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Which conditions promote negative density dependent selection on prey aggregations?

Colin R. Tosh

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1 **Which conditions promote negative density dependent selection on prey**
2 **aggregations?**

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5 Colin R. Tosh

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9 School of Biology, Room 5.67, Ridley Building 2, Newcastle University, Newcastle

10 Upon Tyne NE1 7RU, UK

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12 E-mail: colin.tosh@ncl.ac.uk

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25 Negative density dependent selection on individuals in prey aggregations (negative
26 DDS, the preferential selection by predators of spatially isolated prey) is assumed to
27 contribute in many cases to the evolution and maintenance of aggregation. Both
28 positive and negative DDS on prey groups have been documented in nature but there
29 is no existing framework to predict when each of these forms of natural selection is
30 most likely. By exploiting the tendency of artificial neural networks to exhibit
31 consumer-like emergent behaviours, I isolate at least two environmental factors
32 impinging on the consumer organism that may determine which form of density
33 dependent natural selection is shown: the distribution of prey group size attacked by
34 the predator and the spatial conformation (dispersed or compacted) of the prey group.
35 Numerous forms of DDS on artificial prey (positive, negative, and non DDS) are
36 displayed through different combinations of these factors. I discuss in detail how the
37 predictions of the model may be tested by empiricists in order to assess the usefulness
38 of the framework presented. I stress the importance of understanding DDS on prey
39 groups given the recent emergence of these systems as test beds for ideas on
40 biological self-organisation.

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50 Introduction

51 Selection by predators of individuals from high (positive DDS) or low (negative
52 DDS) density areas of a prey group is assumed to contribute to the evolutionary
53 dynamics of an aggregation's spatial form, with negative DDS contributing to
54 evolution and maintenance of aggregation (Hamilton 1971; Milinski 1977; Krause &
55 Ruxton 2002; Stankowich 2003; Morrell & James 2008; Ioannou et al. 2009). Both
56 positive and negative DDS on prey groups are documented in nature (see above refs.)
57 but we have little idea of the conditions that favour the operation of these different
58 types of natural selection. Understanding this is important for two reasons. Firstly,
59 prey groups are a fundamental part of many animal communities (Fryxell et al. 2007)
60 and many of the best know examples of the demise of animal species apply to large
61 groups of prey (Branch 1929). It is necessary to understand the forms of natural
62 selection imposed on prey aggregations to promote their conservation. Secondly, prey
63 groups have recently become something of a test bed for ideas on the maintenance
64 (Couzin et al. 2002; Ballerini et al. 2008) and evolution (Hamilton 1971; Wood et al.
65 2007) of biological self-organisation. Studies of the evolution of self-organisation in
66 animal groups (Hamilton 1971; Wood et al. 2007) have assumed random selection of
67 prey but, as aforementioned, this is usually not the case in nature. Inevitably, further
68 progress in this area will require a framework for understanding the various forms of
69 DDS imposed on prey animal groups.

70 In this article I analyse the emergent behaviours of artificial neural networks in
71 an attempt to understand some of the dynamics of natural selection on resource
72 organisms (e.g. prey) that may arise from the interaction of consumer organism (e.g.
73 predator), resource group, and key ecological variables associated with this type of
74 system. I and colleagues have successfully modelled the behaviour of consumer

75 organisms using these models in numerous previous studies (see Tosh et al. 2009 and
76 refs. therein) and the tendency of these models to produce consumer-like behaviour is
77 well known (reviewed in Enquist and Ghrilanda 2005; McClelland and Rogers 2003).
78 Nevertheless, as used here, these models are a very simplified and abstracted
79 representation of organic information processing and decision making, and in the
80 discussion of the article I emphasise the need for empirical testing of the predictions
81 arising from the present article and outline how this can be achieved by empiricists. In
82 this article I examine the dynamics of DDS on artificial prey groups emerging from
83 artificial neural networks in relation to two key ecological variables associated with
84 predator prey-group systems: the spatial conformation of the prey group (i.e. the
85 shape of each group – dispersed or compacted) and the statistical distribution of prey
86 group size attacked by predators. I present simple feedforward neural networks with
87 compacted and dispersed artificial prey groups whose size distribution varies
88 according to naturally observed distributions of prey group size attacked by predators.
89 Put another way, a group of a specific size can be compact or dispersed, and size of
90 these groups varies according to different statistical distributions. Networks are
91 trained to optimise strike success on individual prey within the group but are
92 undirected with regard to strategy. Behaviour of the networks is then tested on a
93 separate set of groups, both dispersed and compacted, but standardised with regard to
94 group size distribution. During this testing phase numerous forms of DDS on prey
95 emerge from the system, all of which have been observed in real predator-prey group
96 systems. The presence of ‘consumer’ and ‘resource aggregation’ in the model
97 presented here and the emergence of numerous well documented forms of natural
98 selection from it, indicate that the model could provide a useful framework for

99 understanding and predicting the forms of natural selection imposed on prey groups
100 by predatory animals.

101 Essentially what I am proposing in this paper is that patterns of visual
102 attention and consequent prey preference of predatory animals can arise as an
103 emergent property of their neural information processing systems. Prey preferences
104 that are evolved are efficient (perhaps optimal), as networks are trained to maximise
105 prey capture, but there are thousands of similarly efficient solutions available and the
106 one chosen is simply a function of biases associated with neural information
107 processing in the predator.

108

109 **Materials and Methods**

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111 The network used (fig. S3) was a 3-layer (5x5, 3x4, 1x5) feed-forward network with
112 binary, stochastic artificial neurons (see Electronic Supplementary Information), fully
113 interconnected adjacent layers, and trainable bias weights in the hidden and output
114 layers. Resources in the resource group produced an output of '1' from each of the
115 layer 1 (network input) elements on which they were projected. Background areas in
116 the resource group produced an output of '0'. The five-element output layer produced
117 a maximum of 32 binary codes, five of which were redundant and selected against
118 during training (see below). The remaining 25 codes represented elements of the 5x5
119 input layer. Thus, stimulation of the input surface led to the output of one of these 25
120 codes. The element that was represented by this code was identified, and presence or
121 absence of a resource projected onto that element was determined. The stimulus
122 input-behavioural output sequence just described was designated 'successful' if a
123 resource was projected onto the chosen input element and 'unsuccessful' if

124 background was projected onto that element. This designation forms the basis of
125 training (below). Strictly speaking, within the proposed ecological context of the
126 model, the system represents information processing and decision making after
127 recognition of the prey group by the predatory organism. Different assumptions
128 regarding predator recognition of prey groups are, however, introduced into the model
129 through exposure of networks to different distributions of group size (below). It is
130 assumed that prey selected are always successfully captured and I do not consider the
131 potential effects of motor inefficiency / successful evasion by prey on the evolution of
132 prey selection behaviour in predators. Perfect accuracy is probably not a bad
133 assumption for systems where the predator is more mobile than the prey, and future
134 work is planned to thoroughly investigate the importance of accuracy on the observed
135 effects in this study.

136 Training was accomplished using a simple genetic algorithm in which 30
137 networks were run in each generation and all weights of the top performing five nets
138 were mutated by ± 0.05 (sign random) and cloned six times to form the next
139 generation of networks. Networks weights were initiated from a uniform random
140 distribution between -1 and 1. Five thousand 5x5 arrays, each containing a single
141 resource group (represented by a pattern of 1s – resources – and 0s – background),
142 were input into each network in each generation and the performance of each net at
143 the end of each generation was determined through summation of the following scores
144 over the 5000 inputs: resource selected = 1, background selected = -0.2, redundant
145 code output = -0.2. These scores assume that capturing of a prey item by a predator
146 makes a positive contribution to fitness and selecting and attempting to capture a
147 resource from an empty area makes a small negative contribution to fitness. Training
148 was run for 1000 generations. Finally, because it was observed that training on the

149 same set of inputs could lead to fundamentally different terminal network behaviour
150 (Tosh & Ruxton 2007), all training procedures described were repeated 100 times.

151 The distribution of resource group size within the 5000 training arrays was
152 varied. While the distribution of animal group size in nature often follows a power
153 law with exponent of around -1.5 (Bonabeau et al. 1999), the distribution of prey
154 groups actually attacked by predators (a function of raw group size distribution and
155 predator group recognition capabilities; a measure more appropriate to the present
156 model) varies considerably. Negative, positive and neutral relationships have all been
157 reported (Lindstrom 1989; Cresswell 1994). Here I considered distributions at the
158 extremes and centre of possibilities by running a power law distribution with an
159 exponent of -1.5 (assuming all groups are recognised and attacked), a flip of this
160 relationship (assuming mostly large groups are recognised and attacked), and a
161 uniform distribution of group sizes (recognition and attack somewhere in-between the
162 previous two scenarios) (range 1-25 individuals per group, fig. S1A-C, and see
163 Electronic Supplementary Information).

164 ‘Dispersal’ of resource groups was achieved simply by spatially random
165 placement of all resources within each of the 5000 input arrays. ‘Compaction’ was
166 achieved using an accretion algorithm: the position of the first resource in the group
167 was spatially random. The next resource was placed in the position that maximised
168 the number of resources surrounding it (in the 8-element ring surrounding the
169 individual). If more than one position within the array satisfied this criterion, position
170 within legitimate elements was random. Further elements were filled identically to the
171 second.

172 After training, the behavioural preference of networks for different density
173 types of resource (defined here as the number of other prey surrounding an individual

174 prey animal) was tested. A separate set of groups was created, both dispersed and
175 compacted but standardised with regard to group size distribution(a uniform
176 distribution of group size was used; distribution used for behavioural testing is
177 arbitrary and qualitative model predictions are not sensitive to this arbitrary choice).
178 Only three density types were considered to simplify analysis: low (surrounded by 6-8
179 empty spaces on the network input surface), intermediate (surrounded by 3-5 empty
180 spaces on the network input surface) and high (surrounded by 0-2 empty spaces on the
181 network input surface) density types (see fig. S3). Twenty five sets of 1000 input
182 arrays were created. The first set contained a single resource in each array (a group
183 size of one), the second set two resources in each array (a group size of two), and so
184 on, up to a group size of 25. Each set of input arrays was passed through each of the
185 30 networks after the final generation of training. For each input set, the total number
186 of hits on resources (1s) of a given density type (A_d), the total number of hits on
187 resources of all density types (A_t), the expected (assuming random strike across
188 30,000 presentations) number of hits on resources of a given density type (E_d), and the
189 expected number of hits on resources of all density types (E_t), was determined.
190 ‘Positive behavioural preference’ was defined as $(A_d / A_t) > (E_d / E_t)$. The influence of
191 an alternative definition is considered in the Electronic Supplementary Information.
192 The number of positive behavioural preferences for each resource density type over
193 the 100 repeats of training was plotted against set of input arrays (resource group size)
194 in figs. 1, 2, and 3. Note that while training included resource selections from all
195 elements of the visual field, behavioural testing only considered selections within the
196 inner 3x3 area, to avoid ambiguities in defining density type associated with the edge
197 of the visual field.
198

199 **Results**

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201 This results section only presents a small proportion of the extensive results in full
202 (figs 1, 2, and 3), in order to assist understanding and interpretation. The full results are
203 summarised in fig. 4 and readers are directed to the Electronic Supplementary
204 Information for a detailed description of all the results summarised in fig. 4. Fig. 1
205 shows an example of positive DDS for one combination of three model parameters:
206 (resource groups dispersed during training, dispersed during behavioural testing, and
207 group size following a power law with exponent -1.5 during training). By looking
208 down the dashed lines in fig. 1 it can be seen that when low and intermediate resource
209 density types are equally abundant in the behavioural testing groups (leftmost line) the
210 networks have a preference for the intermediate density types. When intermediate and
211 high density types are equally abundant (rightmost line) the networks have a
212 preference for the high density resource types. Fig. 2 shows an example of negative
213 DDS when one of the three parameters is changed: (resource groups dispersed during
214 training, dispersed during behavioural testing, and group size following a *uniform*
215 *distribution* during training). By looking down the dashed lines in fig. 2 it can be seen
216 that when low and intermediate resource density types are equally abundant in the
217 behavioural testing groups (leftmost line) the networks have a preference for the low
218 density types. When intermediate and high density types are equally abundant
219 (rightmost line) the networks have a preference for the intermediate density resource
220 types. Fig. 3 shows a parameter combination (resource groups dispersed during
221 training, compacted during behavioural testing, and group size following a power law
222 with exponent -1.5 during training) leading to weak DDS relative to other parameter
223 combinations. Network preference for the different density types (part B) does not

224 change much (relative to other parameter combinations, Figs. 1, 2, S1, and S2)
225 regardless of the incidence of density types in the behavioural testing groups (part A).
226 The results shown in figs. 1-3 are summarised in elements 1,1, 1,2, and 1,4 of fig. 4.
227 Fig. 4 shows the form of DDS expressed for all parameter combinations considered.
228 The other data summarised in this fig. is presented in full and can be interpreted as
229 described here in figs. S1 and S2 of the Electronic Supplementary Procedures.

230 Further analyses, including a dissection of mechanisms underlying selected
231 phenomena described, a description of more complex training scenarios, and further
232 discussion of the implications of model output can also be found in the Electronic
233 Supplementary Information.

234

235 **Discussion**

236

237 Accepting the inherent limitations of this highly simplified model and the need for
238 empirical validation of it (see below), let us ask: what does the model presented in
239 this article tell us about natural selection imposed by simple artificial neural networks
240 on aggregated resource groups and what might be biological analogies of these
241 phenomena? Firstly, it appears that experience during ‘training’ and not subsequent
242 behavioural testing is important in determining the form of DDS imposed on resource
243 aggregations (fig. 4). In fig. 4 patterns of DDS on artificial prey are similar within
244 treatments where groups were dispersed or compacted during training but quite
245 different between these treatments and, generally, group conformation during
246 behavioural testing makes little difference to the pattern of natural selection imposed.
247 While the model uses an evolutionary algorithm to optimise networks during training,
248 I make no distinction between evolution of behaviour and within-lifetime learning as

249 an analogy of training. The performance surface of a neural network (the multivariate
250 relationship between network weights and task efficiency) is determined by the task at
251 hand, network architecture, and the functions chosen to embody artificial neurons.
252 The optimisation algorithm simply traverses this surface and evolutionary and
253 ontogenetic optimisation methods will ideally reach the same point on the surface.
254 This claim is consistent with empirical data, which show no intrinsic difference in
255 generalization behaviour for innately recognized stimuli vs. recognition resulting from
256 individual experience (Ghirlanda & Enquist 2003). The prediction that ‘training’ is
257 important in determining the form of DDS imposed on resource aggregations
258 indicates that in consumers that learn little during their lifetime, their evolutionary
259 experience of resources aggregations and not experience during any one lifetime will
260 determine the type of DDS they impose on resource aggregations. In consumers that
261 learn during their lifetime through experience with resource aggregations, it is
262 expected that their within-lifetime history of experience rather than the conformation
263 of any new group encountered will determine the type of DDS they impose. Secondly,
264 the model indicates that evolution of resource aggregation through predator pressure
265 (via negative DDS) is not expected to occur when the distribution of resource group
266 size experienced and processed by the predator nervous system follows a power law
267 with an exponent of -1.5 (fig. 4). In fig. 4 negative DDS is completely absent when
268 networks are trained with this group size distribution. In prey where the raw
269 distribution of group size follows this distribution (Bonabeau et al. 1999), it will be
270 necessary that the smallest resource groups are not recognised by the predator in order
271 for negative DDS and so evolution of aggregation to occur. It should be noted that the
272 first and second predictions above are explicit and amenable to empirical testing.
273 Thirdly, a dynamic for the evolution of resource aggregation through predator

274 pressure is suggested. The presumed conditions for the evolution of aggregation
275 (negative DDS: preferential selection of spatially isolated individuals) does not occur
276 under any circumstances when networks train on compacted resource groups. It only
277 occurs when network train on dispersed groups and even then under a restricted set of
278 circumstances (fig. 4). This indicates that evolution of aggregation from initially
279 dispersed groups through predator pressure will not occur indefinitely to produce
280 extremely compacted aggregations, but rather evolution will proceed until a sufficient
281 level of compaction occurs to terminate the operation of negative DDS, after which it
282 will stop. As selection on compacted groups tends to be positive DDS (fig. 4) one can
283 also envisage how this terminal process could lead to a cyclical evolutionary dynamic
284 of group compaction and dispersal. Fourthly, an alteration in the form of natural
285 selection imposed by predators on aggregated prey is predicted in response to
286 anthropomorphic influences on prey. Mean prey group size is positively related to
287 population density in many prey organisms forming unstable groups (see refs. in
288 Pepin & Gerard 2008). Depletion of prey numbers through human influences is,
289 therefore, likely to change the distribution of group size detected and processed by the
290 predator and so alter the selective regime imposed by it on prey in aggregations (fig.
291 4).

292 Although I have termed the manipulations carried out on resource groups
293 within simulations, ‘changes in the spatial conformation of resource groups’, similar
294 changes in the projection onto the visual sensory surface could be obtained by
295 viewing the same resource group at a different distance. A resource group viewed
296 close up is heterogeneous-looking, like the dispersed groups in the result section, and
297 a resource group viewed at a distance looks like the compacted groups. ‘Spatial
298 conformation’ can, therefore, be considered synonymous with the spatial scale at

299 which a resource group is viewed by the consumer organism. It is within this context
300 that recent empirical results consistent with model output are presented. Ioannou et al.
301 (2009) analysed the behaviour of stickleback fish predating *Daphnia* waterfleas and
302 found that at a distance there is selection on the fish to select fleas in spatially dense
303 regions of the swarm while closer up there is selection to select fleas from less dense
304 areas. These results are consistent with simulations, where selection of resources in
305 dense regions of the group predominates when training is on ‘compacted’ (distant)
306 groups and selection of low density type resources predominates when training is on
307 ‘dispersed’ (close) resources (fig. 4). Another approach colleagues and I have
308 previously used to test neural network models of behaviour (Ruxton et al. 2007) is the
309 use of interactive computer games with humans. To test the present model it would be
310 necessary to assume that the use of an evolutionary training algorithm as in the
311 present study is irrelevant and the same result could be produced by an ontogenetic
312 algorithm (discussed above). A game could be developed that is entirely analogous to
313 procedures within the present modelling study. It could comprise a presentation phase
314 with different resource group configurations and distributions of group size, in which
315 users train to increase their efficiency of resources capture, and a testing phase in
316 which preference for resources with different density type is quantified. There is also
317 potential to modify the protocols of Ioannou et al. (2009) with sticklebacks and
318 waterfleas in order to test the predictions of the model.

319 The model presented here is relatively simple (compared to many other
320 simulations of biological complex systems) and I have tried to investigate some
321 parameters space both in the main results and in Electronic Supplementary
322 Information. Nevertheless, due to time and computing limitations, some aspects of the
323 model are not investigated. These include the influence of artificial neuron

324 characteristics and network architecture. It is possible that varying these could affect
325 the results significantly, however, the results presented represent the first and only
326 values/characteristics chosen for these invariant model parameters at the beginning of
327 simulations. This fact coupled with the robustness of results and the demonstration of
328 biologically interesting phenomena across a wide area of the parameter space
329 investigated, leads me to be optimistic that results of biological interest would remain
330 across a significant proportion of this additional parameter space.

331 This study is part of a wider research program investigating the nature of the
332 evolution of self-organised systems, of which self-organised animal groups have
333 become a model system. Couzin et al. (2002) developed a now widely used model of
334 self-organising fish shoals that, given the number and specificity of shoal behaviours
335 it can reproduce, undoubtedly captures essential elements of these systems. Wood and
336 Ackland (2007) subject this model to evolution by introducing predators that
337 approached and removed individuals prey essentially at random. They demonstrated
338 both the evolution of aggregation and some group-level evasion behaviours. The next
339 stage in this research program is to subject the self-organised prey group to predation
340 that is discriminating with regard to prey individuals chosen. A fully validated version
341 of the model presented in this article is a possible candidate for introduction of
342 predator discrimination. The present study indicates that, just like the group-level
343 behaviours of self-organised shoals, patterns of natural selection imposed on resource
344 aggregation may arise as an emergent property of interactions between interacting
345 agents (neurons) in a complex system.

346

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349

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422 Figure 1. An example of positive DDS for one combination of three model parameter
423 (see plot header). By looking down the dashed lines it can be seen that when low and
424 intermediate resource density types are equally abundant in the behavioural testing
425 groups (leftmost line) the networks have a preference for the intermediate density
426 types. When intermediate and high density types are equally abundant (rightmost line)
427 the networks have a preference for the high density resource types. Data was excluded
428 from graphs in figs. 1, 2, and 3 when fewer than 60 of the 100 training replicates
429 showed an expected number of strikes on the resource type under consideration of
430 less than 20 (results are not sensitive to this criterion, see Electronic Supplementary
431 Information).

432

433 Figure 2. An example of negative DDS when one of the three model parameters in
434 fig. 1 (group size distribution during training) is changed (see plot header). By
435 looking down the dashed lines it can be seen that when low and intermediate resource
436 density types are equally abundant in the behavioural testing groups (leftmost line) the
437 networks have a preference for the low density types. When intermediate and high
438 density types are equally abundant (rightmost line) the networks have a preference for
439 the intermediate density resource types. Data was excluded from graphs in figs. 1, 2,
440 and 3 when fewer than 60 of the 100 training replicates showed an expected number
441 of strikes on the resource type under consideration of less than 20 (results are not
442 sensitive to this criterion, see Electronic Supplementary Information).

443

444 Figure 3. A parameter combination leading to weak DDS relative to other parameter
445 combinations. Network preference for the different density types (part B) does not
446 change much (relative to other parameter combinations, Figs. 1, 2, S1, and S2)

447 regardless of the incidence of density types in the behavioural testing groups (part A).
448 Data was excluded from graphs in figs. 1, 2, and 3 when fewer than 60 of the 100
449 training replicates showed an expected number of strikes on the resource type under
450 consideration of less than 20 (results are not sensitive to this criterion, see Electronic
451 Supplementary Information).

452

453 Figure 4. A summary of the forms of DDS expressed for all parameter combinations
454 considered. Effects illustrated in figs. 1, 2, and 3 are elements 1,1, 1,2, and 1,4 of the
455 figure. A full, detailed description of the results summarised here can be found in the
456 Electronic Supplementary Information.

457

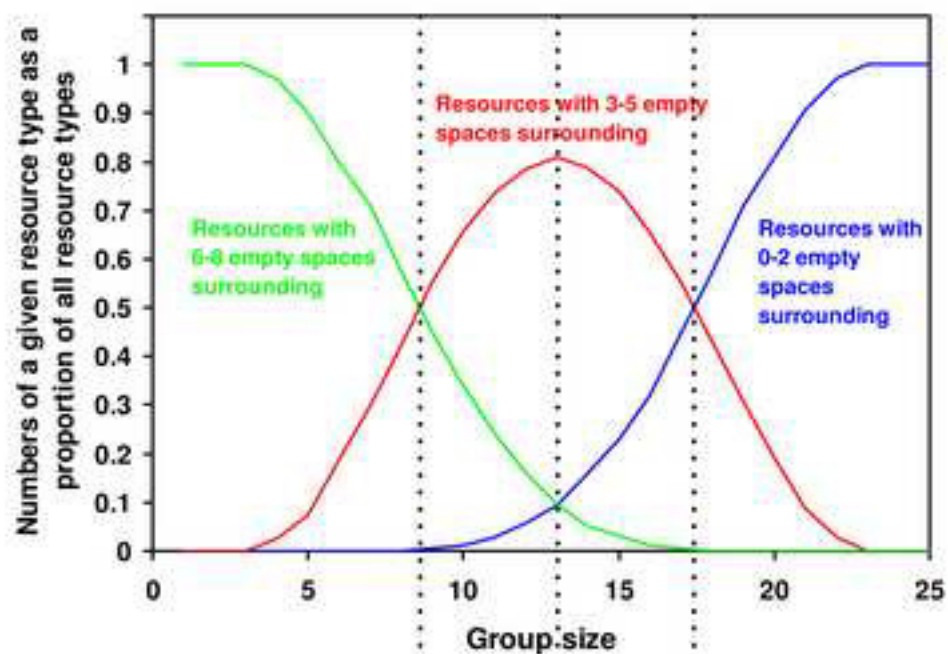
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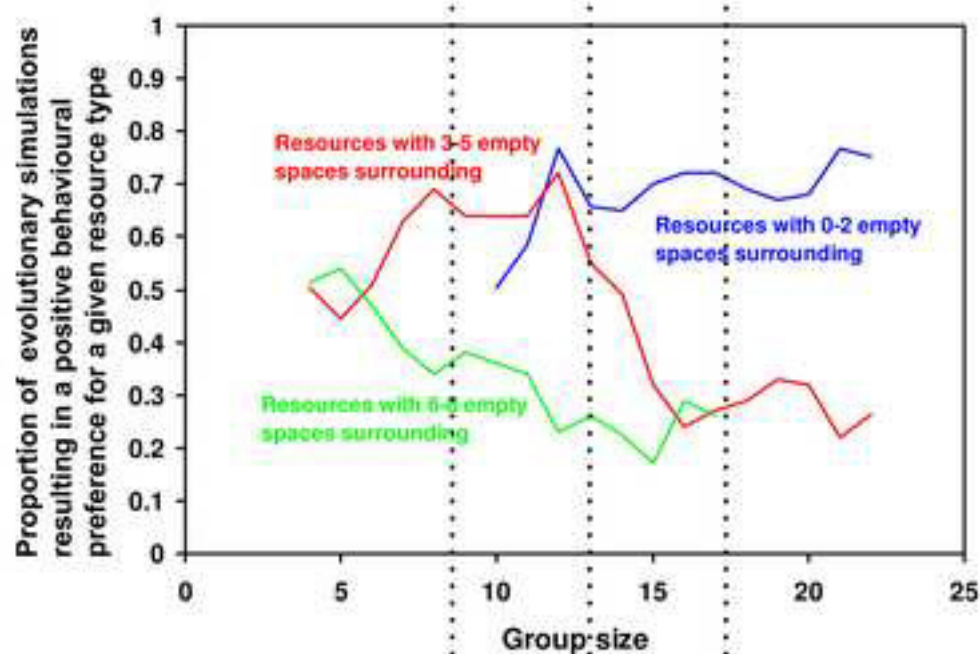
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Spatial conformation of resource groups during training: dispersed
 Spatial conformation of resource groups during behavioural testing: dispersed
 Distribution of group size during training: Power law, exponent = -1.5

Part A) Distribution of resource density types in behavioural testing groups

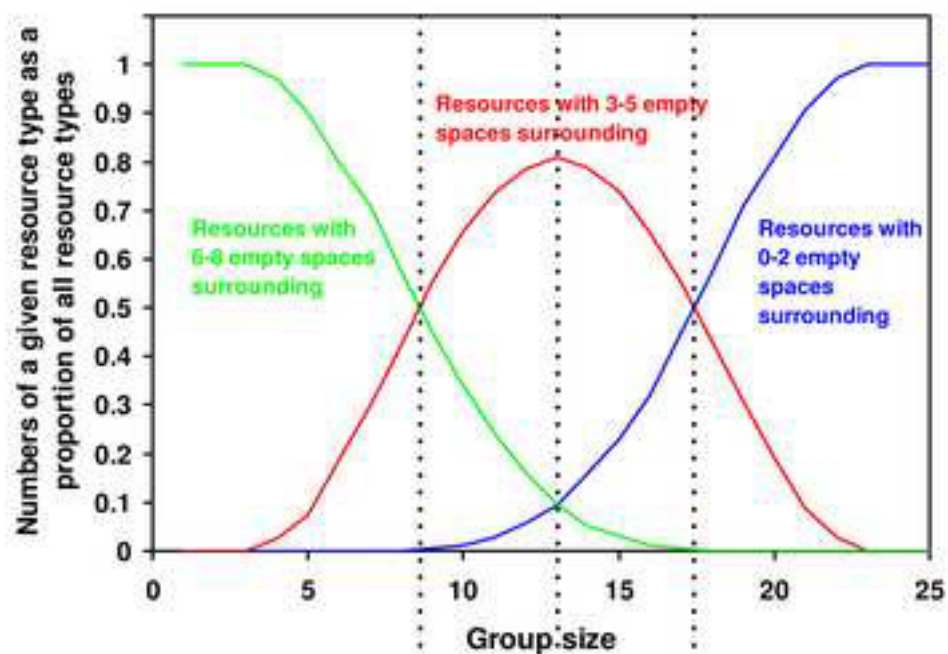


Part B) Preference for different resource density types during behavioural testing

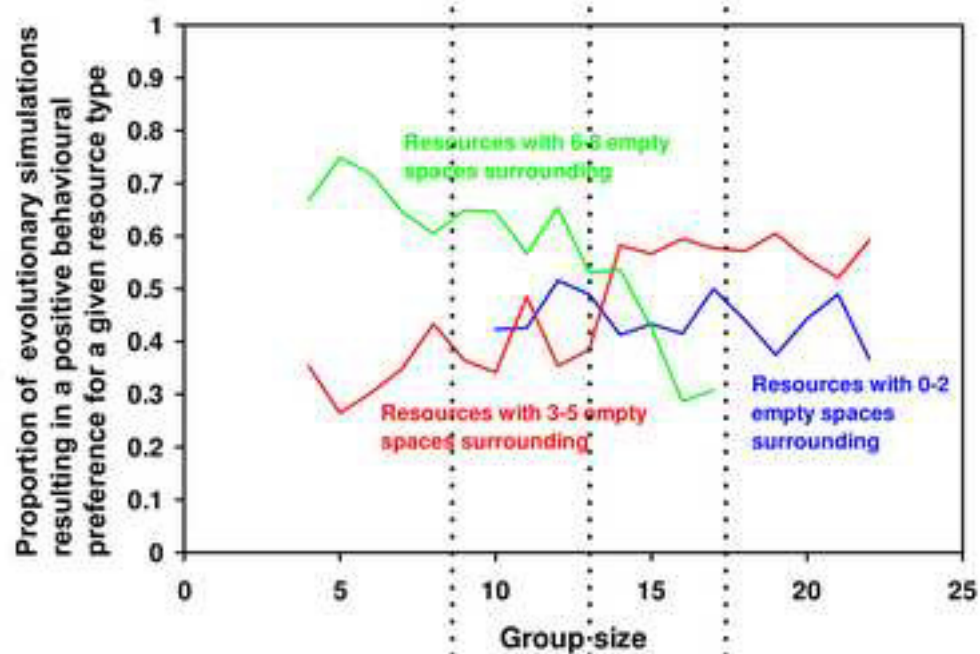


Spatial conformation of resource groups during training: dispersed
 Spatial conformation of resource groups during behavioural testing: dispersed
 Distribution of group size during training: uniform distribution

Part A) Distribution of resource density types in behavioural testing groups

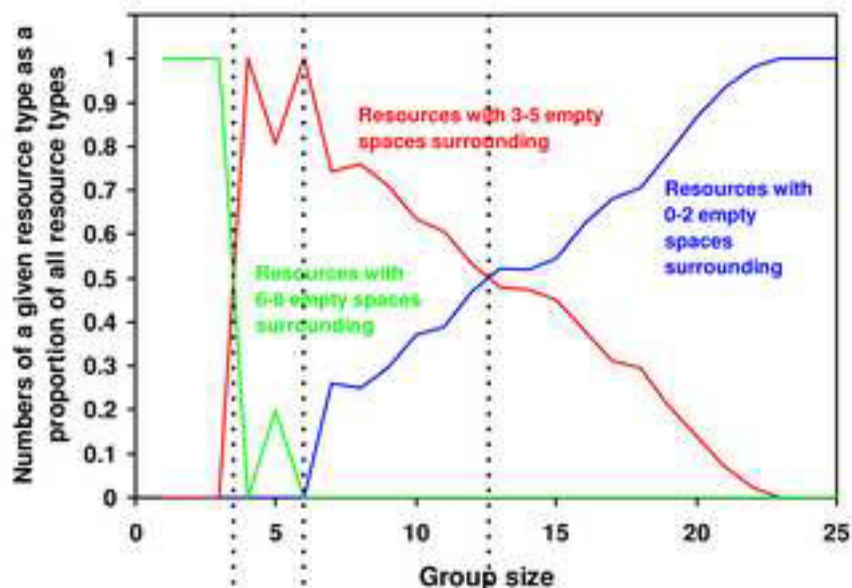


Part B) Preference for different resource density types during behavioural testing

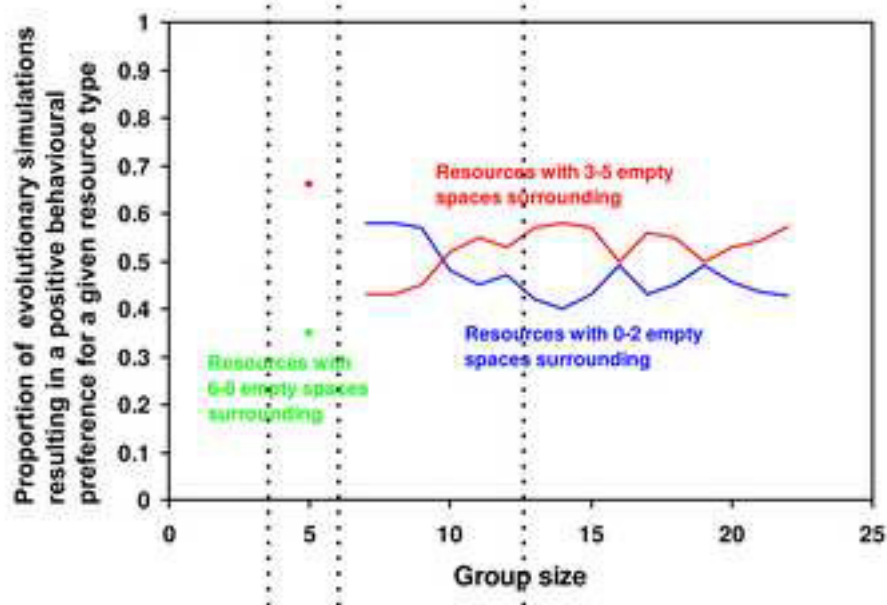


Spatial conformation of resource groups during training: dispersed
 Spatial conformation of resource groups during behavioural testing: compacted
 Distribution of group size during training: Power law, exponent = -1.5

Part A) Distribution of resource density types in behavioural testing groups



Part B) Preference for different resource density types during behavioural testing



	Resource group dispersed during training and dispersed during behavioural testing	Resource group compacted during training and compacted during behavioural testing	Resource group compacted during training and dispersed during behavioural testing	Resource group dispersed during training and compacted during behavioural testing
Distribution of resource group size during training: power law with exponent -1.5	Positive DDS	Positive DDS	Positive DDS	DDS weak
Distribution of resource group size during training: uniform	Negative DDS	Positive DDS	Positive DDS	Negative DDS
Distribution of resource group size during training: flip of power law with exponent -1.5	Negative DDS	Positive DDS	Positive DDS	Negative DDS

461 I analyse the behaviour of artificial neural networks in the context of predator – prey
462 interactions.
463 Networks subject to undirected training impose numerous forms of DDS on artificial
464 prey groups.
465 The study provides an empirically testable framework.
466 It could allow prediction of the forms of natural selection imposed by predators on
467 prey groups.
468

Accepted manuscript