

1 Irrational risk aversion in ants is driven by perceptual mechanisms

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12 Abstract

13 Animals must often decide between exploiting safe options or risky options with a chance for large
14 gains. While traditional optimal foraging theories assume rational energy maximisation, they fail to
15 fully describe animal behaviour. A logarithmic rather than linear perception of stimuli may shape
16 preference, causing animals to make suboptimal choices. Budget-based rules have also been used
17 to explain risk-preference, and the relative importance of these theories is debated. Eusocial
18 insects represent a special case of risk sensitivity, as they must often make collective decisions
19 based on resource evaluations from many individuals. Previously, colonies of the ant *Lasius niger*
20 were found to be risk-neutral, but the risk preference of individual foragers was unknown. Here,
21 we tested individual *L. niger* in a risk sensitivity paradigm. Ants were trained to associate a scent
22 with 0.55M sucrose solution and another scent with an equal chance of either 0.1 and 1.0M
23 sucrose. Preference was tested in a Y-maze. Ants were extremely risk averse, with 91% choosing
24 the safe option. Even when the risky option offered on average more sucrose (0.8M) than the fixed
25 option, 75% preferred the latter. Based on the psychophysical Weber-Fechner law, we predicted
26 that logarithmically balanced alternatives (0.3M vs 0.1M/0.9M) would be perceived as having
27 equal value. Our prediction was supported, with ants having no preference for either feeder (53%
28 chose the fixed option). Our results thus strongly support perceptual mechanisms driving risk-
29 aversion in ants, and demonstrate that the behaviour of individual foragers can be a very poor
30 predictor of colony-level behaviour.

31 Introduction

32 Finding a good meal is not easy: the environment provides a broad variety of food
33 sources, but individuals are not necessarily able to explore all of them before committing to one
34 (Mehlhorn et al., 2015). The food sources the organism inspects will often have different
35 attributes, and options can be compared in order to choose the best one. This economic decision
36 process is so crucial for organisms that the ability to compare options is found not only in animals,
37 but even in non-neuronal organisms such as plants and slime-moulds (Dener et al., 2016; Reid et
38 al., 2015, 2016).

39 Traditionally, organisms were assumed to maximise energetic gains while minimising
40 costs, on the basis that evolution should drive animals to have optimal behavioural strategies.
41 However, the optimal foraging theory framework (Pyke et al., 1977) fails to fully describe
42 behaviour - organisms do not always behave optimally. Extensive examples of violation of
43 optimality in animal species can be found, for example, in the literature about risk sensitivity. We
44 define risk as a situation in which the probabilities associated with an option (e.g. food source) are
45 known, but the exact value of it is not. Conversely, “uncertainty” is when not even the probabilities
46 of the various possible payoffs are known.

47 *Risk sensitivity theories – the budget rule*

48 Risk sensitivity studies were effectively inaugurated by Caraco et al. (1980). They studied
49 the preference of yellow-eyed juncos for different amount of seeds: one of the two alternatives
50 available to the birds was stable, presenting always the same, medium amount of food (safe
51 feeder), while the other one fluctuated in value, but had the same mean pay-out as the safe feeder
52 (risky feeder). The authors then, based on the preference of the animals, designed a utility
53 function (Becker et al., 1964), computing the perceived value (utility) for each number of seeds for
54 the animals. Yellow-eyed juncos presented a concave utility function (and so were risk averse)

55 when in a high energy budget, whereas their utility function was convex (and so they were risk
56 prone) when in a low energy budget. This behaviour was soon formalized as the Energy Budget
57 Rule (Stephens, 1981). However, a growing body of work on risk sensitivity failed to provide
58 consistent empirical support for the budget rule (Kacelnik and Bateson, 1996; Kacelnik and El
59 Mouden, 2013). For this reason the budget rule has recently been reformulated by Lim et. al.
60 (2015). They argue that the classical budget rule is often misused in its binomial interpretation:
61 animals are either risk prone (when in a low energy budget) or risk averse (when in a high energy
62 budget). However, the optimum risk sensitivity in a given situation lies on a continuum, depending
63 on the remaining energy budget of the animal, even arriving at extreme conditions (very low
64 energy budget and very high energy budget) in which risk indifference arise again. Such a
65 continuous interpretation of the budget rule may accommodate results considered as inconsistent
66 the classical budget rule hypothesis (e.g. Hurly, 2003).

67 *Risk-sensitivity theories – Scalar Utility Theory*

68 An alternative to prescriptive theories (based on optimality modelling) are descriptive
69 theories, which explain behaviours in terms of proximate mechanisms. If risk sensitivity arises as a
70 side-effect of the neural or cognitive architecture of an animal, or due to evolutionary constraints,
71 one need not attempt to fit this behaviour to fitness benefits. A striking pattern in risk preference
72 studies is that animals are often risk averse when risking amounts, but risk seeking when risking
73 delays (Kacelnik and Bateson, 1996). Animals (and humans) are also generally risk averse for
74 potential gains, but risk prone for potential losses (Kahneman and Tversky, 1979). These patterns
75 are elegantly explained by an understanding of how animals perceive the world, as described by
76 Psychophysics (Gescheider, 1976; Stevens, 2017; Tuzlukov, 2013). Stimulus strength has a
77 logarithmic relationship with perception, as formalized by the Weber-Fechner law (Fechner, 1860).
78 Thus, a constant feeder that always presents 5 seeds and a variable feeders presenting

79 alternatively 1 or 9 seeds have the same average; however, 5 seeds are perceived as 5 times more
80 than 1 on a logarithmic curve, while 9 is not even twice as good as 5. Thus, while the mathematical
81 average, and so the true energetic value, of the variable feeder is the same as the one of the safe
82 feeder, it's geometric average is lower. On logarithmic distributions, such as the Weber-Fechner
83 law by which animals perceive the world, the median is coincident with the geometrical average,
84 and is the measure that describes the overall perceived value of an option, as it is the middle point
85 between the two alternatives. Based on these insights, Kacelnik & El Mouden (2013) developed
86 Scalar Utility Theory (SUT) to describe risk aversion behaviour. They point out that, based on the
87 Weber-Fechner law, the variance of the memory representation of a food value increases as the
88 value itself increases. For this reason, two options with identical mathematical average (means)
89 but different variances will have different medians, with the more variable option having a lower
90 one (see figure 6 from Kacelnik and El Mouden, 2013 for a complete explanation). However,
91 support for this descriptive theory is also mixed: Lim et al. (2015) argue that SUT has even weaker
92 support than the budget rule, with only 8 of the 35 studies reviewed by Kacelnik & Bateson (1996)
93 finding complete risk aversion when risking potential resource gains. Shafir (2000) argued that it is
94 the strength of risk preference that is driven by perceptual mechanisms, while the direction is
95 driven by budget considerations, and could thus accommodate both risk seeking and risk aversion
96 in a manner consistent with logarithmic perception. However, Shafir's model can only account for
97 alternatives with the same mean value. Whether risk sensitivity is best understood in terms of
98 adaptation or constraints on perceptual mechanisms is thus still under debate.

99 *Ants as a model for risk sensitivity*

100 Risk sensitivity has been studied in a great variety of animals (for a review, see Kacelnik and
101 El Mouden, 2013). Among those, nectarivores have received particular scrutiny (Perez and
102 Waddington, 1996; Shafir, 2000). The majority of studies on nectarivores have been carried out on

103 bees. Results have, however, been unclear: bees have been observed to be risk indifferent
104 (Banschbach and Waddington, 1994; Fülöp and Menzel, 2000; Perez and Waddington, 1996), risk
105 averse (Shapiro, 2000; Waddington et al., 1981), to follow the budget rule (Cartar, 1991; Cartar and
106 Dill, 1990), or a mixture of those depending on risk variability (Dunlap et al., 2017; Mayack and
107 Naug, 2011; Shafir, 2000; Shafir et al., 1999). Bees and other eusocial insects represent a special
108 case for risk sensitivity. For eusocial insects with non-reproductive workers, the colony is the main
109 unit of selection and a colony can be considered a superorganisms (Boomsma and Gawne, 2018;
110 Hölldobler and Wilson, 2009). As such, the foraging successes of the individual workers are pooled.
111 This buffers colonies against short-term (negative) fluctuation coming from risky choices made by
112 individual foragers individuals. Colonies can also visit multiple food sources simultaneously,
113 allowing them to more efficiently exploit their environment (Czaczkes et al., 2015a; Devigne and
114 Detrain, 2005). Lastly, many eusocial insects can make collective foraging decisions, using
115 recruitment mechanisms to channel workers towards certain resources in the environment
116 (Detrain and Deneubourg, 2008; Gordon, 2019).

117 While research on risk preference and collective decision-making is extensive, these have
118 rarely been combined. Collective risk sensitivity has been explicitly studied in ants: Burns et al.
119 (2016) presented colonies of rock ants (*Temnothorax albipennis*) a fixed-quality mediocre nest and
120 a variable quality nest. Ants were allowed to explore (and hence evaluate) each nest and then
121 recruited nestmates, and colonies were found to be risk prone. On the other hand, Hübner &
122 Czaczkes (2017) tested the risk sensitivity of black garden ant (*Lasius niger*) colonies to food values.
123 Each colony was presented with two feeders: a stable one, always presenting the same, medium
124 quality sucrose solution (0.55M), and a variable one, presenting alternatively (changing every 3
125 minutes) either low or high quality sucrose solution (0.1M – 1.0M). Almost all trials showed a clear
126 collective decision for one of the two feeders (as is expected due to symmetry breaking in ants
127 collective decisions, see Beckers et al., 1990, 1993; Czaczkes et al., 2015b; Price et al., 2016), but

128 overall colonies were risk-indifferent: half the colonies chose the safe feeder, and half chose the
129 risky one. This is surprising, as positive feedback from the initially best food source should have
130 resulted in symmetry breaking and a collective choice for that feeder (Beckers et al., 1993;
131 Czaczkes et al., 2015b; Detrain and Deneubourg, 2008; Price et al., 2016).

132 This work aimed to explore individual risk preference in individual *Lasius niger* ant foragers.
133 Although their collective behaviour appears to be rational, individual workers may not be (Sasaki
134 and Pratt, 2011). They could be victims to the same perceptual constraints discussed above and be
135 strongly influenced by expectations, causing disappointment for some food alternatives, triggering
136 risk sensitivity.

137 Materials and Methods

138 *Subjects*

139 8 queenless *Lasius niger* colony fragments of around 1000 ants were used in the
140 experiment. Each fragment was collected from a different wild colony on the University of
141 Regensburg campus. Colonies fragments forage, deposit pheromone and learn well (Evison et al.,
142 2008; Oberhauser et al., 2018). Each fragment was housed in a transparent plastic box
143 (30x20x40cm), with a layer of plaster on the bottom. A circular plaster nest, 14cm in diameter and
144 2 cm thick, was also provided. The colonies were kept at room temperature (21-25 °C) and
145 humidity (45-55%), on 12:12 light:dark cycle.

146 Each colony was fed 0.5mol sucrose solution *ad libitum*, and deprived of food 4 days prior
147 each test. Water was provided *ad libitum* and was always present.

148 *Experiment 1 – Risk preference between options of equal absolute value*

149 The aim of this experiment was to assess the preference of individual ants between two
150 food sources which provide, on average, an equal amount of sucrose: one feeder provided a stable

151 moderate value (0.55M sucrose, the 'safe' option) and one providing a fluctuating value, either
152 high or low (0.1M or 1.0M, the 'risky' option). This was achieved by teaching each individual ant to
153 associate each feeder type (risky or safe) with a different odour, and then testing their preference
154 in a Y-maze. Preliminary tests (see ESM1) and previous work (Czaczkes et al., 2018b, 2018c) shows
155 that *L. niger* foragers learn quickly (within 3 visits to each odour) and reliably to associate odours
156 with feeders of different types.

157 *Training*

158 To begin each experiment ants were allowed onto a 15cm long, 1cm wide runway, with a
159 drop of sucrose at the end. The first ant to encounter the sucrose was marked with a dot of paint,
160 and all other ants were returned to the nest. The marked ant was allowed to drink to satiety and
161 then return to the nest to unload the collected sugar. She was then allowed to make 7 further
162 training visits to the runway and feeder. In each visit we recorded the number of pheromone
163 depositions performed on the runway towards the feeder and towards the nest after foraging.
164 Over the 8 visits the quality and odour of the feeder was varied systematically so that the ant
165 alternately encountered a moderate quality drop of sucrose solution (0.55M, 'safe') scented with
166 one odour, or either a low (0.1M) or high (1.0M) ('risky') drop of sucrose scented with another
167 odour. These values are clearly distinguishable by the ants (Wendt et al., 2018) and correspond to
168 moderate, low, and high value food sources for *L. niger* (Detrain and Prieur, 2014). Note that the
169 average of the low and high quality solutions equals that of the moderate quality. The solutions
170 were scented using either rosemary or lemon essential oils (0.05 μ l per ml). The runway leading to
171 the feeder was covered with a paper overlay scented identically to the sucrose solution being
172 offered. Overlays were scented by storing them in a sealed box containing cotton soaked in
173 essential oil. Overlays were discarded after each return to the nest, to ensure fresh odour and to
174 prevent a build-up of trail pheromone from occurring.

175 *Testing*

176 After the 8 training visits, the runway was replaced with a Y-maze (arm length 10cm,
177 bifurcation angle 120°). The stem of the Y-maze was overlaid with unscented paper, whereas the
178 two other arms were covered with scented overlays – one bearing the ‘risky’ associated scent, and
179 the other the ‘safe’ associated scent. The maze tapered at the bifurcation to ensure that the ant
180 perceives both scented arms at the same time (following Czaczkes, 2018a). No sucrose was present
181 on the Y-maze. We recorded the ants’ initial arm decision, defined by the ants’ antennae crossing a
182 line 2cm from the bifurcation point. We also recorded the ants’ final decision, defined by the ant
183 crossing a line 8cm from the bifurcation point. However, the initial and final decisions of the ants
184 were almost always the same, and analysis of either choice provides the same results (see ESM1).
185 For brevity we henceforth discuss only the initial decision data. On reaching the end of an arm the
186 ant was allowed to walk onto a piece of paper and brought back to the start of the Y-maze stem, to
187 be retested. The Y-maze test was thus repeated 3 times, to assess reliability of the ant choice.
188 However, this handling may have caused some disruption (see ESM1) and repeated unrewarded
189 trials affect motivation, so we conservatively analysed only the first Y-maze test. After testing, the
190 ant was permanently removed from the colony. In total we tested 64 ants equally divided among 4
191 different colonies.

192 For each tested ant, one odour corresponded to the ‘risky’ feeder and one to the ‘safe’
193 feeder. The association between odour and feeder type, the initial feeder type encountered, the
194 initial value of the ‘risky’ feeder, the side on which the ‘risky’ or ‘safe’ associated odours were
195 presented on the Y-maze test, and the scents associated with the ‘risky’ and ‘safe’ options were all
196 balanced between ants. Performing treatments blind was attempted, but due to the clear negative
197 contrast effects shown by ants on encountering a low quality food source after better ones (Wendt
198 et al., 2018), true blinding was not possible.

199 *Experiment 2 – Risk preference between options of different absolute value*

200 Experiment 1 demonstrated very strong risk aversion in individual ant foragers. Experiment
201 2 was designed to test whether risk aversion would be maintained ‘irrationally’, that is, when the
202 ‘risky’ feeder had a higher average quality than the ‘safe’ feeder.

203 As in experiment 1, the ‘safe’ feeder always presented a medium quality drop (0.55M,
204 indistinguishable for the ants from the solution provided ad libitum to the colony). However, the
205 ‘risky’ feeder alternated between a low quality reward (0.1M) and a very high quality reward
206 (1.5M). The average molarity of the risky feeder (0.8M) was thus higher than the average molarity
207 of the safe one. *L. niger* foragers can distinguish between the three presented molarities (Wendt et
208 al., 2018). Moreover, in a pilot experiment, we observed that when presented with three different
209 molarities ants do learn all three molarities and their associated odours (see ESM1). Each ant was
210 tested on the Y-maze 5 times, but as in experiment 1, only data from the first test was ultimately
211 used (see ESM1). In total we tested 64 ants from 8 new colonies. Each condition (scent association,
212 feeder order, risky feeder order, scent side on the Y-maze) was balanced and equally distributed
213 among colonies.

214 *Experiment 3 – Risk preference between psychophysically balanced options*

215 One hypothesis explaining the widespread risk aversion found in animals towards reward
216 quantities arises from the psychophysics of perception: intensity is generally perceived
217 logarithmically (Kacelnik and Bateson, 1996; Kacelnik and El Mouden, 2013; see introduction). It is
218 thus the geometrical average between the two risky alternatives that may describe the perceived
219 value. This hypothesis predicts that animals should be indifferent between a safe and a risky
220 option, if the risky option balances the logarithmic differences between the low and high quality
221 reward. In experiment 2, these were not balanced: the geometrical average of the risky feeder (
222 $\sqrt{0.1 \times 1.5} = 0.387$) was still lower than the one of the safe feeder ($\sqrt{0.55} = 0.55$), thus the

223 risky option may still have been perceived as worse than the safe option. In this experiment we set
224 out to offer a 'risky' option in which the *perceived* qualities of the low and high reward were
225 balanced relative to the moderate reward. We chose a moderate reward of 0.3M, and a low and
226 high reward of 0.1M and 0.9M respectively. The geometrical average of the risky option (
227 $\sqrt{0.1 \times 0.9} = 0.3$) was now equal to the one of the safe option. We thus hypothesised that ants
228 would be indifferent between these two options. Each ant was tested on the Y-maze 5 times, but
229 again only data from the first test was used (see S1). In total we tested 40 ants from 10 different
230 colonies. Each condition (scent association, feeder order, risky feeder order, scent side in the Y-
231 maze) was balanced and equally distributed among colonies.

232 *Statistical analysis*

233 Statistical analyses were carried out in R 3.3.3 (R Core Team, 2017). Following Forstmeier
234 and Schielzeth (2011), we included in the models only factors and interactions for which we had *a*
235 *priori* reasons for including. We employed generalized linear mixed effect models using the
236 package lme4 (Bates et al., 2015), with colonies as a random effect. Y-maze choice data was

$$\begin{aligned} \text{Initial decision} = & \\ & \text{first presented feeder (risky-safe)}^* \\ & \text{first presented risky alternative (good-bad)} + \\ & \text{random effect (colony)} \end{aligned}$$

237 modelled using a binomial distribution and logit link function. We used the following model:

238 We then used the package car (Fox and Weisberg, 2011) to test which factors of the model
239 had a significant effect on the dependent variable. Subsequently, we carried out post-hoc analysis
240 with Bonferroni correction using the package emmeans (Lenth, 2018) both for the general
241 preference of the ants for either the safe or the risky feeder (safe choice probability against
242 random probability), and for the factors with a significant effect to analyse the direction of the
243 difference. Plots were generated using the package ggplot2 (Wickham, 2009).

244 Pheromone deposition count was modelled using a poisson distribution and logit link
245 function. Good model fit was confirmed using the DHARMA package (Hartig, 2018), and the pscl
246 package (Jackman, 2017; Zeileis et al., 2008) was used to produce the zero-inflated poisson models
247 when needed. Pheromone deposition was not the focus of the current study, but we include it as
248 descriptive data since it may shed light on how individual perception can shape group choice. We
249 modelled pheromone deposited towards the nest and pheromone deposited on the way back
250 separately, since these are conceptually very different: depositions towards the food reflect the
251 ants' expectation, and depositions on the return to the nest reflect the ants' perception. The
252 models used were the following:

Pheromone towards the drop =
*visit (2-8)**
value (molarity)+
random effect (ant nested in colony)

Pheromone back to the nest =
*visit (1-8)**
value (molarity)+

254 Pheromone deposition data from each of the three experiments were analysed separately,
255 as they were taken by three separate experimenters, and so could not reliably be compared
256 between experiments. Path choice decisions allow much less observer error, so Y-maze data can be
257 pooled between experiments.

258 Only main results are reported below. For the full analysis see ESM2. The raw data for all
259 the experiments can be found in the supplemental materials ESM3.

260 Results

261 *Experiment 1 – Risk preference between options of equal absolute value*

262 *Y-maze choice tests*

263 Ants were strongly risk averse, with 91% (58/64) ants initially choosing the safe option
264 (figure 1) (GLMM post-hoc with estimated means, probability=0.911, SE=0.36, z=5.142, p<0.0001).
265 We found no effect of the first presented feeder (GLMM Analysis of Deviance, Chi square=0.709,
266 DF =1, p=0.3), nor of the first presented risky alternative (Chi square=0, DF=1, p=1), nor of the
267 interaction between those two factors (Chi square=0, DF=1, p=1).

268 *Pheromone deposition*

269 Considering pheromone deposition towards the feeder, we found an effect of molarity
270 (GLMM Analysis of Deviance, Chi square=12.992, DF=2, p=0.001) and an effect of the interaction
271 between molarity and visit number (GLMM Analysis of Deviance, Chi square=14.469, DF=2,
272 p=0.0007). Specifically, we found that the ants deposited overall more pheromone when going
273 towards the 0.55M drop in comparison to the 1.0M drop (figure 2A, GLMM post-hoc with
274 estimated means, estimate=0.657, SE=0.227, z=2.891, p=0.015). Note that the ant may be
275 expecting to find the 0.1M drop when going towards the 1.0M, because it last experienced the low
276 value associated with that scent. We found no differences in pheromone deposition between the
277 other molarities. Overall, the ants deposited more pheromone on the way to the safe feeder
278 relative to the risky one (GLMM post-hoc with estimated means, estimate=0.498, SE=0.19,
279 z=2.616, p=0.036).

280 Considering pheromone deposited when returning to the nest, we found an effect of
281 molarity (GLMM Analysis of Deviance, Chi square=85.97, DF=2, p<0.0001), an effect of visit (GLMM
282 Analysis of Deviance, Chi square=5.11, DF=1, p=0.024), but no effect of their interaction.

283 Specifically, we found that the ants deposited overall less pheromone when going back from the
284 0.1M drop in comparison to the 0.55M drop (figure 2D, GLMM post-hoc with estimated means,
285 estimate=-2.67, SE=0.154, z=-17.352, p<0.0001) and from the 0.1M drop in comparison to the
286 1.0M drop (GLMM post-hoc with estimated means, estimate=-2.78, SE=0.194, z=-14.308,
287 p<0.0001). However, there was no difference between the 0.55M drop and the 1.0M drop. Overall
288 the ants deposited more pheromone on the way back from the safe feeder relative to the risky one
289 (GLMM post-hoc with estimated means, estimate=1.28, SE=0.14, z=9.149, p<0.0001).

290 *Experiment 2 – Risk preference between options of different absolute value*

291 *Y-maze choice tests*

292 Ants were again strongly risk averse, with 75% (48 / 64) ants initially choosing the safe
293 option (figure 1)(GLMM post-hoc with estimated means, probability=0.792, SE=0.068, z=3.248,
294 p=0.001). We found no effect of the first presented feeder (GLMM Analysis of Deviance, Chi
295 square=2.015, DF=1, p=0.156), nor of the first presented risky alternative (Chi square=0.197, DF=1,
296 p=0.657), nor of the interaction between those two factors (Chi square=1.807, DF=1, p=0.179).

297 *Pheromone deposition*

298 The data for the pheromone deposition are summarized in figure 2B and 2E.

299 Considering pheromone deposited towards the drop, we found an effect of the molarity
300 (figure 2B, GLMM Analysis of Deviance, Chi square=7.489, DF=2, p=0.024). However, post-hoc
301 analysis revealed no difference between any of the molarities: the differences were probably so
302 small that bonferroni correction in the post-hoc analysis brought them above significance.

303 Considering the pheromone deposited back to the nest, we found an effect of molarity
304 (GLMM Analysis of Deviance, Chi square=133.424, DF=1, p<0.0001), an effect of visit (GLMM, Chi
305 square=10.249, DF=1, p=0.001), and an effect of their interaction (GLMM, Chi square=11.339,

306 DF=2, $p=0.003$). Ants deposited less pheromone for the 0.1M drop in comparison to the 0.55M
307 drop (figure 2E, GLMM post-hoc with estimated means, estimate=-2.683, SE=0.17, $z=-15.742$,
308 $p<0.0001$), less pheromone for the 0.1M in comparison to the 1.5M (GLMM post-hoc with
309 estimated means, estimate=-3.474, SE=0.204, $z=-17$, $p<0.0001$) and less for the 0.55M in
310 comparison to the 1.5M (GLMM post-hoc with estimated means, estimate=-0.79, SE=0.19, $z=-$
311 4.144, $p=0.0001$). Overall the ants deposited more pheromone on the way back from the safe
312 feeder relative to the risky one (GLMM post-hoc with estimated means, estimate=0.946, SE=0.14,
313 $z=6.341$, $p<0.0001$).

314 *Experiment 3 – Risk preference between psychophysically-balanced options*

315 *Y-maze choice tests*

316 53% (21/40) of ants chose the safe option (figure 1), a proportion not different from chance
317 (GLMM post-hoc with estimated means, probability=0.535, SE= 0.086, $z=0.403$, $p=0.687$).

318 We found an effect of the first presented feeder (GLMM Analysis of Deviance, Chi
319 square=4.424, DF=1, $p=0.0354$). Specifically, 71% of the ants that were presented with the safe
320 feeder in visit 1 choose the safe smell during testing, while 35% of the ones presented with the
321 risky feeder first did.

322 *Pheromone deposition*

323 Considering pheromone depositions towards the feeder, we found an effect of molarity
324 (GLMM, Chi square=16.133, DF=2, $p=0.0003$). Ants deposited more pheromone when going
325 towards the 0.3M drop in comparison to the 0.9M drop (figure 2C, GLMM post-hoc with estimated
326 means, estimate=10.444, SE=1.751, $z=3.769$, $p=0.0007$), while we found no difference between
327 0.1M and 0.3M (GLMM post-hoc with estimated means, estimate=0.477, SE=0.174, $z=-2.032$,
328 $p=0.169$) and between 0.1M and 0.9M (GLMM post-hoc with estimated means, estimate=4.981,

329 SE=3.452, $z=2.317$, $p=0.082$). Overall, ants deposited more pheromone for the safe feeder (GLMM
330 post-hoc with estimated means, estimate=4.679, SE=1.751, $z=4.124$, $p=0.0001$)

331 Considering pheromone deposition back to the nest, we found an effect of molarity
332 (GLMM, Chi square=47.083, DF=2, $p<0.0001$). Ants deposited less pheromone when returning
333 from the 0.1M drop in comparison to the 0.3M one (figure 2F, GLMM post-hoc with estimated
334 means, estimate=-882, SE=0.143, $z=-6144$, $p<0.0001$), less for the 0.1M in comparison to the 0.9M
335 (GLMM post-hoc with estimated means, estimate=-1.479, SE=0.18, $z=-8193$, $p<0.0001$) and less for
336 the 0.3M in comparison to the 0.9M (GLMM post-hoc with estimated means, estimate=-0.597,
337 SE=0.165, $z=-2.615$, $p=0.001$). Overall the ants deposited the same amount of pheromone on the
338 way back from the safe feeder relative to the risky one (GLMM post-hoc with estimated means,
339 estimate=0.142, SE=0.126, $z=1.134$, $p=1$).

340 Discussion

341 Ants show strong risk aversion given equal average payoffs between the risky and safe
342 options (0.1/1.0M vs. 0.55M, experiment 1). Even if the risky option offers 45% higher mean
343 payoffs than the safe reward (0.1M/1.5M vs. 0.55M), ants still show strong risk aversion
344 (experiment 2). We predicted, based on psychophysical principles, that logarithmically-balanced
345 rewards should be perceived as having equal value. We tested this in a situation where the risky
346 reward offered 66% higher payoffs than the safe reward (0.1/0.9M vs 0.3M) and observed, as
347 predicted, indifference between the two options.

348

349 *Support for the perceptual basis of risk sensitivity*

350 Our demonstration of risk aversion in resource amounts strongly support the perceptual,
351 descriptive theory of risk sensitivity proposed by Kacelnik & Bateson (1996) and developed by
352 Kacelnik & El Mouden (2013). Specifically, our data suggest functional risk aversion arising from risk
353 neutrality filtered through logarithmic perception. Budget Rule theories (Stephens, 1981) would
354 also predict risk aversion in our context, since the ants are on a positive energy budget – *Lasius*
355 *niger* would survive for over a week without feeding. However, our ability to accurately predict an
356 indifference point based on logarithmic perception strongly implies that perceptual mechanisms
357 are driving risk aversion in this species. Alternatively, we may have by chance chosen the precise
358 point where logarithmic balancing matches the balance point between improved average gains
359 from a risky option and the premium garnered by a safe bet according to the budget rule.
360 However, this seems unlikely.

361 The ants in our experiments never showed a preference for the risky alternative. This may
362 seem to imply that the ants were failing to learn the risky option, and associate it with an odour.
363 However, this hypothesis can be ruled out, as it cannot account for the results of experiment 3,

364 where neither food sources is preferred. If the ants were unable to learn the risky option, the only
365 other explanation for experiment 3 would be that a 0.3M is not preferred over complete
366 uncertainty. This can be ruled out, however, as ants clearly prefer 0.3M over 0.1M (ESM1).

367

368 *The Budget Rule is neither supported nor refuted*

369 Budget Rule theories (Stephens, 1981) would also predict risk aversion in our context, since
370 the ants are on a positive energy budget – *Lasius niger* would survive for over a week without
371 feeding. However, our ability to accurately predict an indifference point based on logarithmic
372 perception strongly implies that perceptual mechanisms are driving risk aversion in this species.
373 Our data neither supports nor refutes the Budget Rule (Caraco et al., 1980; Lim et al., 2015;
374 Stephens, 1981): we tested all ants after exactly 4 days of starvation, so we cannot know how ants
375 would have behaved on a different energy budget. Lim et al. (2015) strongly critiques SUT, since it
376 predicts suboptimal behaviour, which should be selected against. Logarithmic perception, however,
377 is a widespread phenomenon in the animal kingdom, from roundworms (Luo et al., 2008) to
378 humans (Fechner, 1860), and is argued that the logarithmic scale is the best possible neural
379 representation of magnitudes among other biologically feasible scales (Portugal and Svaiter, 2011).
380 A more precise food evaluation may require more energy than the energy gained from the
381 additional precision. However, this has never been tested in the context of risk sensitivity (Lim et
382 al., 2015). Even if the benefits accrued from a more linear perception of value would outweigh
383 their costs, developmental constraints or pleiotropy may prevent such perception from evolving.

384

385 *Lack of support for Prospect Theory*

386 Other theories of risk sensitivity based on perceptual mechanisms exist. Prospect Theory
387 (Kahneman and Tversky, 1979), a hugely influential economic theory of decision-making under risk
388 in humans, predicts that an individual should be risk averse in the context of gains but risk prone in

389 the context of losses. This again derives from logarithmic perception of cumulative gains and
390 losses. However, in Prospect Theory the dividing point between gains and losses is not necessarily
391 at zero. Rather, gains and losses are defined relative to a reference point, which is usually the
392 expected payoff, but may be socially induced (e.g. by comparing ones own salary to that of ones
393 colleagues). Anything above the reference point is perceived as a gain and anything below the
394 reference point is a loss. Disappointment for a lower value after a reference has been established
395 has already been demonstrated in the honeybee (Couvillon and Bitterman, 1984) and ants (Wendt
396 et al., 2018), and suggested in bumblebees (Wiegmann et al., 2003). The reference point for our
397 colonies might have been 0.5M: the solution that the ants are regularly fed on. If this were the
398 case, in experiment 1 the true choice would be between an always neutral value (0.55M, safe), and
399 a risk between a gain (1.0M) and a loss (0.1M). This hypothesis is also supported by the fact that
400 almost no pheromone was deposited for the 0.1M drop. In this case Prospect Theory would still
401 predict risk aversion, as losses are assumed to be perceived more strongly than gains. To test this
402 hypothesis we repeated experiment 1, but with colonies that had been fed *ad libitum* 1.5M
403 sucrose 1 month prior testing (data and procedure can be found in ESM1). If the ants were taking
404 their standard feeding solution as a reference point, every presented solution in this experiment
405 should have been perceived as a loss, and so the ants should have showed risk-seeking. However,
406 we observed the same preference that we saw in the main first experiment – strong risk aversion.
407 Either the ants behaviour is poorly described by Prospect Theory, or the normal feeding solution
408 does not set the reference point. Another possibility is that the reference point is not set by the
409 normal feeding solution, as the four-day food deprivation period may erase the ants memory of
410 the feeding solution. Instead, the reference point could be the most common solution in the
411 current context. In experiment 1 this would be 0.55M, maintaining the same situation of one
412 neutral vs. a loss or a gain, and so predicting the same outcome under Prospect Theory. This
413 hypothesis, however, does not fit the result obtained in experiment 3: if the 0.3M would have been

414 taken as a reference, we should still have observed a preference for the safe option. Either
415 Prospect Theory does not well describe the behaviour of ants, or their reference point remains at 0
416 in every situation, with every reward being a gain: in the domain of gains Prospect Theory predicts
417 simple logarithmic value perception.

418

419 *Risk neutrality at the colony level*

420 Does our understanding of individual behaviour in a risk-choice situation help explain the
421 risk indifference of ants at a colony levels (Hübner and Czaczkes, 2017)? Pheromone deposition
422 rates of individual foragers vary hugely between individuals, even when presented with identical
423 food sources. This is to be expected, given the fact that individual variability may aid collective
424 decisions (Dussutour et al., 2009; O'Shea-Wheller et al., 2017). However, the appropriate measure
425 of pheromone for colony-level decisions is total pheromone deposited. Examining the mean
426 deposition rates for both feeders in experiment 1, we see that ants, on average, deposited more
427 pheromone to the safe feeder (5.5 dots per ant) than the risky feeder (3.9 dots per ants). In
428 Hübner & Czaczkes (2017) each ant made only one or two visits to the feeder, but even when
429 considering only the first two visits ants made more pheromone depositions to the safe (1.5 dots
430 per ant) than to the risky (0.89 dots per ant) feeder. The finding of risk neutrality at the colony level
431 is thus still a puzzle. However, the two experiments are not directly comparable. Firstly, in the
432 current experiment pheromone was removed from the trail every visit. Pheromone presence is
433 known to reduce further pheromone deposition (Czaczkes et al., 2013), perhaps damping out the
434 differences between the two feeders. Secondly, the presence of odours on a path affects
435 pheromone deposition: while pheromone deposition on odourless paths is usually higher on the
436 nestward journey (Beckers et al., 1993; Czaczkes and Heinze, 2015; Czaczkes et al., 2013, 2016),
437 pheromone deposition is higher on outward journeys on scented paths (this study, Czaczkes et al.,
438 2018b, 2018c). Finally, it should be noted that perception of pheromone, much like perception of

439 quality, is also logarithmic (von Thienen et al., 2014), thus emphasising initial differences in
440 pheromone concentration but damping out differences between strong trails. Nevertheless, it
441 seems that colony-level decision-making effectively filters out the ants individual perceptual
442 constrains (this study, Sasaki and Pratt, 2011), but the mechanism used to achieve this is still
443 unknown.

444 In this study, we found that ants demonstrate risk aversion due to a logarithmic perception
445 of food value. Individual risk preference does not predict colony behaviour, which seems able to
446 filter out perceptual biases.

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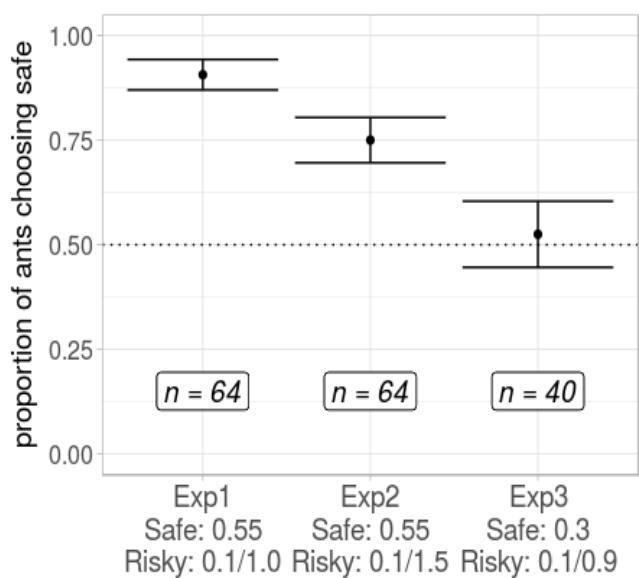
593 Figure legends

594 *Figure 1: Proportion of ants choosing the safe feeder. Ants preference is different from chance level in experiment 1*
595 *(prob.=0.911, SE=0.36, z ratio=5.142, p-value<0.0001) and in experiment 2 (prob.=0.792, SE= 0.068, z ratio = 3.248, p-*
596 *value =0.001), but not in experiment 3 (prob.=0.535, SE=0.086, z ratio=0.403, p-value=0.687).*

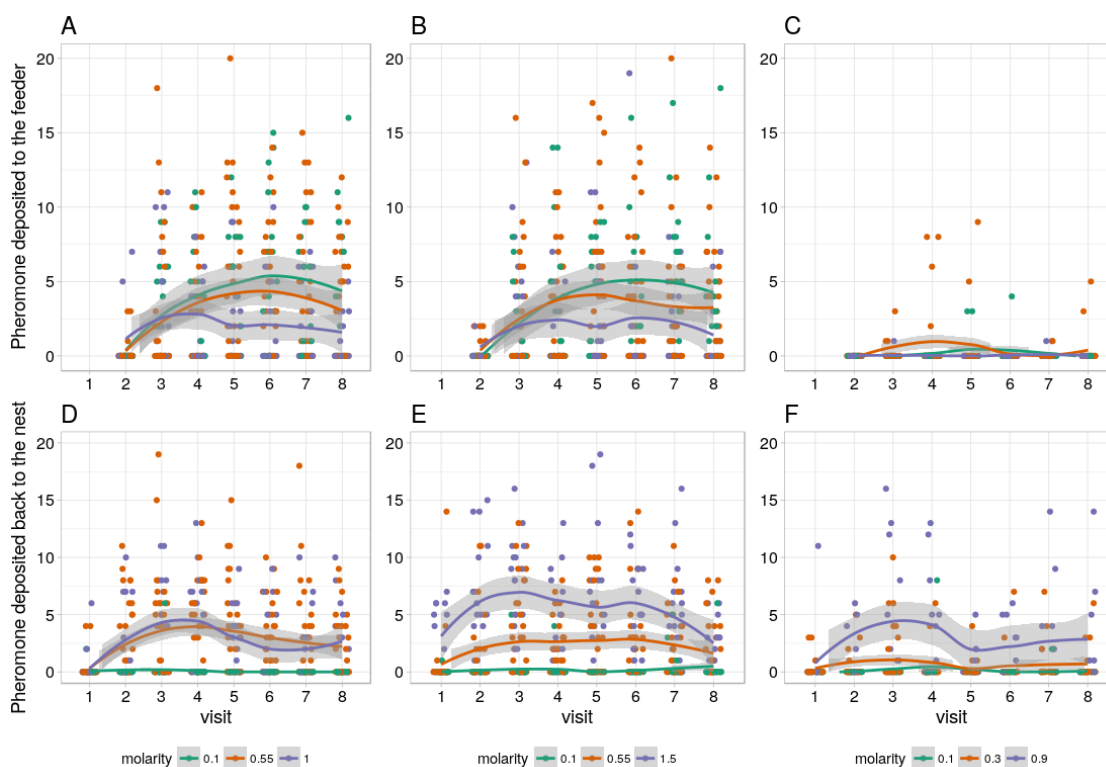
597 *Figure 2: Amount of pheromone deposited by the ants going to the drop and back to the nest across visits in the three*
598 *experiments. Considering the pheromone deposited on the way to the drop, we found a higher deposition rate for the*
599 *safe feeder in experiment 1 (A) and in experiment 3 (C) but not in experiment 2 (B). Considering the pheromone*
600 *deposited on the way back to the nest, we found a higher deposition rate for the safe alternative in experiment 1 (D)*
601 *and experiment 2 (E), but not in experiment 3 (F).*

602

603 Figures



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605