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Indirect genetic effects on the sociability of several group members

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Indirect genetic effects (IGEs) are a major driver of social evolution, but much of the experimental work pertaining to IGEs on social behaviour has focused on the effect of stimulus individuals on single focal individuals. We extended IGE research to examine how stimulus individuals influence social interactions among several focal individuals. Specifically, we relied on recent work on social behaviour in fruit flies to examine whether IGEs cause 12 stimulus flies of distinct genotypes to alter social interactions within groups of six focal flies. The social behaviour of focals was significantly affected by the genotype of the stimulus flies. Focals were closer together when grouped with stimulus flies from genotypes that were close together than when grouped with stimulus flies from genotypes that were farther apart. A mechanism mediating this effect was the encounter rate between focal flies, which was lowest when the focal flies were grouped with stimulus flies of the more cohesive genotypes.

It has long been recognized that the observed behaviour of a social group reflects the characteristics of its individual members, and that some individuals might disproportionally determine group performance (Allee, 1938; Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014; Pentland, 2014). For example, the average social sensitivity of group members was the best predictor of performance on a variety of collective tasks by human groups (Woolley, Chabris, Pentland, Hashmi, & Malone, 2010). And in the social spider *Stegodyphus dumicola*, the presence of a few mature females increased the frequency of attacking prey in small juvenile groups and decreased attack latencies in large juvenile groups (Modlmeier et al., 2015).

When individual traits that influence social behaviour are heritable, the performance of one group member is partially determined by the genotypes of other members. Such indirect genetic effects (IGE) (Griffing, 1967; Moore, Brodie, & Jason, 1997; Scott, 1977) have been documented in a variety of traits and taxa including aggression in deer mice, *Peromyscus maniculatus* (Wilson, Gelin, Perron, & Réale, 2009), domestic pigs, *Sus scrofa* (Camerlink, Ursinus, Bijma, Kemp, & Bolhuis, 2015) and fruit flies, *Drosophila melanogaster* (Saltz, 2013), mate choice in field crickets, *Teleogryllus oceanicus* (Bailey & Zuk, 2012) and tree hoppers, *Enchenopa binotata* (Rebar & Rodríguez, 2013), chemical signalling in fruit flies (*Drosophila* spp.) (Kent, Azanchi, Smith, Formosa, & Levine, 2008; Petfield, Chenoweth, Rundle, & Blows, 2005), and antipredatory behaviour in guppies, *Poecilia reticulata* (Bleakley & Brodie, 2009).

Much of the experimental work on IGEs on social behaviour has focused on the effect of stimulus individuals on focals. The only exception we know of (Saltz, 2013) considered the effect of a stimulus individual on interactions between two focal individuals. Saltz (2013) termed the classically considered interactions between the stimulus and focal individual 'first-order IGEs', and the effect of the stimulus individual on interactions between the two focals 'second-order IGEs'. Social behaviour often involves many individuals. Because theory indicates that IGEs can profoundly influence both the rate and direction of the evolution of social traits (Moore et al., 1997; Wolf & Moore, 2010), it is pertinent that we examine IGEs of stimulus individuals on social interactions among several focal individuals. To this end, we relied on the recent work on social behaviour in fruit flies (Battesti, Moreno, Joly, & Mery, 2012; Krupp et al., 2008; Saltz, 2011; Sarin & Dukas, 2009; Simon et al., 2012) and on our own research documenting significant genetic variation in social behaviour in fruit flies (Anderson, Scott, & Dukas, 2016) to test whether stimulus flies of distinct social genotypes determine social features among groups of six focal flies. While there are different ways to define and measure social behaviour, our focus here is on the tendency of conspecifics to be close to others (Ward & Webster, 2016).

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Specifically, we predicted that six focal flies would be closer together when grouped with 12 flies of stimulus genotypes that were close together than when grouped with 12 flies of stimulus genotypes that were farther apart. In a follow-up experiment, we examined the behavioural mechanism mediating the IGEs.

METHODS

General

We maintained all populations at low density in 40 ml vials each containing 5 ml of standard food (1 litre of which contained 90 g of sucrose, 32 g of yeast, 75 g of cornmeal, 20 g of agar and 2 g of methyl paraben), at 25 °C and 60% relative humidity, on a 12:12 h light cycle with lights on at 1000 hours. These conditions are optimal for fruit fly well-being. Furthermore, we handled flies either by gentle aspiration or with a soft brush following brief anaesthetization with CO_2, and applied no harmful manipulations. Our focal flies belonged to an inbred line of Canton-S, which has been in captivity for decades and in our laboratory for 6 years. Our three stimulus fly lines were two lines of the *Drosophila* Genetic Reference Panel (DGRP; Mackay et al., 2012) and the Canton-S (CS) line. We chose the two DGRP lines (304 and 427) based on our previous work (Anderson et al., 2016) as well as the preliminary experiment described below.

Preliminary Experiment

We collected flies within 8 h of eclosion on day 1 and housed them in mixed-sex vials each containing 20 males and 20 females. On day 4 at 0800 hours, we transferred groups of 18 males from each line each into an 85 mm food dish. The petri dishes contained standard food, with cornmeal omitted to minimize variation in surface texture. The volume of food was sufficient to minimize headspace, such that flies were constrained to two dimensions during observations. At 1300 hours, we placed the dishes inside test boxes (53 × 31 × 30 cm; length × width × height) made of semi-opaque plastic and illuminated by diffused room light. After an additional 2 h of acclimatization, we videorecorded the dishes for 1 h with high-resolution webcams (Logitech C920) through a hole in the centre of each box lid.

During video analyses, we sampled the Cartesian coordinates of each fly at 30 s intervals and calculated a single nearest-neighbour index for the 18 flies in each dish. The nearest-neighbour index is defined by the ratio between the mean observed nearest-neighbour distance and that expected by chance at the given density. Nearest-neighbour indices range from 0, where all points occupy the same region in space, to 2.15, which represents a perfectly uniform distribution (Anderson et al., 2016; Clark & Evans, 1954). Calculations were similar to those illustrated in Fig. 1a for experiment 1 but were based on 18 flies belonging to a single line. Similar measures have been used successfully in numerous studies on social behaviour in a variety of species (Durisko, Kemp, Mubasher, & Dukas, 2014; Evans & Harris, 2008; White & Chapman, 1994). The distance among individuals reflects some balance between the degree of attraction to and avoidance of others, with the latter being either a response to the presence of a nearby individual or a result of some aggressive interactions (Brown & Orians, 1970; Conder, 1949). Hence the average nearest-neighbour distance in a group provides us with a comprehensive and objective measure for comparisons between genotypes and treatments of the outcomes of social interactions among individuals. Nevertheless, a complete characterization of social behaviour will benefit from using a variety of protocols (Saltz, 2011; Schneider, Dickinson, & Levine, 2012).

We intended to use in the main experiment, and hence tested in the preliminary experiment, six DGRP lines (304, 360, 362, 365, 427 and 437) as well as our Canton-S line. We expected to observe two discrete levels of social behaviour from our DGRP lines based on our previous work, which employed a distinct protocol (Anderson et al., 2016). However, only line 304 expressed a social phenotype that was significantly different from the other DGRP lines (all $P < 0.001$, uncorrected pairwise t tests). The nearest-neighbour scores of the remaining five DGRP lines were indistinguishable from one another (all $P > 0.77$), although line 427 was the least variable DGRP line tested. We thus proceeded using only lines 304, 427 and our Canton-S line, which was the least social line of the three (all $P < 0.05$; Fig. 1b).

Experiment 1

We collected flies within 8 h of eclosion on day 1 and housed stimulus and focal males in different mixed-sex vials each containing 14 males and 14 females. Focal and stimulus Canton-S flies always came from distinct vials. On day 4 at 0800 hours, we marked focal and stimulus males with either pink or blue fluorescent powder, which was counterbalanced across days. An hour after marking, we briefly anaesthetized the flies under light CO_2 and transferred six focal males from one vial and 12 stimulus males from another vial into each 85 mm petri dish with food as described above. That is, each experimental dish contained 18 males. At 1300 hours, we transferred six dishes of flies into each of four test boxes described above. Following an additional 2 h of acclimatization, we videorecorded the flies for 60 min as described above. During video analyses, we sampled Cartesian coordinates of each fly at 60 s intervals. Observers blind to fly treatment verified the position of all 18 males and distinguished the six focals from the 12 stimulus males based on colour.

To quantify social behaviour, we calculated two nearest-neighbour indices independently for each dish and time point: one for the six focal males and one for the 12 stimulus males (Fig. 1a). We observed a total of 126 dishes ($N = 42$ per stimulus line), and analysed the data in R version 3.2 (R Core Team, 2014) with a linear mixed model with focal male nearest-neighbour index as a response variable, stimulus genotype and focal colour as fixed effects, day, box and dish as random effects, and time as a repeated measure. Although there was a significant effect of colour ($\chi^2_1 = 14.38$, $P < 0.001$), there was no effect of day ($P = 1.0$), box ($P = 0.15$), nor changes over time ($\chi^2_1 = 0.01$, $P = 0.93$).

Our preliminary data indicated that the nearest-neighbour index is sensitive to the number of individuals when a group of flies is divided into two subgroups of different sizes. This was relevant here, as we observed six focal flies and 12 stimulus flies within the same dish. To verify this outcome, we performed a simulation in which we sampled dishes from our preliminary experiment (with replacement), randomly partitioning each dish into subgroups of six and 12 and calculating a nearest-neighbour index for each subgroup. The nearest neighbour indices were greater for subgroups of six flies (mean and 95% CI = 1.0 (0.46, 1.38)) than for subgroups of 12 flies (0.89 (0.47, 1.14)). This most likely explains the difference in nearest-neighbour indices between the 12 stimulus and six focal Canton-S flies observed when comparing Fig. 1c and d.

To quantify the magnitude of the indirect genetic effect on focal phenotype, we fitted a second model to estimate the interaction coefficient (Ψ) based on the partial regression coefficient between focal and stimulus fly nearest-neighbour indices (Equation 2b in Moore et al., 1997). This model was identical to our initial model, but included stimulus fly nearest-neighbour index and its interaction with genotype as fixed effects. Although the IGE is

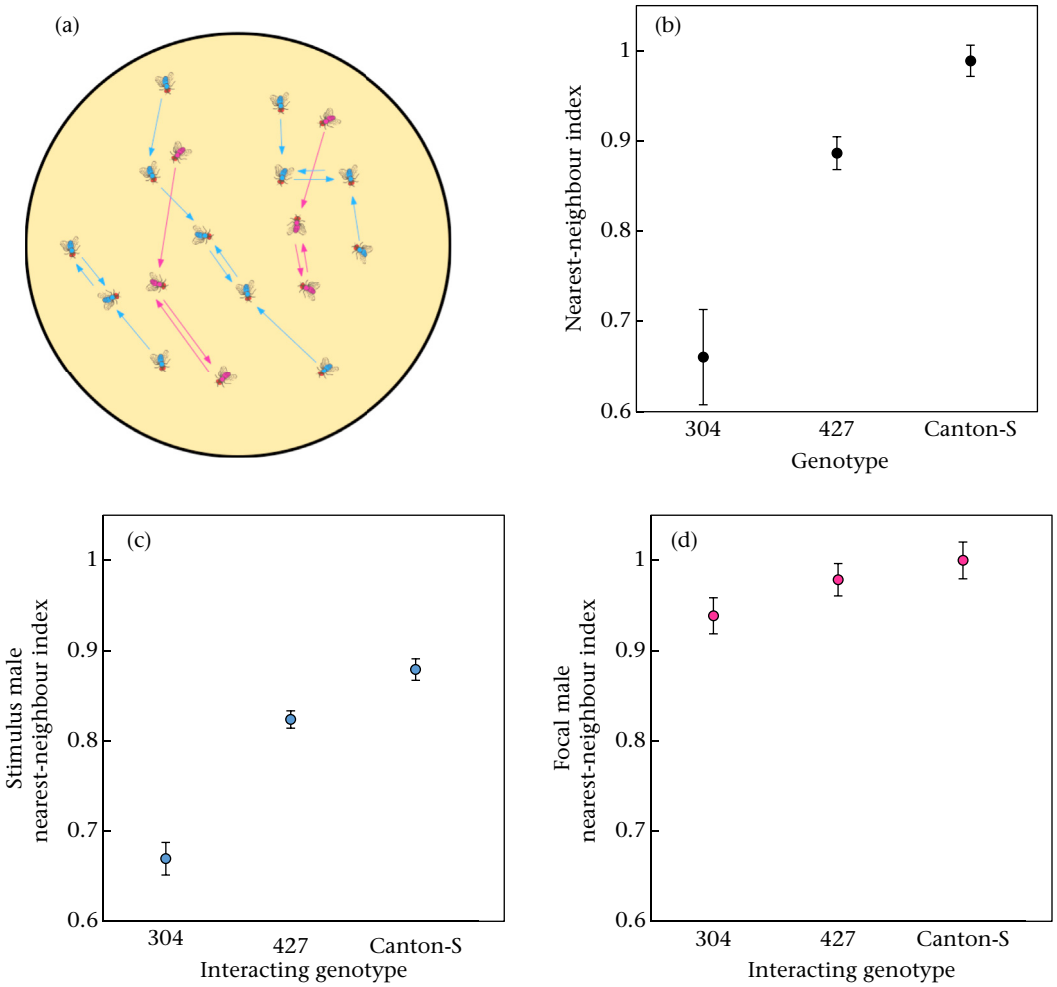

Figure 1. (a) Diagram illustrating nearest-neighbour measurements amongst six focal (pink) and 12 stimulus (blue) flies. Note that, for clarity, flies are drawn larger than their actual size relative to the 85 mm dish. Also note that, in panels (c) and (d), measurements for each focal were done without regard to stimulus flies' positions, and vice versa. (b) Mean ± SE nearest-neighbour index among groups of 18 flies from each stimulus line during the preliminary experiment. (c) Mean ± SE nearest-neighbour index measured amongst groups of 12 stimulus flies from the three different lines. (d) Mean ± SE nearest-neighbour index measured amongst the six focal flies (Canton-S) when grouped with 12 flies from each of three distinct stimulus lines.

presumably driven by the more numerous stimulus males, we corrected Ψ estimates to account for the possibility of a reciprocal IGE (Equation 12 in Bijma, 2014). The interaction between stimulus male nearest-neighbour index and genotype was not significant ($\chi^2_2 = 1.05$, $P = 0.59$), suggesting that the relative strength of the IGE was similar when observed with the related stimulus Canton-S and the unrelated stimulus DGRP.

Experiment 2

In experiment 2, we wished to test whether social interactions among the focals varied when grouped with stimulus flies from each of the three distinct genetic lines. To quantify the encounter rates between stimulus flies and focals, and between focals and focals, we used a protocol similar to that of experiment 1. We had three treatments, one for each line of stimulus flies. Each 85 mm dish contained six focal males and 12 stimulus males. We had 18 dishes, six for each stimulus fly treatment. We placed two dishes in each of three testing boxes, allowing videos of six dishes to be recorded each day over 3 days. Testing box, treatment day and fly colour were counterbalanced for each dish treatment.

For each dish, observers blind to treatment recorded all encounters during the first 10 min of each video. We defined encounters as either a clear inspection by one fly of another (e.g. licking or prodding with legs), or the movement of one fly towards another with a clear reaction from the other fly (e.g. wing fluttering or moving away). We separately recorded encounters between stimulus flies and focals and between focals. For encounters between stimulus flies and focals, encounters included stimulus flies moving towards stationary focals, focals moving towards stationary stimulus flies, and both stimulus and focal flies moving towards each other. For encounters between focals, encounters included one focal moving towards a stationary focal, and two focals moving towards each other.

We analysed the data with a generalized linear model with Poisson distribution and log link function and used sequential Bonferroni for pairwise comparisons. A nonparametric test revealed similar results. In the analysis of encounter rates among focal flies ($N = 18$), focal colour did not have a significant effect (Wald $\chi^2_1 = 0.2$, $P = 0.65$), but both box ($\chi^2_1 = 13.6$, $P < 0.001$) and day ($\chi^2_1 = 30$, $P < 0.001$) effects were significant. In the analysis of encounter rates between stimulus and focal flies, focal colour, box and day effects were all significant ($N = 18$, all $P < 0.001$).

RESULTS

In the preliminary experiment, there was a significant effect of stimulus fly genotype on average nearest-neighbour index ($\chi^2_2 = 74.4$, $P < 0.001$; Fig. 1b). A post hoc analysis of experiment 1 with stimulus male nearest-neighbour index as a response variable showed commensurate differences between genotypes ($\chi^2_2 = 141.0$, $P < 0.001$; Fig. 1c). Most importantly, the average nearest-neighbour index of focal flies differed significantly based on the genotype of the stimulus flies they were paired with, with focals adjusting their social behaviour in response to that of the stimulus flies ($\chi^2_2 = 6.06$, $P < 0.05$; Fig. 1d). The corrected interaction coefficient (Ψ) was positive (partial regression coefficient = 0.084 ± 0.029 SE, adjusted $\Psi \pm SE = 0.042 \pm 0.015$). In experiment 2, the stimulus flies had a significant effect on the encounter rates among focal flies, which were highest when the stimulus flies had the highest nearest-neighbour index (CS line) and lowest when the stimulus flies had the lowest nearest-neighbour index (DGRP 304 line) (Wald $\chi^2_2 = 60$, $N = 18$, $P < 0.001$; $P < 0.01$ for all pairwise comparisons; Fig. 2). The encounter rates between stimulus and focal flies were highest with the line with the highest nearest-neighbour index (CS line), lower with the intermediate line (DGRP 427 line) and lowest with the line with the lowest nearest-neighbour index (DGRP 304 line) (Wald $\chi^2_2 = 341$, $N = 18$, $P < 0.001$; $P < 0.001$ for all pairwise comparisons; Fig. 2).

DISCUSSION

Our major finding was that social behaviour within a group of six focal group members varied as a function of the genotype of 12 other stimulus individuals (Fig. 1). As far as we know, this is the first study that documents IGEs caused by stimulus individuals on the social dynamics among several focal group members. The most relevant previous work involved applied research in a few species of farm animals housed in groups with the goal of reducing overall stress, injury and mortality, and increasing features such as growth rate and egg laying. The key emphasis of that work has been on estimating IGEs and designing the best artificial selection regimens to maximize group features, which are the most relevant to farmers (Bijma, 2010; Ellen, Visscher, van Arendonk, & Bijma, 2008; Muir, 1996; Wade, Bijma, Ellen, & Muir, 2010). While this body of applied research clearly illustrates the importance of IGEs, it has not provided data on how IGEs of stimulus individuals might influence social interactions among several focal individuals. The other relevant work already mentioned in the introduction indicated that levels of aggression by a stimulus male fruit fly influenced aggressive interactions between two focal male fruit flies (Saltz, 2013).

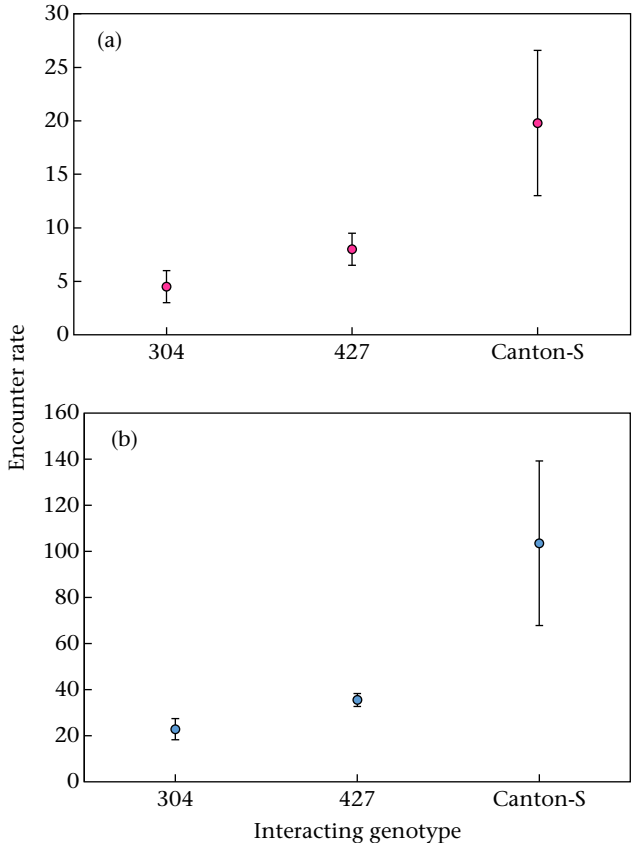

Figure 2. Average number of encounters per 10 min (a) among six focal flies and (b) between stimulus and focal flies in experiment 2.

To some degree, it is intuitive that stimulus individuals can change the social dynamics among several focals. For example, in humans, one can readily envision how a single person would alter the social dynamics at a holiday family dinner. And in the business world, it is widely agreed that a group leader can dramatically affect group performance via the nature of interactions among team members (Hackman, 2002). When it comes to animal behavioural and evolutionary biology, however, we still know little about how IGEs by some individuals influence social interactions among several focals. Another highly relevant issue is the impact such IGEs would have on the rate and direction of social evolution. While we require further empirical data on that topic, it is likely that within-group cohesion and the quantity and quality of its interactions can affect a variety of features linked to fitness. Such factors, which have been documented in fruit flies, include the exchange of social information (Battesti et al., 2012; Sarin & Dukas, 2009), longer life span owing to fewer antagonistic interactions (Carazo, Tan, Allen, Wigby, & Pizzari, 2014), suppression of microbial competitors and pathogens (Rohlfs, 2005; Rohlfs, Obmann, & Petersen, 2005), enhancing the growth of favourable yeast species (Stamps, Yang, Morales, & Boundy-Mills, 2012; Wertheim, Dicke, & Vet, 2002; Wertheim, Marchais, Vet, & Dicke, 2002), locating the best available resources (Durisko & Dukas, 2013) and improved larval digging (Durisko et al., 2014), which could reduce predation risk (Rohlfs & Hoffmeister, 2004).

We chose to use CS males as one of the stimulus fly treatments, meaning that, for that treatment, the focals (always CS males) and stimulus flies came from the same population, but from distinct vials. One would expect the higher relatedness between focal and stimulus males in this treatment to increase cohesion, perhaps through the expected reduced aggression between related males (Carazo et al., 2014; Martin & Long, 2015). It appears, however, that the dominant effect was the tendency of CS males to be the most dispersed, as indicated by their highest nearest-neighbour index (Fig. 1b and d). Furthermore, the fact that the interaction between stimulus male nearest-neighbour index and genotype was not significant (see Methods) suggests that the relative strength of IGEs was similar when the stimulus males were Canton-S and DGRP. Nevertheless, we cannot separate the possible effects of focals' relatedness to and sociability of the stimulus flies. Another issue that we still cannot resolve is the occasional significant effect of the standard fluorescent powder that we use for marking flies.

We have identified one possible mechanism mediating the effect of stimulus flies on focals: the encounter rates among focals were highest when interacting with the least cohesive stimulus line (CS line) and lowest when interacting with the most cohesive stimulus line (Fig. 2a). This is perhaps because the encounter rates

between stimulus flies and focals were highest when the stimulus flies were the least cohesive and lowest when the stimulus flies were the most cohesive (DGRP 304; Fig. 2b). While it is clear that the quantity and quality of interactions determine a group's sociability, we still do not know how the encounter rate may affect our sociability score. We can rule out some artefact of activity levels because our independent analyses indicated no correlation between activity levels and sociability in 29 isofemale lines (Anderson et al., 2016).

In both our previous and current work, we observed no overt aggressive interactions, but we cannot preclude the role of either explicit aggression during the habituation period prior to videorecording or subtle antagonism during videorecording. For example, it is possible that the significant effect of encounter rate is associated with either subtle behavioural cues or odour signals. It is indeed known that olfaction plays a role in fruit fly social interactions (Schneider et al., 2012), and that cuticular hydrocarbons, which can mediate social interactions, may vary in response to social cues (Gershman, Toumishey, & Rundle, 2014; Krupp et al., 2008). Interestingly, encounters involving touch were the mechanism mediating both collective behaviour that enhanced avoidance of an aversive odour in fruit flies (Ramdya et al., 2015) and the switch from solitary to gregarious phase in desert locusts, *Schistocerca gregaria* (Simpson, Despland, Hagele, & Dodgson, 2001). It thus appears that mechanosensory information has a special role in orchestrating social behaviour in insects.

IGEs are widely acknowledged as a major potential factor in social evolution due to their complex effects on the relationships between genotypes and phenotypes and the fact that they themselves can evolve (Wolf, Brodie, Cheverud, Moore, & Wade, 1998). Although fruit flies are not typically considered among the multitude of species serving for research on the mechanisms of social behaviour, recent data (Battesti et al., 2012; Durisko & Dukas, 2013; Saltz, 2011; Schneider et al., 2012), our current demonstration of IGEs of stimulus individuals affecting social behaviour among several focals and the numerous tools available for mechanistic and evolutionary research in this classic model system open up further fruitful directions for research on the role of IGEs in the evolution of social behaviour.

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