

13 **Abstract**

14 Displaced communication, whereby individuals communicate regarding a subject
15 that is not immediately present (spatially or temporally), is one of the key innovations of
16 human language. It also occurs in a few animal species, most notably the honeybee,
17 where the waggle dance is used to communicate the location and quality of a patch of
18 flowers. However, it is difficult to study how it emerged given the paucity of species
19 displaying this capacity and the fact that it often occurs via complex multimodal signals.
20 To address this issue, we developed a novel paradigm in which we conducted
21 experimental evolution with foraging agents endowed with neural networks that regulate
22 their movement and the production of signals. Displaced communication readily evolved
23 but, surprisingly, agents did not use signal amplitude to convey information on food
24 location. Instead, they used signal onset-delay and duration-based mode of
25 communication, which depends on the motion of the agent within a communication area.
26 When agents were experimentally prevented from using these modes of communication,
27 they evolved to use signal amplitude instead. Interestingly, this mode of communication
28 was more efficient and led to higher performance. Subsequent controlled experiments
29 suggested that this more efficient mode of communication failed to evolve because it took
30 more generations to emerge than communication grounded on the onset-delay and length
31 of signaling. These results reveal that displaced communication is likely to initially evolve
32 from non-communicative behavioral cues providing incidental information with evolution
33 later leading to more efficient communication systems through a ritualization process.

34

35 **Author Summary**

36 The evolution of displaced communication, the process through which individuals
37 share information about a remote object (in space or time), is a key innovation in language.
38 By conducting experimental evolution we found that displaced communication is more
39 likely to leverage and evolve from behavioural cues, such as the agent's movement, rather
40 than from dedicated communication modes, such as the amplitude of emitted signals. This
41 phenomenon is shown to happen because communication via signal amplitude -although
42 more efficient- is slower to evolve. The simple behaviors and neural networks of the agents
43 studied here, also suggest that communication may evolve more frequently than expected
44 via ritualization, a process whereby an action or behavior pattern in an animal loses its
45 original function but is retained for its role in display or other social interactions.

46

47 **Introduction**

48 The evolution of communication, wherein privately acquired information is
49 transmitted in a social context, still represents a major issue in evolutionary biology [1, 2,
50 3]. In particular, the origin of displaced communication [4, 5], where the subject of
51 communication is remote in space and/or time, is poorly understood. While displaced
52 communication is a defining feature of human language [5], it has also been documented

53 in a few other animal species such as chimpanzees [6, 7], dolphins [8] and parrots [9].
54 One of the most striking example is the honeybee waggle dance [10], where foragers
55 returning to the hive provide information on the quality and spatial location of foraging sites
56 by modifying the orientation of the dance according to the relative position of the sun to
57 the food source and modulating the length of the waggle proportion according to the
58 distance of the food from the hive [11, 12, 13, 14, 15, 16]. Since historical origins of natural
59 languages cannot be observed directly [17], and because displaced communication often
60 involves complex multimodal signals (e.g., the orientation and the length of the dance in
61 honeybees), studying their origin is challenging [18, 19].

62

63 To investigate the evolution of displaced communication, we conducted
64 experimental evolution with simple simulated robots that could make use of a dedicated
65 communication system to provide information on food location [20, 21, 22, 23]. Each
66 experiment replicates the evolution of these artificial organisms from scratch under new
67 environmental conditions. In each experiment, a signal sender and a signal receiver were
68 placed on a one-dimensional circular environment containing a region ("nest") where they
69 could communicate, and five non-overlapping foraging sites, only one of which contained
70 food at any given time (Fig 1). Importantly, the sender, but not the receiver, could perceive
71 the presence of food when at a site containing food. When back at the nest, the sender
72 could communicate with the receiver by producing a signal whose amplitude could vary
73 continuously. Experimental evolution was conducted over 25'000 generations in 40
74 independent populations each containing 1'000 pairs of senders and receivers. Each pair

75 was evaluated during five trials; food was located once at each of the five foraging sites in
76 random order. The performance of each pair of sender-receiver agents was evaluated in
77 the last 20 time steps of a trial as the proportion of the time spent by the receiver on the
78 foraging site containing food. The specifications of the agents' neural networks were
79 encoded in an artificial genome (Fig 1). The probability of transmission of genomes from
80 one generation to the next was proportional to the performance of the agents. All
81 experiments were initiated with completely naive agents (i.e., with randomly generated
82 genomes that corresponded to randomly wired neural controllers) with no information
83 about how to move and identify foraging sites or the nest location. Mutations occurred with
84 a given probability during each of the 25'000 generations.

85

86 **Fig 1. Illustration of experimental setting.** During each trial, food was randomly located
87 on one of the five foraging sites (marked in red) located on a circle. Both the sender and
88 the receiver always started a trial at position 0 on the circle, inside the communication
89 area, which acted as a “nest” (marked in blue). The agents' controllers were comprised of
90 two continuous-time, recurrent neural networks with a fully connected hidden layer of five
91 neurons. Connections between neurons are represented by black lines and input, hidden
92 and output layers are respectively designated as *I*, *H* and *O*. See Materials and Methods
93 for a complete description of the experimental setup.

94

95 **Results**

96

97 **Role of communication on performance**

98 To determine whether communication evolved and, if so, quantify how it influenced
99 performance, we first conducted experimental evolution under two different treatments. In
100 the communication treatment, the sender could freely signal while in the no-
101 communication treatment we prevented agents from communicating by fixing the signal
102 perceived by the receiver to a constant zero value. Foraging efficiency rapidly increased
103 in both the communication and no-communication treatments (Fig 2), but rose to be over
104 double as high in the communication treatment than in the no-communication treatment
105 (last generation: Mann-Whitney U test, $P < 0.0001$).

106

107 **Fig 2. Performance over generations of evolution depending on communication**
108 **capabilities.** Performance (i.e., proportion of time spent by the receiver on the site
109 containing food) over the 25'000 generations of selection when individuals could freely
110 communicate (green line) and when they were prevented from communicating (orange
111 line). Each experimental treatment was replicated over 40 populations. The colored areas
112 represent the first and third quartiles.

113

114 Analyses of individual behaviors provided an explanation for the higher
115 performance in the communication than in the no-communication treatment. In the no-
116 communication treatment, 67% of the receivers evolved a strategy of always going to the
117 same foraging site. Because food was placed at each of the 5 foraging sites once during
118 the 5 trials, these individuals always found food in one of the five trials, hence leading to
119 a performance close to 0.2 (i.e., nearly 20% of the time spent on a foraging site with food).
120 The remaining 33% of the agents had a very different strategy. They moved slowly
121 throughout the five foraging sites thereby spending about 20% of the time on each of the
122 five foraging sites. Their performance was therefore also close to 0.2 but they were
123 invariably classified as not having found food because they always spent less than 75%
124 of the time on the foraging site containing food. By contrast, in the communication
125 treatment 68% of the agents were able to locate food in two or more of the five trials (Fig
126 3B) This, together with the much higher performance than in the no-communication
127 treatment (Fig 2), revealed that an effective mode of displaced communication evolved
128 between senders and receivers.

129

130 **Fig 3. Repartition of sites found depending on communication capabilities.**

131 Percentage of individuals, which found food 0, 1, 2, 3, 4 or 5 times during the five trials in
132 the (A) no-communication and (B) communication treatments. Receivers were considered
133 to have found food if they spent at least 15 of the last 20 time steps of a trial on the site
134 containing food.

135

136 **Mode of communication**

137 Since the neural networks of the senders were designed to allow senders to vary
138 the signal amplitude as a means of communication, we expected that senders would
139 signal which site contained food by using this mode of communication as this mode of
140 communication would have provided a large potential of expressiveness to evolve.
141 Surprisingly, however, there was no consistent difference at the end of the experiment
142 (generation 25'000) in signal amplitude depending on the site at which food was located.
143 Overall, the variation of signal amplitude between the five trials was only $0.005 \pm 5.03 \cdot 10^{-5}$.
144 This unexpected result suggests that senders did not use signal amplitude to provide
145 information on food location. This was confirmed in an additional experiment where we
146 constrained the evolved senders to produce a signal of fixed amplitude, irrespective of the
147 site at which food was located. This manipulation did not lead to a significant reduction in
148 performance (mean performance: 0.471 ± 0.005) compared to the treatment where signal
149 amplitude was not constrained (mean performance: 0.472 ± 0.005 ; Mann-Whitney U test P
150 > 0.4), confirming that receivers did not use signal amplitude to localize food.

151

152 Given that individuals did not transmit information by means of signal amplitude,
153 we hypothesized that they instead used the timing of onset-delay and/or the duration of
154 signaling as a source of information on food location. In the experiments, receivers could
155 perceive a signal only when both the sender and receiver were simultaneously in the

156 communication area in the nest. Thus, information could be provided by variation in when
157 the signal was first perceived by the receiver or by variation in the duration of the signal.
158 To test these two hypotheses, we experimentally manipulated both the timing of onset-
159 delay and duration of signaling and measured performance during the last generation (see
160 Materials and Methods). These experiments revealed that, depending on historical
161 contingencies, populations evolved to rely on either source of information or both.
162 Delaying the timing of onset-delay of signal production resulted in a significant decrease
163 in performance in 38 out of the 40 populations (Mann-Whitney U test, $P < 0.01$, Fig 4
164 orange bar), indicating that the timing of onset-delay was used as a vector of information
165 in most populations. Constraining the signal duration resulted in a significant decrease in
166 performance in 21 of the 40 populations (Mann-Whitney U test, $P < 0.01$, Fig 4 green bar
167 -see also S1 Fig for the precise influence on performance for every population). In 20 of
168 the 40 populations, performance was significantly decreased both when the timing of
169 onset-delay of signaling was delayed and when the signaling duration was constrained,
170 indicating that these populations relied on both modes of communication for food location
171 (Mann-Whitney U test, $P < 0.01$, Fig 4 purple bar).

172

173 **Fig 4. Percentage of populations with decreased performance depending on**
174 **communication mode.** Percentage of the populations ($n=40$) where performance was
175 significantly (Mann-Whitney U test, $P < 0.01$) decreased by preventing receivers from
176 using information on the timing of signal onset-delay and/or duration. Length (green bar)
177 represents the percentage of populations where performance was decreased when

178 constraining the duration of communication, Onset (orange bar) the percentage of
179 populations where performance was decreased when delaying signal onset-delay and
180 both (purple bar) the percentage of populations where performance was decreased when
181 altering either the timing of signal onset-delay or the duration of signaling.

182

183 The finding that receivers used the timing of onset-delay and duration of signaling
184 as a source of information raises the question of how this evolved. We hypothesized that
185 food location directly influenced the time of arrival of the sender in the communication area
186 and therefore might have affected the timing of onset-delay and/or duration of signaling
187 because senders would arrive earlier and signal longer when food was located at a
188 foraging site close to the nest. Hence, the time of arrival to the nest would have first served
189 as a cue, inadvertently providing information to the receiver about food location. To test
190 this hypothesis, we determined for each population whether there was an association
191 between variation in the timing of signal onset-delay depending on food location and the
192 number of generations required for average performance to become significantly greater
193 than 0.2 (i.e., the highest value reached in no-communication populations; see Materials
194 and Methods). In all the 40 populations there was a close match between these two values
195 with a performance value significantly greater than 0.2 being reached only 1.4 ± 2.1
196 generations (Fig 5) after the sender changed the timing of signal onset-delay depending
197 on the site at which food was located. Accordingly, there was a strong correlation across
198 populations (Pearson correlation, $R = 0.90$, $P < 0.0001$) between the number of
199 generations required for senders to vary in their time of arrival to the nest as a function of

200 food location and the number of generations required for average performance to exceed

201 0.2

202

203 **Fig 5. Number of generations before using signal onset-delay and surpassing**
204 **performance threshold.** For each of the 40 populations, number of generations required
205 before senders changed signal onset-delay depending on the site at which food was
206 located (in green). Number of generations required for the mean population performance
207 to surpass the average performance (i.e., 0.2) in the no-communication populations (in
208 orange).

209

210 **Association between the mode of communication and**
211 **performance**

212 Given the unexpected result that individuals used the onset-delay and duration of
213 signaling in the nest instead of signal amplitude as a mode of communication, we
214 conducted new experiments to investigate whether the agents would evolve the use of
215 signal amplitude when prevented to use variation in signaling onset-delay and duration.
216 This “constrained communication” experiment was performed by forcing senders to
217 always move at a fixed velocity and in the same direction, hence preventing variation in
218 time of arrival and time spent within the nest.

219

220 The elimination of variation in timing of signal onset-delay or signal duration did
221 indeed lead to the evolution of a communication system based on variation in signal
222 amplitude. In this constrained treatment, the mean variation of signal amplitude between
223 trials was 0.185 ± 0.006 , a value significantly greater (Mann-Whitney U test, $P < 0.0001$)
224 than in the unconstrained treatment, where there was almost no variation in signal
225 amplitude between trials ($0.005 \pm 5.03 \times 10^{-5}$). Importantly, at the end of the selection
226 experiment, the performance in the constrained communication treatment (0.510 ± 0.008)
227 was also significantly higher than in the unconstrained treatment (0.472 ± 0.005 ; Mann-
228 Whitney U test, $P < 0.01$).

229

230 The finding that communication mediated by the time of onset-delay/duration of
231 signaling was less efficient than communication mediated by variation in signal amplitude
232 raises the question of why individuals did not use the latter (more efficient) mode of
233 communication when unconstrained. A possible explanation is that a system of
234 communication mediated by signal amplitude is slower to evolve than communication
235 based on signaling onset-delay/duration. To investigate this hypothesis, we analyzed how
236 the performance changes over the first 5'000 generations when the mode of
237 communication was unconstrained and when it was constrained not to use the onset-
238 delay/duration of signaling (Fig 6). This analysis revealed that unconstrained populations
239 quickly reached a performance greater than 0.2 (the value that can be reached without
240 communication) while constrained populations plateaued at this 0.2 performance for
241 almost 800 generations. Overall, unconstrained populations were 42 times faster than the
242 constrained populations to evolve a system of communication with a greater than 0.2
243 performance (Mann-Whitney U test, $P < 0.0001$). The huge variation among the 40
244 constrained populations in the number of generations (range 20-5000 generations)
245 required to surpass the 0.2 performance value further indicates high stochasticity in the
246 number of generations required for effective communication to evolve.

247

248 **Fig 6. Average performance in the first 5'000 generations of evolutions depending**
249 **on treatment.** Average performance in the unconstrained treatment (40 populations) and
250 in the constrained treatment (40 populations) over the 5'000 first generation. Dashed lines

251 show the average performance achieved in the two treatments at the end of the
252 experiments (i.e., in generation 25'000).

253

254 **Discussion**

255 Our analysis showed that experimental evolution with simple artificial agents readily led to
256 the emergence of displaced communication providing information about the location of
257 remote food sources. Surprisingly, although the agents were imbued with a dedicated
258 signaling channel that could vary in amplitude, they did not use this channel as a mode of
259 communication. Instead, they used either the timing of onset-delay and/or duration of
260 signaling in the nest to communicate food location. Importantly, our analysis showed that
261 it was not because the agents were unable to evolve a system of communication based
262 on signal amplitude. When experimentally prevented from using the timing of onset-delay
263 or duration of signaling, the agents were able to make use of signal amplitude as a mode
264 of communication in all of the 40 populations studied. These findings are of particular
265 interest because it has been argued that a satisfactory account of the origins of
266 communication has been hindered by the fact that Artificial Life models have consistently
267 implemented communication as an exchange of signals over dedicated and functionally
268 isolated channels [24]. Our results support Quinn's view that it is possible to evolve
269 communication without dedicated channels and that an understanding of how
270 communication evolves in such situations is of particular interest to our understanding of
271 the evolution of communication in natural systems.

272

273 Interestingly, many intraspecific signaling systems between animals having evolutionary
274 overlapping interests (i.e., when the fitness of one depends, at least in part, on the fitness
275 of the other -a in our experiments) have been shown to also rely on variation in signaling
276 amplitude or duration (e.g. [25, 26, 27]) or variation in the rhythms [28]. This can be
277 understood since such variation readily allows effective communication and because it
278 can quickly evolve, as demonstrated by our experiments.

279

280 A surprising result was that communication via signal amplitude was actually more efficient
281 than communication based on signaling onset-delay/duration, raising the question of why
282 agents invariably evolved the less efficient mode of communication in the unconstrained
283 treatment. We hypothesized that this might be due to communication via signal amplitude
284 taking more time to evolve than communication via the timing of signal onset-delay/signal
285 duration. Our time-course analyses confirmed this hypothesis, showing that on average it
286 took 42 times more generations for communication to evolve (i.e., for populations to reach
287 higher performance than in the no-communication treatment) via signal amplitude than via
288 the timing of signal onset-delay/signal duration. This finding can be explained by the fact
289 that the time taken for agents to return to the nest was rapidly associated with the distance
290 between food and the nest, thereby providing a useful cue to the receiver. By contrast,
291 despite being more efficient, communication via signal amplitude was much slower to
292 evolve - most likely because it first required that signal amplitude varied non-randomly
293 among senders according to food location before the receivers could evolve an

294 appropriate response. In line with this view of a slow stochastic process being required for
295 reaching a difficult evolutionary target, in the experiments where agents were constrained
296 to use signal amplitude there was a large variation across populations in the number of
297 generations required to surpass a performance score of 0.2 (the performance hallmark of
298 some form of communication).

299

300 Interestingly, our analysis revealed that once the populations had evolved a mode of
301 communication based on the timing of signal onset-delay and/or signal duration, none of
302 them were able to switch to the more efficient system of communication via signal
303 amplitude. A likely reason for this is that switching from one system of communication to
304 the other would require passing through a valley of lower performance values [29] where
305 each population would have to abandon their original mode of communication to develop
306 the other. This problem is likely to be particularly acute in the case of communication
307 systems because changes in either the signaling or response strategy would destroy the
308 communication system and result in a performance decrease [30, 31]. A similar
309 phenomenon may account for some of the differences in signaling observed between
310 closely related species or isolated populations of a given species. For example, Anolis
311 lizards originating from different evolutionary ancestors have evolved different signaling
312 systems in response to similar selective pressures [32].

313

314 This study also supports the suggestion that communication may often evolve via
315 ritualization, a process whereby an action or behavior pattern in an animal loses its original
316 function to serve as a mode of display or other role in social interactions [33]. The path to
317 communication revealed by our study is typical of such a process [2, 34]. The variations
318 of motor actions initially acted as non-selected cues (i.e., timing of return to the nest and
319 signal duration) that elicited an adaptive reaction in the receiver. Through selection, these
320 cues then became full-fledged signals that provided reliable information about food
321 location. Similarly, ritualization has been proposed as a route towards the evolution of the
322 waggle dance in honeybees [35, 36]. Because communication based on the timing of
323 signal onset-delay/duration is built from an existing behavior, its evolution was faster than
324 that of communication based on signal amplitude which required the coordinated evolution
325 of signal and response (i.e., coordination between senders and receivers). As a result,
326 communication by signal amplitude never evolved when the agents could use the timing
327 of signal onset-delay and/or signal duration in the unconstrained treatment. In conclusion,
328 our study reveals that ritualization may play a more pervasive role than realized, in
329 particular for the emergence of displaced communication.

330

331 **Materials and Methods**

332 **Experimental Setup**

333 The environment was a one-dimensional circle containing a nest where individuals
334 could communicate with each other and five non-overlapping foraging sites at fixed
335 positions: $\pi/2$, $3\pi/4$, π , $-3\pi/4$ and $-\pi/2$ (Fig 1). Each foraging site's length was $\pi/4$. Each
336 trial was always conducted with a *sender* and a *receiver*, both of which were initially
337 located at position 0 on the circle. Each pair was evaluated over five trials, with food being
338 located at each foraging site once and changed position at each trial in random order. The
339 performance of each pair of sender-receiver agents was proportional to the number of
340 time steps spent by the receiver on the foraging site containing food during the last 20
341 time steps (out of 100) of each of the five trials. Starting from 0, performance was
342 increased by 0.01 for each time step spent at the food location and thus the maximum
343 performance achievable after five trials was equal to 1 [$0.01*20*5$].

344

345 Each agent was controlled by an individual, fully-connected, continuous-time
346 recurrent neural network (CTRNN) [37]. The agent could move around the circle in either
347 direction (i.e., clockwise or counterclockwise) and freely vary their speed (i.e., angular
348 velocity) from zero to a maximum of $\pi/9$. Agents could pass each other without collision.
349 In addition, the sender was equipped with a floor sensor for food detection that would
350 switch from 0 to 1 if food was present at a given foraging site. The sender could emit a

351 signal expressed as a numerical value in the range from 0 to 1, which the receiver could
352 perceive if both agents were in the nest. The nest was centered on 0 and was $\pi/2$ wide
353 (i.e., extending from $-\pi/4$ to $\pi/4$). Outside of this area, the signal strength perceived by the
354 receiver was equal to zero, independent of the strength of the signal sent.

355

356 Both senders and receivers possessed two inputs indicating their own location
357 (expressed as sine and cosine values). The sender had an additional input providing
358 information on whether the foraging site on which it was contained food (1 if food was
359 present, 0 otherwise) and the receiver had an additional input corresponding to the
360 perceived signal strength. Each network included five hidden neurons with recurrent
361 connections and two output neurons. The two output neurons controlled the speed and
362 direction of the agent. Speed was computed as the absolute value of the difference
363 between these two outputs and direction as the sign of this difference. In addition, the
364 sender had a supplementary output encoding the signal strength. Each synaptic
365 connection was encoded in a single gene whose real value was in the $[0, 1]$ range. It was
366 then mapped linearly in the $[-4, 4]$ range to be used as a synaptic weight. The neuron's
367 integration time constant τ and bias term θ were encoded in genes whose values were
368 linearly mapped in the $[0.1, 1.0]$ range and the $[-2, 2]$ range respectively. This amounted
369 to a total genome size of $77 [3 \times 5 + 5 \times 5 + 5 \times 3 + 2 \times 11]$ values for the sender and $70 [3 \times 5 +$
370 $5 \times 5 + 5 \times 2 + 2 \times 10]$ values for the receiver.

371

372 **Artificial Evolution**

373 Each of the 40 independent populations comprised 1'000 pairs of senders and
374 receivers. At generation 0, each gene in the genome was initialized with a random value
375 uniformly sampled from the [0, 1] range. Each sender was randomly paired with a receiver
376 from the same population. The performance of this pair was evaluated across five trials;
377 in each trial, food was randomly positioned at a different foraging site. After the
378 performance of every pair had been evaluated, tournament selection [38] was separately
379 applied to each group (tournament size = 10) to identify the 1'000 senders and 1'000
380 receivers selected to produce the next generation. Each gene of a selected genome was
381 mutated with a mutation rate μ_N which depended on the genome size, as follows:

382

$$383 \quad \mu_N = \frac{\mu}{G},$$

384 where μ is the baseline mutation rate, whose value is set to 0.5, and G is the genome size.
385 Thus, each gene had a mutation probability of $7.1 \cdot 10^{-3}$ for a sender's genome and $6.5 \cdot 10^{-3}$
386 for a receiver's genome. For each mutated gene, we changed the value by a random
387 value sampled according to a standard normal distribution. All populations evolved for
388 25'000 generations.

389

390 **Analysis of Communication Strategies**

391 To assess individuals' performance and strategies, we determined the number of
392 trials in which each receiver successfully found the food location. We considered that food
393 was successfully found when receivers had a performance of at least 0.15 for a given trial
394 (i.e., it spent at least 15 of the last 20 timesteps of a trial on the foraging site containing
395 the food).

396

397 To study how signal amplitude varied according to food location, we considered
398 only the trials in which the receiver found the food location (as per the previous definition).
399 For a given sender, we measured the difference in signal amplitude at the same time step
400 between the five different trials. Mean signal variation \acute{S}_i for each individual i was thus
401 calculated as follows:

402

$$403 \quad \acute{S}_i = \frac{1}{100} \sum_{u=1}^{100} \frac{2}{|T|(|T|-1)} \sum_{t_1 \in T} \sum_{t_2 \in T, t_2 \neq t_1} |s_{ut_1} - s_{ut_2}|,$$

404 where T was a set representing the 5 different trials ($T = \{1, 2, 3, 4, 5\}$, cardinality $|T| = 5$),
405 t_1 and t_2 two different trials, u the time step (in $[1, 100]$) and s_{ut_n} is the signal amplitude
406 emitted by the sender at time step u during trial t_n .

407

408 To study whether receivers relied on signal amplitude, we fed the receivers'
409 sensors with a signal that did not change according to the location of food (i.e., did not
410 change between trials). Specifically, at each time step, the receiver was given a signal
411 whose amplitude was equal, for a given time step, to the average signal amplitude emitted
412 by the sender over the five trials at this time step. As such, the signal amplitude a_u received
413 at time step u was:

414

$$415 \quad a_u = \frac{1}{|T|} \sum_{t \in T} s_{ut},$$

416 where T , t , u and s_{ut} were the same variables as defined in the previous equation.

417

418 We identified the first generation where there was a differences between the 5
419 trials for each sender (i.e., when communication onset-delay was different depending on
420 the foraging site at which food was located) to determine when senders began to actively
421 communicate food location. To determine whether agents relied on the onset-delay of the
422 signal we tested whether performance was affected when changing the onset-delay of
423 signaling. To that end, the onset-delay of the signal was shifted (in time steps) by a value
424 equal to the average difference of onset-delay value between trials. Receivers would thus
425 perceive it earlier or later than it was actually emitted by the sender. To determine whether
426 agents relied on the signal duration, we forced senders to stay in the communication area
427 once they had entered it. In both cases, the average performance was then compared
428 with control trials.

429

430

431 **Acknowledgments**

432 The authors thank Kuniaki Noda, Peter Dür, and Sara Mitri for conceiving and
433 contributing to preliminary experiments that lead to this study and Tom Kay for very useful
434 comments.

435

436 **References**

- 437 1. Di Paolo EA. An Investigation into the Evolution of Communication. *Adapt. Behav.*
438 1997;6: 285-324
- 439 2. Maynard-Smith J, Harper D. *Animal Signal*. Oxford University Press; 2003
- 440 3. Christiansen MH, Kirby S. Language evolution: Consensus and controversies.
441 *Trends Cogn. Sci.* 2003;7: 300-307
- 442 4. Bloomfield L. *Language*. 1993
- 443 5. Hockett CF. The Origin of Speech. *Sci. Am.* 1960;203: 88-111.
- 444 6. Woodruff G, Premack D. Intentional communication in the chimpanzee: the
445 development of deception. *Cognition*. 1979;7: 333-362
- 446 7. Call J. Chimpanzee social cognition. *Trends in Cognitive Sciences*. 2001;5

- 447 8. Herman LM, Forestell PH. Reporting presence or absence of named objects by a
448 language-trained dolphin. Rutgers University Symposium: The question of animal
449 cognition. *Neuroscience and Biobehavioral Reviews*. 1985;9: 667-681
- 450 9. Pepperberg IM. *The Alex studies: cognitive and communicative abilities of grey*
451 *parrots*. Harvard University Press; Cambridge, Massachusetts: 1999
- 452 10. Frisch KV. *The dance language and orientation of bees*. Belknap Press of Harvard
453 University Press; 1967
- 454 11. Dyer FC. The Biology of the Dance Language. *Annu. Rev. Entomol.* 2002;47: 917-
455 949
- 456 12. Michelsen A. Signals and flexibility in the dance communication of honeybees. *J.*
457 *comparative physiology A* 2003;189: 165-174
- 458 13. Nieh JC. Recruitment communication in stingless bees (Hymenoptera, Apidae,
459 Meliponini). *Apidologie* 2004;35: 159-182
- 460 14. Fitch WT. The evolution of language: A comparative review 2005; 20: 193-203
- 461 15. Grüter C, Farina WM. The honeybee waggle dance: can we follow the steps? 2009
- 462 16. Menzel R. *Navigation and Communication in Honeybees* 2012;8
- 463 17. Scott-Philipps TC, Kyrby S. Language evolution in the laboratory. *Trends in*
464 *Cognitive Sciences* 2010; 14: 411-417
- 465 18. Heberts EA, Papaj DR. Complex signal function: Developing a framework of
466 testable hypotheses. *Behav. Ecol. Sociobiol.* 2005;57: 197-214
- 467 19. Bro-Jørgensen J. Dynamics of multiple signalling systems: animal communication
468 in a world in flu. *Trends Ecol. Evol.* 2010;25: 292-300

- 469 20. Endler JA. Signals, signal conditions, and the direction of evolution. *The Am. Nat.*
470 1992;139: 125-153
- 471 21. Wiley HR. Errors, Exaggeration, and Deception in Animal Communication in
472 Behavioral mechanisms in ecology. L Real. University of Chicago Press, Chicago;
473 1994 p. 157-189
- 474 22. Wiley HR. Signal Detection and Animal Communication. *Adv. Study Behav.* 2006
- 475 23. Bradbury JW, Vehrencamp SL. Principles of Animal Communication. Sinauer
476 Associates; 2008
- 477 24. Quinn M. Evolving communication without dedicated communication channels.
478 *Advances in Artificial Life: ECAL6*; 2001; Kelemen, J. and Sosiák, P., eds: Springer;
479 2001. p. 357-366
- 480 25. Fenton M, Audet D, Obrist M, Rydell, J. Signal strength, timing, and self-deafening:
481 The evolution of echolocation in bats. *Paleobiology* 1995;21(2): 229-242
- 482 26. Laidre ME, Johnstone RA. Animal signals. *Current Biology* 2013;23: 829-833
- 483 27. Garcia M, Theunissen F, Sèbe F, Clavel J, Ravignani A, Marin-Cudraz T et
484 al. Evolution of communication signals and information during species
485 radiation. *Nat. Commun.* 2020;11: 4970
- 486 28. Roeske TC, Tchernichovski O, Poeppel D, Jacoby N. Categorical rhythms are
487 shared between songbirds and humans. *Curr. Biol.* 2020;30: 3544-3555
- 488 29. Wright S. The Roles of Mutation, Inbreeding, Crossbreeding and Selection in
489 Evolution. *Proc. The Sixth Int. Congr. Genet.* 1932;1: 356-366
- 490 30. Floreano D, Mitri S, Magnenat S, Keller L. Evolutionary conditions for the
491 emergence of communication in robots. *Curr. Biol.* 2007;17: 514-519

- 492 31. Wischmann S, Floreano D, Keller L. Historical contingency affects signaling
493 strategies and competitive abilities in evolving populations of simulated robots.
494 Proc. Natl. Acad. Sci. 2012;109: 864-868
- 495 32. Ryan MJ. Sexual selection, receiver biases, and the evolution of sex differences.
496 Science 1998;281: 1999-2003
- 497 33. Scott-Phillips TC. Defining biological communication. J. Evol. Biol. 2008;21: 387-
498 395
- 499 34. Scott-Phillips TC, Blythe RA, Gardner A, West SA. How do communication
500 systems emerge? Proc. Royal Soc. B: Biol. Sci. 2012;279: 1943-1949
- 501 35. Barron AB, Maleszka R, Vander Meer RK, Robinson GE. Octopamine modulates
502 honey bee dance behavior. Proc. Natl. Acad. Sci. 2007;104: 1703-1707
- 503 36. Nieh J. The Evolution of Honey Bee Communication: Learning from Asian Species.
504 Formos. Entomol. 2011;31: 1-14
- 505 37. Beer RD. On the dynamics of small continuous-time recurrent neural networks.
506 Adapt. Behav. 1995;3: 469-509

507 38. Goldberg DE. Genetic Algorithms in Search, Optimization, and Machine Learning.

508 1989

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510 **Supporting information**

511 **S1 Fig. Performance difference for every population depending on communication**

512 **constraints.** Performance difference of every population line when (A) communication

513 length was constrained and (B) communication onset was constrained.

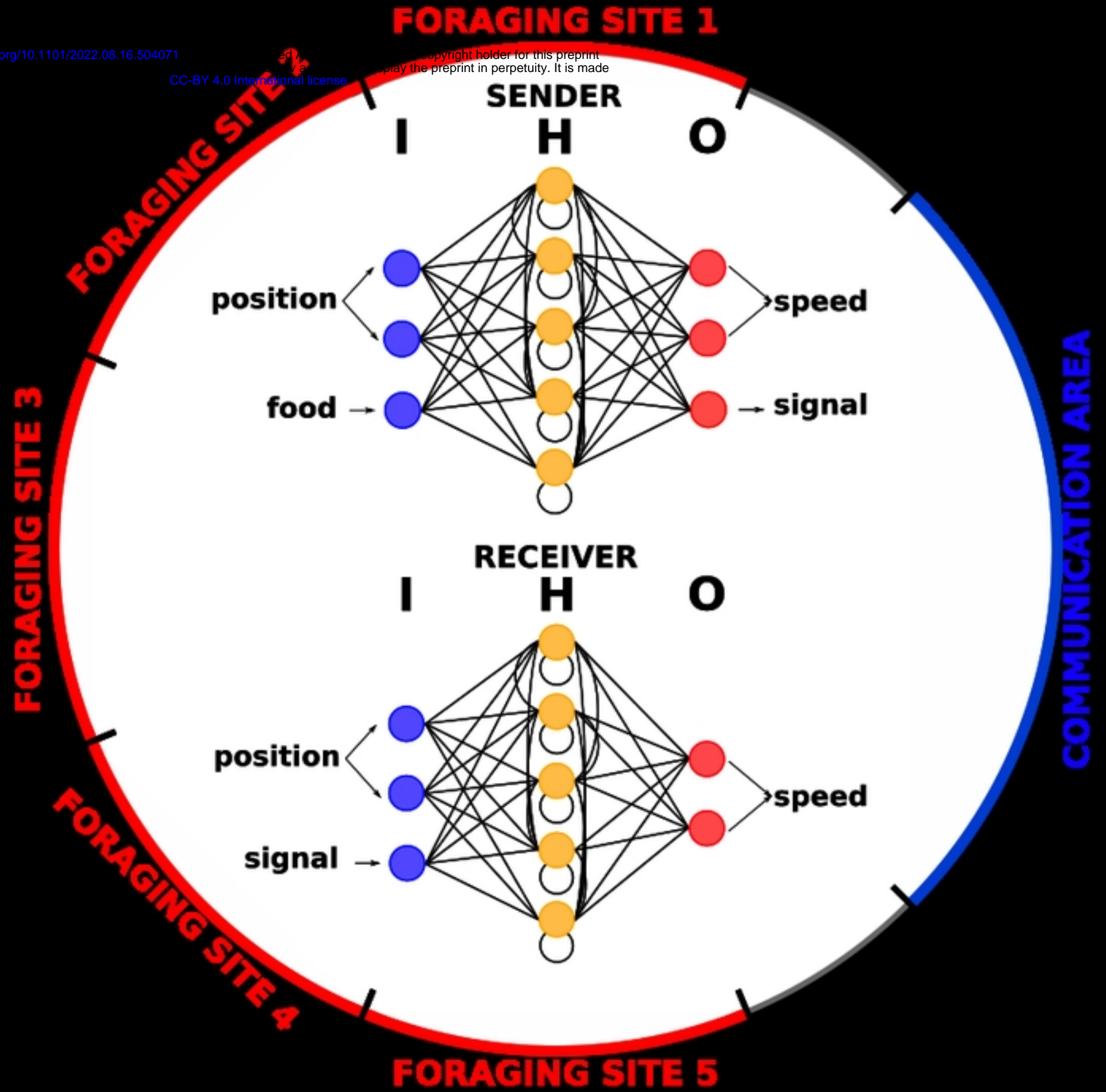


Fig 1

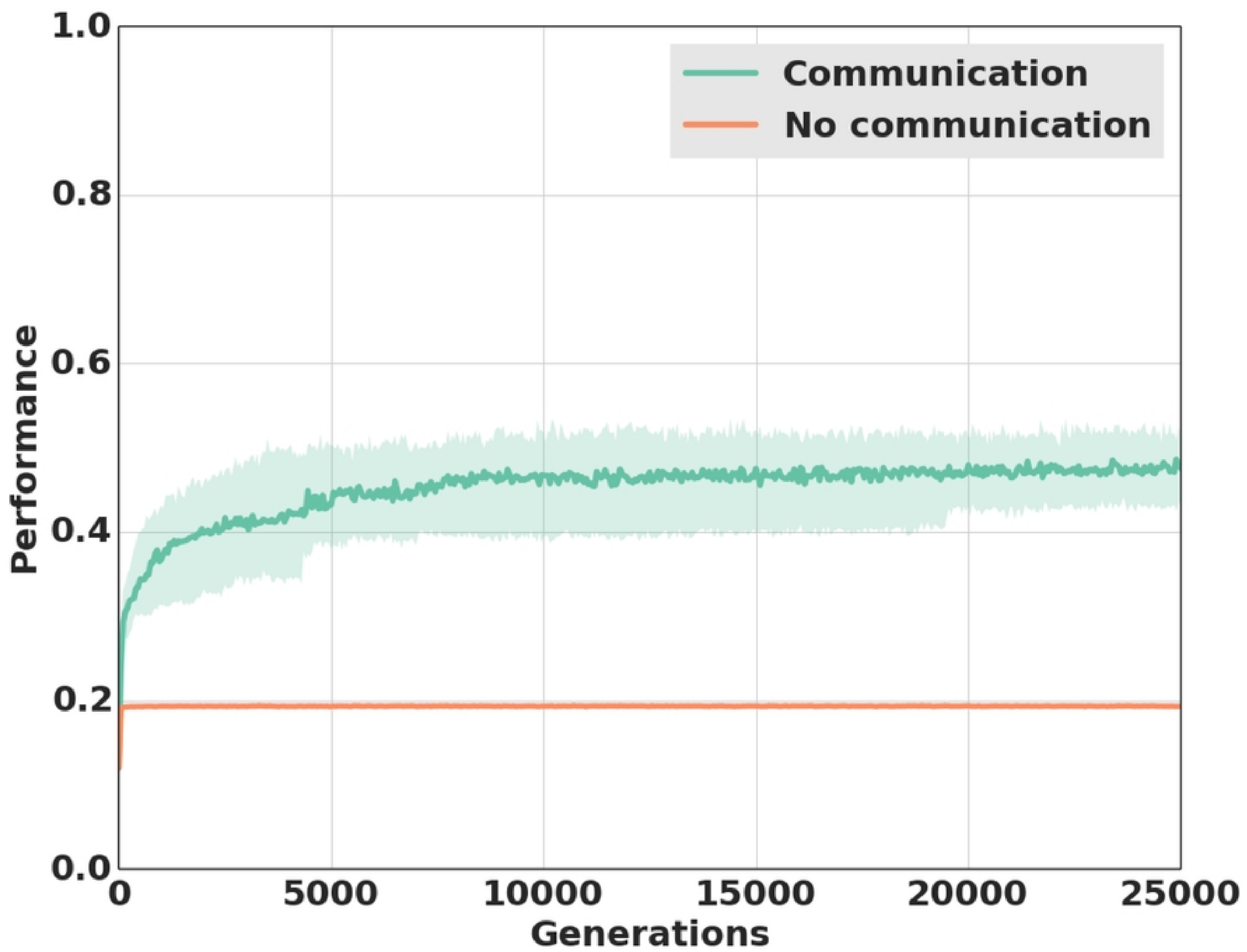


Fig 2

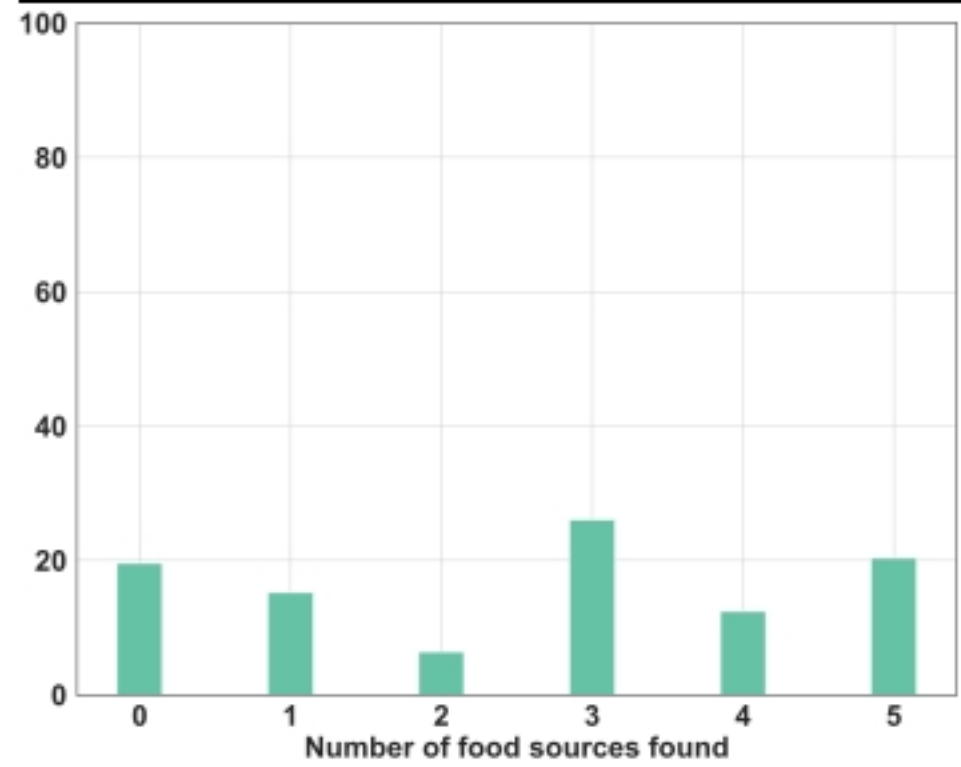
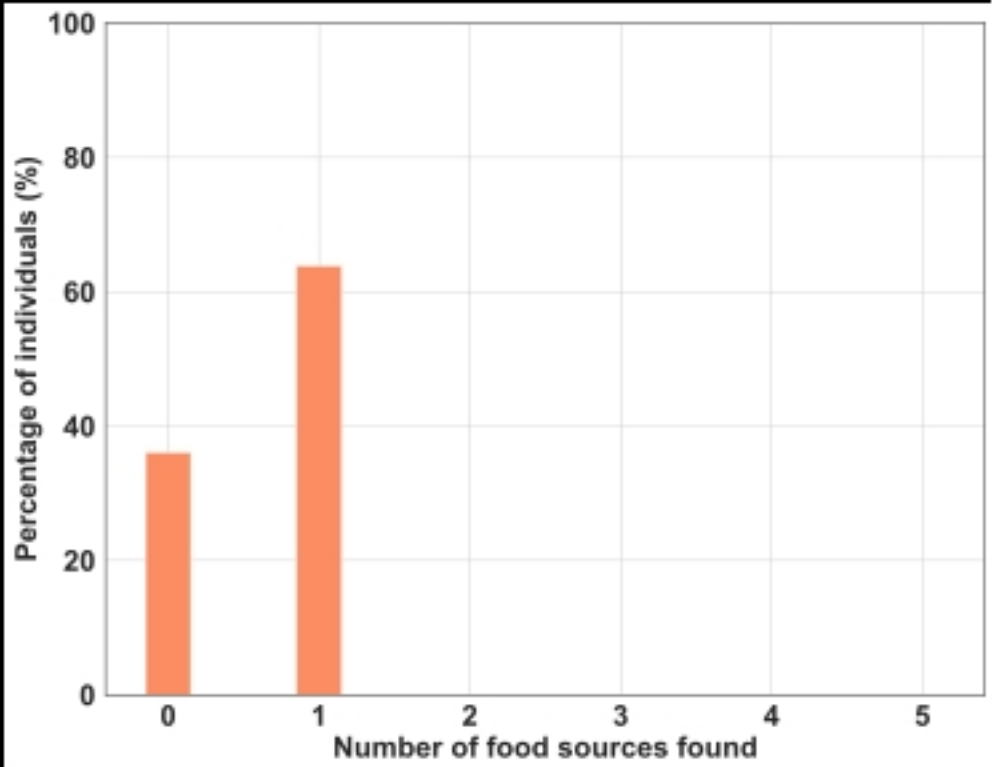


Fig 3

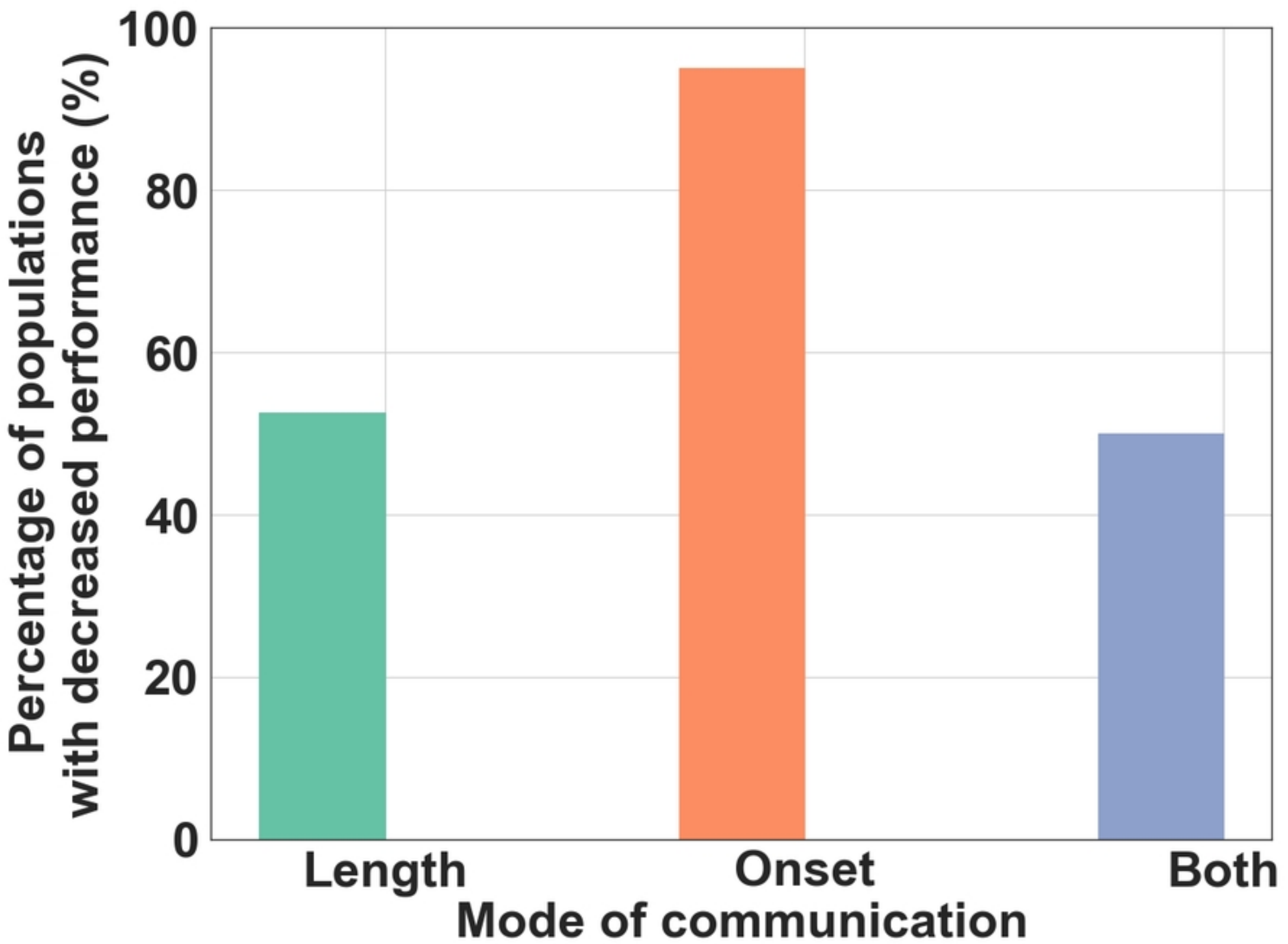


Fig 4

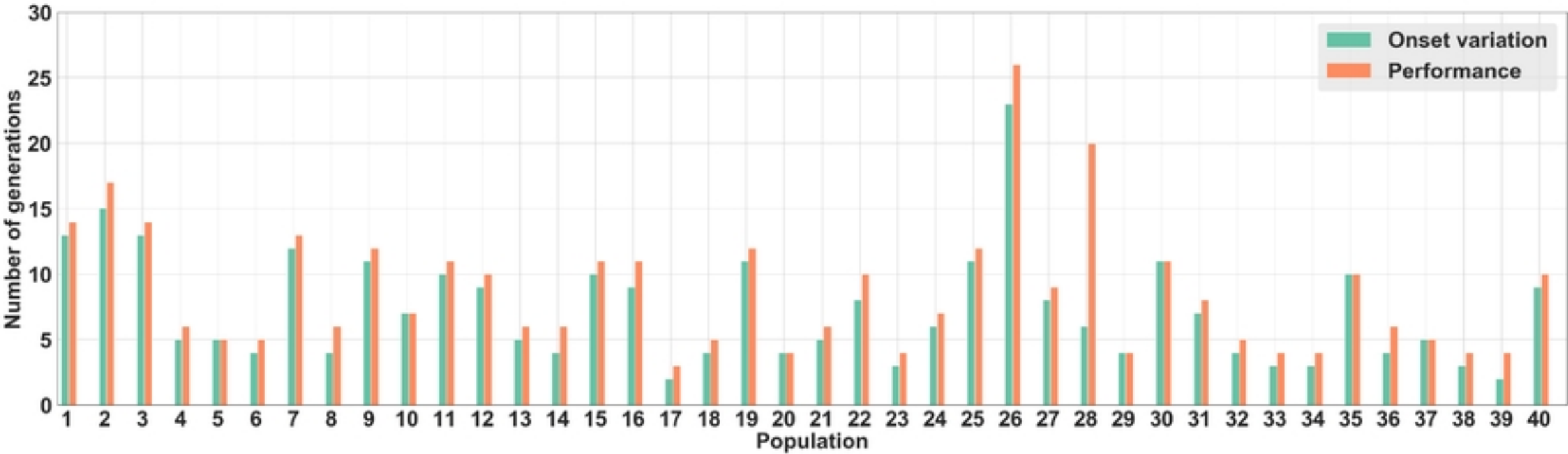


Fig 5

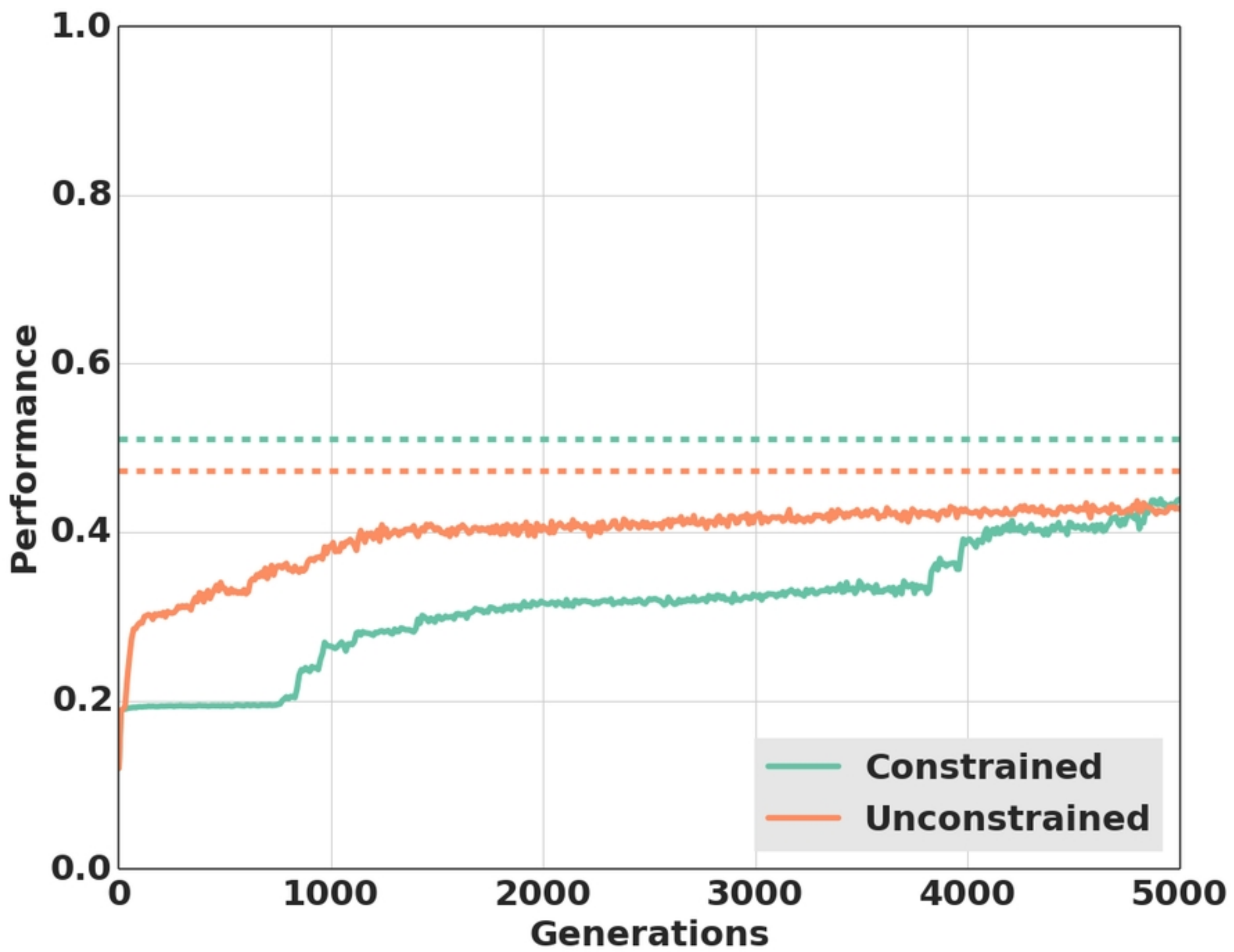


Fig 6