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1 **Title:**

2 Clearing the way to the external world: do ants make optimal decisions when removing
3 obstacles from their subterranean galleries?

4

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13 **Keywords :** decision making, ants, transport, optimality, path clearing

14

15 **Abstract:**

16 Transport tasks are simple tasks whose cost can be easily measured and that are thus well
17 suited to test optimality hypotheses. Here we focus on a particular type of transport that occur
18 when ants are clearing obstacles from their subterranean galleries. In the laboratory we
19 studied how they extract an object from a gallery of various inclinations. We expected that if
20 ants behave optimally, they should remove the object by the gallery extremity requiring the
21 lower energetic effort. At the colony-level, we found that the obstacle was more often
22 extracted by the lower end of the tube, even if this required a higher amount of mechanical
23 work. At the individual level however, ants showed mechanically optimal pulling behaviours
24 in 75% of cases. Our results suggest that individual ants take into account both the inclination
25 of the gallery and the position of the obstacle in it to decide in which direction they pull. In
26 addition, they seem to base their decision to release the obstacle on the relative effort they
27 perceive while pulling. Using a simple simulation model, we argue that the suboptimal
28 extraction bias observed at the colony-level can be explained by the sequential nature of the
29 extraction task.

30 **1. Introduction**

31 The optimality paradigm has been used for more than forty years in behavioral ecology as a
32 powerful method to investigate how animals make decisions to solve a variety of problems
33 involving cost-benefits trade-off, e.g. food or mate choice. However, the optimality approach
34 has often been criticized for investigating too complex tasks and relying implicitly on
35 unrealistic assumptions about the information gathering and cognitive capabilities of animals.
36 Studies on insects are less prone to this criticism because, with their much smaller behavioral
37 repertoire compared to vertebrates, the experimenter can focus on simple tasks that involve a
38 limited amount of information. In addition, because of their small brain and limited lifetime,
39 the experimenter is bound to make simple hypotheses on the cognitive mechanisms
40 underlying the tasks to be optimized by these animals. Insects offer therefore a particularly good
41 model for the study of optimality in behavior [1].

42 Social insects have been for a long time one of the favorite insects scientists have used for
43 testing optimality theory. The optimality approach has been applied in these insects, both at
44 the individual and collective level, to study decisions made in a variety of context such as
45 reproduction, division of labor [2], food choice and foraging [3–6], colony defense, and nest
46 choice [7] and construction [8]. One particular task that lends itself very well to the optimality
47 approach is the transport of items. Ants, in particular, can transport all sorts of objects. They
48 can transport food items such as whole prey, seeds or leaf fragments [9] but they can also
49 transport building material [8,10], brood or nestmates [11] or various types of items when
50 clearing their foraging trails of obstacles [12]. Each of these transports incurs a cost in terms
51 of time and energy which is a function of the weight of the item transported and of the
52 distance covered during the transport [13]. It also provides a benefit which can be assessed
53 quantitatively by the energetic content of the item transported in the case of food or which is

54 directly linked to the function of the object being transported in the case of a non-alimentary
55 item.

56 In this paper, we focus on a particular type of transport that occurs in ants with subterranean
57 nests when a narrow gallery linking their nest to the external world is partially clogged by an
58 object, e.g. a small stone or a vegetation fragment, which has fallen down from the ground
59 surface or which has been brought by the ants themselves. In that case the energetic cost
60 required to transport the object in order to unclog the gallery depends on its inclination and on
61 the distance to travel to reach either of its extremity. The benefit of the transport on the other
62 hand lies in the reestablishment of the flow of ants in the gallery. In this situation, how do ants
63 manage to extract the object from the gallery? do they behave optimally and extract the object
64 in the direction associated with the less energetic cost? And on which basis do they decide to
65 move the object in one or the other direction? In the study presented here we reproduced this
66 situation in the laboratory and investigated the mechanisms by which ants, both at the
67 individual and collective level, manage to extract an object from a narrow gallery with
68 different inclinations. We used the measure of the mechanical work achieved while moving
69 the object as a proxy for the measure of the metabolic energy expended. Since the
70 displacement of the object can be done only in two directions, the relative cost of the two
71 solutions can be easily calculated. We reasoned that if ants behave optimally when moving
72 the object, they should choose, both at the individual and colony-level, the direction requiring
73 the less amount of metabolic energy.

74 We structured our study in three different parts. First, we analyzed the final outcome of the
75 sequence of individual pulling actions leading to the extraction of the obstacle to test whether
76 ants reach energetically optimal solutions at the colony level. To do so we ran a series of
77 experiments to calculate the position of the obstacle in the gallery for which the probability of
78 left/right extraction was the same and compared it to the position for which equal amount of

79 mechanical work was required to extract the obstacle from either end of the gallery. We then
80 turned to the analysis of ant behavior at the individual level and examined whether the
81 decision of individual ants to grasp and pull the object is also energetically optimal. Finally,
82 we present a simple simulation model that aims at reproducing the clearing behavior observed
83 at the collective level from the sequence of pulling actions observed at the individual level.

84 **2. Methods**

85 **(a) Studied species**

86 The study was conducted on *Messor barbarus* (Linnaeus, 1767), a species of seed-harvesting
87 ant commonly found in Mediterranean regions [14–16]. This species builds large
88 subterranean nests and its colonies can be composed of several thousand individuals [15].

89 The worker caste of *M. barbarus* exhibits a continuous size polymorphism, with individuals
90 ranging in length from 2 to 15mm and weighing from 1 to 40mg [17,18]. This size
91 polymorphism can be roughly discretised in three size classes: *minor*, *media* and *major*. The
92 *major* can be particularly well distinguished because of their much larger reddish head
93 compared to the *media* and *minor*.

94 In total seven experimental colonies composed of 300 workers (150 *minor*, 100 *media* and 50
95 *major* individuals) drawn from five colonies collected in Saint-Hippolyte (France) between
96 2018 and 2020 were used in the experiments. The mean body mass of a sample of workers
97 drawn from the experimental colonies was 21.40, 9.66 and 3.60 mg, for *major*, *media* and
98 *minor* workers respectively.

99 **(b) Experimental set-up**

100 Each experimental colony was installed in two transparent plastic boxes of identical size (H x
101 W x L: 54 x 119 x 173mm) covered by a lid and linked together by a rigid tube (5mL
102 Falcon® pipet, internal diameter: 6mm, length: 300mm). One box contained the nest and the

103 other was used as a foraging area. Two plastic tubes were placed in each box. The two tubes
104 in the nest box were used as nesting sites by ants. They were covered with opaque paper and
105 had a water reservoir at their end retained by a cotton plug to provide water to the ants. The
106 two tubes in the foraging box were entirely filled with pure water. In addition, ants had at
107 their disposal a mixture of seeds and small cups filled with a mixed diet of vitamin-enriched
108 food [19]. To avoid water condensation in the tube linking the two boxes, this latter was
109 pierced at 18 mm interval with 2mm diameter holes that were covered with a fine metal mesh
110 to prevent ants from escaping. Each box was placed on an adjustable platform so that the
111 inclination of the tube between the two boxes could be set at a desired angle. In all
112 experiments the nest box was placed on the left-hand side of the experimenter and the
113 foraging box on the right-hand side. In addition, in the experiments in which the tube was not
114 horizontal, the nest box was always at a lower position than the foraging box. Outside
115 experimental sessions the experimental colonies were kept at a mean temperature of 22°C and
116 relative humidity of 40% on a 12:12 L:D cycle.

117 **(c) Experimental protocol, data acquisition and data analyses**

118 The experiments consisted in inserting an obstacle inside the tube linking the nest box and the
119 foraging box and in waiting for the ants to remove it from the tube through one of its ends.
120 The obstacle was a small piece of wood (diameter: 4mm, length: 60mm, mass: 300mg) that
121 was inserted in the tube by one of its ends (either that of the nest box or that of the foraging
122 box, chosen at random). The initial position of the obstacle and the inclination angle of the
123 tube were varied between experiments. Each replicate of the experiment ended when the
124 obstacle had been extracted from the tube by one of its ends or after one hour maximally. The
125 connecting tube was changed for a new one at the end of each daily session of experiments to
126 prevent the inner surface of the tube from too much wear due to the friction of the obstacle
127 and of walking ants.

128 To find the point of equiprobability of left-right extraction of the obstacle and to investigate
129 to what extent the position of this point depends on the initial position of the obstacle in the
130 tube and of its inclination angle, the obstacle was inserted at five possible positions inside the
131 tube, i.e., at 5, 10, 15, 20 or 25cm from the left (nest) end of the tube, and the inclination of
132 the tube could take four different angles i.e., 0, 10, 20 or 30°. To determine the point of
133 equiprobability of left(downward)/right(upward) extraction for each inclination angle of the
134 tube at the colony level, we fitted a logistic regression with a logit link function. The
135 response variable was the final destination of the obstacle in the experiments (set to 1 when
136 the final destination was the right end of the tube, i.e. the foraging box, and to 0 when it was
137 the left end, i.e. the nest box) and the inclination angle of the tube, the obstacle initial position
138 and the interaction between these two variables were entered as independent variables in the
139 model. We then used the equation of this model to compute, for each inclination angle, the
140 position of the obstacle for which ants have equal probability to extract the obstacle to the
141 right or to the left of the tube. We considered this position as the point of equiprobability of
142 left/right extraction.

143 To minimize the error in the location of the point of equiprobability, we adopted a high
144 throughput experimental design by working with four experimental colonies in parallel. For
145 each colony a total of at least 200 replicates of the experiment were run with a given
146 inclination angle and initial position of the obstacle. The inclination angle of the tube was
147 chosen pseudo randomly so that at any time each colony was tested with a different angle. A
148 total of 851 replicates of the experiments were performed on the four colonies. Among these
149 851 replicates, the obstacle was extracted from the tube in less than one hour in 792 replicates
150 (93%).

151 To investigate how individual ants behave towards the obstacle as a function of its position in
152 the tube and of the inclination angle of this latter, we used a different experimental design in

153 which only one colony was tested at a time. First, we ran 144 replicates of the experiment in
154 which the initial position of the obstacle was always set in the middle of the tube, which could
155 be randomly positioned at four possible inclination angles (0° , 10° , 20° , 30°). Second, to
156 create as much variability in the initial position of the obstacle, we changed its initial position
157 systematically between each replicate, depending on the result of the preceding replicates.
158 The result of each replicate was noted as one if the final destination of the obstacle was the
159 foraging box and as zero if it was the nest box. Then, for each inclination angle, we fitted the
160 results with a logistic regression and the equation of the logistic model gave us the theoretical
161 position of the obstacle in the tube for which the odds of extracting the obstacle towards one
162 or the other end of the tube are equal. This position was used in the next replicate as the new
163 initial position of the obstacle. All replicates of the experiment run with this experimental
164 design were videotaped at 50 fps using a JVC GZ-MG505 camera (resolution: 2560 x 1920
165 pixels) on three experimental colonies. Each experimental colony was tested at least six times
166 before changing the inclination angle of the tube. A total of 120 replicates were run on the
167 three experimental colonies with this method.

168 To acquire data on the behaviour of individual ants towards the obstacle we used the software
169 Boris [20](<https://www.boris.unito.it/>). For each grasping event we noted the size class of the
170 worker (*major* or *media* – detecting grasping by *minor* on the videos was too uncertain), its
171 position relative to the obstacle (on its left or right side), as well as the time at which it began
172 to grasp the obstacle and the time at which it released it.

173 To determine the position for which equal mechanical work was required to extract the
174 obstacle from either end of the tube, we needed to calculate the forces applying on the
175 obstacle. These forces depend on whether or not the obstacle is in movement.

176 When the obstacle is *not in movement*, it is subject to three physical forces (Fig. S1A):

- 177 - its weight $F_g = m \cdot g$
- 178 - the reaction force of the tube $F_N = m \cdot g \cdot \cos(\alpha)$
- 179 - a static friction force F_s that prevents the obstacle from sliding along the tube when the
- 180 tube is not horizontal

181 with m the mass of the object, g the gravity vector and α the inclination angle of the tube.

182 When an ant applies a force F_A on the obstacle, the static friction force increases in a direction
183 opposed to the movement until reaching a maximum value $F_{s\ max}$ just before the object starts
184 to move (Fig. S1B). This force can be computed as the product of the coefficient of friction μ_s
185 of the tube by its reaction force F_N . Then, when the obstacle starts to move, one enters in a
186 dynamical friction regime in which the coefficient of friction μ_s becomes slightly less
187 important, thus decreasing the intensity of the friction force F_s . For the sake of simplicity in
188 our study, we estimated the friction force as the maximum static friction force (thus under the
189 hypothesis that the object has a constant velocity).

190 To estimate the coefficient of friction μ_s , we used the following method. We took each tube
191 used in the experiments and we glued it to a vertical surface by plasticine at one of its ends
192 while the other end was held by the experimenter to maintain the tube in a horizontal position.
193 The obstacle was then inserted into the tube close to the attached extremity and the free
194 extremity of the tube was released so that it slowly fell down. A camera was positioned in
195 front of the tube to videotape the falling tube and determine precisely the inclination angle at
196 which the obstacle started to slide down the tube. This angle, θ_i^{thresh} corresponds to the
197 inclination angle for which the friction force applied on the obstacle are not high enough to
198 prevent it from sliding. This operation was repeated 10 times for each tube and we estimated
199 the coefficient of friction μ_s by the average value of the tangent of the inclination angles

200 θ_i^{thresh} . We then computed the maximal friction force exerted on the obstacle as $F_{smax} =$
201 $\mu_s \times F_N$.

202 Our data shows that the value of the coefficient of friction decreases with increasing exposure
203 time of the tube to the ants (Fig S2B), ranging from 1.5 for a brand-new tube to 1 for a tube
204 used for a total of 9 hours. The coefficient of friction in each replicate of the experiment was
205 then estimated from the equation of a linear regression of the value of the friction coefficient
206 against the duration of exposure of the tube to the ants.

207 From the estimation of the coefficient of friction μ_s , one can then compute the minimal force
208 F_{Amin} an ant has to apply on the obstacle to put it in movement for all inclination angles of the
209 tube (0,10, 20, 30°) and the two pulling directions (upward or downward). When the tube is
210 not horizontal, F_{Amin} is equal to the sum of the maximal friction force F_{smax} plus (if the
211 obstacle is pulled upwards) or minus (if the obstacle is pulled downwards) the projection of
212 the gravitational force on the tube axis $F_{g||} = m \cdot g \cdot \sin(\alpha)$:

$$213 \quad F_{Amin} = F_{smax} + \varepsilon F_{g||} = m \cdot g \cdot (\mu_s \cdot \cos(\alpha) + \varepsilon \sin(\alpha)) \quad (1)$$

214 with $\varepsilon = 1$ if the obstacle is pulled upwards and $\varepsilon = -1$ if the obstacle is pulled downwards.

215 When the tube is horizontal, one gets $\alpha = 0$ and thus $\sin\alpha = 0$. Consequently, the force that has
216 to be applied on the obstacle to put it in movement is simply equal to the friction force.

$$217 \quad F_{Amin} = F_{smax} = m \cdot g \cdot \mu_s \cdot \cos(\alpha) \quad (2)$$

218 The mechanical work achieved by ants to extract the obstacle from the tube corresponds to the
219 product of the force it has to apply on the obstacle by the distance it has to travel to reach the
220 end of the tube towards which it is moving. The point of equal mechanical work for upward
221 or downward extraction is thus given by the equation

$$222 \quad F_{A\swarrow} \cdot \gamma d = F_{A\searrow} (1 - \gamma) d \quad (3)$$

223 where $F_{A\swarrow}$ is the force that ants have to apply to extract the obstacle by the left (nest) end of
224 the tube, $F_{A\searrow}$ to extract it by its right (foraging box) end, and γd is the position of the obstacle
225 in the tube (γ is the proportion of the length of the tube $d = 30\text{cm}$)

226 From equation (3) one gets:

$$227 \quad \gamma = \frac{F_{A\searrow}}{F_{A\swarrow} + F_{A\searrow}} = \frac{1}{2} \left(1 + \frac{\tan(\alpha)}{\mu_s} \right) \quad (4)$$

228 The position of the point of equal mechanical work can then be expressed as the distance

229 \tilde{x}_{mecha} from the nest box:

$$230 \quad \tilde{x}_{mecha} = \frac{d}{2} \left(1 + \frac{\tan(\alpha)}{\mu_s} \right) \quad (5)$$

231 We performed all data analysis with R 4.2.1 (2022-06-23 ucrt) [21](RCore team, 2022) run
232 under RStudio (v. 2022.07.0). The package *MuMIn* [22] was used to choose the most likely
233 model among several regression models. In the presentation of the results the coefficients of
234 the regression models are followed by the lower and upper value of the 95% confidence
235 interval indicated in brackets. We used a Cox proportional hazard model to analyse the rate of
236 release of the obstacle by ants. The survival analysis was run with the functions of the
237 package *survival* [21] and the survival curves were drawn with the functions of the package
238 *survminer* [23].

239 **3. RESULTS**

240 **(a) Colony-level extraction behaviour**

241 Both the inclination angle of the tube and the initial position of the obstacle in it had an
242 influence on the probability of observing an upward extraction in the experiments (Fig 1A,
243 Table 1). When the obstacle was in the middle of the tube and the tube was horizontal, ants
244 had equal chances of extracting it in either direction ($\hat{p} = 0.49, N = 41, P = 0.438$). The

245 downward extraction was increasingly preferred when the slope angle of the tube increased,
246 even when the obstacle was placed initially close to the upward end of the tube.

247 The comparison of the line of equiprobability of downward and upward extraction (Fig. 1A:
248 solid purple line) with that for which equal mechanical work is required to extract the obstacle
249 to either end of the tube (Fig. 1A: yellow line), shows that, except when the tube was
250 horizontal, the direction of extraction was overwhelmingly suboptimal from a mechanical
251 point of view, i.e. it did not correspond to the minimum mechanical work required to extract
252 the obstacle. This suboptimal bias is shown in Fig 1B in which the probability of upward
253 extraction is represented as a function of the mechanical fitness of this solution. The value of
254 the probability of upward extraction corresponding to the point of equal mechanical work, i.e.,
255 0.5 on the x-axis, is well below the value of equiprobable downward or upward extraction,
256 i.e., 0.5 on the y-axis. At the colony-level, ants have thus a mechanically suboptimal
257 extraction behaviour since they tend to extract the obstacle downward even when this requires
258 more mechanical work than the upward extraction.

259 **(b) Individual pulling behaviour**

260 All pulls did not necessarily lead to large displacement of the obstacle because ants
261 sometimes released their grasp very rapidly. One can thus make a distinction between *aborted*
262 *pulls*, that led to a very small displacement of the obstacle (≤ 1 cm), and *effective pulls* that led
263 to a larger displacement (> 1 cm). In the remaining analysis only effective pulls will be
264 considered.

265 Both the inclination angle of the tube and the position of the obstacle had an influence on the
266 probability of observing an upward effective pull (Fig. 2A: Table 1). Upward pulling
267 behaviours were adequately distributed from a mechanical point of view, i.e. ants did pull the
268 obstacle upwards when the upward extraction required less mechanical work than the

269 downward one. Besides, when both options require the same amount of work, ants responded
270 randomly (Fig. 2A: yellow dashed lines and area).

271 What kind of proxy could ants use to decide to continue to pull the obstacle once they have
272 grasped it, i.e. to perform an effective pull? One could think of two types of information: the
273 distance to the end of the tube towards which they are moving and the force they have to
274 apply on the obstacle to set it in motion. We used a logistic regression to test to what extent
275 these two criteria, considered independently or as a combination, could influence the
276 probability of pulling the obstacle. The model thus includes as independent variables the force
277 applied on the obstacle, the distance to the end of the tube and the interaction term between
278 these two variables. We found that the probability to continue pulling depended on a
279 combination of the force that has to be applied on the obstacle and of the distance to the end
280 of the tube (Table 1, interaction force x distance). Therefore, ants have to somewhat integrate
281 both metrics to take the decision to continue to pull the obstacle once they have grasped it.

282 Do ants of different sizes use the same decision criteria to decide to continue to pull the
283 obstacle? We tested this by adding the worker size class (media *vs.* major) as a categorical
284 variable in the logistic regression above. The results show that there was indeed an effect of
285 worker size: all things being equal, major ants have a higher probability of continuing to pull
286 the obstacle than media ants (Fig. 2B, Table 1).

287 Once ants have decided to pull the obstacle, they can decide to release it at any moment. One
288 can hypothesize that the ants' decision to release the obstacle could depend on the duration of
289 the pull, on the distance travelled while pulling, or on the mechanical work achieved while
290 pulling. Therefore, we tested three different survival models to explain the rate of release of
291 the obstacle: in the first model we analyzed the rate of release of the obstacle as a function of
292 the time elapsed since the initiation of the pull, in the second as a function of the distance
293 moved while pulling and in the third as a function of both the distance moved and the force

294 applied on the obstacle, equivalent to the mechanical work exerted. To investigate to what
295 extent the rate of release could depend on worker size (major *vs.* media) and pulling direction
296 (downwards *vs.* upwards - experiments with horizontal tubes were not considered in these
297 analyses), these two variables were entered as independent variables in the three survival
298 models.

299 Regarding the effect of worker size, we found that, independent of pulling directions, media
300 ants held the obstacle on average for shorter durations (Fig. 3A, Table 2), shorter distances
301 (Fig. 3B, Table 2), and for less amount of mechanical work (Fig. 3C, Table 2) than their
302 major conspecifics. As for the effect of pulling direction, we found that, independent of
303 worker size, when pulling downward (and thus applying a lower force than when pulling
304 upward), ants tended to pull for shorter durations (Fig. 3A, Table 2) and on longer distances
305 (Fig. 3A, Table 2) compared to when pulling upwards. However, ants released the obstacle
306 after applying on average the same amount of mechanical work in the two different pulling
307 directions (Fig. 3C, Table2).

308 **(c) Modeling colony-level extractions**

309 Our study at the individual level shows that, on average, ants behave optimally from a
310 mechanical point of view, i.e., most ants pull the obstacle in the direction requiring the less
311 amount of mechanical work to extract it from the tube (Fig. 2A). In contrast, the extraction
312 behavior at the colony level is mechanically suboptimal with a downward bias (Fig 1B).
313 Therefore, the question arises of how a mechanically sound pulling behaviour at the
314 individual level can lead to a suboptimal extraction behaviour at the colony-level. We argue
315 that this is can be explained by the sequential nature of the task, i.e. to the repeated pulls and
316 releases of the obstacle by many ants before it is eventually extracted from the tube. In fact,
317 for each pull of the obstacle in the downward direction the probability for the next pull to be
318 again in the downward direction increases more rapidly than if the pull was in the upward

319 direction since, for the same amount of work, the obstacle is displaced on longer distance
320 when it is pulled downwards than when it is pulled upwards.

321 To test whether this explanation is correct, we modelled the extraction behaviour as a
322 sequence of successive downward or upward pulls over a certain distance until the obstacle is
323 extracted from the tube. Each step of a sequence is a two-stage process. First, the decision to
324 pull the obstacle is given by the equation of the logistic regression shown in Figure 2A, which
325 gives the probability of observing an upward effective pull as a function of both the
326 inclination angle of the tube and the position of the object in it. Second, the distance at which
327 ants release the obstacle is based on the mechanical work they have achieved. Our model is
328 based on observed data. Therefore, the mechanical work exerted by ants are randomly drawn
329 from the distribution of the values of mechanical work observed in the experiment,
330 independent of pulling direction and of the inclination angle of the tube. From the inclination
331 angle of the tube and the pulling direction one can then calculate the force exerted by ants
332 while pulling the obstacle and hence deduce from the mechanical work value the distance
333 they travelled before releasing the obstacle. It is this distance that is used in the simulations to
334 move the obstacle.

335 To compare the results of the simulations to those of the experiments, we reproduced in the
336 simulations the same initial conditions as in the experiments (inclination angle of 0° , 10° , 20°
337 or 30° and initial obstacle position ranging from 5 to 25 cm from the lower end of the tube).
338 For each combination of angle and initial obstacle position the simulation was repeated 1000
339 times. We then compared the probability of upward extraction in our simulations for each
340 combination of angle and initial obstacle position to that found in the experiments.

341 The results of the simulations are shown in Fig. 4. There was a relatively good fit of the
342 model with the observed data, except for the highest inclination angle of 30° .

343 4. Discussion

344 When moving between their underground nest and their foraging ground many ant species use
345 narrow galleries that can be temporarily clogged by all sorts of objects. These objects have to
346 be rapidly removed to re-establish the flow of foraging workers between the nest and the
347 ground surface. Here, we reproduced this situation in the laboratory and show that, at the
348 individual level, ants behaved optimally by removing the obstacle most of the times in the
349 direction requiring the less amount of mechanical work (Fig. 2), whereas at the colony-level a
350 strong downward bias in the extraction of the obstacle was observed leading to mechanically
351 non-optimal solutions (Fig. 1). Since ants were as likely to extract the obstacle by either end
352 of the gallery when this latter was horizontal and the obstacle was positioned in its middle,
353 this downward bias was not due to ants preferring to extract the obstacle in the nest direction
354 but rather, as suggested by our simulation model, to the sequential nature of the extraction
355 task.

356 How do individual ants make their decision to pull and release the obstacle in the
357 gallery? Based on our analysis of the behaviour of individual ants, one can imagine a scenario
358 in which each pull of the obstacle made by ants is the result of two successive decisions: i) the
359 decision to grasp the obstacle and to pull it towards either extremity of the gallery, ii) the
360 decision to release the obstacle at a new location after a certain time. Our analysis allows us to
361 make the following assumptions regarding the criteria used by ants to make these two
362 decisions. First, ants decide to continue to pull the obstacle once they have grasped it by
363 considering *both* the distance they have to travel to reach the extremity of the gallery and the
364 force they applied on the obstacle to set it in motion. This is actually equivalent to saying that
365 they base their decision on an assessment of the total mechanical work needed to extract the
366 obstacle from the gallery. Second, the result of our analysis of pulling durations allows us to
367 make the assumption that, whatever the force they apply on the obstacle to set it in motion,

368 ants base their decision to release the obstacle on the mechanical work applied since the
369 beginning of the pulling action. Therefore, ants need to be able to assess two types of
370 information to make mechanically optimal decisions: the position of the obstacle in the
371 gallery and the force they have to apply on it to set it in motion. Below we discuss how these
372 two types of information could be assessed.

373 There are two ways an ant could estimate the position of the obstacle in the gallery in
374 our experiment. The first is by assessing its 3D location based on the surrounding visual cues
375 that can be seen through the transparent wall of the tube used as a gallery. However, this
376 hypothesis can be rejected because the visual landmarks present in the experimental room
377 were too far away to allow for a precise assessment of the obstacle location in the tube by
378 triangulation. The second mechanism which could be used by an ant to estimate the position
379 of the obstacle is odometry, i.e. the assessment of the distance walked between the entrance of
380 the gallery and the location in the gallery where the obstacle was encountered. Indeed, there
381 are now firm evidences that ants can assess distance with a podometer that acts as a stride
382 integrator [24,25], including when they walk on inclined surface as in our experiment [26,27].
383 Although most studies on ant odometry have been achieved over distances of several meters,
384 distance estimation in ants can also be quite accurate on short distances [28], even in complete
385 darkness [29]. Therefore, ants could use their podometer to assess the distance of the obstacle
386 to each gallery extremities in our experiment.

387 Besides the position of the obstacle in the gallery, the second element ants have to take
388 into account to assess the mechanical work required to remove the obstacle from the gallery is
389 the force they have to apply on the obstacle to set it in motion. Insects possess various types
390 of mechanoreceptors distributed over their legs to precisely monitor the position and
391 movement of their limbs during locomotion and to adjust their walking pattern to the
392 characteristics of the substrate on which they are moving (slope, uneven terrain, obstacle

393 crossing...). Some of these mechanoreceptors like the *campaniform sensilla* are known to
394 encode the forces exerted by the leg muscles as cuticular strains [30]. Although mostly
395 studied in cockroaches and stick insects, this type of mechanoreceptors is likely to be also
396 present in Hymenoptera. They could provide ants with proprioceptive feedback on the
397 heightened activity of their leg muscles when they are dragging an object, allowing them to
398 gauge the force they need to exert on it to set it in motion.

399 As mentioned before, independent of the slope of the gallery and of whether they were
400 pulling downwards or upwards, the results of the survival analysis on pulling durations
401 suggest that ants base their decision to release the obstacle on the amount of mechanical work
402 achieved since the beginning of their pulling action. To explain this result, one could
403 hypothesize that the limiting factor for continuing pulling is either the amount of energy that
404 can be mobilized per unit time, i.e., the metabolic power, or, alternatively that ants have a
405 limited amount of energy available to pull the obstacle and thus that they release their grip
406 before using up this energy. Below we examine these two hypotheses.

407 The mechanical power required by ants for pulling the object is equal to the product of
408 the force they apply on the object to set it in motion by the speed at which they move. This
409 corresponds in our experiments to about $4.52\mu\text{W}$ [4.11 4.94] and $4.30\mu\text{W}$ [3.97 4.63] for
410 media and major workers, respectively. Assuming that the work efficiency of ant leg muscles
411 is about the same as that of the cockroach *Periplaneta americana*, i.e. around 1% [31], this
412 amounts to a metabolic power of $452.0\mu\text{W}$ [411.0 494.0] and $430.0\mu\text{W}$ [397.0 463.0] for
413 media and major workers, respectively. The specific metabolic power is thus $46790.89\mu\text{W}\cdot\text{g}^{-1}$
414 [42546.58 51138.72] and $20093.46\mu\text{W}\cdot\text{g}^{-1}$ [18551.40 21635.51] for media and major
415 workers, respectively. In comparison, the specific metabolic power required for a worker of
416 the seed-harvesting ant *Pogonomyrmex maricopa* to walk at a speed of $3\text{cm}\cdot\text{s}^{-1}$ is about

417 10000.00 μ W.g⁻¹ [32], which represents 21% and 50% of the specific metabolic power of
418 media and major workers while pulling the object, respectively. Therefore, at least in the case
419 of media workers, the metabolic energy cost per unit time may well be a limiting factor to
420 continue pulling the obstacle.

421 The second hypothesis to explain why ants decide to release the obstacle is that they
422 would have at their disposal a limited amount of energy available. But how much energy do
423 ants expend when pulling the obstacle and what does this amount of energy actually
424 represent? In our experiments ants released their grip after producing on average 0.124mJ
425 [0.112 0.137] and 0.157mJ [0.144 0.171] an of mechanical work, for media and major ants
426 respectively. Assuming, as above, that the work efficiency of ant leg muscle is about 1%, this
427 would result in the use of 12.40mJ [11.20 13.70] and 15.70mJ [14.40 17.10] of metabolic
428 energy for media and major ants respectively. Note that these values of metabolic cost are
429 probably somewhat underestimated since they are not based on the total mechanical work
430 achieved by ants, which includes the mechanical cost of locomotion, i.e. the mechanical work
431 required to accelerate the center of the mass of the ants [33] as well as the internal energy they
432 use to accelerate their limbs during locomotion, but just on the mechanical work required to
433 pull the obstacle. Nonetheless, the metabolic cost of locomotion is likely to represent only a
434 small fraction of the cost of pulling the obstacle. If one hypothesizes that the metabolic cost of
435 locomotion in *M. barbarus* is about the same as that in *Pogonmyrmex maricopa*, i.e. around
436 129 J.kg⁻¹.m⁻¹ [32], a *M. barbarus* worker weighing 9.66mg, the average weight of a media
437 worker in our experiment, could walk on average 9.95m [8.99 11.00] with the amount of
438 metabolic energy required to pull the obstacle. And for a major worker weighing on average
439 21.4mg the distance covered would be on average 5.68m [5.20 6.18]. These figures are a few
440 meters less than the average length of foraging trails observed in *M. barbarus* [34]. There are
441 no data available in the literature on the maximal distance foraging workers of *M. barbarus*

442 can travel per hour. As in most ant species, they can probably perform several round trips
443 between their nest and a seed patch within the same hour and, what is more, with a load in
444 their mandibles on their way back to the nest, which requires more energy than unloaded
445 locomotion [35]. However, in *M. barbarus* [36] as in other ant species carrying external loads
446 [37–40] the existence of transport chains, i.e. food transfer between workers along the
447 foraging trails, is well documented. This means that loaded ants may not necessarily travel the
448 whole length of the foraging trails with their load which may be a strategy to spare energy. Of
449 particular interest is the fact that in *M. barbarus* the first workers in the chain tend to have a
450 high loading ratio [36]. Therefore, although the amount of metabolic energy expended by ants
451 while pulling the obstacle is not negligible, it may nonetheless be a factor that could
452 contribute to limit the duration of pulling.

453 In conclusion, the distance at which ants release the obstacle may depend both on the
454 metabolic power and on the amount of energy required to pull the obstacle. However, ants
455 have no way to directly measure metabolic power or metabolic energy. Therefore, what are
456 the criteria they could use to decide to release the obstacle? One of the criteria one could think
457 of is the relative effort they perceive while pulling. This relative effort is linked to the relative
458 force exerted by ants while pulling. The force exerted by a muscle depends on its cross-
459 sectional area which increases with body mass raises to the $2/3$ power [41]. Therefore, if the
460 decision to release the obstacle depended on the relative effort perceived by ants one would
461 expect that the differences between major and media found in the rate of release of the object
462 calculated on the mechanical work achieved (Fig. 3C) would disappear if the mechanical
463 work were normalized by body mass raises to the $2/3$ power. This is actually what happens
464 (Table 2, Fig. 3D). This suggests that ants could use the relative effort they perceive while
465 pulling as a heuristic to decide when to release the obstacle. A similar heuristic has been
466 shown in the ant *Pheidole pallidula* whose scout workers modulate their trail-laying behavior

467 to recruit nestmates as a function of the tractive resistance of the prey they find [42]. In the
468 same way, it is likely that the size-matching between body mass and load mass observed in
469 several ant species transporting external loads could be explained on the basis of an
470 assessment of the relative effort. Further experiments would be needed to test this hypothesis.
471 For example, one could think of manipulating the force required to pull the obstacle by using
472 a rough substrate to increase the coefficient of friction of the tube or by attaching a thread to
473 its two ends so that the experimenter can decrease or increase the force ants have to apply to
474 set the obstacle in motion and pull it in either direction. One could also place individual ants
475 in a respirometric chamber and use flow-through respirometry to measure gas exchanges
476 during pulling to assess the metabolic cost of pulling.

477 Our experiments show that the complete extraction of the obstacle from the tube by a
478 single ant was very rarely observed. In fact, it was overwhelmingly the result of a series of
479 successive pulls made by individual ants and it is the sequential nature of the task that
480 explains the downward bias observed at the colony-level. The simulations we ran which
481 modelled the extraction behaviour as a sequence of successive downward or upward pulls
482 confirms this explanation. The poorest fit was obtained when the slope of the tube was 20° or
483 30° and the obstacle was very close to the upward end of the tube. The following hypothesis
484 may explain this poor fit. In our model the decision to pull the obstacle at each step of a
485 sequence is based on the probability of ants to perform an upward *effective* pull, i.e. to
486 continue pulling once they have grasped the obstacle and started to pull it. However, when the
487 force required to move the obstacle was maximum, i.e. when pulling upwards for the highest
488 value of the inclination angle of the gallery, it is likely that many ants, especially media ants
489 which have less force, quickly released the obstacle just after grasping it. The capacity of ants
490 to pull the obstacle upwards for high inclination angles was thus overestimated in our model,
491 leading to an overestimation of the probability of upward extraction.

492 In conclusion our study on gallery clearing shows that a mechanically optimal
493 response at the individual level can sometimes lead through an amplification process to a
494 mechanically non-optimal response at the collective level. This is reminiscent of the
495 maladaptative response resulting from negative information cascade that are sometimes
496 observed in group-living animals and that occur through direct [43] or indirect [44]
497 information transfer. However, the situation we studied here is singular. While each
498 individual makes a correct decision based on the relative effort required to move the obstacle,
499 the maladaptive response at the colony-level occurs as a consequence of its action which is
500 strictly governed by the law of physics.

501 **Data accessibility:**

502 **Author's contributions:** L.D. conceived the project and designed the experiments, L.D., and
503 C.C. performed the experiments, L.D. and ZBM processed the videos, L.D. analyzed the data.
504 V.F. and L.D. wrote the manuscript. V.F. and G.L. supervised the work.

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622 **Table 1:** Output of model statistics for the regression analyses.

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Variable	β	CI _{95%}	z	P	N
<i>Probability of upward extraction</i>					792
Angle	-0.08	[-0.16 -0.00]	-1.947	0.052	
Position	23.91	[18.45 29.86]	8.273	<0.001	
Angle x Position	-0.43	[-0.87 0.01]	-1.926	0.054	
<i>Probability of observing an upward effective pull</i>					579
Angle	-0.11	[-0.18 -0.03]	-2.644	0.008	
Position	16.69	[11.28 22.48]	8.858	<0.001	
Angle x Position	0.33	[-0.13 0.80]	1.379	0.167	
<i>Probability of observing an effective pull after grasping the object</i>					3257
Distance	-18.68	[-26.54 -10.97]	4.706	<0.001	
Force	-943.70	[-1255.34 -622.17]	-5.842	<0.001	
Distance x Force	3629.97	[364.27 5912.78]	3.129	<0.001	
Size class	-0.43	[-0.61 -0.24]	-4.531	<0.001	

646

647 **Table 2:** Output of the Cox proportional hazard analyses on the rate of release of the object.
 648 The hazard ratio (HR) is the ratio of the rate of release of the object observed for media vs.
 649 major workers for the size class, and that of downwards vs. upwards pulling for the pulling
 650 direction. $N=729$ pulls.

651

652	Variable	HR	CI _{95%}	z	P
653	<i>Calculated on time</i>				
654	Size class	1.657	[1.288 2.131]	3.931	<0.001
655	Pulling direction	0.486	[0.370 0.638]	-5.190	<0.001
656	<i>Calculated on distance pulled</i>				
657	Size class	1.513	[1.175 1.949]	3.213	<0.001
658	Pulling direction	1.916	[1.443 2.544]	4.498	<0.001
659	<i>Calculated on mechanical work</i>				
660	Size class	1.627	[1.266 2.090]	3.798	<0.001
661	Pulling direction	0.875	[0.670 1.142]	-0.985	0.324
662	<i>Calculated on mechanical work normalized by body mass^{2/3}</i>				
663	Size class	0.885	[0.692 1.132]	-0.913	0.331
664	Pulling direction	0.856	[0.673 1.089]	-1.263	0.207
665					
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669 **FIGURE CAPTIONS**

670 **Figure 1.** Colony-level extraction of the obstacle. (A) Probability of upward extraction of the
671 obstacle as a function of both the inclination angle of the tube and the initial distance of the
672 obstacle from the downward end of the tube (0m = downward end, 0.3m = upward end). The
673 blue dashed lines are the lines of isoproability of upward extraction. The solid purple line is
674 the line of equiprobability of downward/upward extraction. The yellow line corresponds to the
675 isowork line, i.e., to the values of slope and distance to the downward end of the tube for which
676 the mechanical work required for an upward or downward extraction of the obstacle is the same.
677 The yellow area around the line is the 95% confidence interval (based on the 95% confidence
678 interval of the friction coefficient μ_s) (B) Probability of upward extraction of the obstacle as a
679 function of the mechanical fitness of the upward solution. The average empirical probabilities
680 of upward extraction (along with their 95% confidence interval), calculated for 10 bins of 0.1,
681 are shown as green dots. The purple line is the logistic fit surrounded by its 95% error bounds
682 (purple area). The horizontal yellow dashed line shows the value of probability of upward
683 extraction for which equal mechanical work is required to extract the obstacle by either end of
684 the tube. The yellow area around the line is the 95% confidence interval (based on the 95%
685 confidence interval of the friction coefficient μ_s). $N = 792$ extractions.

686

687 **Figure 2.** Individual pulling behavior. (A) Probability of observing an upward effective pull of
688 the obstacle as a function of both the inclination angle of the tube and the distance of the
689 obstacle from the downward end of the tube (0m = downward end, 0.3m = upward end). The
690 dashed lines are the lines of isoproability of upward pull. The solid purple line is the line of
691 equiprobability of downward or upward pull. The yellow line corresponds to the isowork line,
692 i.e., to the values of slope and distance to the downward end of the tube for which the

693 mechanical work required for an upward or downward extraction of the obstacle is the same.
694 The yellow area around the line is the 95% confidence interval (based on the 95% confidence
695 interval of the friction coefficient μ_s) (B) Probability of observing an upward effective pull on
696 the obstacle as a function of the mechanical fitness of the upward solution. The purple line is
697 the logistic fit surrounded by its 95% error bounds (purple area). The average empirical
698 probabilities of upward extraction (along with their 95% confidence interval), calculated for 10
699 bins of 0.1, are shown as green dots. The purple line is the logistic fit surrounded by its 95%
700 error bounds (purple area). The horizontal yellow dashed line shows the value of probability of
701 upward effective pulls for which equal mechanical work is required to extract the obstacle by
702 either end of the tube. $N=579$ pulls.

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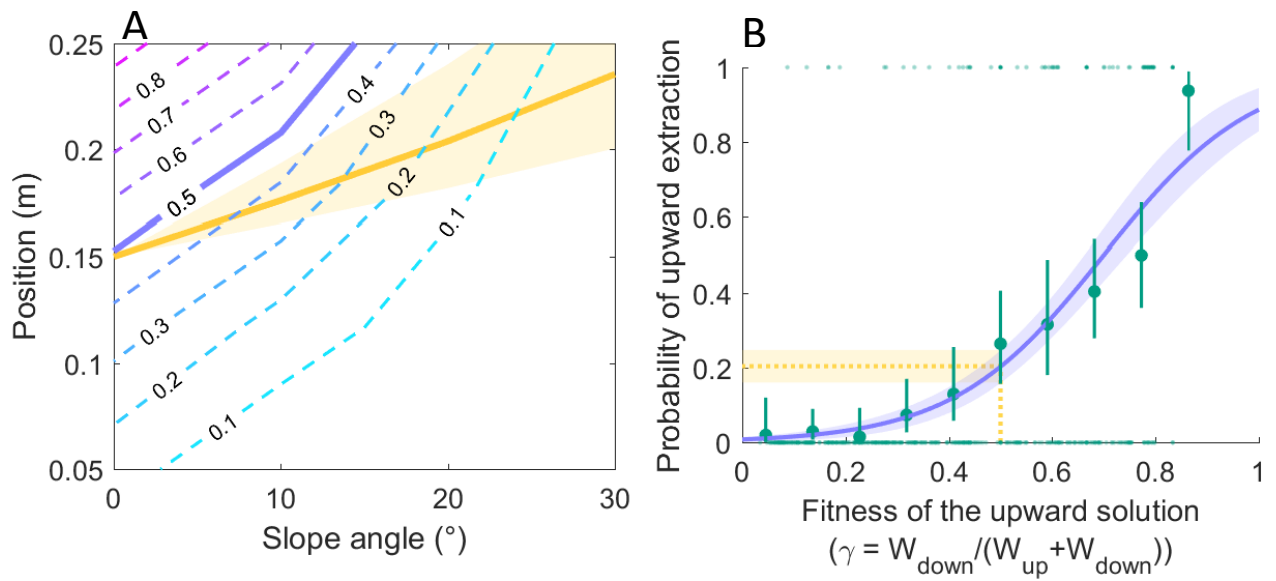
704 **Figure 3.** Kaplan-Meier survival curves of pulling behaviour, partitioned by worker size
705 category (media/major) and pulling direction (upwards/downwards), as a function of (A) the
706 time elapsed since the initiation of the pull, (B) the distance travelled while pulling and (C) the
707 mechanical work achieved. (D) the mechanical work normalized by the mass^{2/3} of the workers.
708 $N = 729$ pulls.

709

710 **Figure 4.** Comparison of the probabilities of upward extraction, calculated from the
711 experiments and from the results of the simulations, as a function of the distance from the
712 downward (nest) end of the tube and of its inclination angle. The green dots show the value of
713 average empirical probabilities (along with their 95% confidence interval) calculated for five
714 5cm-distance bins. The probabilities calculated in the simulations are shown in purple. 1000
715 runs of the simulations were achieved for each combination of angle and initial obstacle position
716 in the tube.

717 **FIGURES**

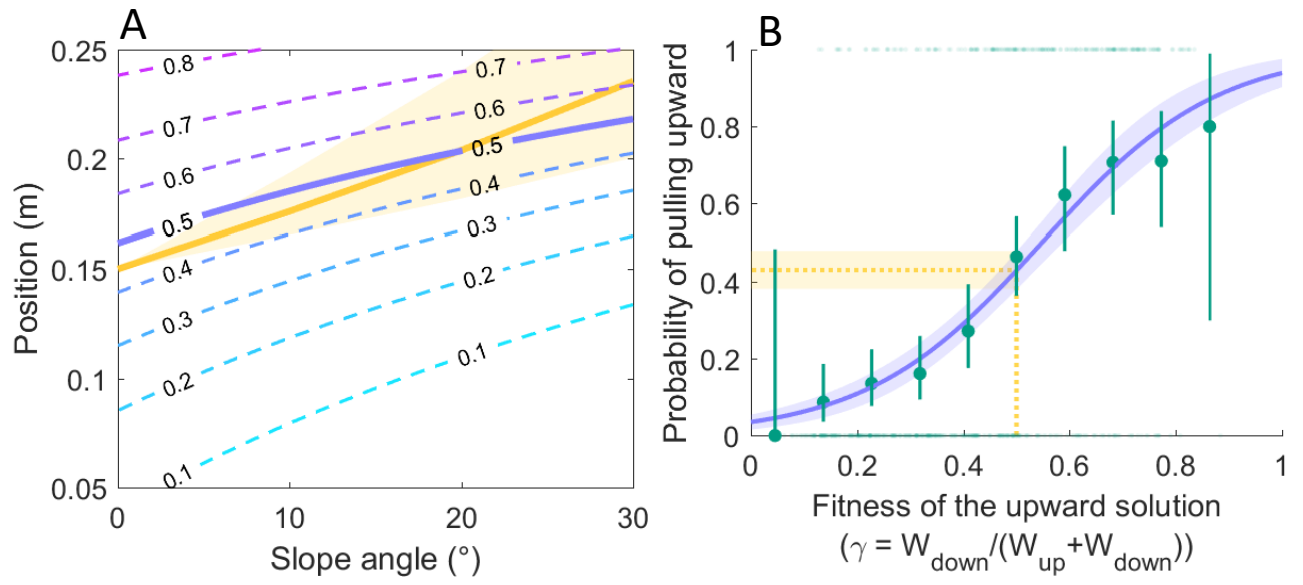
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721 Figure 1

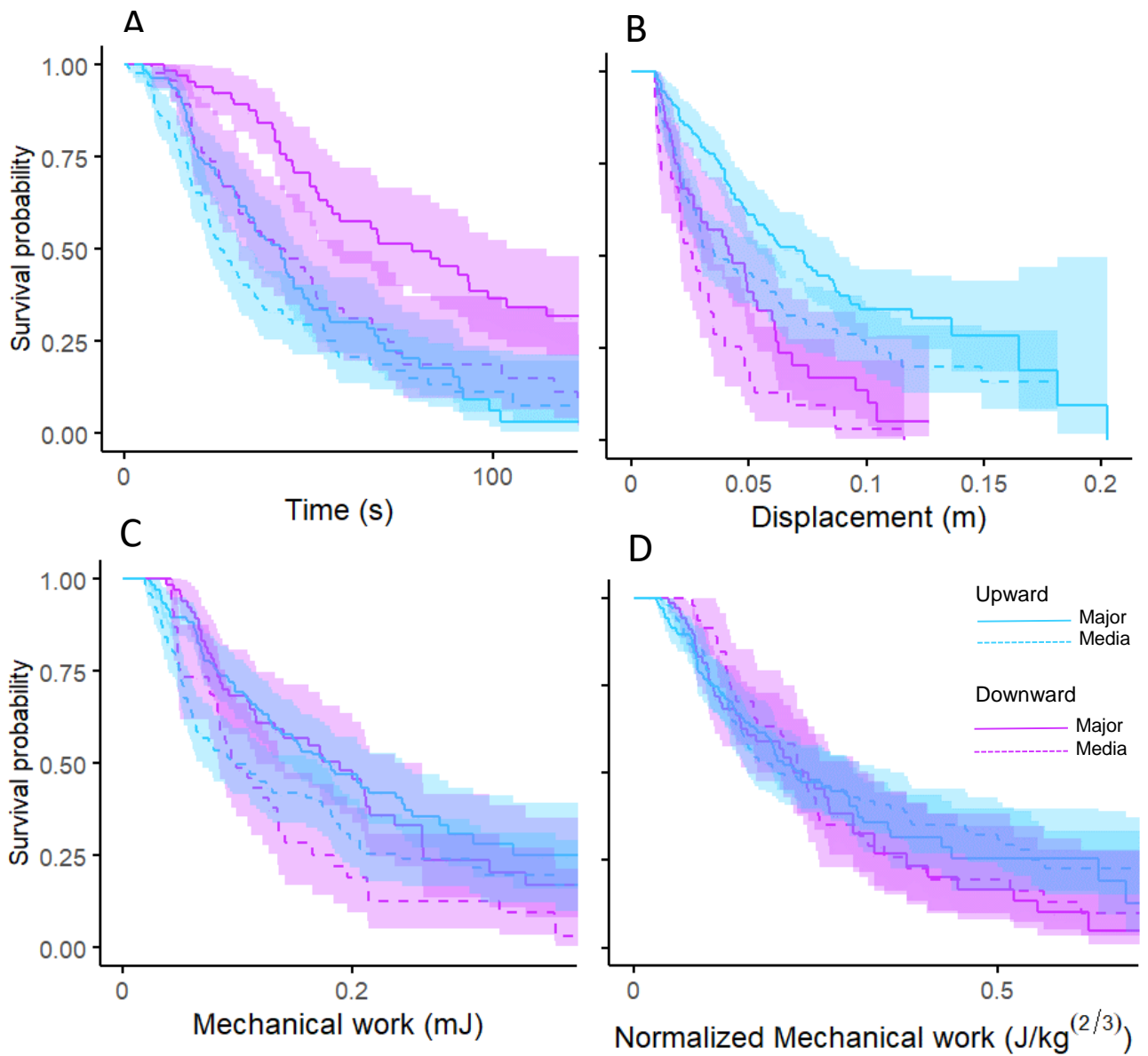


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723 Figure 2

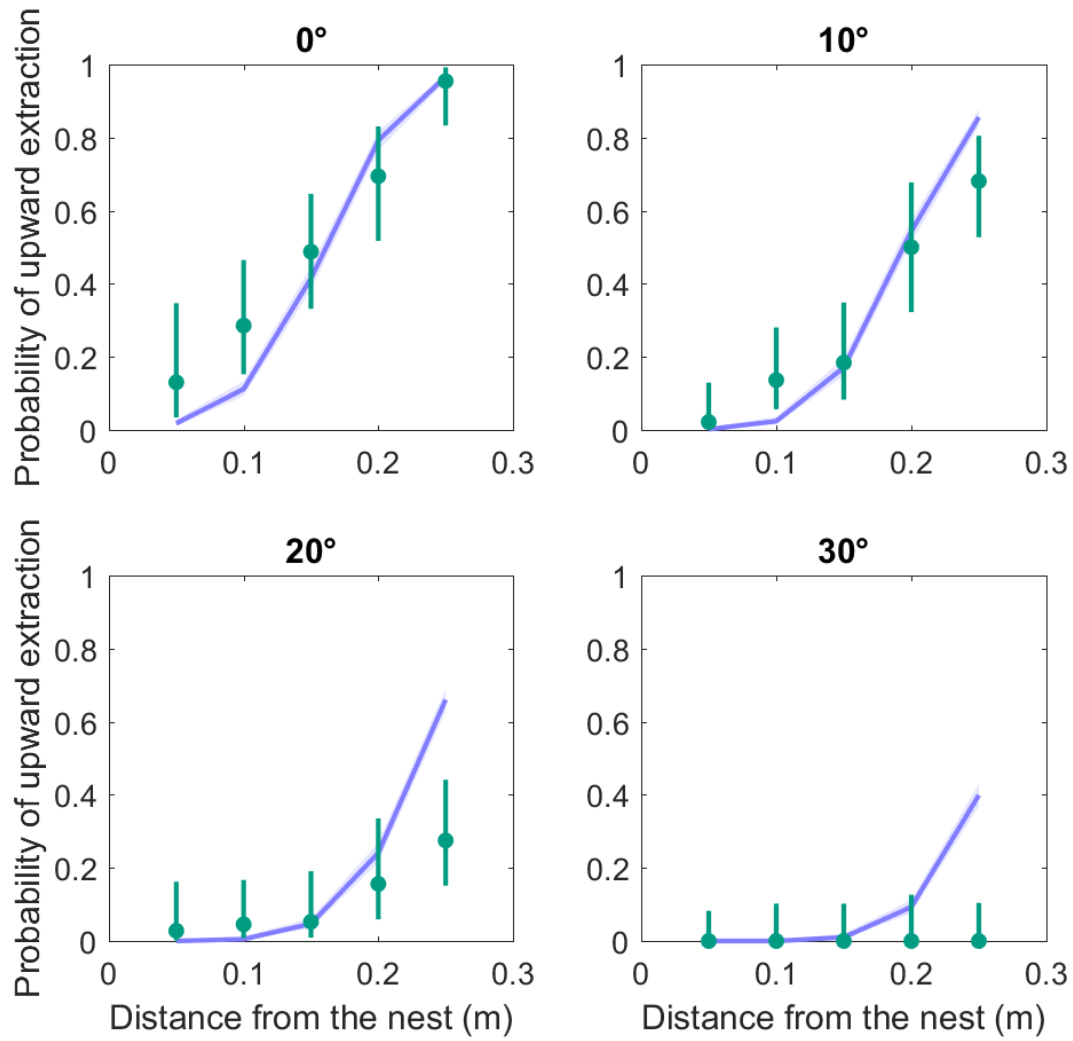
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727 Figure 3



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729 Figure 4

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