Mating affects resource selection and modulates associational effects between neighbouring resources

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Associational effects occur when the attack rate on a resource depends on neighbouring resources in the environment. These effects are predicted to result from mismatches experienced by the consumer organism in resource selection along hierarchical search levels. As resource selection depends on sensory information used during search behaviour, we expected that different physiological states of an insect might modulate the outcome of associational effects due to differences in resource selection. We used *Drosophila melanogaster* as a model organism for olfactory-guided behaviour in insects, to study the effects of mating induced behavioural changes on associational effects between two alternative resources. We found that mating has no effect on the ability of *D. melanogaster* to locate resource patches, but rather affects the perception of the resources within the patch. Consequently, we only found associational effects in the experiments with unmated females and not in the experiments with mated females. Our results suggest that the lack of associational effects for mated females resulted from changes in the use of short-range olfactory cues, leading to random selection among the resources. In conclusion, our results suggest that the physiological state of an insect modulates associational effects by affecting resource selection rates within the patch.

Interactions between consumer and resource organisms have historically been viewed as processes between two interacting organisms, but many of these interactions are also modified by the presence of neighbouring species (Tahvanainen and Root 1972, Atsatt and O’Dowd 1976). In complex environments it is expected that neighbouring species diversify the availability of sensory cues experienced by consumer organisms (Schröder and Hilker 2008, Webster and Cardé 2016). However, many insect species are constrained in their neural abilities to process the multitude of sensory cues experienced in such complex environments (Bernays 2001, Grippenberg et al. 2010, Bruce and Pickett 2011). As a consequence, the quality of a suitable resource patch, and the actual quality of the individual resources within that patch might be misinterpreted by the insect (Hambäck and Beckerman 2003, Underwood et al. 2014). Therefore, the presence of a neighbouring resource can either decrease or increase the probability that an insect detects an individual resource within a patch. These effects of neighbouring resources, on the interactions between individual consumers and their focal resources, are commonly referred to as associational effects (Barbosa et al. 2009, Underwood et al. 2014).

While various studies focussing on associational effects have studied the consequences of resource selection by insects in complex environments (Barbosa et al. 2009, Underwood et al. 2014), most studies have neglected to recognize that resource selection is influenced by the sensory traits or physiological state of the consumer organism (Underwood et al. 2014). When insects mate, for example, females allocate large quantities of their internal resources to progeny production, and they might have to adjust their dietary requirements to resources with higher nutritional gain (Harshman and Zera 2007, Jervis et al. 2008). In many insect species these changes in dietary requirements are initiated through a combination of physiological changes affecting neural processes connected to behavioural decisions (Dickson 2008, Avila et al. 2010, Hussain et al. 2016). In *Drosophila melanogaster*, for example, male-derived seminal peptides increase the females’ preference towards resources rich in yeasts (Ribeiro and Dickson 2010, Vargas et al. 2010, Becher et al. 2012), and salts (Zhang et al. 2013, Walker et al. 2015). Other studies have shown that changes in physiological needs also increase the sensitivity for specific olfactory cues associated with oviposition (Joseph et al. 2009, Dweck et al. 2013, Hussain et al. 2016), and decrease the
sensitivity for olfactory cues associated with mating (Barrozo et al. 2010, Saveer et al. 2012). While these examples provide compelling evidence that mating, and potentially other states, induces physiological changes in the chemosensory systems of insects, the consequences of these changes on resource selection in complex environments have largely been neglected.

To address this issue, we studied the consequences of mating induced behavioural changes on resource selection in complex environments using *D. melanogaster* as a model organism for olfactory-guided behaviour in insects. We used a wind tunnel experiment previously described by Verschut et al. (2016), which showed that the attraction rate towards preferred resources increases (i.e. associational susceptibility), while the attraction rate towards less preferred resources decreases (i.e. associational resistance), when both odour sources co-occur in complex environments. In our current study, we used this experimental framework to compare resource selection by mated and unmated *D. melanogaster* in complex olfactory environments. The specific aim of our study was to determine whether the mating state of *D. melanogaster* females affects the likelihood that neighbouring resources experience associational susceptibility, or associational resistance, due to changes in the probability that individual resources are detected. For this purpose, we determined how mating affected the attraction rates of *D. melanogaster* females towards patches composed of different frequencies of apple and banana odour sources. Subsequently, we determined the selection rates of the fruit flies for the individual odour sources within the patches, and determined how long it took the females to select a resource within the patch. By comparing the selection rates of the fruit flies for the individual odour sources within our patches, we determined whether associational effects occur between those odour sources (Hambäck et al. 2014, Verschut et al. 2016). We expect that mating modulates the chemosensory system, and changes search behaviour priorities, which eventually could affect the outcome of associational effects between neighbouring resources.

More specifically, based on the work of Hambäck et al. (2014) we expected that differences in the selection between apple and banana would result in a significant effect of both odour source type and odour source frequency (as in Fig. 1a). This outcome would imply that the fruit flies have a higher landing rate on one odour source in presence of an alternate odour source (i.e. associational susceptibility), and a lower landing rate on the alternate odour source in presence of the first odour source (i.e. associational resistance). Additionally, the work of Hambäck et al. (2014) also suggests that an interactive effect between odour source type and odour source frequency may occur when the relative roles of long distance detection of resource patches and the selection of odour source types within those patches differs (as in Fig. 1b). Finally, a non-significant main effect of odour source type and a non-significant interaction (as in Fig. 1b) would indicate that the consumer insects randomly select resources within the patches, and that neither odour source will experience associational effects. With our study we thus link mating induced behavioural changes of consumer organisms, to the consequences of these changes for the resource organisms through the scope of associational effects.

Material and methods

**Fly husbandry and mating state of the females**

We used *Drosophila melanogaster* (Diptera: Drosophilidae) from the wild-type Dalby-HL strain (Ruebenbauer et al. 2008), which we reared on a standard sugar–yeast–cornmeal diet in 25 × 95 mm rearing vials kept under controlled conditions (25°C, 60% RH, 12:12 L:D). Each morning we anesthetized the newly eclosed fruit flies with CO₂ and separated them by sex. The females were divided into two groups, which received different treatments prior to the experiments. The first group of females was transferred into vials only containing a humidified piece of cotton for a starvation period of 48 h prior to the experiments.
Throughout the article we denote these starved and virgin females as unmated females. The second group of females and all males were kept separately in rearing vials containing the normal diet for 72 h to allow them to reach reproductive maturity before using them in the experiments. We did not starve these females before mating, as trials experiments showed that this strongly diminishes their probability to initiate mating. On the morning prior to the experiment these fruit flies were transferred into rearing vials in a 1:3 female to male ratio to allow for mating. We checked the rearing vials every five minutes, and only those females that had mated and remained copulated for a minimum of 20 min were used in the experiments. Approximately 60 min after copulation the mated females were transferred into glass tubes (Ø 2.2 × 14 cm) closed with humidified pieces of cotton. Subsequently, these mated females were acclimatized for another 60 min before using them in the wind tunnel experiments. This ensured us that the females had copulated and had the time to initiate egg development (Heifetz and Wölfner 2004). Throughout the rest of the article these females will be denoted as mated females.

**Wind tunnel experiments**

We first examined whether patch attraction rates of unmated and mated *D. melanogaster* females were affected by the frequency of ripe apple (variety: Discovery) and over-ripe banana (Organic Cavendish – Dole, Dominican Republic) odour sources in a four-odour point source wind tunnel experiment described in full detail by Verschut et al. (2016). In this experiment we released individual fruit flies at a 100 cm downwind distance into the wind tunnel where they were exposed to a patch releasing four distinct odour sources at once into a 25 cm s⁻¹ airstream. The fruit odours were released by bubbling air through fruit pulp contained in four separate gas-washing bottles (outlet Ø 5 mm) at a rate of 0.8 l min⁻¹. The gas-washing bottles were placed 7.5 cm from each other to prevent instant mixing of the odour plumes. We tested five separate treatments consisting of two pure resource patches of only apple or banana odour sources (i.e. homogeneous), and three mixed resource patches containing all possible frequency combinations of apple and banana odour point sources (i.e. heterogeneous). We randomized the positions of the odour sources within the patches to control for potential bias caused by the spatial arrangement of odour point sources.

After determining whether resource frequency affects patch attraction rates we determined the absolute and relative resource selection rates of unmated and mated *D. melanogaster* females in one-, two- and four-odour point source experiments. More specifically, the one-odour point source experiments were used to determine the absolute landing rate on an odour source, and the multi-odour point source experiments were used to determine differences in selection rates for apple and banana odour point sources by the unmated and mated females. While in the one-odour point source experiments the females could only select one resource, the multiple odour point source experiments allowed the fruit flies to make an initial selection, and then move back downwind into the odour plume, to a point where the plumes were fully mixed before make a landing choice. Therefore, we distinguished between these two selection steps, and recorded the attraction rate when the attracted fruit flies would hover for at least five seconds in a 1.5 cm vicinity of the odour release point, and landing was recorded when a fruit fly would land within 10 min on a metal mesh (pore Ø 1 mm) placed in front of the outlet of the gas-washing bottles.

To account for the time invested in resource selection we measured the time that a female needed from takeoff until making a landing decision in the patch. Some of the females that were first attracted towards apple odours rather selected banana, and vice versa, during landing. Consequently, longer flight durations represent the decision of those females that moved back downwind into the odour plume before selecting an odour source to land on.

**Statistical analysis**

To determine whether mating affects the attraction of *D. melanogaster* females to patches composed of different resource frequencies, we first analysed the absolute attraction rates for the four-odour point source patches using a generalized linear model (GLM) with binomial error distribution. We defined the absolute attraction rate as the sum of all flies attracted to any of the odour point sources in a patch. The different patches were characterized by a numerical factor with values of 0, 0.25, 0.50, 0.75 or 1 to account for resource frequency as the proportion of the banana odour point sources in the patch. Because inspection of the data indicated that attraction rates might be non-linearly related to the resource frequency, we included resource frequency as an additional squared fixed effect in the model to examine whether heterogeneous patches caused a higher, or lower, landing rate than homogeneous patches.

Subsequently, we determined whether *D. melanogaster* females of both mating states showed different absolute selections rates in the one-, two- and four-odour point source experiments. We denoted the total attraction and total landing rates on the odour point sources as the absolute rates, and considered them to account for the odour source preferences of *D. melanogaster* females. For the one-odour point source experiment we tested for the effects of mating state, odour source type (i.e. apple or banana), and the interaction between the two factors using a GLM with binomial error distribution. For the two-and four-odour point source experiment we extended this analysis by including an additional factor separating attraction and landing rates (i.e. selection step). This selection step accounted for the fact that some fruit flies where first attracted to one odour source type and then decided to land on the other type.

To determine the consequence of resource selection by the fruit flies among the individual odour point sources we performed generalized linear mixed-effects models (GLMM) with the individual trial as a random factor. This random factor effectively estimates relative, rather than absolute, landing or attraction rates by correcting for the number of release points per odour source type in the patch. In other words, the analysis of relative rates compares rates among single odour point sources and identifies potential associational effects between individual resources (Hambäck et al. 2014, Verschut et al. 2016). We performed
separate GLMMs on both mating states and selection steps to determine whether associational effects occurred within any of these subsets.

Finally, we tested whether the flight duration in the two- and four-odour point source experiments were affected by the mating state of the fruit fly, the odour source on which the fruit fly eventually landed, or by an interaction between those factors using a GLM with a Gaussian error distribution. Prior to each analysis we used Bartlett’s tests to check for homogeneity of variances and found that we did not meet the model requirements for some patch compositions. Therefore, we did not include the patch resource composition as a factor, but performed the analysis on pooled and log-transformed data.

All models were selected using likelihood ratio tests based on $\chi^2$ and Akaikes information criterion in a step-wise backward selection process. After each analysis, we estimated over-dispersion and visually inspected the normality of the residuals and the Q-Q plots, but did not find any indications that necessitated corrections of the tests or data distributions. Where necessary, we used either planned comparisons, or Tukey HSD post hoc tests to perform pairwise comparisons across selection rates for the odour sources. The analyses were carried out in R (ver. 3.3.0; <www.r-project.org>) using the lme4 package (Bates et al. 2013) for fitting the mixed effect models, the car package (Fox and Weisber 2011) for likelihood ratio tests, the multcomp package (Hothorn et al. 2008) for pairwise comparisons and the ggplot2 package (Wickham 2009) to visualize binomial analysis.

Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8sj63> (Verschut et al. 2017).

Results

Patch attraction rates

The overall patch attraction rate did not differ between unmated and mated females, but was affected by an interaction between mating state and odour source type (GLM: $\chi^2_{1,297} = 3.87, p = 0.05$; Supplementary material Appendix 1 Table A1). This interaction depended on non-linear differences in resource frequency and optimum patch attraction. More specifically, for the unmated females patch attraction increased with an increasing frequency of banana odour point sources in the patch (GLM: $\chi^2_{1,297} = 5.46, p = 0.02$), and showed a tendency towards a hump-shaped but non-significant relationship between attraction rates and the frequency of banana odour sources in the patch (GLM: $\chi^2_{1,297} = 3.63, p = 0.057$; Fig. 2, Supplementary material Appendix 1 Table A2). For the mated females, on the other hand, the predicted resource frequency that resulted in the highest attraction was closely connected to an evenly mixed patch (GLM: $\chi^2_{1,297} = 10.14, p = 0.001$), and caused a relationship that was non-linearly affected by the frequency of resources in the patch (GLM: $\chi^2_{1,297} = 9.92, p = 0.002$; Fig. 2, Supplementary material Appendix 1 Table A2).

Absolute attraction and landing rates

The absolute landing rates of Drosophila melanogaster females in the one-odour point source experiments were affected by the odour source type, but not by the mating state of the female or by an interaction between mating state and odour source (Fig. 3a, Supplementary material Appendix 1 Table A3). The attraction- and landing rates followed the same behavioural patterns in the two-odour point source experiment, and both were affected by an interaction between mating state and odour source (Fig. 3b, Supplementary material Appendix 1 Table A3). This interaction seemingly occurred because the unmated females had a stronger selection for banana than apple odour sources (GLM: $\chi^2_{1,99} = 7.84, p = 0.005$), while the mated females showed no selection towards either odour source (GLM: $\chi^2_{1,99} = 0.26, p = 0.61$). In the four-odour point source experiment a proportion of initially attracted mated females landed elsewhere in the wind tunnel, which resulted in lower absolute landing rates for the mated females (Supplementary material Appendix 1 Table A4, Fig. A1). Both the absolute attraction and landing rates were affected by an interaction between mating state and odour source. This interaction occurred as the absolute selection rates of unmated females were highest for the more dominant odour source in the patch, while the selection of

![Figure 2. Total patch attraction rate ± 95% confidence intervals (n = 60 per treatment) and fitted model outcomes (Supplementary material Appendix 1 Table A1) of unmated (white points – solid line) and mated Drosophila melanogaster females (black points – dashed line). The position of the data points was slightly jittered to prevent overlapping error bars. The x-axis represents the frequency of apple and banana odour point sources in the patch. Above the graph a simplified representation of the experiment is illustrated. The square represents the location where individual females were released. The odour source patch, in this example consisting two apple- (red) and two banana-odour point sources (yellow), is illustrated at the upwind end of the wind tunnel. The odour cues travel with the direction of the airflow until they reach the point where the flies were released at the downwind end of the wind tunnel.](image-url)
When separating the analysis for the two mating states, we found that the interactions occurred because mated females had a neutral response to odour source type and frequency, while unmated females responded to both factors (Table 1). For unmated females, relative attraction and landing rates were higher on banana than on apple, and both rates decreased with the increasing frequency of banana in the patch. This means that when we translate these selection rates into associational effects, apple experienced associational resistance as the relative landing rate on apple odour point sources was lowered with the increasing frequency of banana odour point sources in the patch. Alternatively, banana experienced associational susceptibility as the landing rate on banana increased with the decreasing frequency of banana in the patch (Fig. 4a–b). As neither the relative attraction rates nor the landing rates showed significant interactions between odour source frequency and the type of odour source (Table 1), the outcome for the unmated females corresponds with the pattern described in Fig. 1a, in which the hypothesized lines for associational resistance and associational susceptibility follow a parallel pattern without crossing each other.

In the experiments with the mated females neither the attraction rates of (Fig. 4c), nor the landing rates on apple or banana odour point sources (Fig. 4d), were affected by resource frequency or any other factor (Table 1). This shows that in the presence of mated females the apple and banana odour sources experienced no associational interactions (i.e. neutral response). This response corresponds with the pattern described in Fig. 1b where a changing frequency of either odour sources does not result in a change in the attraction or landing rates of either odour source.

Flight duration

The mated females maintained longer flight durations than the unmated females in both the two-odour point source experiments (GLM: \( \chi^2 = 12.04, p < 0.001 \)), and the four-odour point source experiments (GLM: \( \chi^2 = 16.92, p < 0.001 \)). However, the flight duration was not affected by the odour source on which the female landed or by the interaction between the factors odour source and

Supplementary material Appendix 1 Table A5). When separating the analysis for the two mating states, we found that the interactions occurred because mated females had a neutral response to odour source type and frequency, while unmated females responded to both factors (Table 1). For unmated females, relative attraction and landing rates were higher on banana than on apple, and both rates decreased with the increasing frequency of banana in the patch. This means that when we translate these selection rates into associational effects, apple experienced associational resistance as the relative landing rate on apple odour point sources was lowered with the increasing frequency of banana odour point sources in the patch. Alternatively, banana experienced associational susceptibility as the landing rate on banana increased with the decreasing frequency of banana in the patch (Fig. 4a–b). As neither the relative attraction rates nor the landing rates showed significant interactions between odour source frequency and the type of odour source (Table 1), the outcome for the unmated females corresponds with the pattern described in Fig. 1a, in which the hypothesized lines for associational resistance and associational susceptibility follow a parallel pattern without crossing each other.

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and differed in their resource selection within the patches (Fig. 4). These results suggest that mating has no effect on the ability of *D. melanogaster* females to locate suitable resource patches, but rather that mating affects the perception of the resources within the patch. This behavioural difference is likely the reason why we only observed associational resistance for apple, and associational susceptibility for banana in the experiments with unmated *D. melanogaster* females, and not in the experiments with mated females (Fig. 4). More specifically, our results suggest that mating affects the response to short-range olfactory cues used by *D. melanogaster* females while selecting among resources within the patch, which could be a potential mechanism causing the behavioural mismatch in the perception of patch quality versus the quality of individual resources that is expected to underlie associational effects (Hambäck and Beckerman 2003, Hambäck et al. 2014).

Many empirical studies have failed to determine how variation in the behavioural traits of consumer organisms generates associational effects (Hambäck et al. 2014, Underwood et al. 2014). Our results are the first to show that physiologically induced behavioural changes have consequences on associational effects between neighbouring resources through a modulation in the use of sensory cues used to select resources at different hierarchical levels. We hypothesized that patterns of associational effects could not be explained by differences in the patch selection ability of *D. melanogaster* females, and that the observed differences might be due to the mating state (Supplementary material Appendix 1 Fig. A2, Table A6).

**Discussion**

It has been hypothesized that associational effects are caused by a behavioural mismatch in the ability of consumer organisms to discriminate between the overall patch quality and the quality of individual resources within the patch (Stephens and Krebs 1986, Hambäck and Beckerman 2003). Especially insects have been found to make decisions along different hierarchical levels while searching for resources (Saint-Germain et al. 2004, Bukovinszky et al. 2005), and provide a perfect model system to test how resource heterogeneity leads to associational effects between neighbouring resources. However, most studies have overlooked that the sensory traits and the physiological state of an insect can affect their ability to locate suitable resource patches, and change their selection behaviour among the resources within that patch. In our experiments we found that the total attraction rate at the patch level did not differ between unmated and mated *Drosophila melanogaster* females (Supplementary material Appendix 1 Table A1), but that the mated females responded differently to resource frequency (Fig. 2), maintained longer flights to find the patches (Fig. 2A), and differed in their resource selection within the patches (Fig. 4). These results suggest that mating has no effect on the ability of *D. melanogaster* females to locate suitable resource patches, but rather that mating affects the perception of the resources within the patch. This behavioural difference is likely the reason why we only observed associational resistance for apple, and associational susceptibility for banana in the experiments with unmated *D. melanogaster* females, and not in the experiments with mated females (Fig. 4). More specifically, our results suggest that mating affects the response to short-range olfactory cues used by *D. melanogaster* females while selecting among resources within the patch, which could be a potential mechanism causing the behavioural mismatch in the perception of patch quality versus the quality of individual resources that is expected to underlie associational effects (Hambäck and Beckerman 2003, Hambäck et al. 2014).
either result from differences in resource selection rates (as in Fig. 1a), or by changes in the relative roles of long- and short-range olfactory cues (as in Fig. 1b). Even for a generalist species like *D. melanogaster* (Jenike 1983, Whitman and Pierce 2008, Dweck et al. 2013), it is expected that the perceived quality of alternative resources depends on the physiological needs of the individual. These differences in resource perception generally translate into associational susceptibility for higher quality resources, and associational resistance for lower quality resources (Pfister and Hay 1988, Hjältén et al. 1993, Hambäck and Beckerman 2003, Hambäck et al. 2014), which we also observed in the experiments with the unmated females. This outcome confirmed our hypothesis that differences in the selection rates causes associational effects between resources as explained in Fig. 1a.

Our results also suggest that the loss of associational effects in the experiments with mated females resulted from a change in the use of short-range olfactory cues, leading to random selection among the resources (as in Fig. 1b). Moreover, our results suggest that the overall attraction rates to the resource patches were not affected by the starvation period of the unmated females (48 h), compared to lack of starvation for the mated females prior to the experiments. While these results suggest that both mating states equally relied on fruit-derived odours for long-range attraction, the non-linearity of the relationships with resource frequency still suggests a qualitative difference of the resource patches for the mating states. As these qualitative differences are presumably a mechanism to match the specific internal needs of the physiological state of the consumer organism (Harshman and Zera 2007, Billeter et al. 2012, Saveer et al. 2012), it is of interest to speculate how the divergence in the physiological needs of the two mating states can serve as an underlying mechanism of associational effects. Firstly, the importance of banana-derived odours was evident for the unmated females, as long-range attraction increased with the frequency of banana resources in the patch (Fig. 2), and as they strongly selected for banana in mixed resource patches (Fig. 3b, 4). In a previous study with unmated females we found that the prerequisites for the combination of associational susceptibility and associational resistance to occur is that the insects use similar olfactory cues for both long- and short-range attraction (Verschut et al. 2016). Considering that banana is an important adult food resource (Lachaise and Silvain 2004, Schubert et al. 2014), our results suggest that the observed pattern depended on a stronger selection for the preferred banana odours at both hierarchical levels of search behaviour.

For mated *D. melanogaster* females, however, attraction is largely modulated by the presence of yeast odours (Starmer and Fogleman 1986, Becher et al. 2012, Christiaens et al. 2014), which indicate suitable oviposition sites where larvae can feed on yeasts and other microorganisms growing on the fruit substrates (Starmer and Fogleman 1986, Becher et al. 2012, Stamps et al. 2012). As we only used ripe, but undamaged fruits, we excluded the possibility that yeast-derived odours dominated the fruit-derived odour emitted by our resources (Dweck et al. 2013), and as we found no differences in the overall attraction rates to the patches (Fig. 2, Supplementary material Appendix 1 Table A1), we can rule out the importance of yeast in the long-range attraction of the mated females to our patches. As the mated females showed the highest attraction rates to evenly mixed patches, and maintained longer flight durations than the unmated females (Supplementary material Appendix 1 Fig. A2, Table A6), we can hypothesize that evenly mixed patches advertised mixtures of adult food resources and suitable oviposition sites (Bernays 2001, Janz 2005), while the lowered attraction rate to patches with high frequencies of banana might have been caused by the high emission of odours exclusively indicating adult food resources (Lachaise and Silvain 2004, Schubert et al. 2014).

While our results suggest that both mating states strongly relied on fruit-derived odours for long-range attraction, the short-range olfactory preference for oviposition substrates has been found to be mediated through a single olfactory channel in which apple and banana odours induce very similar physiological responses (Dweck et al. 2013). Moreover, as other studies have shown that oviposition behaviour is governed by a combination of olfactory (Ruebenbauer et al. 2008, Dweck et al. 2013, Hussain et al. 2016), visual (Del Solar et al. 1974) and gustatory information (Clyne et al. 2000, Thorne et al. 2004), we expect that the change in the use of short-range cues and the lack of additional sensory cues lowered the interest of the mated females to select among our odour sources (Supplementary material Appendix 1 Fig. A1, Table A3), and eventually removed the competitive interactions between apple and banana odour sources in our mixed resource environments (Fig. 1, 4). This suggests that behavioural mismatches in the ability to discriminate between the overall quality of patches and the quality of the individual resources within a patch do not only cause associational effects between resources, but can also relieve resources from experiencing associational effects. In conclusion, our results suggest that mating affects olfactory-guided resource selection behaviour and modulate associational effects between alternative resources. As the mated females lost their interest in the short-range differences between the resources it is possible that associational effects under more natural conditions might actually depend on whether the consumer organisms are searching for food or oviposition resources. It would be of interest to extend the theoretical framework of associational effects further by including the modulations of behavioural traits after mating of the consumer insects. Moreover, it would be interesting to determine whether the resource selection behaviour we observed for *D. melanogaster* is affected by other sensory cues when the fly can be in direct contact with the substrates within the patch. Such additional experiments would, consequently, separate the role of pre-alighting behaviour, such as finding a patch or a resource, from the effects caused by post-alighting behaviour, such as patch residence time and giving up densities (Stephens and Krebs 1986, Hambäck and Beckerman 2003, Bukovinszky et al. 2005).

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Supplementary material (available online as Appendix oik-04315 at <www.oikosjournal.org/appendix/oik-04315>). Appendix 1.