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The use of conspecific phenotypic states as information during reproductive decisions

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Conspecifics that individuals encounter while foraging can provide a rich source of information about resource quality and levels of competition in the environment. Social learning theory predicts that animals should respond to cues from those individuals that provide the most reliable information. In this study, we explored the effect of the reproductive state and behaviour of individual sources of information on the behavioural and physiological reproductive decisions of the walnut-infesting fruit fly, *Rhagoletis suavis*. We demonstrate that female flies held in the presence of reliable sources of information about resource quality and/or level of local competition (reproductively active females) mature and lay eggs more readily than those in the presence of unreliable information sources (reproductively inactive females). The occurrence of such sophisticated use of social information in a nonsocial insect indicates its potential ubiquity and importance in the ecology and evolution of populations.

The use of inadvertent social information in adaptive decision making is widespread among animals (Leadbeater & Chittka 2007; Valone 2007). Animals can use the presence of conspecifics as indicators of environmental parameters, such as resource quality and levels of competition, to reduce the costs of extensive personal sampling (Laland 2004; Dall et al. 2005). Theory predicts that animals can gather more reliable information about environmental parameters by not only responding to the presence of conspecifics, but also by responding to the phenotypic state or behaviour of those conspecifics (Valone 1989, 2007; Danchin et al. 2004; Witte & Godin 2010). For example, stickleback fish (*Pungitius pungitus*) preferentially foraged in patches where they had previously observed a small group of fish feeding at a high rate over patches where they had previously observed a larger group of fish feeding at a lower rate (Coolen et al. 2005), indicating that these fish use the reliable information about food availability contained in behaviour, rather than just responding to the presence of conspecifics.

In this paper, we explore how two reproductive decisions, egg maturation and oviposition, are affected by the inadvertent social information present in the behaviour and physiological state of conspecifics in the walnut-infesting tephritid fruit fly, *Rhagoletis suavis*. The use of conspecific behaviour as a source of information has been demonstrated in several vertebrate species (Valone 2007), but only one recent study has demonstrated that insects respond to more than just the mere presence of conspecifics (or their eggs) when making foraging and reproductive decisions. In that study, Sarin & Dukas (2009) demonstrated that female *Drosophila melanogaster* preferentially use the location of mated reproductively mature females as indicators of larval resource quality over the location of virgins, suggesting that females discriminate between ovipositing and nonovipositing individuals when gathering information about potential larval resources.

Because members of the *R. suavis* species group are larval specialists on the husk of walnut fruit, adult females save energy by delaying the development of eggs until ripe walnuts are available. In the most extensively studied member, *R. juglandis*, females mature eggs sooner when held with visual models of ripe unused walnuts (Lachmann & Papaj 2001; Papaj 2005). Females could potentially use conspecifics as indicators of the availability of walnuts as well. Since females that have encountered ripe walnuts will begin developing eggs, the presence of reproductively mature females will typically indicate the presence of ripe fruit. Conversely, females without eggs provide little reliable information about the local abundance of hosts.

Tephritid fruit fly oviposition decisions are relatively well studied. In addition to responding to visual and chemical cues emanating from the fruit, several species are more likely to oviposit

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when held in the presence of conspecifics (Prokopy & Reynolds 1998; Prokopy & Roitberg 2001; Díaz-Fleischer & Aluja 2003; Rull et al. 2003; Piñero & Prokopy 2004; Davis et al. 2011). However, none of these studies tested whether flies were responding to the mere presence of conspecifics, or whether observing those conspecifics oviposit was necessary to elicit a response. Ovipositing flies are more reliable indicators of both host quality and the presence of larval competitors than are nonovipositing flies, and should therefore have a stronger effect on the oviposition decisions of conspecifics.

Here, we present two experiments that test the ability of *R. suavis* to use the physiological and behavioural states of conspecifics when making important reproductive decisions. In our first experiment, we tested whether recently emerged females develop more eggs when held in the presence of ovigerous females than when held in the presence of reproductively immature females. In our second experiment, we tested whether ovipositing females stimulate motivation to oviposit in conspecifics more than do nonovipositing females.

METHODS

The walnut husk maggot, *R. suavis*, uses fruit from the black walnut, *Juglans nigra*, as a site for mating and larval development (Bush 1966). Flies were collected as larvae from infested fruit in Dutchess County, NY, U.S.A. (41°43′ 22″N, 73°35′4″W) in the autumn of 2008. Pupae were refrigerated at 4 °C for 9–11 months and then relocated to room temperature conditions. Adults began to emerge in 3–5 weeks. All flies were provided an ad libitum diet of sugar, distilled water and hydrolysed yeast (unless otherwise noted) and were held on a 14:10 h light:dark cycle. In all phases of the two experiments, cages/cups were visually isolated from each other with sheets of white printer paper. Cages from different treatments were arranged alternately on shelves.

Effect of Conspecific Reproductive State on Egg Maturation

We assessed the role of the reproductive state of conspecifics in the facilitation of egg maturation by comparing how the eggload of (focal) females was affected by (demonstrator) females that did or did not possess eggs themselves. At emergence, all demonstrators were provided with a wood model walnut to stimulate egg development. To produce demonstrators with and without eggs, females were randomly split into two equal groups, and only one group was provided with hydrolysed yeast. Since a protein source is necessary for developing mature eggs, only those demonstrators provided yeast could become reproductively mature. Focal females were all provided hydrolysed yeast, but were not given model walnuts until they were placed in experimental treatments. This ensured that focal females were in similar physiological condition, and that the only difference between treatments was the reproductive state of demonstrator females.

When focal flies were split into experimental treatments, demonstrators were 21–29 days old and focal females were 14–16 days old. Focal females were randomly placed in pairs or triplets in 20 3.8-litre cages, half of which were also supplied with a pair of 'reproductively mature' (RM) demonstrators (those previously fed yeast) and the other half of which were provided a pair of 'reproductively inhibited' (RI) demonstrators. Focal female pairs and triplets were spread evenly between the two treatments. Each cage was provided a 5 mm diameter artificial host in which flies could oviposit (an agar sphere prepared using a 1:2:40 agar to sucrose to water solution, coloured with green and yellow food colouring, and dipped in wax (1:1 blend of TeCe-Ozokerit 6270:TeCe-Ceresin W46 waxes from Tromm in Cologne, Germany)). After 7 days in experimental treatments, all flies were frozen and the abdomen of each female was dissected under microscopy. The mature oocytes of both demonstrators and focal females were counted. Individual eggload data were not normally distributed, and there was evidence of cage effects, so we took a conservative statistical approach and analysed cage-level data (mean number of mature eggs in focal and demonstrator females in each cage) using t tests. We also tested for a correlation (Spearman's rank correlation, r_S) between the mean eggload of demonstrators and focal females within cages (SPSS v.17.0, Chicago, IL, U.S.A.).

Effect of Conspecific Presence and Behavioural State on Oviposition Decisions

We examined how the social facilitation of oviposition was modulated by the types of behavioural cues provided by conspecifics. At the beginning of this experiment, mature females (28–45 days old) were transferred to four 3.8-litre cages in groups of 10–15 females. Ripe walnuts were suspended in each of these group cages, and the first 18 females to alight on a fruit were selected for use as 'focal females', thus ensuring that test subjects were reproductively active. Focal females were immediately transferred to 473 ml cups where they were maintained in isolation for 24 h prior to the first trial.

The reproductive behaviours of each female were observed on four fruits representing distinct social contexts: an uninfested fruit (Control); a fruit in which a clutch of eggs had been laid in the previous 60 min (Eggs); a fruit and a female that had previously alighted on fruit (♀); and a fruit in which a female from the group cage was actively ovipositing (Ovip ♀). All fruits used were readily alighted upon and probed by females in pretests, indicating that they were attractive hosts. Extra females were gently removed from the fruit as it was being transferred to the focal female's cup. During the Ovip ♀ treatment, all females transferred while ovipositing continued to oviposit.

Females were observed for 30 min after the fruit and any associated flies were added to the focal female's cup. We recorded the latency at which the female alighted on the nut and/or attempted oviposition. Females were always given at least 40 h between each treatment, and the order in which they experienced each social context was randomized.

We analysed the proportions of individuals performing each behaviour with chi-square and Fisher's exact tests using α values adjusted for multiple comparisons. Latency scores for those females that performed each behaviour were log-transformed to fit the normality and equality of variance assumptions, and analysed with a type III ANOVA (SPSS v.17.0, Chicago, IL).

RESULTS

Effect of Conspecific Reproductive State on Egg Maturation

The reproductive state of demonstrator females had a strong effect on the eggload of focal females. The eggload of focal females housed with reproductively mature (RM) females (mean + SE = 17.4 + 4.2) was significantly higher than the average eggload of females housed with reproductively inhibited (RI) females (6.1 + 1.6; $t_{12.3} = 2.28$, two-tailed $P = 0.027$). Moreover, eggload among RM demonstrators was variable, and this variation influenced focal female eggload within the RM treatment. In cages with RM demonstrators, there was a strong correlation between demonstrator and focal female eggload ($r_S = 0.71, N = 10, P = 0.023$), but not in cages with RI demonstrators ($r_S = 0.28$, $N = 10$, $P = 0.5$; Fig. 1).