test with equal probability 0.5 of choosing either side,  $P<0.05$ ) initially doubled with increasing group size, from 29.4% in groups of four to 61.9% in groups of 100, before decreasing again to 30.9% in groups of 200 ( $\chi^2=18.47$ , d.f.=7,  $P=0.010$ ; Table 1). Additionally, the time at which the winner patch was selected (attracted the majority of the group until the end of the observations) decreased from  $36.7\pm2.5$  min (mean $\pm$ s.e.m.,  $n=34$ ) in groups of four to  $26.7\pm2.3$  min ( $n=42$ ) in groups of 100, before increasing again to  $35.4\pm2.6$  min ( $n=42$ ) in groups of 200 (one-way ANOVA, effect of group size on time elapsed until winner patch was selected:  $F_{1,491}=14.24$ ,  $P<0.001$ ). Therefore, both the magnitude and speed of collective decisions varied with group size. Selection of the winner patch was independent of patch side (sign test with equal probability 0.5 of choosing either side,  $P>0.16$  in all group sizes).

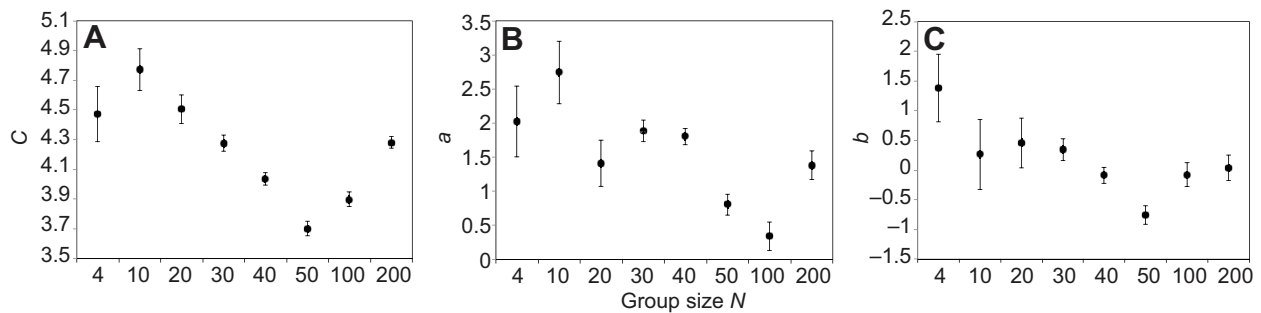
### Probability of joining food patches

To further explore the mechanisms mediating the collective decisions by groups of different sizes, we performed a logistic regression on the experimentally measured probabilities of choosing a focal patch for all group sizes. In performing a logistic



**Fig. 2. Effect of group size on choice dynamics.** (A) Proportion of individuals (number of flies normalized to the maximum of individuals seen on patches during the experiment) on food patches through time. (B) Time elapsed until 50% of individuals in the group were on foods. Different letters above bars indicate significant differences (Tukey's HSD after ANOVA,  $P<0.05$ ). The same color code is used in A and B.  $n$  is the number of groups. Data are means $\pm$ s.e.m.





**Fig. 3. Estimates of the logistic regression parameters.** Estimates of  $C$ ,  $a$  and  $b$  (shown in A, B and C respectively) are shown as a function of group size  $N$  (see details in Eqn 6). Data are means  $\pm$  s.e.m.

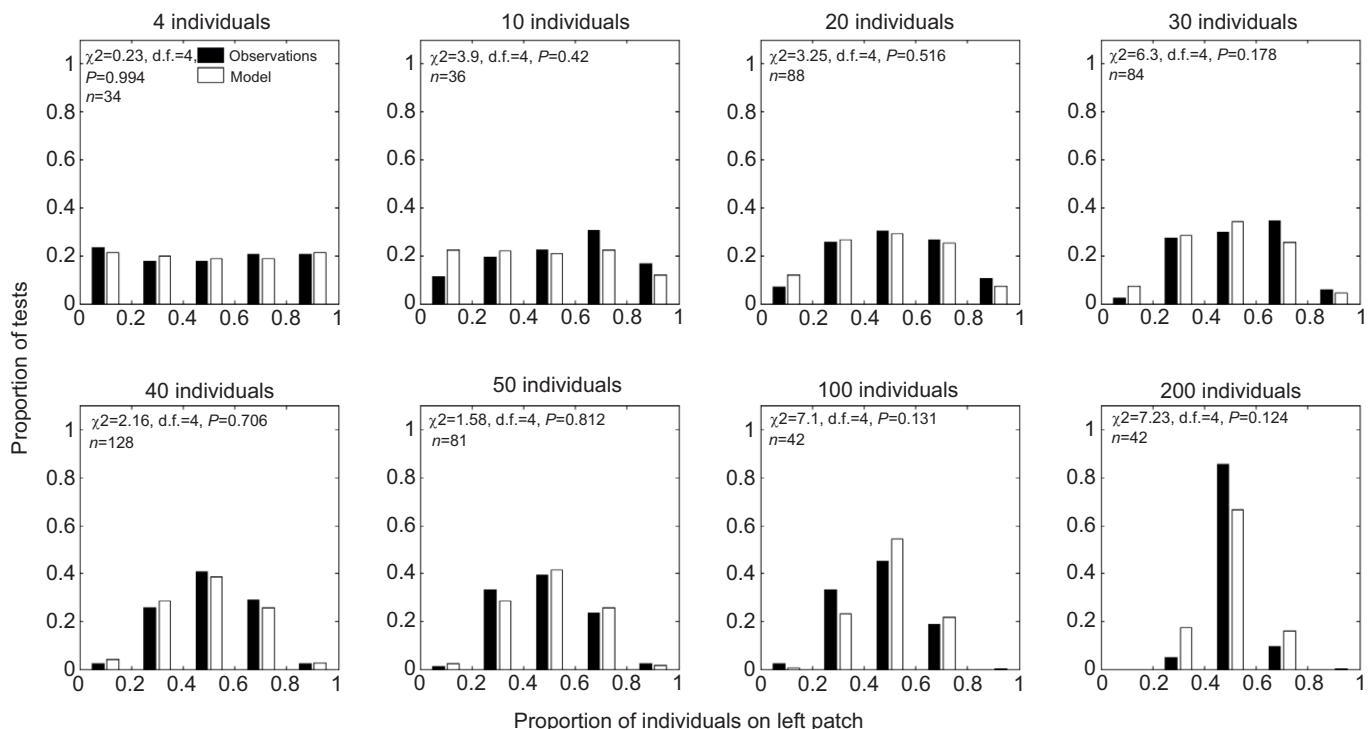
regression, each individual's choice is fitted sequentially. For each individual, the dependent variable is 1 if it joins the focal (right) patch and 0 if it joins the other patch. The dependent variable is the number of individuals that have previously chosen the focal side patch or the other side patch earlier in the arrival sequence. We fitted the rate of individual flies joining a focal food patch per minute as follows:

$$P_{\text{join}} = \frac{1}{[1 + \exp(C - a \frac{F}{N} - b \frac{O}{N})]}, \quad (6)$$

using a binomial link function.  $F$  is the number of individuals on the focal patch (right side);  $O$  is the number of individuals on the other patch (left side);  $N$  is the total number of individuals in the test; and  $C$ ,  $a$  and  $b$  are constants (see details in Table S2).

Variation of  $C$  confirms our observation that the speed at which flies join food patches increases with group size until reaching a plateau for groups of 50 or more individuals (Fig. 3A). Variations

of  $a$  and  $b$  provide further information about the recruitment mechanism of new individuals to patches. For small groups (four to 30 individuals), both  $a$  and  $b$  are positive (Fig. 3B,C). This means that the probability of joining a given patch increases with increasing numbers of flies on both patches (Fig. S4A). Such cumulative attraction of patches suggests that the presence of flies on foods attracts new foragers in the area containing both patches without favoring one of them, presumably through the perception of volatile cues such as a pheromone (Bartelt et al., 1985). For moderate group sizes (40 to 100 individuals),  $a$  remains positive (Fig. S3B) but  $b$  becomes negative (Fig. S3C). The probability of joining one patch decreases with increasing numbers of flies on the other patch, which may result in the selection of one of the two patches by the majority of the group (Fig. S4B). For very large group sizes (200 individuals),  $a$  and  $b$  are both positive again (Fig. S3B,C). In this case, there is no longer competitive attraction between patches, so flies are more equally attracted towards both patches.



**Fig. 4. Comparison between observed and simulated final choices.** Black bars show the observed frequency distribution of individuals on the left food patch ( $n$  is the number of groups). White bars show the simulated distributions ( $c=5.3$ ,  $n=10,000$  runs; see details of the model in Materials and methods). Observed and simulated data were compared with chi-square tests.  $n$  is the number of groups.

### Simulations of the individual-based model

The model produces an arrival distribution at the food patches similar to that seen in the experiments (Fig. 4). Specifically, the model predicts that significant asymmetrical distributions only emerge in groups exceeding four individuals. It also replicates the tendency of flies to produce more unimodal distributions in groups of 200 individuals. This effect arises without implementing any avoidance behavior, for instance, as a result of overcrowding on food patches. As the number of flies on both patches increases, the combined attraction of the two patches ( $A+B$ ) becomes stronger than the difference ( $A-B$ ), so that the flies show a lower tendency to choose one side or the other. Our model also explains the tendency of flies to arrive faster on food patches with increasing group sizes, although the time difference is relatively small in this case (Fig. S6).

The model fit shown here is for the best-fit value of the only free parameter,  $c$ , the degree of randomness. We determined this value ( $c=5.3$ ) by minimizing the chi-squared statistic between simulations and the observational data (for the best fit  $\chi^2 < 7.78$ , d.f.=4,  $P > 0.1$  for all group sizes; Fig. 4). Although this parameter is not estimated independently from the data, the same parameter value reproduces the experimental results for all of the different group sizes. The large value of  $c$  indicates a large variation in the movement of the flies (Fig. S5 shows examples of simulations for each group size). Our model thus suggests a common underlying process of attraction towards the patches across all experimental conditions. Individual flies have a (weak) social attraction to food patches.

### DISCUSSION

It has long been known that fruit flies tend to aggregate on food patches (Prokopy and Roitberg, 2001; Wertheim et al., 2005 and references therein). However, the collective dynamics by which groups initially develop and disperse have never been quantified in detail. Using symmetry-breaking experiments, we showed that groups of *D. melanogaster* larvae and adults make collective foraging decisions, the speed and magnitude of which vary with group size and composition. These complex dynamics may emerge from simple social amplification rules, a widespread phenomenon across animal societies (Camazine, et al., 2001; Sumpter, 2010), including in the simplest groups where individuals form temporary aggregations on food resources (Costa, 2006).

Both our observations and our model indicate that the collective decisions of fruit flies are mediated by social attraction to occupied patches. Previous studies point towards a role of long-distance chemical communication leading to aggregation (Dubnau, 2014; Sokolowski, 2010). For instance, feeding larvae are attracted to each other by odors derived from the gut bacteria of conspecifics as well as by physical heterogeneities generated on the substrate surface as a result of their digging activities (Durisko and Dukas, 2013; Venu et al., 2014). Adults respond to a volatile sex pheromone (cVA) produced by males and transferred to females during copulation (Bartelt et al., 1985; Butterworth, 1969; Wertheim et al., 2005). Interestingly, the fact that virgin females lacking cVA also showed tendency to aggregate on foods indicates that additional social cues are involved (Stamps et al., 2005). Contact chemicals such as cuticular hydrocarbons, which are known to complement the action of cVA during sexual interactions (Billeter et al., 2009; Everaerts et al., 2010; Tompkins et al., 1980), could play a role over short distances. The utilization of cuticular lipids as communication cues by many insects is often combined with responses to physical stimulation by conspecifics, as, for instance, in locusts (Anstey et al., 2009) and cockroaches (Lihoreau and Rivault, 2008), where both olfaction and touch are necessary to mediate aggregation.

Although we cannot exclude a role of acoustic cues, sound production in *D. melanogaster* typically requires stereotyped behavioral sequences, such as wing vibrations during the sexual courtship (Tauber and Eberl, 2003), which we did not observe in our experiments. In contrast to previous studies reporting gregarious behavior in male flies (Saltz, 2011; Saltz and Foley, 2011), we found that males were not attracted to each other on foods. Presumably, their territorial interactions involving aggression and avoidance behaviors (Wang and Anderson, 2010; Yurkovic et al., 2006) impaired the development of aggregations on food patches in our experimental conditions with relatively large population densities.

Manipulating group sizes affected the dynamics and the magnitude of collective responses of flies, a predicted property of collective decisions based on non-linear amplification loops (Sumpter and Pratt, 2009; Jeanson et al., 2012). As more individuals interact, the intensity of amplification processes and the degree of choice asymmetry increases, often leading to phase transitions from groups of uncoordinated to coordinated individuals (e.g. ants, Beekman et al., 2001; locusts, Buhl et al., 2006; cockroaches, Lihoreau et al., 2010). Our model shows how social attraction to occupied patches can reproduce these complex dynamics. The weak collective decisions observed in groups of only four flies indicate that a minimum number of individuals (quorum) must be reached for aggregation to emerge. Although amplifications are at work, they are not strong enough to induce a collective response. However, above this critical group size (between five and 10 individuals in our experimental conditions), the magnitude of asymmetrical distributions increased with the total number of foraging individuals. In larger groups, the amount of social cues on foods becomes higher and thus easier to pinpoint by exploring flies, so that individuals arriving in the food area are more likely to join the most populated patch, a result that is compatible with the known dose-dependent effect of cVA on female aggregation behavior (Datta et al., 2008; Kurtovic et al., 2007). Competition between the attractive effects of the two patches, whereby increased attraction at one patch decreases attraction at the other patch, leads to a faster and stronger aggregation response on one patch. In very large groups, however, the cumulative attraction of the two patches becomes stronger than the difference (possibly because of a local saturation of social cues), so that flies show a lower tendency to choose one patch or the other, leading to a reduction of symmetry breaking as previously observed in similar systems (e.g. earthworms, Zirbes et al., 2010). Although this effect can emerge independently of any explicit avoidance behavior, additional factors such as competition for space because of overcrowding on foods could also be at play, resulting in a more symmetrical distribution of individuals on patches (Amé et al., 2006).

Aggregation on foods provides several benefits to fruit flies that may counterbalance the increased risks of competition and predation (Wertheim et al., 2005). Adults acquire social information for selecting mating partners (Mery et al., 2009) and oviposition sites (Battesti et al., 2012, 2015; Sarin and Dukas, 2009), while also vectoring yeast communities that are beneficial for the development of future larvae (Durisko and Dukas, 2013; Stamps et al., 2012; Wertheim et al., 2002). Larvae collectively alter the foraging substrate, which may facilitate burrowing for nutrient acquisition and predator avoidance (Durisko et al., 2014; Reaume and Sokolowski, 2006). Our results now indicate that socially interacting fruit flies also make faster foraging choices through collective decisions, an emergent property of collective decisions often associated with an increased accuracy of individual choices

(Krause et al., 2010; Sumpter and Pratt, 2009). Although little is known about the nutritional ecology of *D. melanogaster* in natural conditions (Reaume and Sokolowski, 2006), social attraction to food patches may facilitate the localization of resources with nutrient amounts and balances that maximize growth and reproduction (Lee et al., 2008, 2013). In the case of gravid females, social cues may also help in finding high-quality oviposition substrates, optimizing egg hatching success and larval survival.

Social interactions considerably complicate the foraging decisions of animals that must trade off between choosing foods that will address their own nutrient needs and following others to maintain group cohesion (Simpson et al., 2015). Combining experimental approaches of nutritional ecology and collective animal behavior will allow for an empirical examination of how examine how nutrient regulation can be achieved simultaneously at multiple organizational levels, by individuals and groups (Lihoreau et al., 2014, 2015). Our study establishes *D. melanogaster* as a promising model for initiating such research, with the prospect of using the unique combination of behavioral and neurogenetic approaches available in a model organism.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

M.L. designed the experiments. M.L. and I.M.C. collected the data. M.L., J.B. and D.J.T.S. analysed the data. M.L., I.M.C., J.B., D.J.T.S. and S.J.S. wrote the manuscript.

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#### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.127431/-DC1>

#### References

- Amé, J.-M., Halloy, J., Rivault, C., Detrain, C. and Deneubourg, J. L. (2006). Collegial decision making based on social amplification leads to optimal group formation. *Proc. Natl. Acad. Sci. USA* **103**, 5835–5840.
- Anstey, M. L., Rogers, S. M., Ott, S. R., Burrows, M. and Simpson, S. J. (2009). Serotonin mediates behavioral gregarization underlying swarm formation in desert locusts. *Science* **323**, 627–630.
- Attanasi, A., Cavagna, A., Del Castello, L., Giardina, I., Melillo, S., Parisi, L., Pohl, O., Rossaro, B., Shen, E., Silvestri, E. et al. (2014). Collective behaviour without collective order in wild swarms of midges. *PLoS Comp. Biol.* **10**, e1003697.
- Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Lecomte, V., Orlandi, A., Parisi, G., Procaccini, A. et al. (2008). Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study. *Proc. Natl. Acad. Sci. USA* **105**, 1232–1237.
- Bartelt, R. J., Schaner, A. M. and Jackson, L. L. (1985). Cis-vaccenyl acetate as an aggregation pheromone in *Drosophila melanogaster*. *J. Chem. Ecol.* **11**, 1747–1756.
- Battesti, M., Moreno, C., Joly, D. and Mery, F. (2012). Spread of social information and dynamics of social transmission within *Drosophila* groups. *Curr. Biol.* **22**, 309–313.
- Battesti, M., Pasquaretta, C., Moreno, C., Teso, S., Joly, D., Klensch, E., Petit, O., Sueur, C. and Mery, F. (2015). Ecology of information: social transmission dynamics within groups of non-social insects. *Proc. R. Soc. B Biol. Sci.* **282**, 20142480.
- Beckers, R., Deneubourg, J. L., Goss, S. and Pasteels, J. M. (1990). Collective decision making through food recruitment. *Insectes Soc.* **37**, 258–267.
- Beekman, M., Sumpter, D. J. T. and Ratnieks, F. L. W. (2001). Phase transition between disordered and ordered foraging in Pharaoh's ants. *Proc. Natl. Acad. Sci. USA* **98**, 9703–9706.
- Billeter, J.-C., Atallah, J., Krupp, J. J., Millar, J. G. and Levine, J. D. (2009). Specialized cells tag sexual and species identity in *Drosophila melanogaster*. *Nature* **461**, 987–991.
- Bourke, A. F. G. (2011). *Principles of Social Evolution*. Oxford, UK: Oxford University Press.
- Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R. and Simpson, S. J. (2006). From disorder to order in marching locusts. *Science* **312**, 1402–1406.
- Butterworth, F. M. (1969). Lipids of *Drosophila*: a newly detected lipid in the male. *Science* **163**, 1356–1357.
- Camazine, S., Deneubourg, J.-L., Franks, N., Sneyd, J., Theraulaz, G. and Bonabeau, E. (2001). *Self-Organization in Biological Systems*. Princeton, NJ: Princeton University Press.
- Conradt, L. and Roper, T. J. (2005). Consensus decision making in animals. *Trends Ecol. Evol.* **20**, 449–456.
- Corder, G. W. and Foreman, D. I. (2014). *Nonparametric Statistics: a Step-by-Step Approach*. 2nd edn. Hoboken, NJ: Wiley.
- Costa, J. T. (2006). *The Other Insect Societies*. Cambridge, MA: Harvard University Press.
- Couzin, I. D. (2009). Collective cognition in animal groups. *Trends Cogn. Sci.* **13**, 36–43.
- Datta, S. R., Vasconcelos, M. L., Ruta, V., Luo, S., Wong, A., Demir, E., Flores, J., Balonze, K., Dickson, B. J. and Axel, R. (2008). The *Drosophila* pheromone cVA activates a sexually dimorphic neural circuit. *Nature* **452**, 473–477.
- Del Solar, E. (1968). Selection for and against gregariousness in the choice of oviposition sites by *Drosophila pseudoobscura*. *Genetics* **58**, 275.
- Detrain, C. and Deneubourg, J.-L. (2008). Collective decision-making and foraging patterns in ants and honeybees. *Adv. Insect Phys.* **35**, 123–173.
- Dubnau, J. (2014). *Behavioural Genetics of the Fly (Drosophila melanogaster)*. Cambridge, UK: Cambridge University Press.
- Durisko, Z. and Dukas, R. (2013). Attraction to and learning from social cues in fruitfly larvae. *Proc. R. Soc. B Biol. Sci.* **280**, 20131398.
- Durisko, Z., Kemp, R., Mubasher, R. and Dukas, R. (2014). Dynamics of social behavior in fruit fly larvae. *PLoS ONE* **9**, e95495.
- Everaerts, C., Farine, J.-P., Cobb, M. and Ferveur, J.-F. (2010). *Drosophila* cuticular hydrocarbons revisited: mating status alters cuticular profiles. *PLoS ONE* **5**, e9607.
- Heisenberg, M. and Buchner, E. (1977). The role of retinula cell types in visual behavior of *Drosophila melanogaster*. *J. Comp. Physiol. A* **117**, 127–162.
- Jeanson, R., Dussutour, A. and Fourcassié, V. (2012). Key factors for the emergence of collective decision in invertebrates. *Front. Neurosci.* **6**, 121.
- Krause, J., Ruxton, G. D. and Krause, S. (2010). Swarm intelligence in animals and humans. *Trends Ecol. Evol.* **25**, 28–34.
- Kurtovic, A., Widmer, A. and Dickson, B. (2007). A single class of olfactory neurons mediates behavioural responses to a *Drosophila* sex pheromone. *Nature* **446**, 542–546.
- Lee, K. P., Simpson, S. J., Clissold, F. J., Brooks, R., Ballard, J. W. O., Taylor, P. W., Soran, N. and Raubenheimer, D. (2008). Lifespan and reproduction in *Drosophila*: new insights from nutritional geometry. *Proc. Natl. Acad. Sci. USA* **105**, 2498–2503.
- Lee, K. P., Kim, J.-S. and Min, K.-J. (2013). Sexual dimorphism in nutrient intake and life span is mediated by mating in *Drosophila melanogaster*. *Anim. Behav.* **86**, 987–992.
- Lihoreau, M. and Rivault, C. (2008). Tactile stimuli trigger group effects in cockroach aggregations. *Anim. Behav.* **75**, 1965–1972.
- Lihoreau, M., Deneubourg, J.-L. and Rivault, C. (2010). Collective foraging decision in a gregarious insect. *Behav. Ecol. Sociobiol.* **64**, 1577–1587.
- Lihoreau, M., Buhl, J., Charleston, M. A., Sword, G. A., Raubenheimer, D. and Simpson, S. J. (2014). Modelling nutrition across organizational levels: from individuals to superorganisms. *J. Insect Physiol.* **69**, 2–11.
- Lihoreau, M., Buhl, J., Charleston, M. A., Sword, G. A., Raubenheimer, D. and Simpson, S. J. (2015). Nutritional ecology beyond the individual: a conceptual framework for integrating nutrition and social interactions. *Ecol. Lett.* **18**, 273–286.
- Lizé, A., McKay, R. and Lewis, Z. (2014). Kin recognition in *Drosophila*: the importance of ecology and gut microbiota. *ISME J.* **8**, 469–477.
- Mailleux, A.-C., Astudillo Fernandez, A., Martin, G. S., Detrain, C. and Deneubourg, J.-L. (2011). Collective migration in house dust mites. *Ethology* **117**, 72–82.
- Mery, F., Varela, S. A. M., Danchin, E., Blanchet, S., Parejo, D., Coolen, I. and Wagner, R. H. (2009). Public versus personal information for mate copying in an invertebrate. *Curr. Biol.* **19**, 730–734.
- Moussaid, M., Helbing, D. and Theraulaz, G. (2011). How simple rules determine pedestrian behavior and crowd disasters. *Proc. Natl. Acad. Sci. USA* **108**, 6884–6888.

- Prokopy, R. J. and Roitberg, B. D. (2001). Joining and avoidance behavior in nonsocial insects. *Annu. Rev. Entomol.* **46**, 631–665.
- Ramdy, P., Lichocki, P., Cruchet, S., Frisch, L., Tse, W., Floreano, D. and Benton, R. (2014). Mechanosensory interactions drive collective behaviour in *Drosophila*. *Nature* **519**, 233–236.
- Reaume, C. J. and Sokolowski, M. B. (2006). The nature of *Drosophila melanogaster*. *Curr. Biol.* **16**, R623–R628.
- Saltz, J. B. (2011). Natural genetic variation in social environment choice: context-dependent gene-environment correlation in *Drosophila melanogaster*. *Evolution* **65**, 2325–2334.
- Saltz, J. B. and Foley, B. R. (2011). Natural genetic variation in social niche construction: social effects of aggression drive disruptive sexual selection in *Drosophila melanogaster*. *Amer. Nat.* **177**, 645–654.
- Sarin, S. and Dukas, R. (2009). Social learning about egg-laying substrates in fruitflies. *Proc. R. Soc. B Biol. Sci.* **276**, 4323–4328.
- Sasaki, T., Granovski, B., Mann, R., Sumpter, D. J. T. and Pratt, S. C. (2013). Ant colonies outperform individuals when a sensory discrimination task is difficult but not when it is easy. *Proc. Natl. Acad. Sci. USA* **110**, 13769–13773.
- Schneider, J. M., Dickinson, M. H. and Levine, J. D. (2012). Social structures depend on innate determinants and chemosensory processing in *Drosophila*. *Proc. Natl. Acad. Sci. USA* **109**, 17175–17179.
- Seeley, T. D., Visscher, P. K., Schlegel, T., Hogan, P. M., Franks, N. R. and Marshall, J. A. R. (2012). Stop signals provide cross inhibition in collective decision-making by honeybee swarms. *Science* **335**, 108–111.
- Simon, A. F., Chou, M.-T., Salazar, E. D., Nicholson, T., Saini, N., Metchev, S. and Krantz, D. E. (2012). A simple assay to study social behavior in *Drosophila*: measurement of social space within a group. *Genes Brain Behav.* **11**, 243–252.
- Simpson, S. J., Clissold, F. J., Lihoreau, M., Ponton, F., Wilder, S. M. and Raubenheimer, D. (2015). Recent advances in the integrative nutrition of arthropods. *Annu. Rev. Entomol.* **60**, 293–311.
- Sokolowski, M. B. (2010). Social interactions in “simple” model systems. *Neuron* **65**, 780–794.
- Stamps, J., McElreath, R. and Eason, P. (2005). Alternative models of conspecific attraction in flies and crabs. *Behav. Ecol.* **16**, 974–980.
- Stamps, J. A., Yang, L. H., Morales, V. M. and Boundy-Mills, K. L. (2012). *Drosophila* regulate yeast density and increase yeast community similarity in a natural substrate. *PLoS ONE* **7**, e42238.
- Stevens, A. and Othmer, H. G. (1997). Aggregation, blowup, and collapse: the ABC's of taxis in reinforced random walks. *SIAM J. Appl. Math.* **57**, 1044–1081.
- Strandburg-Peshkin, A., Farine, D., Couzin, I. D. and Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science* **348**, 1358–1361.
- Sumpter, D. J. T. (2010). *Collective Animal Behaviour*. Princeton, NJ: Princeton University Press.
- Sumpter, D. J. T. and Pratt, S. C. (2009). Quorum responses and consensus decision making. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 743–753.
- Tauber, E. and Eberl, D. F. (2003). Acoustic communication in *Drosophila*. *Behav. Processes* **64**, 197–210.
- Tinette, S., Zhang, L. and Robichon, A. (2004). Cooperation between *Drosophila* flies in searching behavior. *Genes Brain Behav.* **3**, 39–50.
- Tompkins, L., Hall, J. C. and Hall, L. M. (1980). Courtship-stimulating volatile compounds from normal and mutant *Drosophila*. *J. Insect Physiol.* **26**, 689–697.
- Venu, I., Durisko, Z., Xu, J. and Dukas, R. (2014). Social attraction mediated by fruit flies' microbiome. *J. Exp. Biol.* **217**, 1346–1352.
- Wang, L. and Anderson, D. J. (2010). Identification of an aggression-promoting pheromone and its receptor neurons in *Drosophila*. *Nature* **463**, 227–231.
- Ward, A. J. W., Herbert-Read, J. E., Sumpter, D. J. T. and Krause, J. (2011). Fast and accurate decisions through collective vigilance in fish shoals. *Proc. Nat. Acad. Sci. USA* **108**, 2312–2315.
- Wertheim, B., Marchais, J., Vet, L. E. M. and Dicke, M. (2002). Allee effect in larval resource exploitation in *Drosophila*: an interaction among density of adults, larvae, and micro-organisms. *Ecol. Entomol.* **27**, 608–617.
- Wertheim, B., van Baalen, E.-J. A., Dicke, M. and Vet, L. E. M. (2005). Pheromone-mediated aggregation in nonsocial arthropods: an evolutionary ecological perspective. *Ann. Rev. Entomol.* **50**, 321–346.
- Yurkovic, A., Wang, O., Basu, A. C. and Kravitz, E. A. (2006). Learning and memory associated with aggression in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. USA* **103**, 17519–17524.
- Zirbes, L., Deneubourg, J.-L., Brostaux, Y. and Haubruge, E. (2010). A new case of consensual decision: collective movement in earthworms. *Ethology* **116**, 546–553.