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19 **Abstract**

20 Self-organised systems of collective behaviour have been demonstrated in a number of group-living
21 organisms. There is, however, less research relating to how variation in individual assessments may
22 facilitate group decision-making. Here, we investigate this using the decentralised system of
23 collective nest choice behaviour employed by the ant *Temnothorax albipennis*, combining
24 experimental results with computational modelling. In experiments, isolated workers of this species
25 were allowed to investigate new nest sites of differing quality, and it was found that for any given nest
26 quality, there was wide variation among individuals in the durations that they spent within each nest
27 site. Additionally, individual workers were consistent in spending more time in nest sites of higher
28 quality, and less time in those of lower quality. Hence, the time spent in a new nest site must have
29 included an assessment of nest quality. As nest site visit durations (henceforth termed assessment
30 durations) are linked to recruitment, it is possible that the variability we observed may influence the
31 collective decision-making process of colonies. Thus, we explored this further using a computational
32 model of nest site selection, and found that heterogeneous nest assessments conferred a number of
33 potential benefits. Furthermore, our experiments showed that nest quality assessments were flexible,
34 being influenced by experience of prior options. Our findings help to elucidate the potential
35 mechanisms underlying group behaviour, and highlight the importance of heterogeneity among
36 individuals, rather than precise calibration, in shaping collective decision-making.

37 **Keywords:** Self-organisation, decision-making, heterogeneity, behavioural-thresholds, *Temnothorax*
38 *albipennis*.

39 **Introduction**

40 Collective decision-making has been studied in a wide variety of group-living organisms, especially
41 in relation to self-organisation (1,2). However, its underlying mechanisms at the individual level are
42 less well understood, and behavioural thresholds are frequently postulated to play a role (3,4).
43 Threshold-based systems form an integral part of the life history strategies of numerous organisms,

44 spanning a broad range of genera (5–7). The use of such thresholds facilitates flexibility, decentralised
45 control, and additionally, reduces the need for more cognitively taxing decision-making processes
46 (8,9). Colonies of social insects constitute systems that readily make use of threshold-determined
47 behaviours, employing them to shape complex group organisation (10,11). Indeed, many problem-
48 solving heuristics utilise the same rules applied by social insects at their core, and ant colonies remain
49 one of the key sources of data for informing algorithmic architecture (12,13). One reason for this is
50 that within insect societies, thresholds relating to activity and decision-making allow the effective
51 allocation of workers to various tasks, without the need for direct central control (10,14).
52 Accordingly, insect colonies can solve complex organisational problems, while retaining the
53 robustness inherent to self-organised networks (15,16).

54 In the ant species *Temnothorax albipennis*, colonies undertake emigrations to new nest sites, and often
55 have to choose among multiple options of differing quality (17). Emigrating to the best possible nest
56 site is of paramount importance, as nest structure may influence a colony's future success (18,19).
57 Previous work has shown that ants can choose between nests without directly comparing them, and
58 thus save both time and cognitive effort (9). The exact mechanism underpinning such decentralised
59 nest choice remains unclear, but it has been hypothesised that workers may have considerable
60 variation in their individual quality thresholds, each accepting a nest option only if it meets their
61 individual 'quality standards' (20,21). For this system to be effective, however, differing worker
62 quality assessments would need to be flexibly distributed within colonies, in order to ensure the best
63 possible emigration decisions, and avoid the pitfalls of becoming locked into sub-optimal choices.
64 Specifically, this would mean that some individuals almost always reject a nest, while others almost
65 always accept it; thus stopping the colony as a whole from making poor choices when better options
66 are present, and simultaneously, allowing emigration choices to occur if only low quality nests are
67 available.

68 Earlier work has shown that individuals do indeed differ in their preference for accepting the same
69 quality nest (22). Yet, while adaptive threshold distributions have been indicated through modelling to
70 be plausible (20,23), to date, there remains a paucity of empirical evidence to support the theory.

71 There is, however, a method by which the supposed quality of nests to individual workers may be
72 measured. Chiefly, this emerges from evidence showing that when assessing a nest site, ants spend
73 longer within the nest if they deem it to be of higher quality, while attempting to leave if it is of lower
74 quality (9,22,24). Furthermore, although the pre-recruitment latency of ants is shorter for higher
75 quality nests (20), they spend a greater *proportion* of this latency inside the new nest, if it is of better
76 quality (25). It has been hypothesised that such a trend exists, as by spending longer within a nest,
77 workers may better contribute to a quorum threshold prior to recruiting (24,26,27). Specifically,
78 experiments have shown –simply by introducing workers to a new nest site by hand– that ants within
79 a new nest will contribute to a quorum (27). Moreover, while recruitment is the principal method of
80 nest choice, in certain minority cases, when the current nest is destroyed and new nests are nearby,
81 colonies are also able to choose nests without recruiting to them, instead relying on independent
82 worker discoveries to build up a quorum within (24,28). As such, the persistence of workers within
83 nests, and subsequent recruitment decisions, constitute major factors in colony decision-making
84 (21,25). Thus, by use of a simple measure; individual visit durations, there is the potential to
85 determine how different individuals assess the quality of various nest sites.

86 Here, we investigate experimentally whether workers of *Temnothorax albipennis* do indeed differ in
87 their quality assessments of potential new nest sites, and using a computational model, evaluate the
88 implications of this for self-organised collective decision-making.

89 **Materials and methods**

90 **a) Ant colonies**

91 Ten *Temnothorax albipennis* colonies were collected from the Isle of Portland, Dorset, UK, on the
92 29th of January, 2016, they all contained a queen and from 59 to 280 workers. Each was assigned a
93 random ID number, and was maintained under standard laboratory conditions, within artificial nests
94 housed in Petri dishes (29). All experimental work was undertaken in February 2016.

95

96 **b) Experiments**

97 Our experimental setup consisted of a sequence of three 100x100mm Petri dishes with Fluon-coated
98 sides, each containing a single unoccupied nest site (fig. 1). These nest sites were of three different
99 qualities, determined by their attributes; a ‘poor’ quality nest, a ‘good’ quality nest, and an ‘excellent’
100 quality nest (fig.1). In *T. albipennis*, nest quality preferences have been well studied, and thus we used
101 these to inform nest design (30). During experiments, 16 individual scouting workers from each of 10
102 colonies were tested, taking two days per colony, for a total duration of 20 days.

103 At the initiation of each experiment, a colony was selected at random, and placed into a 230x230mm
104 arena, to stimulate scouting activity. We then removed a single scouting worker at random, and using
105 a fine-tipped paint brush, placed it into one of the three petri dishes (fig. 1). Depending on its
106 treatment group, the ant was placed into either the dish containing the ‘poor’ nest first, or the dish
107 containing the ‘excellent’ nest first. The intermediate ‘good’ nest was always second. In each colony,
108 half of the ants were subjected to the former treatment, and half to the latter. This controlled for any
109 effect of whether ants would encounter new nests in order of increasing or decreasing quality (31).

110 From this point, each ant was allowed to investigate its dish, and once it entered the empty nest site, a
111 timer was started. For every individual, we recorded the time spent within the nest until the point that
112 it exited, as first nest visits comprise a principal stage in nest quality assessment (32). The ant was
113 then moved into the next petri dish, and allowed to assess the nest within, until it had visited all three
114 nests. As these ants use pheromone trails to measure nest cavity area (32), the empty nests and dishes
115 were cleaned with alcohol and detergent between visits, removing any residues. In this way, the
116 potential for pheromonal build-up was eliminated. Once they had assessed all three nests in turn, ants
117 were transferred into a separate holding dish, to avoid re-sampling.

118 This process was repeated for all 160 ants, producing three visit duration values for each individual,
119 corresponding to the three nest qualities. Experiments provided 469 visit duration observations out of
120 a possible total of 480, as in some cases, workers failed to investigate a nest site.

121

122 **c) Computational model**

123 To investigate how heterogeneous nest assessments may affect collective choices, we developed a
124 computational model. The model compared the performance of colonies with heterogeneous nest
125 acceptance, to those with homogeneous acceptance, building on established models of nest site choice
126 with recruitment (20,23). Assessment time is linked to nest acceptance, and hence to recruitment
127 (22,25). Thus, heterogeneous visit durations are likely to correspond to heterogeneous acceptance
128 thresholds, and homogeneous visit durations to homogeneous thresholds, providing comparability
129 with our empirical data. Our model did not explore collective nest choice in the absence of
130 recruitment, as this occurs only when the current nest is destroyed and a new nest is nearby (24,28),
131 and in such cases, the relationship between individual and collective behaviour is linear. In the model,
132 colonies were presented with two potential new nest sites, A and B (fig. S1). Each ant was assigned an
133 acceptance threshold (with the addition of a random error), which was used to decide whether to
134 recruit to a nest, or leave and search for alternatives. Ants had two potential states; assessor and
135 recruiter, and switched from assessors to recruiters once they had accepted a nest site, subsequently
136 recruiting their nest mates to the chosen site (fig. S1). Once a quorum was reached in a given nest site;
137 defined as at least half of the colony (assessors and/or recruiters) being present in a site at any single
138 time point, the colony was assumed to have made a choice, and the simulation was ended. All
139 simulations were run with two potential assessment distributions among workers; a homogeneous
140 case in which all workers had the same acceptance threshold value (with the addition of a random
141 error), and a heterogeneous case in which threshold values were normally distributed. The model was
142 run for different scenarios in which the qualities of the potential new nest sites (A and B) were varied,
143 and the fractions of correct choices, and times until quorum, were compared for the two assessment
144 distributions (figs. 2c-f, S2). For full model parameters, see supplementary material 1.

145 **d) Statistical analyses**

146 To determine how worker visit durations varied with nest quality, and how treatment order influenced
147 this, we employed a Generalised Linear Mixed Model. This used Log10 visit duration (s) as a normal

148 response variable, nest quality and assessment order as fixed factor predictors, the interaction between
149 the two, and worker ID nested within colony ID as random factors. Model fit was validated via
150 evaluation of the standardised residuals.

151 To determine if within individuals, visit durations for the three nest qualities were correlated, and if
152 treatment order influenced this, we used a Spearman's rank correlation. All statistical analyses were
153 performed in SPSS (Release version 23.0.0.0).

154 **Results**

155 **a) Experiments**

156 Nest quality had a significant effect on visit duration (GLMM, effect of nest quality: $F_{2,464}=75.334$,
157 $P<0.001$, $\text{mean}_{\text{excellent}}=714.496\text{s}$, $\text{mean}_{\text{good}}=249.459\text{s}$, $\text{mean}_{\text{poor}}=126.474\text{s}$), while assessment order did
158 not (GLMM, effect of assessment order: $F_{1,464}=2.144$, $P=0.144$). However, the interaction between
159 nest quality and assessment order was significant (GLMM, effect of interaction: $F_{2,464}=12.373$,
160 $P<0.001$, fig. 2a, b), and thus we focussed upon it.

161 Within the 'poor first' assessment order, differences were explained by ants spending significantly
162 more time in the 'excellent' quality nests than in either the 'good' (GLMM, Bonferroni post-hoc test:
163 $t=7.724$, $df=464$, $P<0.001$, $\text{mean}_{\text{excellent}}=1148.154\text{s}$, $\text{mean}_{\text{good}}=319.154\text{s}$), or 'poor' quality nests
164 (GLMM, Bonferroni post-hoc test: $t=11.477$, $df=464$, $P<0.001$, $\text{mean}_{\text{excellent}}=1148.154\text{s}$,
165 $\text{mean}_{\text{poor}}=93.325\text{s}$). Furthermore, ants also spent significantly more time in the 'good' quality nests
166 than in the 'poor' nests (GLMM, Bonferroni post-hoc test: $t=5.599$, $df=464$, $P<0.001$,
167 $\text{mean}_{\text{good}}=319.154\text{s}$, $\text{mean}_{\text{poor}}=93.325\text{s}$).

168 Within the 'excellent first' assessment order, again, differences were accounted for by ants spending
169 significantly more time in the 'excellent' quality nests than in either the 'good' (GLMM, Bonferroni
170 post-hoc test: $t=4.961$, $df=464$, $P<0.001$, $\text{mean}_{\text{excellent}}=444.63\text{s}$, $\text{mean}_{\text{good}}=194.536\text{s}$), or 'poor' quality
171 nests (GLMM, Bonferroni post-hoc test: $t=4.270$, $df=464$, $P<0.001$, $\text{mean}_{\text{excellent}}=444.63\text{s}$,
172 $\text{mean}_{\text{poor}}=171.002\text{s}$). However, ants did not spend significantly more time in the 'good' nests

173 compared to the ‘poor’ nests (GLMM, Bonferroni post-hoc test: $t=0.570$, $df=464$, $P=0.569$,
174 $mean_{good}=194.536s$, $mean_{poor}=171.002s$).

175 Across all nest qualities and assessment orders, worker ID had a significant random effect (Worker
176 Random effect: $Z=4.397$, $P<0.001$), indicating that different workers were spending different amounts
177 of time in the nests. However, colony ID did not have a significant effect (Colony Random effect:
178 $Z=1.812$, $P<0.070$) suggesting that visit duration distributions may have been stable across colonies.

179 Consistent variation among workers was then confirmed by the finding that the time spent by any
180 given ant within nests of one quality was significantly positively correlated with the time it spent
181 within nests of other qualities. This held true for both the ‘poor first’ treatment (Spearman’s rank
182 correlation ‘poor first’: excellent/good= 0.501 , $n=78$, $P<0.001$, excellent/poor= 0.250 , $n=78$, $P=0.027$,
183 good/poor= 0.440 , $n=80$, $P<0.001$), and ‘excellent first’ treatment (Spearman’s rank correlation
184 ‘excellent first’: excellent/good= 0.429 , $n=77$, $P<0.001$, excellent/poor= 0.307 , $n=75$, $P=0.007$,
185 good/poor= 0.362 , $n=75$, $P=0.001$, fig. S3a, b).

186 **b) Computational model**

187 In all cases, a quorum was reached more, or as, rapidly when nest acceptance thresholds were
188 heterogeneously distributed, suggesting that heterogeneity confers a decision speed advantage (fig.
189 2d, f). When the better quality nest was close to, or greater than, the acceptance threshold of ants,
190 homogeneous assessments produced a higher percentage of optimum choices (fig. 2c), however, when
191 both nest qualities were significantly below the acceptance threshold of homogeneous ants,
192 heterogeneous assessments produced a far higher percentage of correct choices (fig. 2e). In cases
193 where the new nest sites were of equal quality, percentages of correct choices were the same for both
194 groups, but heterogeneous acceptance thresholds again provided a speed advantage (fig. S2).

195

196

197 **Discussion**

198 Our data show that individual ants do indeed spend differing periods of time within nests of different
199 quality, and that for any given nest quality, there exists a wide distribution of visit durations across
200 workers, spanning several orders of magnitude. In general, workers spend more time within nests as
201 nest quality increases. However, even at the two extremes of quality, some individuals still invest a
202 large amount of time within nests, while others invest very little. This suggests that some ants are
203 always satisfied with a nest, while others almost never are. Furthermore, we find that the time spent
204 by any given individual within a nest of one quality significantly, and positively, correlates with the
205 time it spends within nests of other qualities. Such a trend indicates that ants are heterogeneous in
206 their assessment of quality, yet remain consistent in their weighting of different nest options.
207 Moreover, the order in which ants encounter new nests also has a significant influence upon the time
208 that they spend within them, implying that prior experience may alter quality assessment. These
209 results provide, to our knowledge, some of the first direct empirical evidence for the use of
210 heterogeneous quality assessments in collective choice. Furthermore, our modelling results suggest
211 that such heterogeneity may confer advantages in collective choice, especially in cases where only
212 mediocre options are available.

213 In the ‘poor first’ treatment, mean visit durations significantly increased with nest quality, consistent
214 with previous work (9,24). However, the variation among ants within each quality represents a novel
215 discovery, and suggests that individuals assess nests of the same quality differently. As quality
216 increased, more individuals began to spend longer within a nest, and the distribution of visit durations
217 became more right-skewed with increasing nest quality (fig. 2a). A possible underlying mechanism is
218 that workers were using an internal measure of quality assessment, and hence adjusting visit duration
219 in relation to how well a nest met their own ‘standards’. This concept is strongly supported by the
220 finding that individuals were consistent in spending either a longer or shorter average time assessing
221 all nests, but still proportionally differed in their visit durations based on nest quality (fig. S3a). It
222 should be noted that the role of visit duration in collective choices is likely to be proximate, as final

223 recruitment decisions are more important for overall colony emigration dynamics (9). However, our
224 results provide evidence that individuals do differ widely in their assessments of nests, thus acting as a
225 foundation for subsequent heterogeneity in recruitment.

226 Experimental evidence shows that as nest quality increases, a greater proportion of workers will
227 accept it, but that some are still not satisfied and will leave to search for alternatives, indicative of
228 varying acceptance thresholds (9,22). Moreover, our empirical results demonstrate strong
229 heterogeneity in assessment durations (fig. 2a, b), and as assessment time predicts nest acceptance
230 (22,25), they also suggest heterogeneous recruitment. Thus, the results from our model, which aimed
231 to assess the potential benefits of heterogeneity in the context of recruitment, link the two findings. In
232 simulations, colonies were able to make more rapid decisions in the presence of heterogeneous
233 acceptance thresholds, although often at the cost of accuracy, a trend that has been observed
234 previously in this species (fig. 2c, d) (33). Furthermore, when presented with nests of relatively low,
235 but differing qualities, heterogeneity was essential to allowing correct choices, while homogeneity led
236 to an inability to distinguish between options (fig. 2e, f). This is particularly relevant, as in nature,
237 colonies often have to choose between mediocre nest sites, a trend evident from the need to construct
238 new walls within cavities after emigrating (34). As such, it seems likely that heterogeneity is an
239 important factor enabling rapid emigrations, and providing flexibility when facing a range of different
240 nest choice scenarios.

241 When ants encountered the ‘excellent’ nest first, although the mean time spent within nests still
242 increased with nest quality, visit durations in the ‘poor’ and ‘good’ nests did not significantly differ
243 from each other (fig. 2b). Interestingly, this indicates that prior exposure to an ‘excellent’ nest
244 depressed the supposed quality of ‘good’ nests, while raising the supposed quality of ‘poor’ nests,
245 consistently across individuals (fig. S3b). It has been shown that at the colony level, prior knowledge
246 of options strongly influences nest assessment behaviour (35), and indeed, the presence of this process
247 at the individual level would further improve the robustness of variable quality assessments during
248 nest choice. Specifically, if the quality assessments of individuals are influenced by experience, this
249 would stop workers from being locked into repeatedly rejecting a nest that they deemed poor, even

250 though it constituted the only viable option. Furthermore, as supported by previous experimental and
251 modelling results, experiential influence would also help to ensure that even when multiple options of
252 very high quality were present, the best nest would still be preferred (20,36).

253 A simplistic view of decision-making thresholds might involve swift and categorical outcomes of
254 either rejection or acceptance. Here, by contrast, we suggest that the visit duration to a potential new
255 nest site, a continuous variable positively associated with its quality, may underpin a probabilistic
256 threshold rule, as observed in other biological systems (37). Such a system would need to take many
257 nest attributes into consideration, as is well established for these ants at a collective level (36).

258 Specifically, as an ant evaluates each quality metric in turn, it may take a variable amount of time
259 before finding one that fails to meet its threshold, and so durations until nest rejection will vary.
260 Hence, the overall visit time will increase as a function of nest site quality, effectively prolonging a
261 worker's contribution to a quorum in a continuous fashion, prior to recruitment (fig. 2a, b).

262 Earlier work by Pratt et al. (27,38) demonstrated that workers introduced to, or removed from, a new
263 nest site by hand, directly influenced other ants' assessments of whether a quorum threshold had been
264 achieved. Thus, individual nest visit durations that are positively associated with overall nest quality,
265 as demonstrated here, may influence quorum attainment at the collective level, both directly via
266 worker presence, and indirectly via recruitment decisions, favouring the choice of the highest quality
267 nest site available. Indeed, previous studies suggest that, in some cases, emigration choices based on
268 visit durations alone are possible, although these are in a minority, and occur absent positive feedback
269 (21,24).

270 Notably, the variation we observed in assessment durations among ants is unlikely to be accounted for
271 simply by differences in individual movement speeds. This is because the same individuals were
272 tested for all three nest qualities, and thus interindividual speed variation would not explain the
273 consistent increase in assessment durations seen with increasing nest quality. Consequently, we
274 postulate that this variation is instead due to assessment differences, and so may subsequently
275 influence recruitment likelihoods, as demonstrated by our model.

276 In summary, our experimental results demonstrate that a distribution of differing, but flexible, worker
277 quality assessments does exist within *T. albipennis*. Modelling suggests that such heterogeneity may
278 allow colonies to make optimal and self-organised emigration decisions, while negating the need for
279 direct comparisons, and circumventing the dangers of sub-optimal choices. Thus, while assessments
280 are highly variable among individuals, it is from this very heterogeneity that adaptive behaviours can
281 emerge at the level of the society.

282 **Ethical standard statement**

283 All applicable institutional and/or national guidelines for the care and use of animals were followed.

284 **Data accessibility**

285 All data are included in the electronic supplementary data, computational model details and figures
286 are included in supplementary material 1.

287 **Competing interests**

288 We have no competing interests.

289 **Author Contributions**

290 TAOW and NRF conceived the study and wrote the manuscript; TAOW conducted the experiments;
291 NM developed the computational model; TAOW and ABSF carried out the statistical analysis. All
292 authors gave final approval for publication.

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386

387 **Figure captions**

388

389 **Figure 1. Nest characteristics and experimental setup.** (a) Nest characteristics: Poor; clear cover,
390 1mm wall height, 6mm entrance width, Good; clear cover, 2mm wall height, 2mm entrance width,
391 Excellent; Red filter cover, 2mm wall height, 1mm entrance width. (b) Experimental setup, crosses
392 mark the introduction point of individual ants in each Petri dish. Ants were placed into the holding
393 dish upon completion of all three assessment trials.

394 **Figure 2. Frequency of worker visit durations by nest quality, and computational model**

395 **comparing the performance of colonies with homogeneous and heterogeneous nest acceptance**

396 **thresholds.** Frequency of worker visit durations by nest quality, in the (a) ‘poor first’ $n=238$ ($n_{\text{poor}}=80$,

397 $n_{\text{good}}=80$, $n_{\text{excellent}}=78$) and (b) ‘excellent first’ $n=232$ ($n_{\text{poor}}=75$, $n_{\text{good}}=77$, $n_{\text{excellent}}=80$) treatment orders.

398 (c)-(f) Comparison between the performance of colonies with homogeneous acceptance thresholds

399 ($\sigma=0$) and heterogeneously distributed acceptance thresholds ($\sigma=1$) using a computational model, with

400 a mean threshold value of 5 and the addition of a Gaussian distributed error (mean=0, $\sigma=0.5$). The

401 quality of nest B (q_B) was set to a constant value, while that of nest A (q_A) was varied. (c) Fraction of

402 correct choices when $q_B=4$, (d) mean time to quorum when $q_B=4$, (e) fraction of correct choices when

403 $q_B=3$, (f) mean time to quorum when $q_B=3$. For full model parameters, see supplementary material 1.

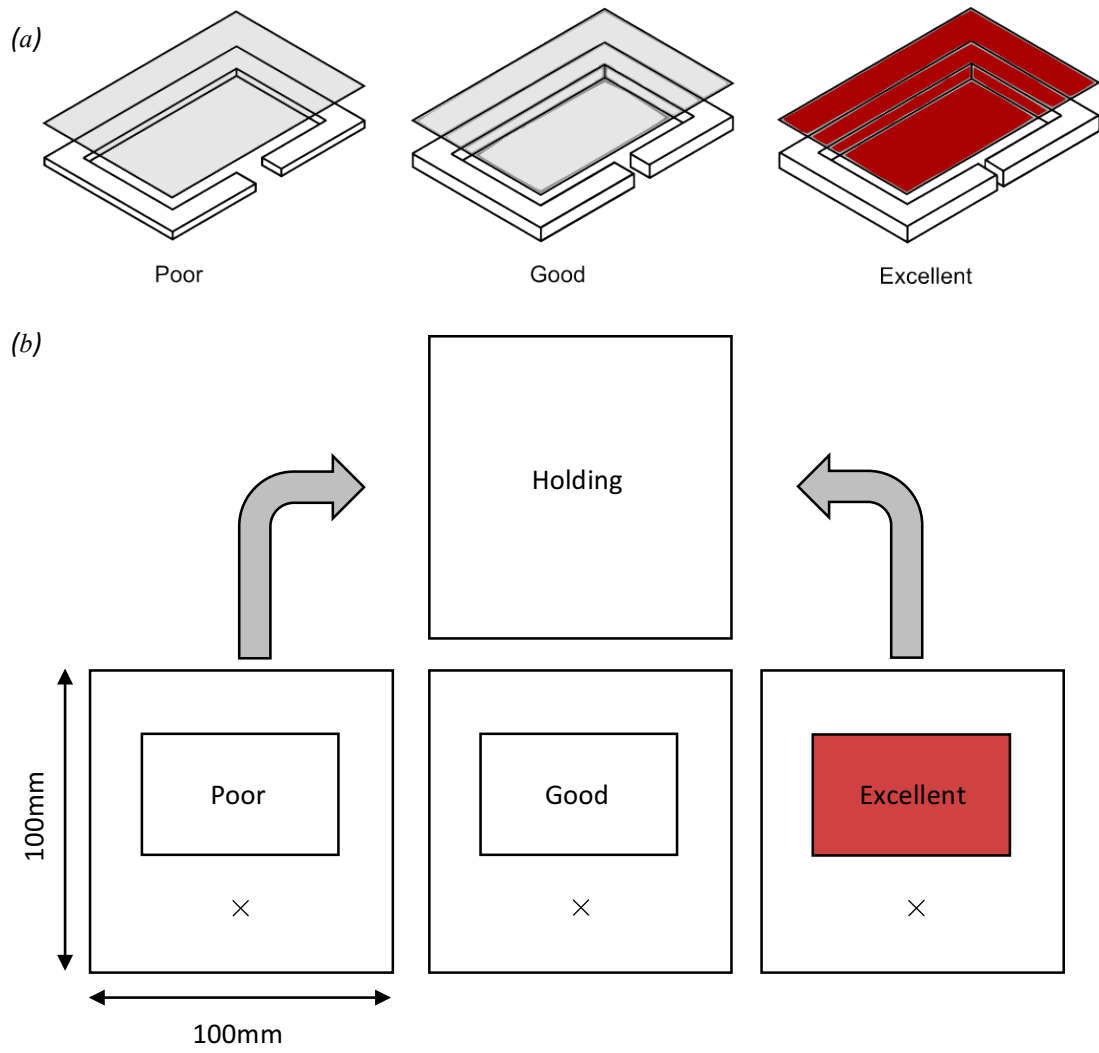


Figure 1.

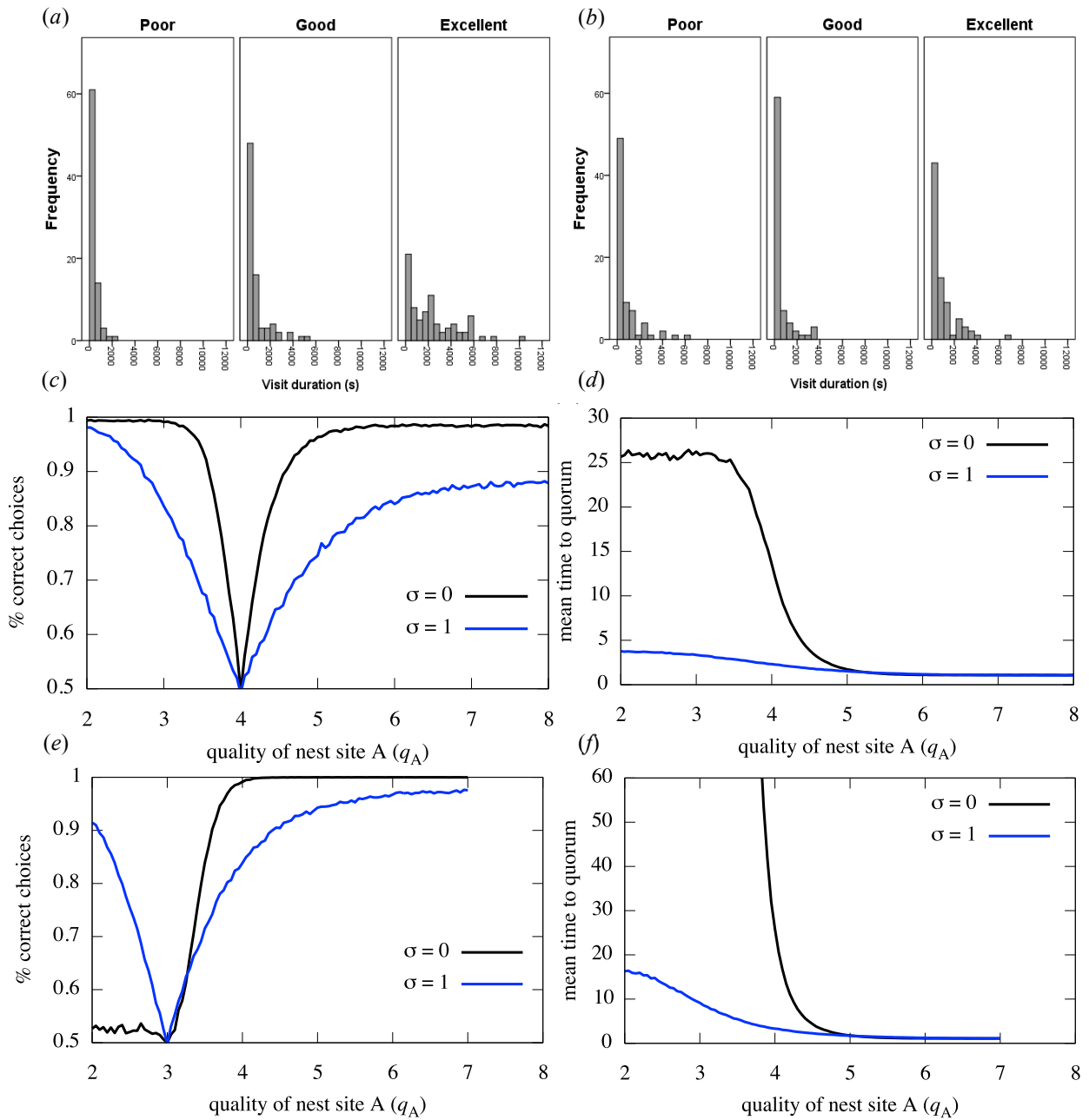


Figure 2.