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2 Labelling effect in insects: cue associations influence

3 perceived food value in ants (*Lasius niger*)

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19
20 **Abstract**

21 Humans usually assess options not in terms of absolute value, but relative to reference
22 points. The framing of alternatives can strongly affect human decision-making, leading to different
23 choices depending on the context within which options are presented. Similar reference-point
24 effects have been recently reported in ants, in which foragers show contrast effects: ants overvalue
25 a medium-quality food source if they were expecting a poor one, and vice versa for expectations
26 of good food. However, studies of human consumer psychology have demonstrated that
27 expectations, for instance from product labels, can drive value perception in the opposite direction,
28 via a process of assimilation. For example, an expensive bottle of wine is perceived as more
29 enjoyable compared to a cheaper bottle, even if the wine is the same. In this study, we demonstrate
30 a similar labelling-association effect in an insect: ants showed assimilation effects by spending
31 twice as long drinking at medium quality food if it was scented with an odour previously associated
32 with high quality than if it was scented with a poor-quality label. The presence of odour cues in the
33 food during consumption and evaluation is critical, as without them, odour-driven expectations of
34 quality result in contrast, not assimilation effects. The addition of a quality label in the food thus

35 reverses contrast effects and causes value to be aligned with expectations, rather than being
36 contrasted against them. As value judgement is a key element in decision-making, relative value
37 perception strongly influences which option is chosen, and ultimately how choices are made.

38 *Keywords:* Product labels; Associative learning; Relative value perception; Assimilation;
39 Branding

40

Introduction

41 A decision is often made by evaluating and comparing available options. This comparison
42 usually leads to a choice for the option promising the greatest profit (von Neumann and
43 Morgenstern 1944). The way in which options are evaluated may, however, strongly influence
44 which option is ultimately chosen. Thus, understanding the factors influencing the perceived value
45 of available options helps us understand human behaviour and decision making (Slovic 1995;
46 Thaler and Sunstein 2008; Tversky and Kahneman 1981). Understanding the drivers of option
47 evaluation and comparison are thus central to the study of behavioural economics and consumer
48 psychology.

49 Although early economic theories described humans as rational decision-makers who
50 always choose the option with the greatest utility regardless of other factors (von Neumann and
51 Morgenstern 1944; Vlaev et al. 2011), a large body of evidence has accumulated demonstrating
52 that this is not always the case. Kahneman and Tversky (1979) suggested that decision-making is
53 not based on absolute outcomes, but rather on the relative perceptions of gains and losses.
54 According to Prospect Theory, which incorporates these assumptions, the value of options being
55 evaluated is determined relative to a reference point, such as the status quo or former experience
56 (Kahneman and Tversky 1979; Parducci 1984; Tversky and Kahneman 1992; Ungemach et al.
57 2011; Vlaev et al. 2011). Thus, the same option can be perceived more negatively if a reference
58 point is high, and more positively given a lower reference point (Kahneman and Tversky 1979).
59 For example, satisfaction gained from income is perceived not absolutely, but relative to the income
60 of one's colleagues (Boyce et al. 2010). Therefore, human decision making tends to be relative
61 rather than rational.

62 The concept of malleable value perception is not just relevant to humans. Value judgments
63 in non-human animals are also influenced by factors apparently independent of the absolute value
64 of options, such as the state an animal is in during learning in birds (Aw et al. 2011), rats (Lydall
65 et al. 2010), fish (Aw et al. 2009) and insects (Czaczkes et al. 2018a; Pompilio et al. 2006), and
66 expectations about upcoming rewards in dogs (Bentosela et al. 2009), rats (Annicchiarico et al.
67 2016; Crespi 1942; Flaherty 1982; 1999; Papini et al. 2001; Webber et al. 2015; Weinstein 1970),
68 mice (Mustaca et al. 2000) and insects (Bitterman 1976; Couvillon and Bitterman 1984;
69 Oberhauser and Czaczkes 2018; Roces and Núñez 1993; Roces 1993; Wendt et al. 2019). Banded
70 tetra fish and desert locusts, for example, prefer cues associated with food presented when they
71 were very hungry compared to identical food received when they were less hungry (Aw et al. 2009;
72 Pompilio et al. 2006). Expectations can make animals perceive identical options differently
73 depending on whether a better or worse option was expected instead of the presented one. For
74 example, capuchin monkeys refuse otherwise acceptable pay (cucumber) in exchanges with a
75 human experimenter if they had witnessed a conspecific obtain a more attractive reward (grape)
76 for equal effort (Brosnan & de Waal, 2003; van Wolkenten, Brosnan, & de Waal, 2007). Similarly,
77 *Lasius niger* ants showed lower food acceptance towards medium quality food when they expected
78 high quality food (negative contrast) and higher acceptance of medium food when expecting poor
79 food (positive contrast) (Wendt et al. 2019). Honeybees too rejected otherwise acceptable lower

80 quality food when they expected high quality food due to previous experience (Bitterman 1976;
81 Couvillon and Bitterman 1984). Such incentive contrast effects (Flaherty 1999) represent one of
82 the main influences on subjective value. We see incentive contrasts as a subset of relative value
83 perception.

84 Other factors altering perceived value in humans are product and brand labels, which can
85 also directly affect purchasing decisions. Such labels convey expectations and thus act as reference
86 points for judging an option (French and Smith 2013). Depending on previous associations with
87 the label, perceived option value can increase (Breneiser and Allen 2011; Fornerino and
88 d’Hauteville 2010; Kühn and Gallinat 2013; Lee et al. 2013; Nevid 1981; McClure et al. 2004;
89 Wansink 2000; Woodside and Taylor 1978; Yamada et al. 2014) or decrease (Lee et al. 2006;
90 Wansink 2000). For example, drinks presented along with strong brands such as “Coca Cola”
91 (which has strong positive associations due to successful marketing campaigns) tend to be rated as
92 being tastier or more attractive compared to identical drinks which were presented with weaker
93 brand labels or without any labels, even though there is rarely a preference found in blind tests
94 (Breneiser and Allen 2011; Fornerino and d’Hauteville 2010; Kühn and Gallinat 2013; McClure et
95 al. 2004; Yamada et al. 2014). Compared to these strong international brands, store brands are often
96 perceived as offering lower product quality and nutritional value (Cunningham et al. 1982; Dick et
97 al. 1995). If the difference between a label-driven expectation and the products’ objective value is
98 small, the perceived value aligns with the expectation in a process called assimilation (Cardello
99 and Sawyer 1992; Hovland et al. 1957; Schnurr et al. 2017). For example, a soft drink, which
100 previously received a low rating, may receive a significantly better rating when subjects were told
101 that it is of a favourable brand (Cardello and Sawyer 1992). In humans, labels are an accumulation
102 of various associative cues which evoke a positive or negative response once the label is seen
103 (French and Smith 2013; Macklin 1996). Such associated attributes may affect value perception in
104 animals as well.

105 Associative learning, through which cues or actions are learned to predict a positive or
106 negative experience, is almost ubiquitous in the animal kingdom as well, including insects
107 (Couvillon and Bitterman 1980; Giurfa 2007; Menzel 1993; Siwicki and Ladewski 2003; Spatz et
108 al. 1974) and other invertebrates (Hawkins and Byrne 2015; Rankin 2004; Sahley et al. 1981). Like
109 associative labelling in humans, perceived option value varies for nonhuman animals as well. Naïve
110 *Camponotus mus* ants, for example, prefer food presented alongside an odour which had already
111 been received through food exchanges inside the nest over food presented with a novel odour,
112 because the familiar odour was previously associated with a positive event (Provecho and Josens
113 2009). An example of negative associations was shown in the leaf cutter ants *Acromyrmex*
114 *ambiguus* and *Acromyrmex lundii*: odour cues associated with damage to the ants’ cultivated fungus
115 drive aversion to otherwise acceptable fungal substrate, with the odour cue acting as a negative
116 food label (Roces 1994; Saverschek and Roces 2011).

117 The aim of this study was to investigate whether labelling effects as shown in humans can
118 be demonstrated in insects, whether they could act against contrast effects and whether this is
119 affected by the timing of cue presentation. Specifically, we ask whether ants align their perception

120 of a food source's value with value-associated odour cues presented in the food during consumption.
121 We previously demonstrated a contrast effect in ants, whereby ants undervalue or overvalue food
122 if they were expecting a better or worse food quality, respectively (Wendt et al. 2019). In the
123 previous study, expectations generated *before* perception of the objective food quality drove value
124 perception. Here, we ask how value-related labels experienced *during* consumption affect
125 perceived value and whether the time of label-presentation changes the perceived value of an option
126 in ants. In order to counteract contrast effects, one first has to elicit them – hence we first aimed
127 to form a cue-based expectation of different molarities, which would normally result in contrast
128 effects during the test, and added assimilation-driving cues within the food (flavour cues previously
129 associated to either high or low quality food), in order to counteract this assimilation. We
130 hypothesized that incentive contrast effects could be counteracted by the mere presence of
131 associative odour cues during consumption.

132

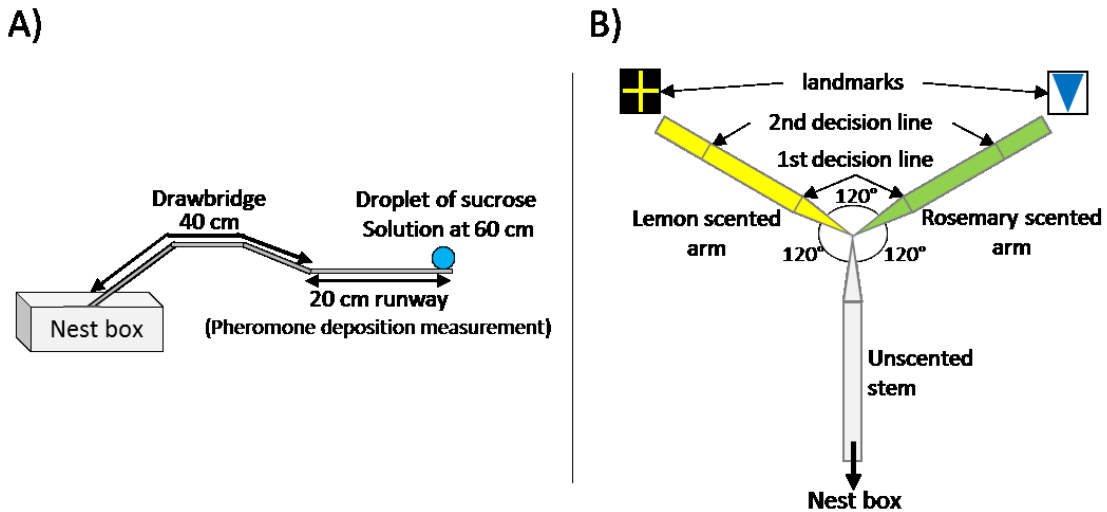
Methods

133 Study animals

134 Eight colonies of the black garden ant *Lasius niger* were collected on the University of
135 Regensburg campus. The colonies were housed in 30 x 30 x 10 cm foraging boxes with a layer of
136 plaster covering the bottom. Each box contained a circular plaster nest box (14 cm diameter, 2 cm
137 height). The colonies were queenless with around 1000-2000 workers and small amounts of brood.
138 Workers from queenless colonies forage and lay pheromone trails, and are frequently used in
139 foraging experiments (Detrain et al. 2019; Dussutour et al. 2004). The colonies were fed with 0.5M
140 sucrose solution and received *Drosophila* fruit flies once a week. Colonies were deprived of
141 sucrose solution four days prior to the experiments in order to achieve a uniform and high
142 motivation for foraging (Mailleux, Detrain, and Deneubourg 2006; Josens and Roces 2000). Water
143 was always available *ad libitum*.

144 General setup

145 The setup consisted of a 1 cm x 20 cm long paper-covered runway which was connected to
146 the colony's nest box via a 40 cm long drawbridge (figure 1A). A 5 mm diameter drop of sucrose
147 solution (Sigma-Aldrich) was placed on an acetate feeder (2 x 1.5 cm) at the end of the runway (60
148 cm from the nest).



149

150

151 Figure 1: A) Setup used during training (visits 1 to 8) and on the 9th (test) visit of ants. The 20 cm long runway was
 152 connected to the nestbox via a 40 cm long drawbridge. The droplet of sucrose solution was placed at the end of the
 153 runway (60 cm distance to the nest). All runways were covered with paper overlays. The overlay on the last 20 cm
 154 was replaced by pheromone-free ones each time an ant had walked over it. B) Y-maze used on the 10th visit of the ants to
 155 conduct a memory probe. All Y-maze arms were 10 cm long. The arm connected to the nest box was covered with
 156 unscented paper overlays while the other two arms were covered with lemon and rosemary scented paper overlays (one
 157 odour on each side). Visual cues (landmarks) were placed right behind the two scented Y-maze arms (at a distance of
 158 about 5 cm from the Y-maze arm end, so that ants could not walk onto it). The first decision line was located 2 cm
 159 from the y-maze centre and marked the initial decision of an ant while the second decision line was placed 8 cm from
 160 the centre and marked the final decision.

161

162 To begin an experimental session, the colony was connected to the runway via the
 163 drawbridge. Two to four ants were allowed onto the runway, and the first ant to reach the feeder
 164 was marked with a dot of acrylic paint on its abdomen. The marked ant was allowed to drink to
 165 repletion at the food source, while all other ants were returned to the nest. As the ant drank at the
 166 droplet it was given one of three food acceptance scores, following Wendt et al. (2019). Full
 167 acceptance (1) was scored when the ant remained in contact with the drop from the moment of
 168 contact and did not interrupt drinking within 3 seconds of initial contact (see video B1 in Appendix
 169 B). Partial acceptance (0.5) was scored if feeding was interrupted within 3 seconds after the first
 170 contact with the food source, but the ant still filled its crop within 10 minutes (as can be seen by
 171 the distention of the abdominal tergites). Ants that interrupt feeding within the first seconds after
 172 contacting the food usually show successive feeding interruptions and generally show a rather
 173 ‘impatient’ behaviour compared to ants that show a food acceptance score of 1 (see video B2 in
 174 Appendix B). Lastly, rejection (0) was scored if the ant refused to feed at the sucrose solution and
 175 either returned to the nest before filling its crop or failed to fill its crop within 10 minutes.
 176 Regardless of whether the ant had drunk to satiety or failed to feed to repletion within 10 minutes,
 177 it was freely allowed to return to the nest at any time. Inside the nest, the ant unloaded the collected
 178 sugar load to its nestmates and was then allowed back onto the runway for another visit. The
 179 drawbridge connecting the nest with the runway leading to the food source was now used

180 selectively to allow only the marked ant onto the runway by lowering it only for the marked ant
181 and quickly raising it once the marked ant had moved onto the bridge. As an additional measure of
182 perceived value, we counted the pheromone depositions the ant performed on the way to and from
183 the feeder. Individual pheromone deposition behaviour correlates with the (perceived) quality of a
184 food source (Beckers et al. 1993; Czaczkes et al. 2018b; Hangartner 1970; Wendt et al. 2019).
185 Individual ants can adapt the strength of a pheromone trail by either depositing pheromone or not,
186 or varying the intensity of pheromone depositions (Hangartner 1970; Beckers et al. 1993).
187 Pheromone deposition behaviour in *Lasius niger* is highly stereotypic. To deposit pheromone, an
188 ant briefly interrupts running to bend its abdomen and press the tip onto the ground (Beckers et al.
189 1992). This allows the strength of a pheromone trail to be quantified by counting the number of
190 pheromone depositions over the 20 cm runway leading to the feeder. Pheromone depositions were
191 measured each time the ant moved from the food source back to the nest (inward trip), and each
192 time the ant moved from the nest towards the food source (outward trip). Because *Lasius niger*
193 foragers almost never lay pheromone when they are not aware of a food source (Beckers et al.
194 1992), we did not measure pheromone depositions for the very first outward trip (visit 1). The
195 presence of trail pheromone on a path depresses further pheromone deposition (Czaczkes et al.
196 2013). Thus, each time an ant had passed the 20 cm runway, the paper overlay covering the runway
197 was replaced by a fresh one. All experimental runs were recorded with a Panasonic DMC-FZ1000
198 camera to allow for later video analysis.

199 **Experimental Procedure**

200 **Overview**

201 A total of 70 ants (7-11 ants per colony) were trained to associate a high sucrose molarity
202 (1.5M) with one odour, and a low molarity (0.1M) with a different odour. Then, in the testing phase,
203 odours were placed on the runway to trigger an expectation of either high or low molarity, which
204 was then contrasted with a medium (0.387M) solution containing one of the learned odour cues.
205 The molarity of the medium quality solution (0.387M) was chosen because we wanted to present
206 the ants with identical relative increases in sucrose molarity. 0.1M was chosen as the low food
207 quality as it is suggested to be the minimum sucrose concentration which *L. niger* ants reliably
208 detect, distinguish, and accept (Detrain and Prieur 2014). 1.5M was chosen as the high food quality
209 as acceptance scores plateau after 1.5M (Wendt et al. 2019).

210 **Detailed methods**

211 Training to associate food quality with odour cues took place over eight visits. The quality
212 of the sucrose solution offered at the end of the runway alternated each visit, always beginning
213 with the low quality solution. The solutions were scented using either rosemary or lemon essential
214 oils (0.5 µl essential oil per ml sucrose solution, rosemary: *Rosmarinus officinalis*; lemon: *Citrus*
215 *limon*, Markl GbR, Grünwald). Molarities were presented along with the same odours throughout
216 a whole training run (i.e. 1.5M presented with rosemary and 0.1M presented with lemon). For half
217 of the trained ants the 1.5M solution was scented with lemon and the 0.1M with rosemary, while
218 for the other half 1.5M was scented with rosemary and 0.1M with lemon. In addition, to support
219 learning and to allow anticipation of solution quality (Czaczkes et al. 2018b), the paper overlays

220 covering the runway leading to the feeder were also scented. Paper overlays were scented by storing
221 them for at least one day in an airtight box containing a drop of essential oil on filter paper in a
222 Petri dish. Finally, in addition to odours cueing sucrose molarity, visual cues were also provided at
223 the end of the runway. These consisted of printed and laminated pieces of paper (22 x 16.5 cm,
224 figure 1B) displayed at the end of the runway, directly behind the sucrose droplet. Each odour was
225 presented along with another visual cue (a yellow cross on black background when lemon odour
226 was presented and a blue triangle on white background when rosemary odour was presented, figure
227 1B). Runways were scented on both outbound and inbound visits of the ant.

228 On the 9th (test) visit, the odour and visual cue associated with either 1.5M or 0.1M were
229 presented, while the sucrose solution provided was of intermediate (0.387M) quality, but also
230 scented according to the runway odour. Runway odours in the test visit were varied systematically
231 between ants, but each ant was confronted with only one of the two runway odours coupled with
232 scented 0.387M sucrose. This resulted in a balanced experimental design in which half of the ants
233 were confronted with the odour associated to 1.5M (for half of the ants, the odour was lemon, for
234 the other half rosemary) and the same flavour in a 0.387M sucrose drop on the 9th visit, and the
235 other half was confronted with the odour associated to 0.1M sucrose and the same flavour in
236 0.387M sucrose. These methods are nearly identical to those used in Wendt et al. (2019) in which
237 contrast effects in ants are reported. The key difference is that in Wendt et al. (2019) odours were
238 presented only on the runway on the 9th (test) visit, but not in the food. In contrast, in the current
239 study the medium quality food (0.387M) was scented in addition to presenting the associated
240 odours on the runway leading to the food source.

241 Previous work has shown that *L. niger* foragers can form robust expectations of upcoming
242 reward quality based on runway odour after four visits to each odour/quality combination
243 (Czaczkes et al. 2018b; Wendt et al. 2019). Nonetheless, to ensure that learning had taken place,
244 we carried out a memory probe at the end of each training and test run, i.e. on the 10th visit. The
245 linear runway was thus replaced with a Y-maze (figure 1B), with two 10 cm long arms and a 10
246 cm long stem. The Y-maze stem was covered with an unscented paper overlay while one arm was
247 covered with the 1.5M-associated odour overlay, and the other with the 0.1M-associated odour
248 overlay. The matching visual cues were placed directly behind the relevant Y-maze runways (ca.
249 5 cm from the end of the Y-maze arms, so that ants could not walk onto it and escape from the
250 setup). The odours and quality associated to odours were evenly distributed throughout all tested
251 ants, so that half of the tested ants were trained to lemon with high molarity food, and the other
252 half to rosemary. The odour associated to high molarity food was presented on the right side of the
253 Y-maze for half of the ants, and on the left for the other half. Trained ants were allowed to walk
254 onto the Y-maze on their 10th visit (after 8 training visits and the 9th test visit) and their Y-maze
255 arm choice was noted. We used two decision lines to define Y-maze arm choice – an initial decision
256 line (figure 1B, 2 cm after the bifurcation) and a final decision line (8 cm after the bifurcation).
257 The majority of ants (98.5%) chose the side in the Y-maze which was covered in an odour
258 previously associated to high molarity food and thus made a correct decision, suggesting that ants
259 had successfully formed an association between both given sucrose/odour combinations (1.5M

260 with one odour and 0.1M with another odour) and showed a strong preference for the odour
261 previously associated to high molarity. Furthermore, on the 9th (test) visit, ants deposited
262 significantly more pheromone when presented with an odour associated with high quality on the
263 runway on their way to the food source compared to when the runway was impregnated with an
264 odour associated with low quality (figure A1B in Appendix A). Pheromone depositions towards
265 the high quality odour increased with increasing experience with the food source during training,
266 while they decreased for the low quality odour (figure A1A in Appendix A). This shows that ants
267 were able to associate a given odour to a food quality and formed a robust expectation of upcoming
268 food qualities based on the odour. After testing on the Y-maze, the ants were permanently removed
269 from the colony. A complete experimental session with 10 trials took around 1.5 hours. Each day,
270 two colonies were tested, with 3-4 ants per colony, and thus, at best, 8 ants a day.

271 **Statistical Analysis**

272 Statistical analyses were carried out in R v. 3.5.0 (R Core Team 2016) using Generalized
273 Linear Mixed Models (GLMMs) in the LME4 package (Bates et al. 2014) to analyse first
274 interruption times, total drinking times and pheromone depositions data. Cumulative Link Mixed
275 Models (CLMMs) in the ordinal package (Christensen 2015) were used to analyse food acceptance
276 scores. CLMMs were used to analyse the acceptance data since we used an ordered factor with
277 three levels (1 = full acceptance, 0.5 = partial acceptance, 0 = rejection).

278 As multiple ants were tested per colony, colony identity was added as a random effect to
279 each model. GLMMs were tested for fit, dispersion and zero inflation using the DHARMA package
280 (Hartig 2017). The model predictors and interactions were defined *a priori*, following Forstmeier
281 and Schielzeth (2011). All p-values presented were corrected for multiple testing using the
282 Benjamini–Hochberg method (Benjamini and Hochberg 1995). A total of 70 ants were tested – 34
283 with low quality associated cues and 36 with high quality associated cues.

284 **Food acceptance data**

285 Model formulas slightly differed depending on the experimental phase (training = visits 1
286 to 8, test = visit 9). Fixed factors used for statistical analysis of the training phase were “presented
287 molarity” (1.5M or 0.1M) interacting with the “visit number” (1 to 8). Visit number was brought
288 into the model as an interaction with presented molarity, because molarities were presented in an
289 alternating order, always starting with low molarity on the first visit. Because individual ants were
290 tested multiple times, we included AntID nested in colony as a random factor for statistical analyses
291 of the training visits.

292 We used the following model formula for statistical analysis of the training visits:

293
$$\text{FoodAcceptance} \sim \text{Molarity} * \text{scale}(\text{visit}) + (\text{random factor: colony/AntID})$$

294 The fixed factor used for statistical analysis of the test visit was “high or low molarity
295 associated odour cues” (odours were associated to 1.5M and 0.1M during the training phase).

296 This resulted in the following model formula for the test visit:

297 $\text{FoodAcceptance} \sim \text{AssociatedMolaritytoOdour} + (\text{random factor: colony})$

298 **First Interruption Times, Total Drinking Times & Pheromone Deposition Data**

299 The total drinking times and pheromone deposition data were analysed using a GLMM with
300 a Poisson distribution for total drinking time during the test visit, and first interruption times and
301 pheromone depositions for the training phase and the test visit. Total drinking times of the training
302 phase were tested with a negative binomial distribution to receive a better model fit.

303 Model formula again slightly differed depending on the experimental phase (training =
304 visits 1 to 8, test = visit 9). Fixed factors used for statistical analysis of the training phase were
305 “presented molarity” (1.5M or 0.1M) interacting with the “visit number” (1 to 8). Visit number
306 was brought into the model as an interaction with presented molarity, because molarities were
307 presented in an alternating order, always starting with low molarity on the first visit. Because
308 individual ants were tested multiple times, we included AntID nested in colony as a random factor
309 for statistical analyses of the training visits.

310 We used the following model formulas for statistical analysis of the training visits:

311 $\text{FirstInterruptionTime} \sim \text{Molarity} * \text{scale}(\text{visit}) + (\text{random factor: colony/AntID}), \text{distribution} = \text{poisson}$

312 $\text{TotalDrinkingTime} \sim \text{Molarity} * \text{scale}(\text{visit}) + (\text{random factor: colony/AntID}), \text{distribution} = \text{negative binomial}$

313 $\text{NumberPheromoneDepositions} \sim \text{Molarity} * \text{scale}(\text{visit}) + (\text{random factor: colony/AntID}), \text{distribution} = \text{poisson}$

314 The fixed factors used for statistical analysis of the test visit were “high or low molarity
315 associated odour cues” (odours were associated to 1.5M and 0.1M during the training phase) and
316 the used odours (rosemary or lemon).

317 This resulted in the following model formulas for the test visit:

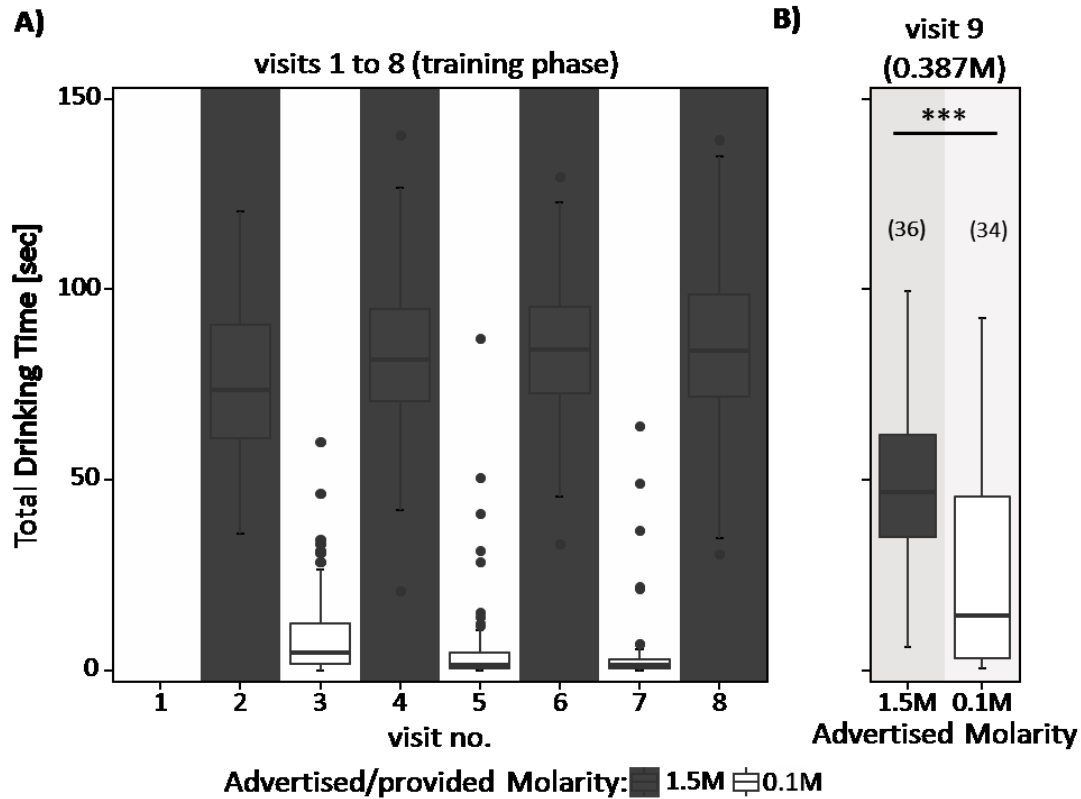
318 $\text{FirstInterruptionTime} \sim \text{AssociatedMolaritytoOdour} + \text{Odour} + (\text{random factor: colony}), \text{distribution} = \text{poisson}$

319 $\text{TotalDrinkingTime} \sim \text{AssociatedMolaritytoOdour} + \text{Odour} + (\text{random factor: colony}), \text{distribution} = \text{poisson}$

320 $\text{NumberPheromoneDepositions} \sim \text{AssociatedMolaritytoOdour} + \text{Odour} + (\text{random factor: colony}), \text{distribution} =$
321 poisson

322 **Results**

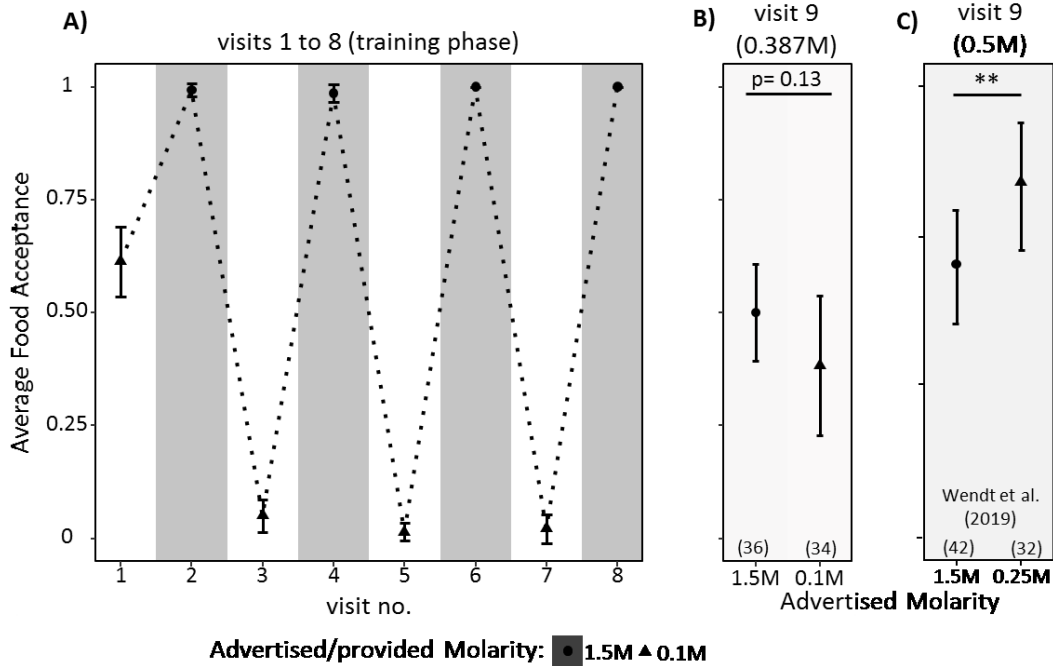
323



324
 325 Figure 2: A) & B) Total Drinking Time in seconds for A) the eight training visits (visits 1-8) in which ants received
 326 0.1M coupled with one odour and 1.5M coupled with another odour in an alternating order, always starting with 0.1M,
 327 B) the test visit (visit 9) in which ants always received 0.387M sucrose solution. Both the sucrose solution and the
 328 runway leading towards the food source were impregnated with one of the learned odours, triggering an expectation
 329 towards receiving either high or low molarities at the end of the runway. There is no data for total drinking time of the
 330 first visit displayed, because ants were sometimes disturbed when marking them, occasionally resulting in unclear
 331 feeding patterns. Shown are the median, the 75%/25% quantiles, and the range of total drinking time for each visit.
 332 Sample sizes for the 9th visits of both experiments are displayed in parentheses of B). *: $p < 0.05$; **: $p < 0.01$; ***: p
 333 < 0.001 .

334
 335 During training (visit 1 to 8), ants showed a higher total drinking time in seconds when
 336 confronted with the high molarity than when confronted with the low molarity (*GLMM*: estimate
 337 = -3.02, $z = -41.81$, $p < 0.001$, *OR* = -3.02, 95% C.I. [-3.16, -2.88], figure 2A). On the 9th (test)
 338 visit, the quality indicated on the runway and in the medium quality (0.387M) food strongly
 339 affected total drinking times. Drinking times were significantly higher when high-quality
 340 associated odours were present than when low-quality odours were present (median drinking time
 341 with high molarity cues: 44.63 seconds, low molarity cues 21.38 seconds, *GLMM*: estimate = -
 342 1.18, $z = -4.47$, $p < 0.001$, *OR* = -1.18, 95% C.I. [-1.7, -0.66], figure 2B).

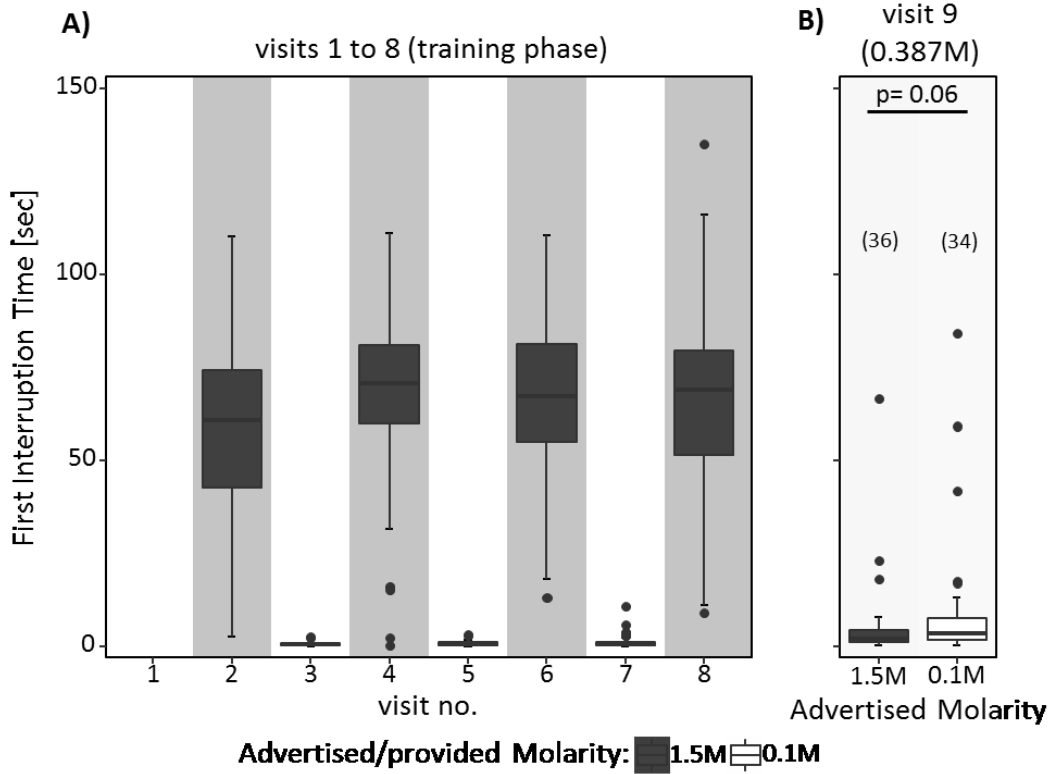
343 Because we believe that a direct comparison of the current study to those of Wendt et al
 344 (2019) is important in order to fully explain the experimental differences included to counteract
 345 contrast effects, we reproduce the key results of Wendt et al (2019) in figures 3C and 5C.



346
 347 Figure 3: Average food acceptance for A) the eight training visits (visits 1-8) B) the 9th (test) visit and C) the 9th (test)
 348 visit of ants tested in Wendt et al. (2019) in which only the runway, but not the medium quality food (0.5M) was
 349 impregnated with learned odours. Shown are the mean food acceptance (points) and the 95% confidence intervals
 350 (error bars) for each visit. Sample sizes for the 9th (test) visits of both experiments are displayed in parentheses of B)
 351 and C). *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

352
 353 Acceptance scores during training mirrored total drinking times, with ants showing a
 354 significantly higher food acceptance when confronted with the high molarity than when confronted
 355 with the low molarity (*CLMM*: estimate = -4.54, $z = -4.97$, $p < 0.001$, *OR*: 95% C.I. [-12.99, -9.11],
 356 figure 3A). However, even though food acceptance scores were higher on average when high
 357 quality food was advertised, they did not differ significantly in the 9th (test) visit between the two
 358 advertised qualities (*CLMM*: estimate = -0.69, $z = -1.51$, $p = 0.13$, *OR*: 95% C.I. [-1.62, 0.18],
 359 figure 3B). This is in contrast to the pattern found in Wendt et al. (2019), in which ants exposed to
 360 1.5M-associated cues during the 9th (test) visit showed significantly lower food acceptance towards
 361 the unscented 0.5M feeder than ants exposed to 0.25M-associated cues (figure 3C).

362

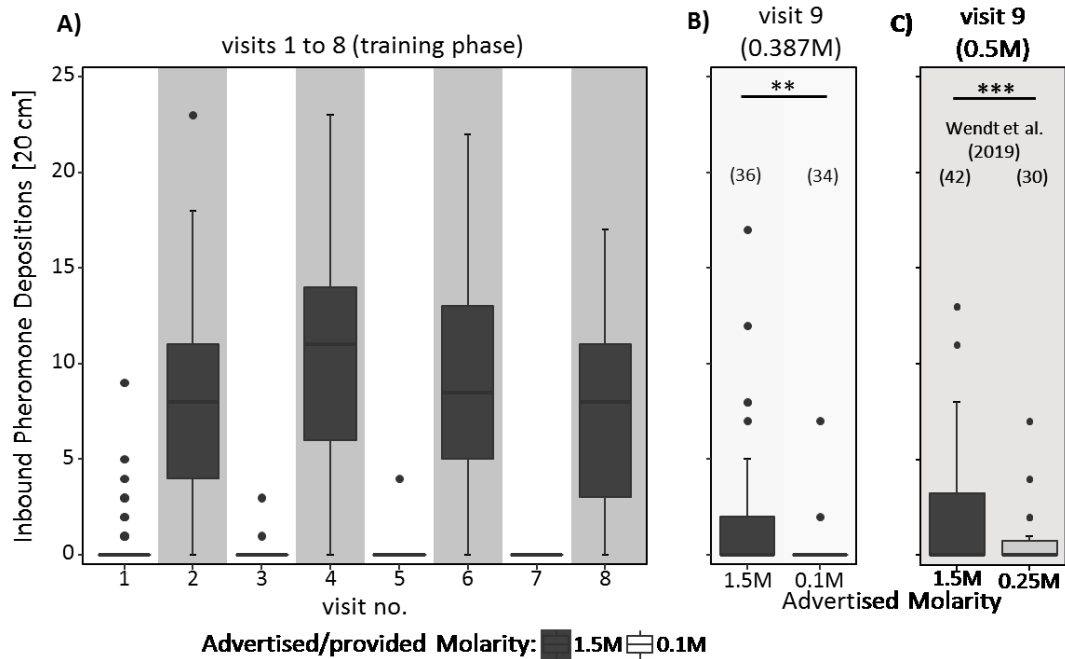


363

364 Figure 4: A) & B) First interruption time in seconds for A) the eight training visits and B) the 9th (test) visit. See figure
 365 legend 2 for details.

366

367 First interruption times also mirrored acceptance scores and total drinking times during
 368 training, with higher first interruption times for the high quality food (*GLMM*: estimate = 0.53, z
 369 = 3.60, p < 0.001, *OR* = -5.21, 95% C.I. [-5.45, -4.97], figure 4A). In the 9th (test) visit, there was
 370 a strong tendency towards ants showing lower first interruptions times for medium quality food
 371 advertised as high quality (*GLMM*: estimate = 0.71, z = 1.88, p = 0.06, *OR* = 0.71, 95% C.I. [-0.03,
 372 1.46], figure 4B).



373
 374 Figure 5: Phomone depositions towards the nest [20 cm] (inbound phomone depositions) for A) the eight training
 375 visits (visits 1-8), B) the 9th (test) visit and C) the 9th (test) visit of ants tested in Wendt et al. (2019) in which only the
 376 runway, but not the medium quality food (0.5M) was impregnated with learned odours. Shown are the median number
 377 of phomone depositions on the measured 20 cm track on the way back to the nest and the 75%/25% quantiles for
 378 each visit. *: p < 0.05; **: p < 0.01; ***: p < 0.001.
 379

380 Finally, phomone depositions when returning from the feeder to the nest also mirrored
 381 the other measured variables, with higher phomone deposition for higher quality (*GLMM*:
 382 estimate = -1.58, z = -5.28, p < 0.001, *OR* = -5.46, 95% C.I. [-6.27, -4.65], figure 5A). On the 9th
 383 (test) visit, advertised food quality affected phomone deposition, with ants depositing more
 384 phomone having consumed medium food advertised as high quality (*GLMM*: estimate = -3.19, z
 385 = -3.24, p < 0.01, *OR* = -3.19, 95% C.I. [-5.12, -1.26], figure 5B). However, note that ants deposited
 386 much less phomone on the return from the 9th (test) visit than on training visits (*GLMM*: estimate
 387 = 1.15, z = 9.37, p < 0.001). The data reported are similar to Wendt et al. (2019). In Wendt et al.'s
 388 (2019) study, ants experiencing 1.5M-associated cues during the 9th visit – provided only through
 389 runway odours towards the food, but not in the food – showed a significantly higher number of
 390 phomone depositions on their return than ants exposed to 0.25M-associated cues (figure 5C).

391 Discussion

392 Ants spent more time feeding at medium quality sucrose solution when it was accompanied
 393 by a flavour previously associated to high molarity food compared to a flavour associated to low
 394 molarity food (figure 2B). The number of phomone depositions performed after feeding on
 395 medium quality food was also significantly higher when ants returned to the nest from medium
 396 food accompanied with high quality flavour compared to low quality odour, suggesting
 397 assimilation effects both in the feeding times and inbound phomone depositions. Food acceptance
 398 scores, although probabilities did not reach or exceed 0.05, displayed a similar pattern (figure 3B):

399 Ants showed higher acceptance of the medium quality food when it was presented along with a
400 high molarity odour. Thus, ants reacted differently to food sources of identical sucrose solution,
401 depending on the associative cue presented before, during, and after consumption.

402 However, ants also showed some evidence of contrast effects in the first few seconds after
403 finding the food. The time until first feeding interruption at medium quality food was almost twice
404 as long when ants expected low quality compared to expecting high quality food, suggesting that
405 the medium quality food was initially perceived as better when ants expected to find poor food,
406 and vice versa (figure 4B).

407 Finally, as in Wendt et al. (2019), there was a significant difference in pheromone
408 deposition depending on the ants' expectations (figure 5B & C), with ants experiencing good food-
409 associated cues depositing on average more pheromone than those experiencing poor food-
410 associated cues. However, our experimental manipulation seems to interfere with pheromone
411 laying, and the number of pheromone depositions is generally so low on the 9th (test) visit that the
412 difference does not seem biologically meaningful.

413 Wendt et al. (2019) showed clear contrast effects in ants of this species in terms of food
414 acceptance, where expectations caused an inversion in perception, so that high expectations caused
415 an undervaluing of medium quality, and vice versa for low expectations. Here, with the minor
416 addition of odour in the food, we eliminated the acceptance contrast effects reported in Wendt et
417 al. (2019), and even found the reverse pattern in terms of drinking times (figure 2B), indicating an
418 assimilation effect: if a label was present in the food indicating high quality during consumption,
419 the perceived quality of the food increased. The assimilation effect can be very clearly seen in the
420 total drinking time data (figure 2B), and also, though to a lesser extent, in the pheromone deposition
421 data (figure 5B). Hovland et al. (1957) argued that assimilation effects are likely to occur in humans
422 when the expectation is not very different from reality, whilst contrast effects are more likely to
423 occur when the expectation is very different from reality. The results of this study together with
424 those of Wendt et al. (2019) support this assumption in ants as well. The presence of an associated
425 odour during consumption leads to a higher similarity between expectation and experience in the
426 current experiment, in turn leading to assimilation rather than contrast effects, which were shown
427 in the previous study (Hovland et al. 1957).

428 We argue that this is directly analogous to the labelling effect described in humans. There,
429 brand labels are based upon an accumulation of associative cues, which have been linked to a label
430 affecting perceived value (Levin et al. 1998; Macklin 1996; Mao et al. 2013; van Osselaer and
431 Janiszewski 2001). For example, our social environment has led us to assign a negative value to
432 fat and a partly negative value to soy. Humans tend to assign greater value to meat advertised as
433 75% lean compared to when it was advertised as containing 25% fat (Levin et al. 1998). Soy as a
434 product label decreases the perceived quality of taste while at the same time increasing the
435 perceived healthiness of a product (Wansink 2000). In this case, the label forms an expectation
436 about taste and healthiness mostly based on cultural biases and advertisements. Products can thus
437 be paired with already positively or negatively associated labels to influence costumers' perception

438 of product value. Just as humans prefer to purchase a brand with which they have previously had
439 positive experiences over a novel brand (Russo et al. 1996), ants may also be affected by a familiar
440 food label (associated odour), which previously offered positive (or negative) experiences, and may
441 thus be more (or less) likely to “buy” a novel medium-quality food source if it is presented with
442 the familiar odour cue.

443 Our findings extend those of Oberhauser & Czaczkes (2018), who trained *Lasius niger*
444 workers to a 1M food source presented along with either lemon or rosemary odour. After training,
445 ants received a food source of identical quality, but presented with an unfamiliar odour. Ants
446 showed significantly lower food acceptance towards the unfamiliar odour. There, as in this study,
447 it is likely that the naturally value-neutral odour cue gained an associated value, which affected
448 value perception. Once the associated cue was missing, the reward lost part of its assigned value,
449 leading to contrast effects, as also shown in Wendt et al. (2019). We propose that in the current
450 experiment the odour on the runway and the taste of the food are playing different roles in the ant’s
451 evaluation process: the odour is signalling what to expect, setting a reference point against which
452 the measure of value obtained during feeding is contrasted. The taste is adding an associated value
453 (positive or negative) during feeding, which is added to the objective sensory measure of food
454 quality to form the complete measure of value obtained during feeding. This is then contrasted
455 against the ant’s expectation. The results of this study support the prediction that the presence of
456 an associative cue during food consumption affects value perception, and that it can counteract
457 expectations – even if the expectations and the associations are triggered by the same cue.

458 However, in some ways the odour cues used in this study may not be directly analogous to
459 brand labels affecting perceived value in humans. Odours often have important innate biological
460 meanings, whereas brand labels in humans are naturally value neutral and biologically meaningless.
461 Indeed, ants strongly rely on odour cues both in navigation (Czaczkes et al. 2014; Josens et al.
462 2009; Oberhauser et al. 2019; Provecho and Josens 2009; Roces 1994) and nestmate recognition
463 (Akino et al. 2004; Brandstaetter et al. 2008; Sturgis and Gordon 2012). However, since *Lasius*
464 *niger* ants mainly feed on honeydew (Detrain et al. 2017; Devigne and Detrain 2002; Völkl and
465 Mackauer 1993; Völkl et al. 1999) it is unlikely that a positive value is assigned to the odours used
466 in this study (rosemary and lemon), even though they may be naturally available to ants. Previous
467 studies show no innate preference for either of the odours (Oberhauser and Czaczkes 2018). In
468 contrast to odours, the value assigned to brand labels in humans comes from social knowledge and
469 marketing, not solely from direct experience. The cues used in this study may thus not be the
470 completely equivalent to brands and food labels used in human studies, but seem to be the best
471 alternative for investigating value distortion effects in ants. We demonstrated an assimilation effect
472 driven by labels in feeding time and recruiting behaviour of ants (and a tendency in food acceptance
473 scores), mirroring effects found in humans. In contrast, ants showed weak contrast effects in first
474 interruption times.

475 This study shows that the time of cue presentation strongly influences its effect on perceived
476 value in ants. When odours were presented *before* food consumption, ants showed clear contrast
477 effects (Wendt et al. 2019). Presenting odours *during* food consumption, however, reversed the

478 perceived value of a medium quality food source, resulting in assimilation (this study). The fact
479 that we see weak contrast effects during the first reactions of ants (first interruption times), but not
480 later during or after feeding (total drinking time and inbound pheromone depositions) furthermore
481 suggests that contrast effects can be acted against by presenting a label during consumption and
482 that this change in value perception happens while the label is presented, and not through
483 expectations induced before food consumption or through other factors. Because contrast effects
484 can be seen in the first interruption times, but not in the acceptance scores which measure the first
485 three seconds of an ant's response, we argue that a food label gradually counteracts and
486 overwhelms contrast effects over the course of several seconds. To further pin down contrast and
487 assimilation effects, future studies may wish to investigate consummatory effects without first
488 inducing contrast effects. This would give a clear picture of ants' responses to food labels alone,
489 and allow for a clearer interpretation of both contrast and assimilation effects, because assimilation
490 effects will likely be stronger when odour labels do not have to overcome contrast effects.

491 The evidence presented in this study adds to prior studies showing parallel value-distorting
492 effects in humans and insects, including decoy effects (Sasaki and Pratt 2011; Tan et al. 2014;
493 2015), risk aversion (De Agrò et al. 2019; Shafir et al. 1999; Shapiro 2000; Waddington et al. 1981),
494 discounting (Cheng et al. 2002; Wendt and Czaczkas 2017) and expectation-driven valuation
495 (Bitterman 1976; Couvillon and Bitterman 1984), suggesting that insights into human behaviour
496 can, in part, be transferred to insects. Insect-based comparative psychology studies allow much
497 tighter control over experimental subjects and conditions, offering stringent tests of basic insights
498 from human psychology, and the experimental flexibility to test hypotheses untestable on human
499 subjects. We hope that our work inspires consumer psychologists and behavioural economists to
500 consider insects as a viable model system in which to test their underlying assumptions and
501 thinking, in order to gain deeper insights into both human and animal behaviour.

502 **Author contributions**

503 SW performed the experiments and analysed the data. SW and TJC designed the study,
504 interpreted the data and wrote the manuscript. All authors gave final approval for publication and
505 agree to be held accountable for the content therein.

506 **Conflict of interest**

507 The authors declare that they have no conflict of interest.

508 **Ethical approval**

509 All animal treatment guidelines applicable to ants under German law have been followed.

510

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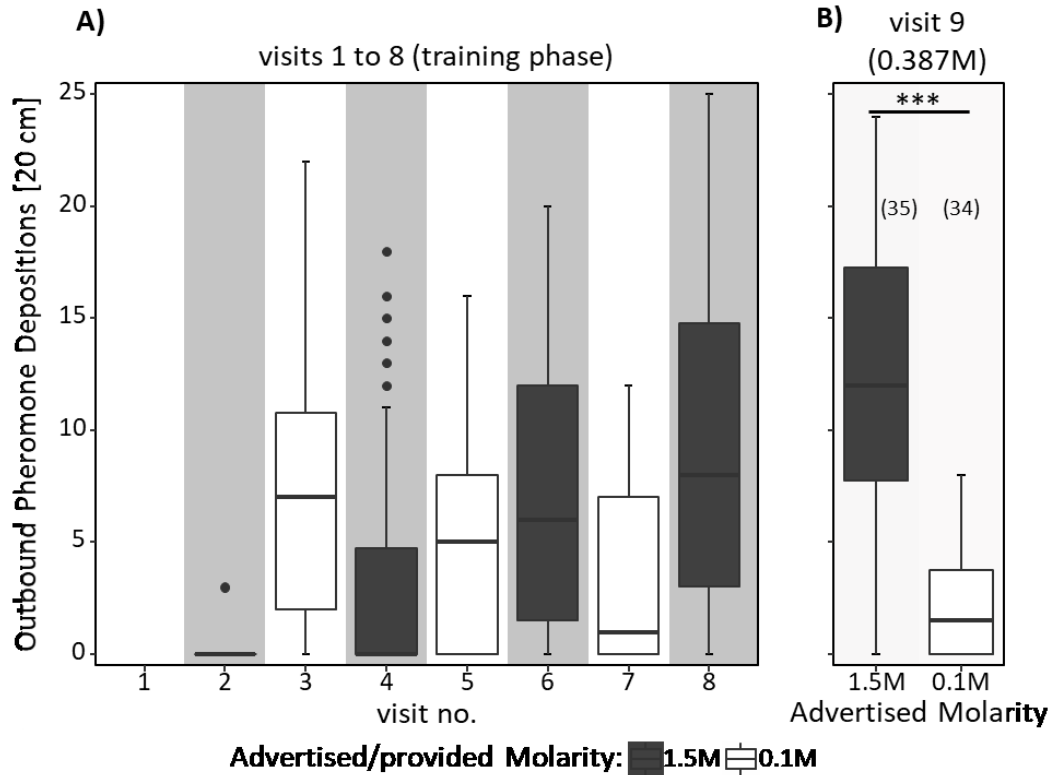
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784 Figure A1: A) & B) Outbound Pheromone Depositions [20 cm] (to the Food Source) for A) the eight training visits
 785 (visits 1-8) in which ants received 0.1M coupled with one scent and 1.5M coupled with another scent in an alternating
 786 order, always starting with 0.1M, B) the test visit (visit 9) in which ants always received 0.387M sucrose solution.
 787 Both the sucrose solution and the runway leading towards the food source were impregnated with one of the learned
 788 scents, triggering an expectation towards receiving either high or low molarities at the end of the runway. Shown are
 789 the median number of pheromone depositions on the measured 20cm track on the way to the food source and the
 790 75%/25% quantiles for each visit.

791

792 During training (visit 1 to 8), ants deposited significantly more pheromone on the measured
 793 20 cm track on the way to the food source when confronted with the high molarity than when
 794 confronted with the low molarity (*GLMM*: estimate = 0.52, $z = 4.65$, $p < 0.001$, $OR = 0.52$, 95%
 795 C.I. [0.3, 0.73], figure A1 A). The number of visit also had a significant effect on the number of
 796 deposited pheromone with pheromone depositions towards high molarity scent generally
 797 increasing and pheromone depositions towards low molarity scents generally decreasing over time
 798 (*GLMM*: estimate = 1.14, $z = 13.64$, $p < 0.001$, $OR = 1.14$, 95% C.I. [0.97, 1.3]). Ants which
 799 expected high molarity on the 9th visit (test visit) deposited significantly more pheromone than ants
 800 which expected to find low molarity food at the end of the runway (*GLMM*: estimate = -1.80, $z =$
 801 -8.85 , $p < 0.001$, $OR = -1.81$, 95% C.I. [-2.21, -1.41]). Number of outbound pheromone depositions
 802 were also significantly higher for ants confronted with the high molarity scent on the 9th visit
 803 compared to the training phase (visit 2 vs 9: estimate = 0.46, $z = 11.14$, $p < 0.001$, visit 4 vs 9:
 804 estimate = 0.57, $z = 13.96$, $p < 0.001$, visit 6 vs 9: estimate = 0.59, $z = 14.5$, $p < 0.001$, visit 8 vs 9:
 805 estimate = 0.58, $z = 14.36$, $p < 0.001$).

806 **Appendix B**

807 **Captions for Supplementary Videos B1 and B2**

808 Video B1: ant displaying food acceptance score 1. It shows no food interruptions within the

809 first seconds of feeding.

810 Video B2: ant displaying food acceptance score 0.5. It interrupts feeding within the first

811 seconds of feeding and repeatedly interrupts feeding, but still feeds at the food source until the crop

812 is filled (an ant displaying food acceptance score 0 would refuse to feed at the sucrose solution and

813 either returned to the nest immediately or fail to fill its crop within 10 minutes).

814