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Original Article

Flexible habitat choice by aphids exposed to multiple cues reflecting present and future benefits

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Mothers choose suitable habitats for laying offspring to maximize fitness. Because habitat quality varies in space and time, mothers gather information to choose among available habitats through multiple cues reflecting different aspects of habitat quality at present and in the future. However, it is unclear how females assess and integrate different cues associated with current rewards and future safety to optimize oviposition/larviposition decisions, especially across small spatial scales. Here, we tested the individual and interactive effects of leaf surface, leaf orientation, and leaf bending direction on larviposition site choice and fitness benefits of wheat aphids (*Metopolophium dirhodum*) within individual leaves. We found that females preferred upper over lower surfaces for gaining current food-related rewards, downward- over upward-facing surfaces for avoiding potential abiotic risks, and sunken over protruding surfaces for avoiding potential biotic risks. When facing conflicting cues during larviposition, females preferred downward-facing/sunken surfaces over upper surfaces, suggesting that females prioritize potential safety at the cost of current rewards during decision making. Most importantly, our combined-cue experiments showed females still assessed secondary cues (i.e., the upper surface) when first-ranked cues (i.e., the downward-facing/sunken surface) are available, even though females only gained relatively small fitness rewards through secondary cues, and females can integrate different cues associated with current rewards and potential safety in a multiplicative way to make flexible and complex larviposition decisions. Overall, our findings provide new insights into how animals collect and process multi-cue information associated with current rewards and potential safety to maximize fitness at small spatial scales.

Key words: **current benefits, flexible decision making, *Metopolophium dirhodum*, microhabitat choice, multiple cues, potential risks**

INTRODUCTION

Habitat-choice decisions can have a critical influence on animal fitness (Refsnider and Janzen 2010; Schmidt and Massol 2019). Because habitat quality is determined by multiple factors such as food resources, predation risks, and weather threats, individuals are expected to assess multiple cues from different aspects of habitat quality in order to make optimal habitat-choice decisions (Nonacs and Dill 1990; Rittschof and Ruggles 2010; Pintar et al. 2018; Yin et al. 2020b). In spatio-temporally varying environments, individuals need to collect information to assess habitat quality not only at varying spatial scales but also at varying temporal scales, allowing them to compare, for example, immediate versus future benefits (Schmidt et al. 2010; Addis and Lowe 2020). However, few studies have explored in detail how individuals assess and integrate multiple cues associated with two or more aspects of present and future habitat quality, especially at a small spatial scale.

Cues that reflect present habitat quality and provide an indication of current fitness benefits are known as direct cues (Thorson et al. 1998; Janz et al. 2005; Schmidt 2006). For example, most animals are able to detect olfactory cues produced by predators and prefer to deposit eggs in low-predation habitats (e.g., Binckley and Resetarits 2002; Silberbush and Blaustein 2011; Mitchell et al. 2017; Beermann et al. 2018). In contrast, other cues may provide

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individuals with information on future habitat quality (Schlaepfer et al. 2002; Stamps and Krishnan 2005). For example, individuals often prefer complex structured habitats that provide protection against predators, even in the absence of direct predator-produced cues. As habitat structures can provide refuges, this habitat-choice decision can increase survival after the appearance of predators in the future (e.g., Mammalia: Thorson et al. 1998; Amphibians: Sadeh et al. 2009; Insects: Pöykkö 2011). While future abiotic and biotic risks cannot be directly evaluated, indirect cues can guide individuals to avoid them and make optimal habitat-choice decisions (see also Jordan and Ryan 2015). Therefore, individuals are expected to use direct and indirect cues to assess current and future habitat quality, especially when selecting sites where offspring can develop.

Due to the limited mobility and high vulnerability of newly laid offspring to abiotic and biotic risks, temporal-scale habitat assessment by females is crucial for offspring survival (Refsnider and Janzen 2010, and references therein). Because indirect cues often correlate with the habitat safety in the future, numerous studies have found that females across taxa can use indirect cues to decide where to place their offspring (Spieler and Linsenmair 1997; Spencer 2002; Vosteen et al. 2016; Baleba et al. 2019). Yet, indirect cues also represent an unknown potential source of information to females during decision-making. The magnitude of fitness enhancement brought about by indirect cues depends on the occurrence frequency and degree of associated selective factors in the near future, which cannot be directly and accurately evaluated by females during the process of decision-making (Yang 2006; Touchon and Worley 2015). In contrast, response to direct cues can yield current fitness benefits to females such as by increasing the number of eggs laid. Therefore, breeding habitat-choice decisions are complicated for females when facing multiple direct and indirect cues among habitats.

In most studies, direct and indirect cues that females use to assess habitat quality have been studied independently (Janz et al. 2005; Fievet et al. 2008; Raitanen et al. 2013; Morinay et al. 2020), whereas direct and indirect cues need to be weighted and integrated when animals decide on responses. In particular, when females face conflicting direct and indirect cues associated with different microhabitats factors, it can be unclear how females assess tradeoffs between current rewards and potential safety through direct and indirect cues; furthermore, it can be unclear whether females can assess secondary cues when prioritized cues are available during decision-making, especially when secondary cues indicate relatively small fitness benefits. If adaptive responses to both sets of cues are possible, we then want to know whether and how females integrate direct and indirect cues to make decisions when choosing a microhabitat.

To explore these issues, we used the rose grain aphid (*Metopolophium dirhodum*), a major wheat pest that occurs worldwide, to test larviposition site choices between neighboring leaf surfaces. The differences in physical and chemical components in the tissues of upper versus lower leaf surfaces can directly affect feeding efficiency and oviposition habitat choice (Reavey and Gaston 1991; Lundgren et al. 2008; Ayabe et al. 2017). In addition, downward-facing surfaces and sunken inward bending surfaces can separately provide females with information on avoiding potential weather stress (Chu et al. 1995; Ohtsuka and Osakabe 2009; Yin et al. 2018) and potential predation risks (Danks 2002; Oku and Yano 2007). Thus, oviposition/larviposition decisions informed by leaf tissue surface (upper vs. lower), leaf orientation (upward vs. downward), and whether the leaf surface is bent inwards or outwards (sunken vs. protruding) are expected to affect fitness through immediate food-related rewards or future potential safety. Because flat or curled wheat leaves are often naturally twisted with the upper surface facing downwards (Yin et al. 2018; Supplementary Figure S1), *M. dirhodum* aphids often encounter in their natural habitat cues with potentially conflicting or consistent fitness effects based on the leaf tissue surface, leaf orientation, and bending direction when making larviposition decisions. This provides an opportunity to study how different cues are weighted and integrated in the decision-making process.

We first examined whether *M. dirhodum* females: 1) prefer upper to lower leaf surfaces for direct food-related rewards; 2) prefer a downward-facing to upward-facing leaf orientation for potential safety against adverse weather; and 3) prefer an inward bending leaf that produces a sunken surface from an outward bending leaf that produces a protruding surface for potential safety against natural enemies. Based on these results, we then determined 4) how females prioritize cues by separately offering females a choice between multiple preferred options. To help interpret the results, we tested the relative magnitude of fitness benefits derived from direct responses versus future risk avoidance behavior. Finally, we considered how females simultaneously assess cues associated with current versus future benefits when the cues are presented together.

MATERIAL AND METHODS

An overview of the experiments and questions being tackled is provided in Table 1. This table also provides a list of the abbreviations used in the paper, which involve the upper versus lower leaf tissue surfaces (Usur and Lsur), upward versus downward-facing leaf orientations (Ufac and Dfac), and inward versus outward bending direction of leaves that separately produce sunken and protruding surfaces (Ibent and Obent). The questions addressed consider fitness effects of larviposition preference and various choice experiments when cues are presented singly or in combination.

Insects and plants

Laboratory experiments were conducted on the potted wheat seedlings. Wheat seeds (Zhoumai 22) were sown in plastic pots (10 cm in diameter and 15 cm in height) containing water-absorbent roseite. Seedlings grown to 15–20 cm in greenhouses were collected for the laboratory experiments. *Metopolophium dirhodum* were collected from a winter wheat field near Beijing (39°48 N, 116°28 E), China, and were reared on 10–15 cm high wheat seedlings in screen cages (80 × 80 × 80 cm) in climate incubators (18 ± 1 °C and 16:8 h photoperiod). Field observations took place in a winter wheat field at Kaifeng (34°80 N, 114°30 E), Henan province, China in early April and early May 2019. No pesticides were applied during experiments.

Fitness-related comparisons

Does leaf tissue surface affect aphid performance in the laboratory?

To explore immediate fitness benefits of preferred leaf tissue surface, we measured the life-time fecundity of *M. dirhodum* females on upward-facing upper surfaces and lower surfaces of wheat leaves. This experiment was carried out on potted wheat seedlings in an insectary set at 18 ± 1 °C, 50% ± 10 RH, and 16:8 h photoperiod. To restrict aphids feeding to either the lower or upper leaf surface,

Table 1

Main questions addressed in study and treatments/traits compared. Expectations are based on observations prior to experiments or results from initial trials

Question	Treatments compared	Trait	Expectations
Fitness-related comparisons			
Does leaf tissue surface affect aphid performance in the laboratory?	Upper surfaces (Usur) versus lower surfaces (Lsur)	Lifetime fecundity	Upper leaf surfaces generate a fecundity advantage.
Does leaf orientation/leaf tissue surface affect aphid performance in the field?	Upward-facing lower surfaces (Ufac, Lsur) versus downward-facing lower surfaces (Dfac, Lsur) versus upward-facing upper surfaces (Ufac, Usur)	Development time, survival and 7-day fecundity	Under field conditions, downward-facing surfaces have a performance advantage. There is a conflict in performance advantages between upper surfaces and downward-facing surfaces.
Does leaf bending affect aphid performance in the presence of predators?	Leaves bent to produce inward sunken surfaces (Ibent) versus outward protruding surfaces (Obent)	Survival with the predatory ladybird	The presence of an inward bent sunken surface decreases predation risk.
Larviposition preference			
What is the individual effect of leaf tissue surface, leaf orientation, and bending direction on larviposition site choice?	Pairwise comparison of leaves with different tissue surface (Usur vs. Lsur), orientation (Ufac vs. Dfac), and bending direction (Ibent vs. Obent)	Number of nymphs deposited on different surfaces	Aphids separately prefer to place offspring on upper, downward, and inward bent sunken surfaces.
What surfaces are preferred by females when there are conflicting preferred cues?	Pairwise comparison of leaves with preferred tissue surface versus preferred orientation, preferred tissue surface versus preferred bending direction, and preferred orientation versus preferred bending direction	Number of nymphs deposited on different surfaces	Cues leading to potential safety are favored compared with cues leading to current rewards.
Can females consider multiple preferred cues simultaneously?	Four-way comparison of leaves with two combined preferred cues versus no preferred cues versus one preferred cue	Number of nymphs deposited on different surfaces	If females consider the secondary cue when the prioritized cue is available, females prefer combined preferred cues over the single preferred cue.
What happens when females are presented with two combined preferred cues compared to a different preferred cue?	Pairwise comparison of leaves reflecting the different preferred cues	Number of nymphs deposited on different surfaces	They combine direct and indirect cues in a multiplicative way and make flexible larviposition decisions.

we attached individual wheat leaves to paper with double adhesive tape to have either upper (n = 33) or lower (n = 34) surfaces exposed. An adult female < 24 h old was transferred to each leaf surface inside a clip cage (2 × 2 × 2 cm). The number of larvae produced by the female was recorded every 2 days until she died. Tested females were transferred to fresh leaves every 2 days.

Does leaf orientation and its interaction with leaf tissue surface affect aphid performance in the field?

To explore potential fitness benefits of preferred leaf orientation and the relative magnitude of effects of preferred leaf tissue surface and preferred leaf orientation on fitness enhancement, we compared *M. dirhodum* performance (development time, survival and 7-day fecundity) on leaves with an 1) upward-facing lower surface, 2) downward-facing lower surface, or 3) upward-facing upper surface in a wheat field. By comparing treatments (1) and (2), effects of leaf orientation (downward vs. upward) on aphid performance were assessed; by comparing treatments (2) and (3), the potential fitness benefits of the downward leaf orientation were compared against immediate benefits of the upper leaf surface (see Results). There were 25 replicates for each treatment.

For each treatment, we selected 25 healthy wheat plants. Two adult females (adapted to field environments for 3–5 days before experiments) were transferred onto tested surface of a flag leaf at about 1800 h and the clip cage was used to confine females there. Bamboo sticks (1 m high × 1 cm in diameter) were sunk into the ground adjacent to experimental plants, and iron wire was used to secure clip cages to the sticks and assisted in maintaining the expected orientation of tested leaf surfaces according to the requirements of each treatment. After 24 h, the adults and all but one nymph were removed from each surface of every wheat leaf. Overall, we tested 25 nymphs for each treatment. Nymphs were monitored daily until they reached adulthood. After emergence of females, nymphs produced by females each day were observed within 7 days. Aphids were transferred to a fresh leaf every 4 days.

Does leaf bending affect aphid performance in the presence of predators?

This experiment explored potential fitness benefits of surfaces produced from leaf bending at the midrib (producing sunken inward bending surfaces or protruding outward bending surfaces) on offspring survival in the presence of a predatory ladybird, *Propylaea japonica*. Each treatment was replicated 20 times. Because we found that predation risk on a protruding surface was similar to the risk on a flat surface in preliminary experiments, we used for convenience a flat surface to replace the protruding surface in this experiment.

Each treatment was applied to wheat seedlings grown in a disposable paper cup (5 cm in diameter). Each cup included four wheat seedlings that passed through a circular (5 cm in diameter) piece of paper at half height of the wheat seedlings (Supplementary Figure S2). Because there were sheltered sites in the lower part of wheat seedlings, the paper was used to prevent aphids from escaping to these lower parts. An adult female was transferred to a predetermined surface of a wheat seedling in each cup, which was then confined by a clip cage for feeding and larviposition for about 1.5 days. Then we removed the clip cage and counted the number of nymphs on the predetermined surfaces in different treatments after removing the adult. A male adult ladybird was then transferred into each cup. After 0.5 days, we counted the number of remaining aphids in each cup. To prevent the aphids and ladybird from dispersing outside the potted plant, we inserted a transparent cylindrical plastic sheet (diameter = 5 cm, height = 30 cm) into the cup along its outer wall and taped a piece of nylon gauze on top of the cylinder for ventilation.

Larviposition preference

All choice experiments were conducted inside clip cages, where aphids could crawl freely between different surface micro-habitats within an individual leaf or neighboring leaves (Figure 1). An adult female (*n* = 50 for each treatment described below) was introduced into each clip cage and left to deposit nymphs for 24 h. The number of newly produced nymphs on each surface microhabitat was recorded. All choice experiments were conducted under dark conditions to exclude light effects in a climate cabinet (20 ± 1 °C, 50% ± 5RH). The choice set-up (*n* = 50) for each treatment was described separately below and illustrated in Figure 1.

Experiment 1: Do females prefer upper versus lower, downward versus upward, sunken versus protruding positions?

To answer this question, we conducted three treatments (Figure 1a–c). In the first (A), a flat wheat leaf was presented with an upper and lower surface (Usur vs. Lsur) in a vertical orientation. The flat leaf and vertical orientation were separately used to exclude the effect of leaf bending (sunken inward/protruding outward bending) and upward/downward orientation (as below). In the second (B), a double-leaf arrangement in a horizontal orientation was used with two lower leaf surfaces facing upward and downward (Ufac vs. Dfac). This double-leaf arrangement (DLA) involved sticking two similarly sized leaves together using double adhesive tape such that only lower surfaces were exposed (Figure 1b). The DLA excluded the effects of leaf surface tissue (as below). In the third arrangement (C), a sunken inward and protruding outward bending midrib surface (Ibent vs. Obent) were produced by using a curved DLA with two lower surfaces bent either inwards or outwards in a vertical orientation. The artificially curved DLA was made by folding a flat DLA along its central axis and fixing the arrangement by a fine cotton thread.

Experiment 2: What surfaces are preferred by females when there are conflicting preferred cues?

Because aphids preferred the upper (Usur as a preferred cue) over lower surface (Lsur), downward-facing (Dfac as a preferred cue) over upward-facing leaf orientation (Ufac), and inward (Ibent as a preferred cue) over outward bending direction (Obent) based on the above experiments (see results), we conducted three treatments to determine the relative importance of these preferred cues on larviposition site choice of *M. dirhodum* within an individual leaf (Figure 1d–f). The first of these (D) considered a flat wheat leaf in a horizontal orientation with an upper surface facing upward and a lower surface facing downward (cues preferred in initial choice tests are displayed in bold: **Usur**, Ufac vs. Lsur, **Dfac**). The second (E) considered a curved wheat leaf with an upper surface bent outward and protruding and a lower surface bent inward and sunken in a vertical orientation (**Usur**, Obent vs. Lsur, **Ibent**). Finally, the third comparison (F) considered a curved double-leaf arrangement in a horizontal orientation with a protruding outward bending lower surface facing downward and a sunken inward bending lower surface facing upward (Obent, **Dfac** vs. **Ibent**, Ufac).

Experiment 3: Can females consider multiple preferred cues simultaneously?

To study whether females consider a secondary cue when a prioritized cue is available for choosing larviposition habitats, we conducted two experiments (Figure 1g,h). We predicted that if females consider the secondary and prioritized cues simultaneously, they would prefer combined preferred cues over a single preferred cue. In the first treatment (G), there were two side-by-side flat leaves in a horizontal orientation; the upper surfaces of two leaves faced opposite orientation. This resulted in four surfaces: a leaf with a downward-facing lower surface (**Dfac**, Lsur; one preferred cue) and an upward-facing upper surface (Ufac, **Usur**; one preferred cue), another leaf with a downward-facing upper surface (**Dfac**, **Usur**; two preferred cues) and an upward-facing lower surface (Ufac, Lsur; no preferred cue). Two flat leaves were connected using double adhesive tape (0.5 cm width and 4 cm length). Joint edges between two leaves were smoothed to ensure that aphids could move freely among four surfaces.

In the second treatment (H), we provided four choices consisting of an individual leaf with two artificially curved sites in a vertical orientation; one curved site produced a sunken inward bending lower surface and a protruding outward bending upper surface, another curved site produced a sunken inward bending upper surface and a protruding outward bending lower surface (Figure 1h). This resulted in four surfaces: two had one preferred cue (**Ibent**, Lsur; Obent, **Usur**), one combined two preferred cues (**Ibent, Usur**) and one lacked preferred cues (Obent, Lsur). Two curved sites were made by tying two fine cotton threads at a distance of 1 cm (Figure 1h).

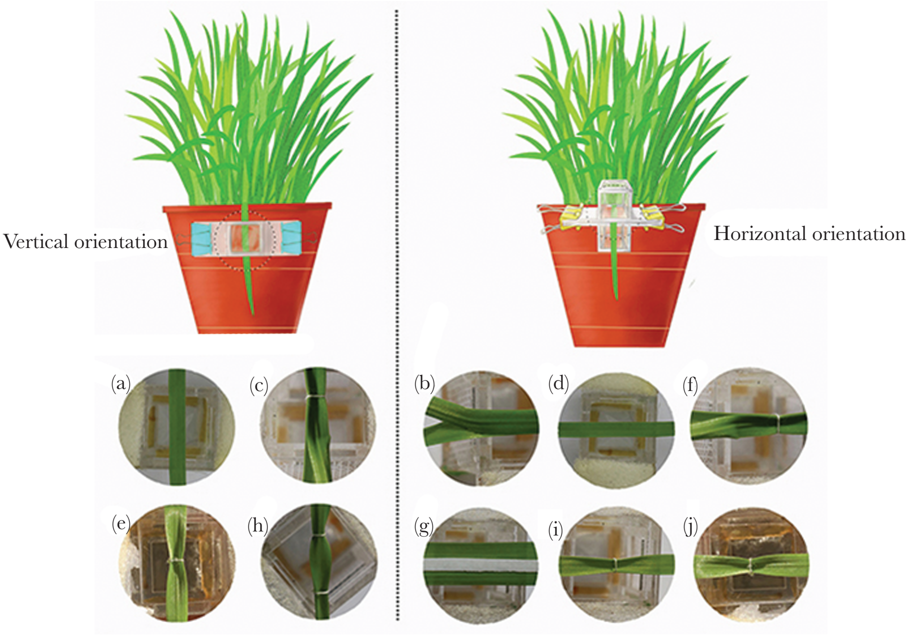
Experiment 4: What happens when females are presented with two preferred cues compared to a different preferred cue?

We investigated this question with two treatments (Figure 1i,j). The first (I) considered a curved leaf with a sunken inward bending upper surface facing upward (**Ibent, Usur**, Ufac; two preferred cues) versus a protruding outward bending lower surface facing downward (Obent, Lsur, **Dfac**; one different preferred cue). The second (J) considered a curved leaf with a protruding outward bending upper surface facing downward (Obent, **Usur, Dfac**; two preferred cues) versus a sunken inward bending lower surface facing upward (**Ibent**, Lsur, Ufac; one different preferred cue).

Statistical analyses

We used a generalized liner model (GLM) with gamma distributed errors to analyze how leaf surface tissue (upper versus lower) affected life-time fecundity of aphids and how leaf bending direction (sunken inward versus protruding outward) affected aphid survival in the presence of predators using the “glm” function and “car” package in R 3.5.2. We used the gamma distribution after testing several distributions with the “fitdist” function and finding that the gamma distribution had the lowest Akaike Information Criterion.

To analyze how the influence of leaf orientation (upward versus downward) and its interactions with leaf tissue surface



(a) Usur *vs.* Lsur
(b) Dfac, Lsur *vs.* Ufac, Lsur
(c) I bent, Lsur *vs.* Obent, Lsur
(d) Usur, Ufac *vs.* Lsur, Dfac
(e) Usur, Obent *vs.* Lsur, I bent
(f) I bent, Ufac, Lsur *vs.* Obent, Dfac, Lsur

(g) Usur, Ufac *vs.* Lsur. Dfac *vs.*
Usur, Dfac *vs.* Lsur, Ufac
(h) Usur, Obent *vs.* Lsur. I bent *vs.*
Usur, I bent *vs.* Lsur, Obent
(i) Usur, I bent, Ufac *vs.* Lsur, Obent, Dfac
(j) Usur, Obent, Dfac *vs.* Lsur, I bent, Ufac

Figure 1

Schematic of 10 microhabitat-choice treatments. A single female *M. dirhodum* ($n = 50$ per treatment) was presented with two (a–f, i, and j) or four (g and h) neighboring surface microhabitats inside clip cages (2 × 2 × 2 cm). The detailed information of different surface microhabitats in each treatment is shown below the pictures. Experiment 1: Do females prefer upper versus lower (abbreviated Usur vs. Lsur; a), downward versus upward (abbreviated Dfac vs. Ufac; b), sunken versus protruding (abbreviated Ibent vs. Obent; c) positions? Experiment 2: What surfaces are preferred by females when there are conflicting preferred cues (d–f)? Experiment 3: Can females consider multiple preferred cues simultaneously (g, h)? Experiment 4: What happens when females are presented with two preferred cues compared to a single different preferred cue (i, j)? The surface habitat with underlining in each treatment is shown in the corresponding circle picture and the rest of the surface habitat is in the back of each leaf. The leaf held in a vertical orientation in a, c, e, and h excluded surface orientation effects and allowed only surface tissue and/or bending effects to be compared. The double leaf arrangement with two lower surfaces exposed in b, c, and f excluded surface tissue effects to allow surface orientation and/or bending effects to be tested. The flat leaf in a, b, d, and g excluded surface bending effects and allowed surface tissue and/or orientation effects to be tested (see text for further details).

(downward-facing lower surfaces versus upward-facing upper surfaces) affected aphid performance, we first analyzed the raw data from different treatments in accordance with age-stage two-sex life table theory (Chi and Liu 1985) and estimated the intrinsic rate of increase (r) by using the iterative bisection method based on the Euler-Lotka formula: $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$ where l_x is the age-specific survival rate and m_x is the age-specific fecundity. We calculated the means and corresponding 95% confidence intervals of r by using the bootstrap procedure ($n = 999$). We then used GLM with gamma distributed errors to separately analyze the individual effect of leaf orientation and its interactions with leaf tissue surface on development time, 7-day fecundity and r using the "glm" function and "car" package in R. We further used the Cox proportional hazard regression model to analyze the individual effect of leaf orientation and its interactions with leaf tissue surface on aphid survival with "survival" and "survminer" package in R.

For the two-way choice experiments, the proportion of newly produced nymphs between two tested surfaces was compared using Wilcoxon's signed rank test. For the four-way choice experiments, the proportion of newly produced nymphs among four tested surfaces were compared using Friedman tests and their pairwise comparison were performed using Conover's test with the "PMCMR" package.

RESULTS

Does leaf tissue surface affect aphid performance in the laboratory?

Leaf tissue surface significantly affected total fecundity of *M. dirhodum* (Figure 2a). Females reared on upper leaf surfaces produced 34.42 (± 1.10 SE) nymphs during their lifetime, which was significantly higher than females reared on lower leaf surfaces (29.15 ± 0.93 SE; $X^2 = 13.56$, $P < 0.001$).

Does leaf orientation and its interaction with leaf tissue surface affect aphid performance in the field?

Leaf orientation has significant effects on aphid life history traits in terms of offspring survival rate ($X^2 = 6.76$, $P < 0.01$) and fecundity

($X^2 = 13.96$, $P < 0.001$) in the field (Figure 3). As an important integrative index of aphid performance, intrinsic rate of increase was significantly higher on downward-facing lower surfaces (DL) than upward-facing lower surfaces (UL) ($X^2 = 97.63$, $P < 0.001$).

Aphid performance significantly varied between upward-facing upper surfaces (UU) and downward-facing lower surfaces (DL) in the field (Figure 3). There was no significant difference in the development time of nymphs between UU and DL ($X^2 = 0.055$, $P = 0.81$). However, the 7-day fecundity was an average of 134% higher on DL than UU ($X^2 = 11.59$, $P < 0.001$). The aphid survival was significantly higher on DL than UU after 9 days ($X^2 = 7.60$, $P < 0.01$). Intrinsic rate of increase was significantly higher on DL than UU ($X^2 = 97.63$, $P < 0.001$).

Does leaf bending affect aphid performance in the presence of predators?

Leaf surface bending significantly affected aphid survival in the presence of predators (Figure 2b). When the predator was present, aphid survival was significantly higher on sunken inward bending surfaces (65.7%) than flat leaf surfaces (34.9%; $X^2 = 6.67$, $P < 0.01$).

Do females prefer upper versus lower, downward versus upward, sunken versus protruding positions?

When separately offered paired surfaces within individual leaves, female *M. dirhodum* significantly preferred to deposit nymphs on upper over lower surfaces ($P < 0.001$), downward- over upward-facing surfaces ($P < 0.001$) and sunken inward over protruding outward bending surfaces ($P < 0.001$) (Supplementary Table S1, Figure 4).

What surfaces are preferred by females when there are conflicting preferred cues?

There were significant differences among the relative strength of Usur, Dfac, and Ibent in larviposition microhabitat choice of female *M. dirhodum* (Supplementary Table S1, Figure 5). Females on average deposited more offspring on downward-facing lower surfaces (1.62 ± 0.13 SE) than upward-facing upper surfaces (0.3 ± 0.07 SE) in the treatment of Dfac versus Usur ($P < 0.001$), more offspring on sunken inward bending lower surfaces (1.3 ± 0.13 SE) than protruding outward bending upper surfaces (0.48 ± 0.10 SE) in the treatment of Ibent versus Usur ($P < 0.001$), and more offspring on protruding outward bending lower surfaces facing downward (1.14 ± 0.12 SE) than sunken inward bending lower surfaces facing upward (0.54 ± 0.11 SE) in the treatment of Dfac versus Ibent ($P < 0.01$). Overall, the relative strength of Usur, Dfac, and Ibent was ranked from high to low as Dfac > Ibent > Usur.

Can females consider multiple preferred cues simultaneously?

Over all treatments, female *M. dirhodum* preferred to produce their offspring on microhabitats with two combined preferred larviposition cues (Supplementary Table S1, Figure 6). Females deposited a higher proportion of their offspring on downward-facing upper surfaces (i.e., combined Dfac and Usur) than downward-facing lower surfaces (i.e., Dfac), upward-facing upper surfaces (i.e., Usur) and upward-facing lower surfaces (i.e., no preferred cue) ($P < 0.001$). Females deposited a higher proportion of their offspring on sunken inward bending upper surfaces (i.e., combined Ibent and Usur) than sunken inward bending lower surfaces (i.e., Ibent), protruding outward bending upper surfaces (i.e., Usur) and protruding outward bending lower surfaces (i.e., no preferred cue) ($P < 0.001$).

What happens when females are presented with two preferred cues compared to a single different preferred cue?

Over all treatments, female *M. dirhodum* preferred to deposit their offspring on surface microhabitats with two combined preferred larviposition cues over surface microhabitats with only one different preferred cue (Supplementary Table S1, Figure 7). Females deposited a higher proportion of offspring on sunken inward bending upper surfaces facing upward (i.e., combined Ibent and Usur) than protruding outward bending lower surfaces facing downward (i.e., Dfac) ($P < 0.01$), and a higher proportion on protruding outward bending upper surfaces facing downward (i.e., combined Dfac and Usur) than sunken inward bending lower surfaces facing upward (i.e., Ibent) ($P < 0.001$).

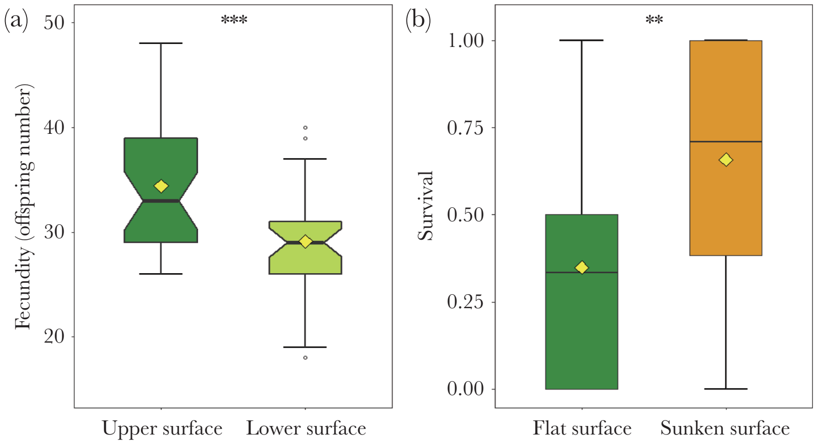


Figure 2

Fitness-related comparisons. (a) Total fecundity of *M. dirhodum* females on upper and lower surfaces of wheat leaves at 18 ± 1 °C and a photoperiod of 16:8 (L:D) (***$P < 0.001$); boxes represent interquartile ranges, the solid centerline inside the boxes represents the median value, the red dashed line inside the boxes indicates the mean value, the tails represent the nonoutlier range, and dots represent outlier values. (b) Survival of *M. dirhodum* nymphs on flat surfaces and sunken inward bending surfaces of wheat leaves in the presence of predatory ladybird (*Propylaea japonica*) (**$P < 0.01$).

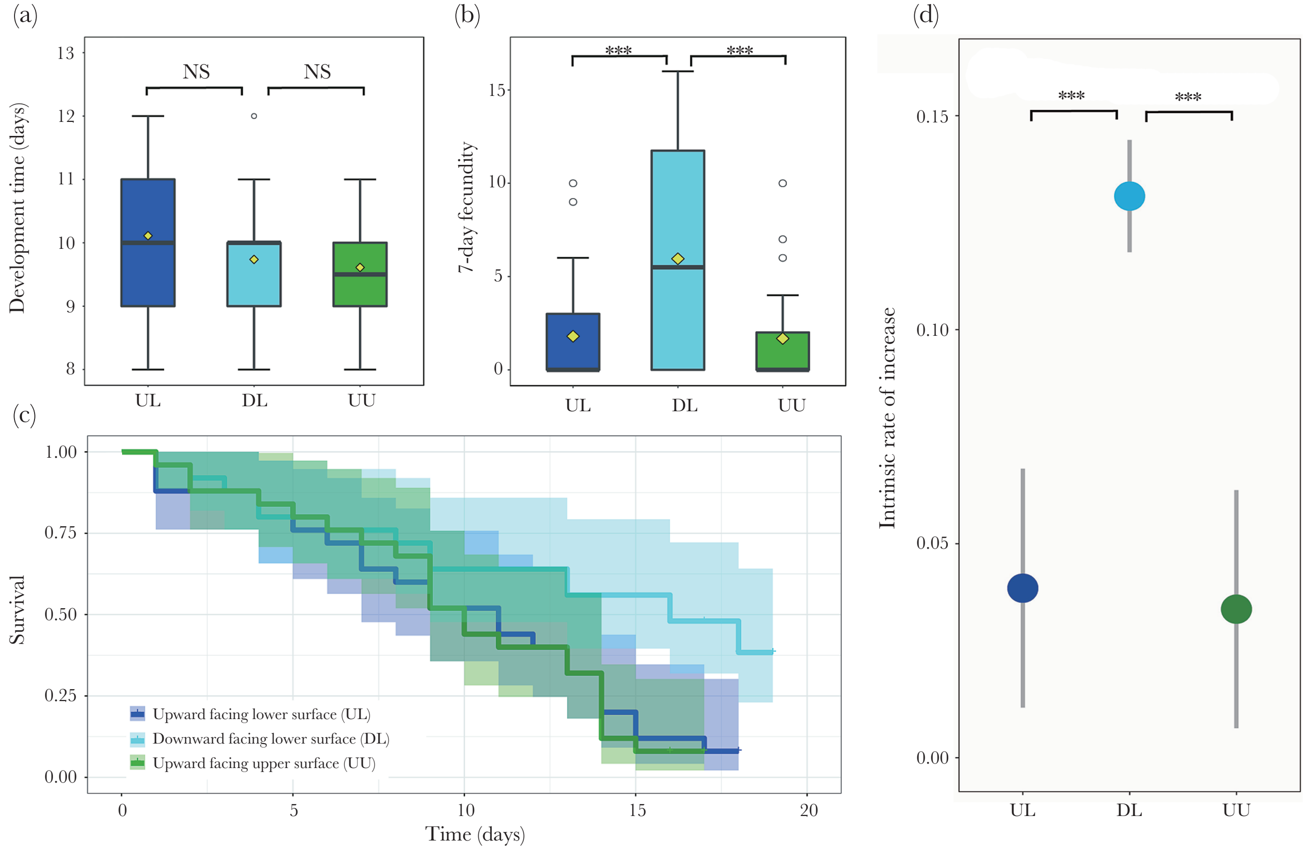


Figure 3
Fitness-related comparisons. Development time (a), 7-day fecundity (b), survival (c) and intrinsic rate of increase (d) of *M. dirhodum* on upward-facing lower (UL), downward-facing lower (DL) and upward-facing upper (UU) leaf surfaces in the wheat field (***$P < 0.001$; NS, not significant).

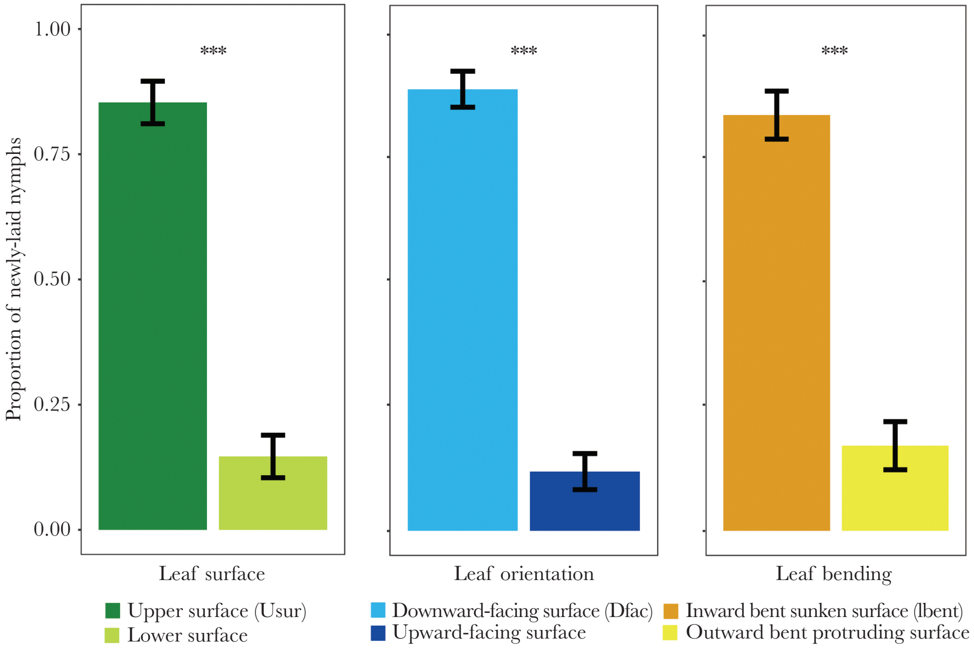


Figure 4
Larviposition preference. The proportion of offspring (means ± SE) laid by *M. dirhodum* females ($n = 50$ per treatment) within individual leaves when separately given a choice between upper versus lower surfaces, downward-facing versus upward-facing surfaces, and sunken inward versus protruding outward bending surfaces (Wilcoxon's signed-rank test: ***$P < 0.001$).

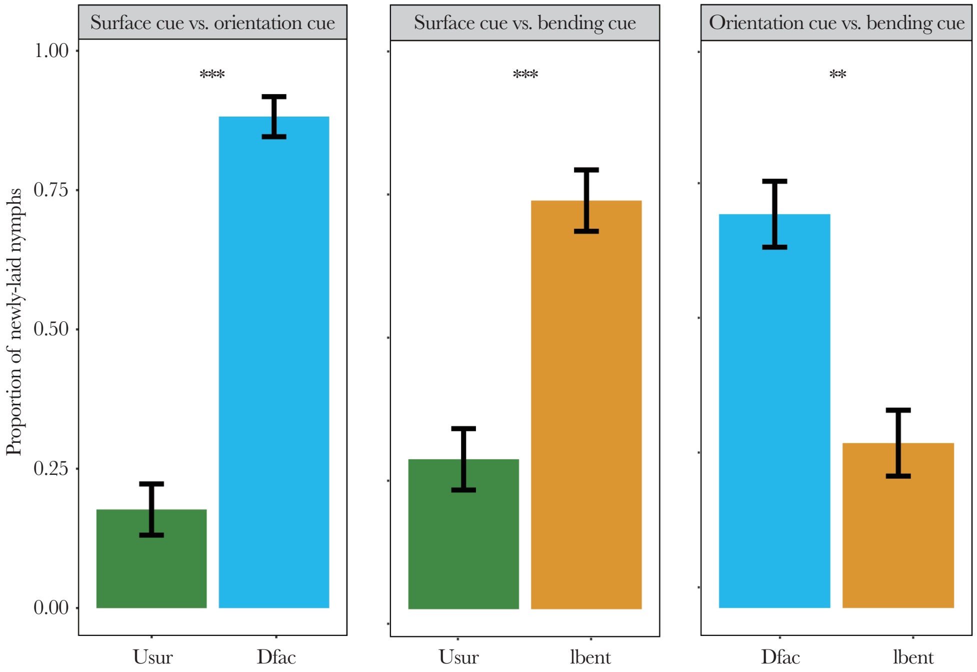


Figure 5

Larviposition preference. The proportion of offspring (means ± SE) laid by *M. dirhodum* females (*n* = 50 per treatment) within individual leaves when separately given a choice between upper surfaces facing upward (Usur, only preferred cues showed in the x-axis title based on above choice treatments) versus lower surfaces facing downward (Dfac), between protruding outward bending upper surfaces (Usur) versus sunken inward bending lower surfaces (Ibent), and between protruding outward bending lower surfaces facing downward (Dfac) versus sunken inward bending lower surfaces facing upward (Ibent) (Wilcoxon's signed-rank test: ***$P < 0.001$, ** $P < 0.01$).

DISCUSSION

Despite interest in multiple-cue habitat choice, there is still little understanding of the basic decision rules involved (Huijbers et al. 2012; Cayuela et al. 2017; Ashur and Dixson 2019). Here, we found clear evidence that females used different cues in their breeding microhabitat choice depending on how these were presented, and we provide connections to the relative fitness benefits of each preferred cue. To the best of our knowledge, this is the first time female insects have been shown to assess secondary cues at the same time as prioritized cues with indirect safety benefits, even when they only indicate small current rewards, and that females may integrate different cues associated with current and potential benefits in a multiplicative way rather than in an additive way to make flexible larviposition decisions. This study is unique in considering the individual effects of cues that reflect future safety and immediate benefits of habitat choice, and then considering their interactions when they are presented together.

Adaptive response to different cues at the leaf habitat level

Metopolophium dirhodum females showed an evident preference for upper surfaces rather than lower surfaces of wheat leaves (Figure 4). Since piercing-sucking herbivores, including aphids, penetrate the epidermis before gaining nutrition (Pollard 1973; Walling 2008), mechanical barriers such as a thicker wax layer could make stylet penetration difficult, which can affect female feeding/oviposition choices (Reavey and Gaston 1991; Peeters 2002; Ayabe et al. 2017). Previous studies have shown that the wax layer was thinner on upper than lower surfaces of wheat leaves (Troughton and Hall 1967). Aphids may more easily ingest nutrients from upper surfaces of wheat leaves, which likely increase their nutritional intake efficiency. This direct feeding benefit is reflected by the difference in female performance between two leaf surface tissues, that is, females produced more nymphs when feeding on upper than on lower surfaces of wheat leaves (Figure 2a). Note that we have not recorded the process of *M. dirhodum* larviposition between upper and lower surface, further study is needed to explore how females make larvaposition decision based on leaf surface cue.

In accordance with the results of previous studies in other herbivores (Li and Margolies 1991; Chu et al. 1995), *M. dirhodum* females showed an evident preference for downward-facing rather than upward-facing leaf surface orientation (Figure 4). Because herbivores, especially at a young stage, are sensitive to adverse weather such as extreme temperatures, detrimental ultraviolet-B and rain, adverse weather is often considered a driving force for inhabiting downward-facing leaf surfaces (Chu et al. 1995; Ohtsuka and Osakabe 2009; Yin et al. 2018). As expected, our results showed that aphids performed much worse on sun-exposed upward-facing than downward-facing leaf surfaces in the field (Figure 3). Thus, larviposition habitat selection based on a downward orientation allows female *M. dirhodum* to avoid future abiotic risks.

Herbivores are generally under strong predation pressure in nature and thus natural selection favors females that use complex habitat structures for oviposition site choice even without predator threats (Schlaepfer et al. 2002; Stahlschmidt and Adamo 2013). We found that *M. dirhodum* females showed an evident preference for sunken rather than protruding surfaces (Figure 4), and that aphids suffered less mortality in sunken than protruding/flat surfaces in the presence of predatory ladybirds (Figure 2b). In the field, wheat leaves are often naturally curled or rolled (Supplementary Figure

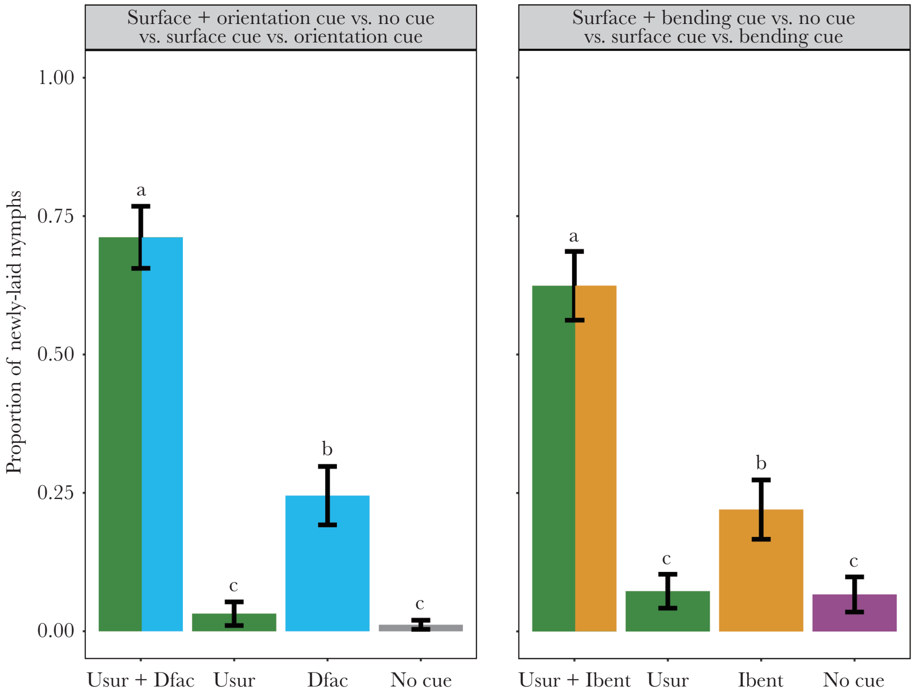


Figure 6

Larviposition preference. The proportion of offspring (means ± SE) laid by *M. dirhodum* females (n = 50 per treatment) within individual leaves when separately given a choice among upper surfaces facing upward (Usur) versus lower surfaces facing upward (Dfac) versus upper surfaces facing downward (Usur + Dfac) versus lower surfaces facing upward (no preferred cue), and between protruding outward bending upper surfaces (Usur) versus sunken inward bending lower surfaces (Ibent) versus sunken inward bending upper surfaces (Ibent + Usur) versus protruding outward bending lower surfaces (no preferred cue) (Friedman test: $***P < 0.001$).

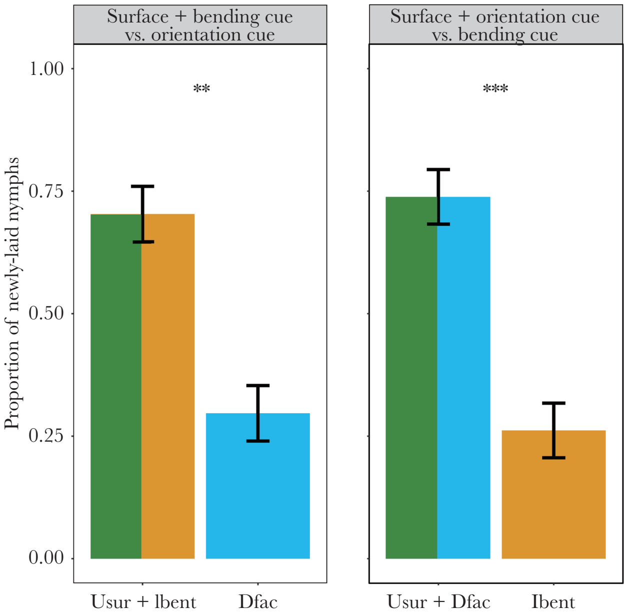


Figure 7

Larviposition preference. The proportion of offspring (means ± SE) deposited by *M. dirhodum* females (n = 50 per treatment) when separately given a choice between sunken inward bending upper surfaces facing upward (Ibent + Usur) versus protruding outward bending lower surfaces facing downward (Dfac), and between protruding outward bending upper surfaces facing downward (Usur + Dfac) versus sunken inward bending lower surfaces facing upward (Ibent) (Wilcoxon's signed-rank test: $***P < 0.001$, $**P < 0.01$).

S1), which can offer aphids natural shelters against predators. Aphids on sunken surfaces are also less likely to be paralyzed by parasitic wasps than on flat or protruding surfaces in the wheat field (Yin, unpublished data). So, *M. dirhodum* females using the sunken inward bending surface of curled leaves for larviposition avoid potential biotic risks. Overall, our results support the prediction that *M. dirhodum* females can use the upper leaf surface as a direct cue for current food-related rewards, and separately use the downward-facing surface and sunken inward bending surface as indirect cues for potential safety.

Effects of conflicting/consistent direct and indirect cues on breeding site choice

Abundant evidence has shown that females will under-utilize habitats with predators even if these same habitats are high in food availability (Nonacs and Dill 1990; Binckley and Resetarits 2008; Beermann et al. 2018). We found that female aphids prioritized the downward-facing or sunken inward bending surface over the upper surface (Figure 5), even without biotic and abiotic risks being present during larviposition. This implies that females can rely heavily on potential safety at the cost of current food-related rewards when choosing larviposition sites. Previous studies showed that indirect cues of predation risk are often used as primary indicators of behavioral decisions in animals compared with direct cues of predation produced by predator itself (Thorson et al. 1998; Orrock et al. 2004; Leaver et al. 2017). Our results also suggest that indirect cues of abiotic/biotic risks (i.e., the downward /sunken surface) are more important in larviposition decision making than direct cues of food rewards (i.e., the upper surface). We further experimentally demonstrated that the relative importance of direct and indirect cues in decision making was positively correlated with their benefits on fitness enhancement. Our results showed that in the field aphids had extremely low performance on upward-facing upper surfaces compared to downward-facing lower surfaces of wheat leaves (Figure 3). Although aphids can obtain direct food rewards from upper leaf surfaces, the magnitude of fitness benefits by avoiding potential weather risks may outweigh those gained through food rewards. Females thus optimize their lifetime fitness based on indirect cues instead of direct cues when making larviposition decisions.

These findings pose an additional question as to whether females can consider secondary direct cues when prioritizing indirect cues in making decisions. Due to limitations on information processing and integration in animals (Lewis 1986; Bernays 2001), decision making is expected to be based on prioritized cues to expedite and simplify the process (Mönkkönen et al. 2009; Leaver et al. 2017). Especially when secondary direct cues bring only a relatively small fitness benefits compared with prioritized indirect cues, it would seem unlikely that direct cues might still play a role in decision making. Nevertheless, our results showed that females considered prioritized and secondary cues simultaneously during larviposition rather than only considering the prioritized cue as females deposited most of their offspring on the microhabitat combining upper surface cue and downward-facing cue rather than only downward-facing cue, and also on the microhabitat combining upper surface cue and sunken inward bending cue rather than only the sunken inward bending cue (Figure 6). Our results also suggest that females are integrating different preferred cues when making larviposition decisions.

In general, there are three forms of synergistic effects of multiple signals/cues on behavioral decisions: 1) enhancement (increased response over either component alone), 2) additive effects (equal to levels of response to each component combined), and 3) multiplicative effects (response greater than the sum of responses to components) (Partan and Marler 2005). Our studies found that the proportion of offspring deposited in microhabitats with sunken inward bending cue (27%) by females was significantly lower than microhabitats with downward-facing cue (73%), and a similar trend was found in upper surface cue (16%) versus downward-facing cue (84%) (Figure 5). However, females deposited most of their offspring on microhabitats with combined sunken inward bending cue and upper surface cue (70%) compared with downward-facing cue (30%) (Figure 7). This strongly suggests that females can combine an indirect cue (i.e., sunken inward bending surface) and direct cue (i.e., upper surface) in a multiplicative way rather than in an additive way, and make flexible rather than fixed decisions when choosing larviposition habitats. Of course, whether such larviposition decisions are adaptive in nature will require further research.

The significance of flexible multi-cue microhabitat choice

Multiple-cue decision making has primarily been studied within the context of mate choice (Candolin 2003; Taylor and Ryan 2013). Few studies explore habitat choice related to larviposition or oviposition (Kivelä et al. 2014). Due to the limited mobility and high vulnerability of newly deposited offspring to abiotic and biotic risks, selecting safe habitats is critical for offspring survival and growth in most animals (Gripenberg et al. 2010: Refsnider and Janzen 2010). By using multiple cues, females obtain more reliable information about different factors affecting fitness, which reduces uncertainty and increases their likelihood of choosing a high-quality habitat for their offspring (Spieler and Linsenmair 1997; Stahlschmidt and Adamo 2013; Touchon and Worley 2015). Moreover, since reproductive success is not only caused by offspring survival but also by the number of offspring laid, females may adjust their behavioral decisions in response to cues which can bring direct benefits to their own performance during oviposition (Scheirs et al. 2000, Spencer 2002). Therefore, evaluating different direct and indirect cues and making flexible decisions in breeding site choice is crucial for female reproductive success in dynamically changing and unpredictable environments.

Inevitably, multiple-cue decisions might be costly in terms of direct search cost (Candolin 2003; van Doorn and Weissing 2004). However, unlike mating/habitat-choice behaviors across a large area, female aphids can easily search for and detect fine-scale multiple cues between neighboring surfaces, which should decrease the time and energy spent on habitat assessment. A reduction in the cost of choice should promote the evolution of preferences for multiple cues, including cues that do not indicate large fitness benefits (Candolin 2003). Thus, natural selection may favor female making larviposition decision based on multiple cues within microhabitats.

Different kinds of fine-scaled cues used for choosing microhabitats are widespread in nature, and reported in birds (e.g., Pärt and Doligez 2003), amphibians (e.g., Osbourn et al. 2014), fishes (e.g., Huijbers et al. 2012), shrimps (e.g., Ashur and Dixson 2019), and reptiles (e.g., Spencer 2002) among others. Thus, our findings on aphids may relate more generally to how animals flexibly collect and process multi-cue information to maximize their fitness at small spatial scales.

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