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Which conditions promote negative density dependent selection on prey aggregations?

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

Introduction

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

In this article I analyse the emergent behaviours of artificial neural networks in an attempt to understand some of the dynamics of natural selection on resource organisms (e.g. prey) that may arise from the interaction of consumer organism (e.g. predator), resource group, and key ecological variables associated with this type of system. I and colleagues have successfully modelled the behaviour of consumer organisms using these models in numerous previous studies (see Tosh et al. 2009 and refs. therein) and the tendency of these models to produce consumer-like behaviour is well known (reviewed in Enquist and Ghrilanda 2005; McClelland and Rogers 2003). Nevertheless, as used here, these models are a very simplified and abstracted representation of organic information processing and decision making, and in the discussion of the article I emphasise the need for empirical testing of the predictions arising from the present article and outline how this can be achieved by empiricists. In this article I examine the dynamics of DDS on artificial prey groups emerging from artificial neural networks in relation to two key ecological variables associated with predator prey-group systems: the spatial conformation of the prey group (i.e. the shape of each group – dispersed or compacted) and the statistical distribution of prey group size attacked by predators. I present simple feedforward neural networks with compacted and dispersed artificial prey groups whose size distribution varies according to naturally observed distributions of prey group size attacked by predators. Put another way, a group of a specific size can be compact or dispersed, and size of these groups varies according to different statistical distributions. Networks are trained to optimise strike success on individual prey within the group but are undirected with regard to strategy. Behaviour of the networks is then tested on a separate set of groups, both dispersed and compacted, but standardised with regard to group size distribution. During this testing phase numerous forms of DDS on prey emerge from the system, all of which have been observed in real predator-prey group systems. The presence of ‘consumer’ and ‘resource aggregation’ in the model presented here and the emergence of numerous well documented forms of natural selection from it, indicate that the model could provide a useful framework for understanding and predicting the forms of natural selection imposed on prey groups by predatory animals.

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

Materials and Methods

The network used (fig. S3) was a 3-layer (5x5, 3x4, 1x5) feed-forward network with binary, stochastic artificial neurons (see Electronic Supplementary Information), fully interconnected adjacent layers, and trainable bias weights in the hidden and output layers. Resources in the resource group produced an output of ‘1’ from each of the layer 1 (network input) elements on which they were projected. Background areas in the resource group produced an output of ‘0’. The five-element output layer produced a maximum of 32 binary codes, five of which were redundant and selected against during training (see below). The remaining 25 codes represented elements of the 5x5 input layer. Thus, stimulation of the input surface led to the output of one of these 25 codes. The element that was represented by this code was identified, and presence or absence of a resource projected onto that element was determined. The stimulus input-behavioural output sequence just described was designated ‘successful’ if a resource was projected onto the chosen input element and ‘unsuccessful’ if background was projected onto that element. This designation forms the basis of training (below). Strictly speaking, within the proposed ecological context of the model, the system represents information processing and decision making after recognition of the prey group by the predatory organism. Different assumptions regarding predator recognition of prey groups are, however, introduced into the model through exposure of networks to different distributions of group size (below). It is assumed that prey selected are always successfully captured and I do not consider the potential effects of motor inefficiency / successful evasion by prey on the evolution of prey selection behaviour in predators. Perfect accuracy is probably not a bad assumption for systems where the predator is more mobile than the prey, and future work is planned to thoroughly investigate the importance of accuracy on the observed effects in this study.

Training was accomplished using a simple genetic algorithm in which 30 networks were run in each generation and all weights of the top performing five nets were mutated by ± 0.05 (sign random) and cloned six times to form the next generation of networks. Networks weights were initiated from a uniform random distribution between -1 and 1. Five thousand 5x5 arrays, each containing a single resource group (represented by a pattern of 1s – resources – and 0s – background), were input into each network in each generation and the performance of each net at the end of each generation was determined through summation of the following scores over the 5000 inputs: resource selected = 1, background selected = -0.2, redundant code output = -0.2. These scores assume that capturing of a prey item by a predator makes a positive contribution to fitness and selecting and attempting to capture a resource from an empty area makes a small negative contribution to fitness. Training was run for 1000 generations. Finally, because it was observed that training on the same set of inputs could lead to fundamentally different terminal network behaviour (Tosh & Ruxton 2007), all training procedures described were repeated 100 times.

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

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

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

Results

This results section only presents a small proportion of the extensive results in full (figs 1, 2, and 3), in order to assist understanding and interpretation. The full result are summarised in fig. 4 and readers are directed to the Electronic Supplementary Information for a detailed description of all the results summarised in fig. 4. Fig. 1 shows an example of positive DDS for one combination of three model parameter: (resource groups dispersed during training, dispersed during behavioural testing, and group size following a power law with exponent -1.5 during training). By looking down the dashed lines in fig. 1 it can be seen that when low and intermediate resource density types are equally abundant in the behavioural testing groups (leftmost line) the networks have a preference for the intermediate density types. When intermediate and high density types are equally abundant (rightmost line) the networks have a preference for the high density resource types. Fig. 2 shows an example of negative DDS when one of the three parameters is changed: (resource groups dispersed during training, dispersed during behavioural testing, and group size following a *uniform distribution* during training). By looking down the dashed lines in fig. 2 it can be seen that when low and intermediate resource density types are equally abundant in the behavioural testing groups (leftmost line) the networks have a preference for the low density types. When intermediate and high density types are equally abundant (rightmost line) the networks have a preference for the intermediate density resource types. Fig. 3 shows a parameter combination (resource groups dispersed during training, compacted during behavioural testing, and group size following a power law with exponent -1.5 during training) leading to weak DDS relative to other parameter combinations. Network preference for the different density types (part B) does not change much (relative to other parameter combinations, Figs. 1, 2, S1, and S2) regardless of the incidence of density types in the behavioural testing groups (part A). The results shown in figs. 1-3 are summarised in elements 1,1, 1,2, and 1,4 of fig. 4. Fig. 4 shows the form of DDS expressed for all parameter combinations considered. The other data summarised in this fig. is presented in full and can be interpreted as described here in figs. S1 and S2 of the Electronic Supplementary Procedures.

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

Discussion

Accepting the inherent limitations of this highly simplified model and the need for empirical validation of if (see below), let us ask: what does the model presented in this article tell us about natural selection imposed by simple artificial neural networks on aggregated resource groups and what might be biological analogies of these phenomena? Firstly, it appears that experience during ‘training’ and not subsequent behavioural testing is important in determining the form of DDS imposed on resource aggregations (fig. 4). In fig. 4 patterns of DDS on artificial prey are similar within treatments where groups were dispersed or compacted during training but quite different between these treatments and, generally, group conformation during behavioural testing makes little difference to the pattern of natural selection imposed. While the model uses an evolutionary algorithm to optimise networks during training, I make no distinction between evolution of behaviour and within-lifetime learning as an analogy of training. The performance surface of a neural network (the multivariate relationship between network weights and task efficiency) is determined by the task at hand, network architecture, and the functions chosen to embody artificial neurons. The optimisation algorithm simply traverses this surface and evolutionary and ontogenetic optimisation methods will ideally reach the same point on the surface. This claim is consistent with empirical data, which show no intrinsic difference in generalization behaviour for innately recognized stimuli vs. recognition resulting from individual experience (Ghirlanda & Enquist 2003). The prediction that 'training' is important in determining the form of DDS imposed on resource aggregations indicates that in consumers that learn little during their lifetime, their evolutionary experience of resources aggregations and not experience during any one lifetime will determine the type of DDS they impose on resource aggregations. In consumers that learn during their lifetime through experience with resource aggregations, it is expected that their within-lifetime history of experience rather than the conformation of any new group encountered will determine the type of DDS they impose. Secondly, the model indicates that evolution of resource aggregation through predator pressure (via negative DDS) is not expected to occur when the distribution of resource group size experienced and processed by the predator nervous system follows a power law with an exponent of -1.5 (fig. 4). In fig. 4 negative DDS is completely absent when networks are trained with this group size distribution. In prey where the raw distribution of group size follows this distribution (Bonabeau et al. 1999), it will be necessary that the smallest resource groups are not recognised by the predator in order for negative DDS and so evolution of aggregation to occur. It should be noted that the first and second predictions above are explicit and amenable to empirical testing. Thirdly, a dynamic for the evolution of resource aggregation through predator pressure is suggested. The presumed conditions for the evolution of aggregation (negative DDS: preferential selection of spatially isolated individuals) does not occur under any circumstances when networks train on compacted resource groups. It only occurs when network train on dispersed groups and even then under a restricted set of circumstances (fig. 4). This indicates that evolution of aggregation from initially dispersed groups through predator pressure will not occur indefinitely to produce extremely compacted aggregations, but rather evolution will proceed until a sufficient level of compaction occurs to terminate the operation of negative DDS, after which it will stop. As selection on compacted groups tends to be positive DDS (fig. 4) one can also envisage how this terminal process could lead to a cyclical evolutionary dynamic of group compaction and dispersal. Fourthly, an alteration in the form of natural selection imposed by predators on aggregated prey is predicted in response to anthropomorphic influences on prey. Mean prey group size is positively related to population density in many prey organisms forming unstable groups (see refs. in Pepin & Gerard 2008). Depletion of prey numbers through human influences is, therefore, likely to change the distribution of group size detected and processed by the predator and so alter the selective regime imposed by it on prey in aggregations (fig. 4).

Although I have termed the manipulations carried out on resource groups within simulations, ‘changes in the spatial conformation of resource groups’, similar changes in the projection onto the visual sensory surface could be obtained by viewing the same resource group at a different distance. A resource group viewed close up is heterogeneous-looking, like the dispersed groups in the result section, and a resource group viewed at a distance looks like the compacted groups. ‘Spatial conformation’ can, therefore, be considered synonymous with the spatial scale at which a resource group is viewed by the consumer organism. It is within this context that recent empirical results consistent with model output are presented. Ioannou et al. (2009) analysed the behaviour of stickleback fish predating *Daphnia* waterfleas and found that at a distance there is selection on the fish to select fleas in spatially dense regions of the swarm while closer up there is selection to select fleas from less dense areas. These results are consistent with simulations, where selection of resources in dense regions of the group predominates when training is on ‘compacted’ (distant) groups and selection of low density type resources predominates when training is on ‘dispersed’ (close) resources (fig. 4). Another approach colleagues and I have previously used to test neural network models of behaviour (Ruxton et al. 2007) is the use of interactive computer games with humans. To test the present model it would be necessary to assume that the use of an evolutionary training algorithm as in the present study is irrelevant and the same result could be produced by an ontogenetic algorithm (discussed above). A game could be developed that is entirely analogous to procedures within the present modelling study. It could comprise a presentation phase with different resource group configurations and distributions of group size, in which users train to increase their efficiency of resources capture, and a testing phase in which preference for resources with different density type is quantified. There is also potential to modify the protocols of Ioannou et al. (2009) with sticklebacks and waterfleas in order to test the predictions of the model.

The model presented here is relatively simple (compared to many other simulations of biological complex systems) and I have tried to investigate some parameters space both in the main results and in Electronic Supplementary Information. Nevertheless, due to time and computing limitations, some aspects of the model are not investigated. These include the influence of artificial neuron characteristics and network architecture. It is possible that varying these could affect the results significantly, however, the results presented represent the first and only values/characteristics chosen for these invariant model parameters at the beginning of simulations. This fact coupled with the robustness of results and the demonstration of biologically interesting phenomena across a wide area of the parameter space investigated, leads me to be optimistic that results of biological interest would remain across a significant proportion of this additional parameter space.

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

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

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

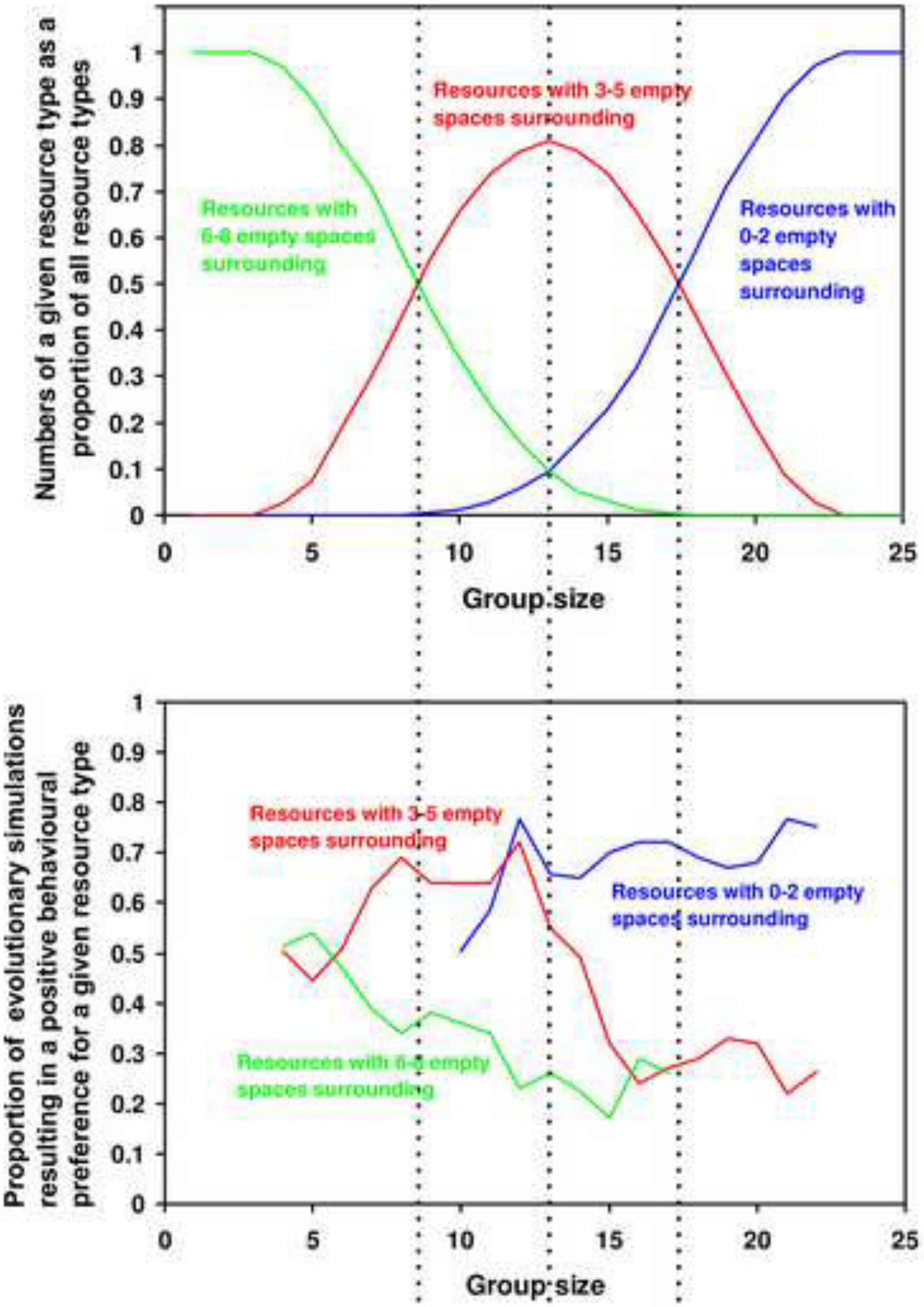
Figure 3. A parameter combination leading to weak DDS relative to other parameter combinations. Network preference for the different density types (part B) does not change much (relative to other parameter combinations, Figs. 1, 2, S1, and S2)

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

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

4. Figure

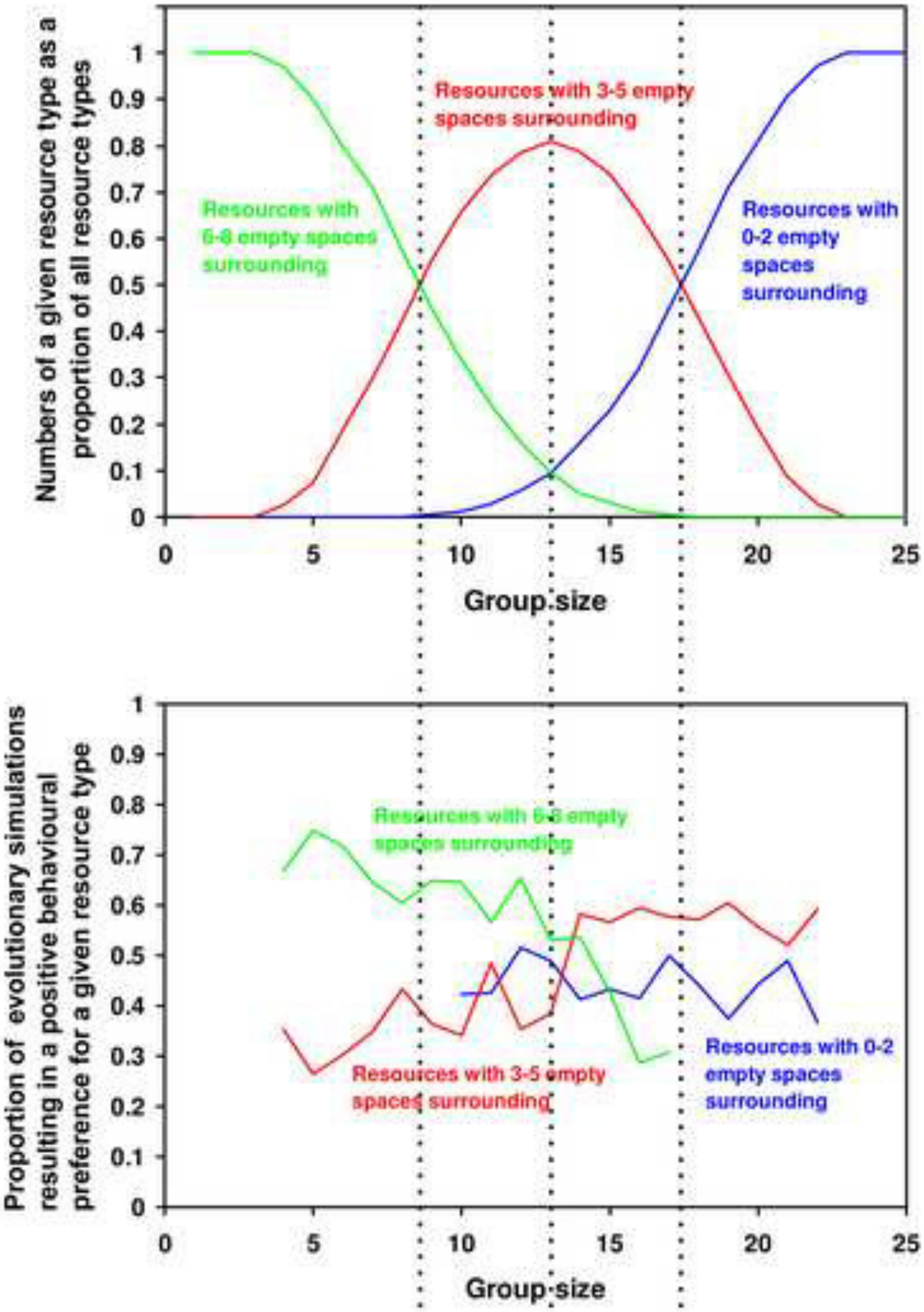
Spatial conformation of resource groups during training: dispersed
Spatial conformation of resource froups during behavioural testing: dispersed
Distribution of group size during training: Power law, exponent = -1.5



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

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

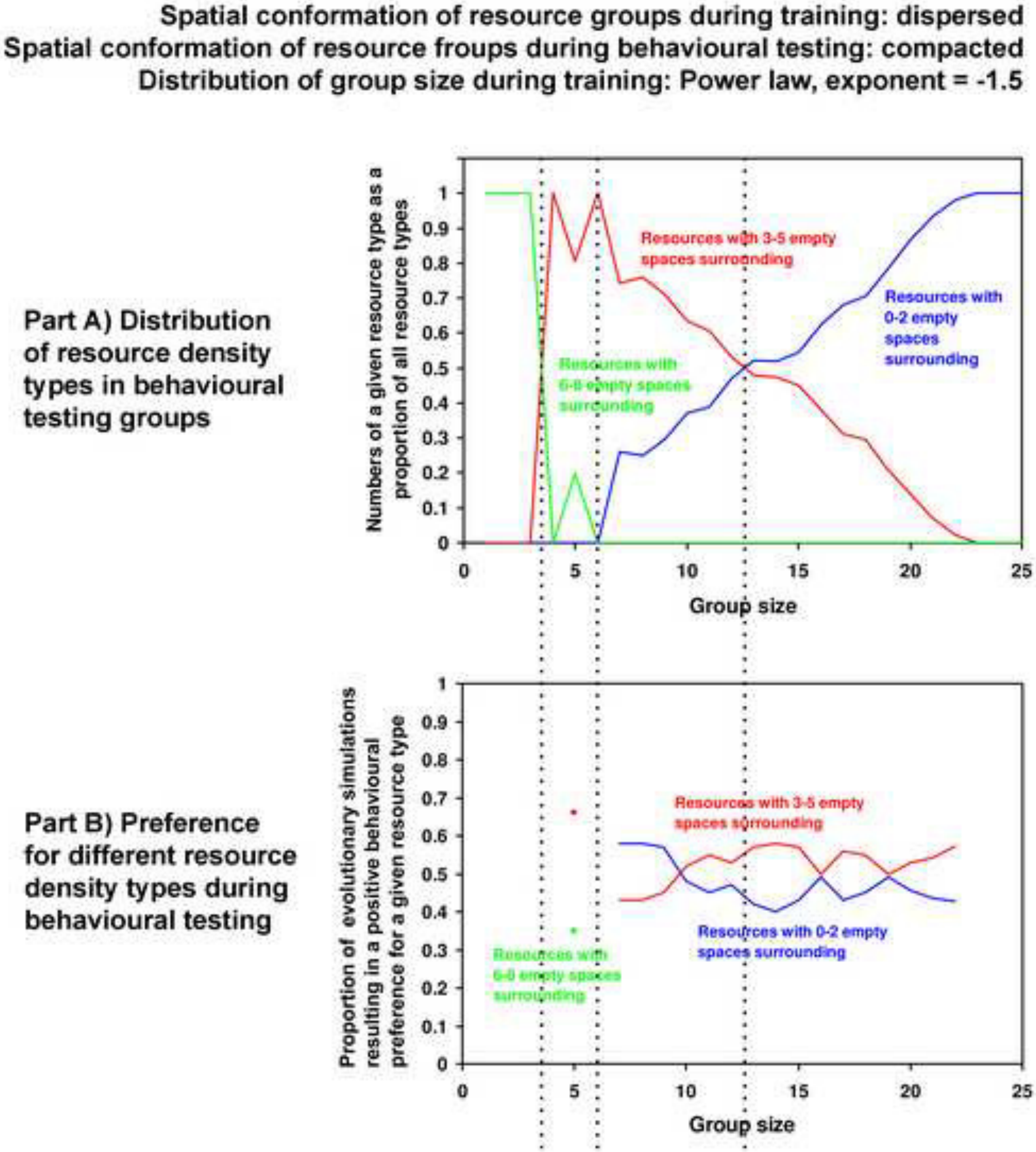
Spatial conformation of resource groups during training: dispersed
Spatial conformation of resource froups during behavioural testing: dispersed
Distribution of group size during training: uniform distribution



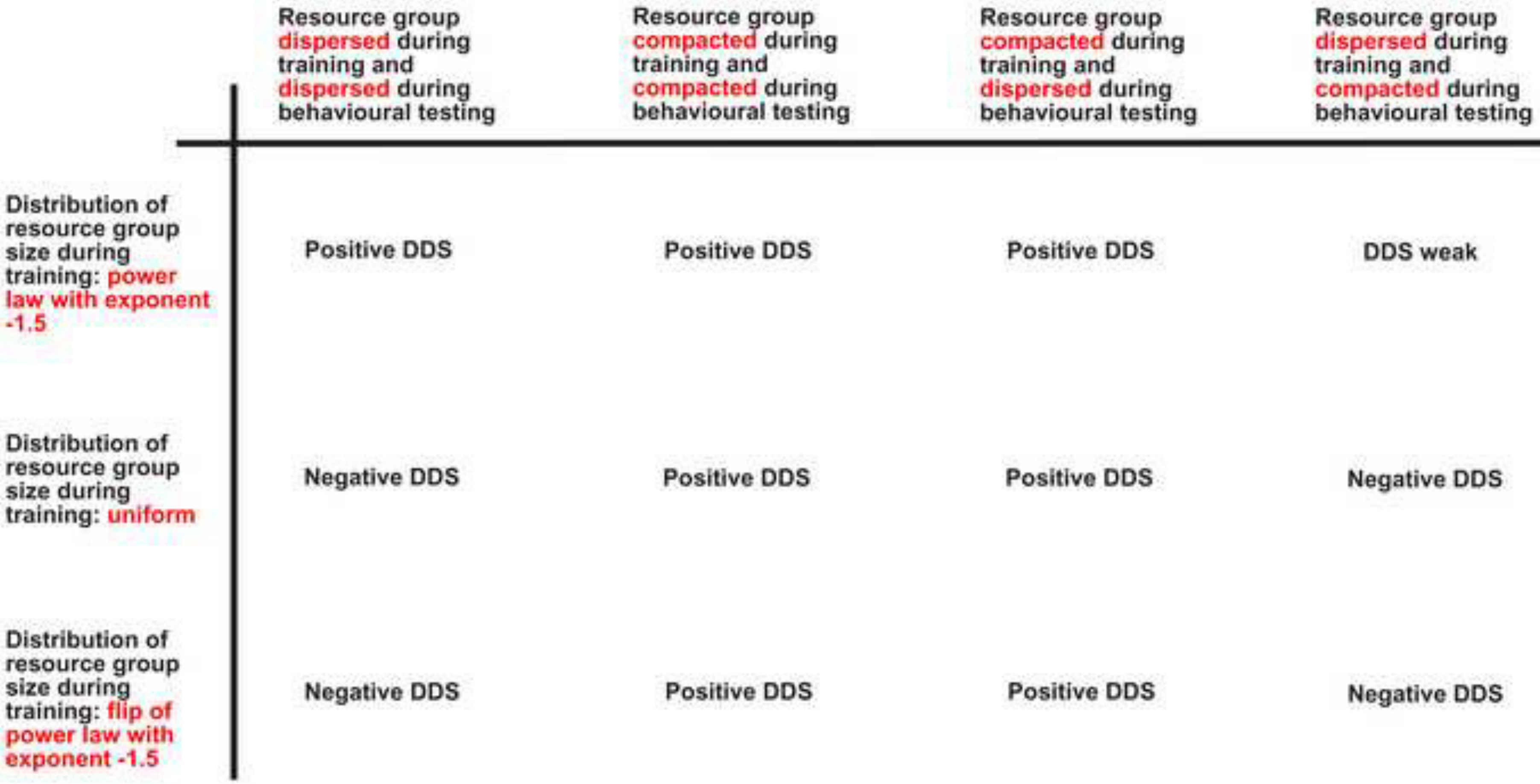
Part A) Distribution of resource density types in behavioural testing groups

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

4. Figure


Spatial conformation of resource groups during training: dispersed
Spatial conformation of resource froups 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
Numbers of a given resource type as a proportion of all resource types
Resources with 3-5 empty spaces surrounding
Resources with 0-2 empty spaces surrounding
Resources with 6-8 empty spaces surrounding
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
5
10
15
20
25
Group size
Part B) Preference for different resource density types during behavioural testing
Proportion of evolutionary simulations resulting in a positive behavioural preference for a given resource type
Resources with 3-5 empty spaces surrounding
Resources with 0-2 empty spaces surrounding
Resources with 6-8 empty spaces surrounding
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
5
10
15
20
25
Group size

4. Figure



	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

I analyse the behaviour of artificial neural networks in the context of predator – prey interactions.

Networks subject to undirected training impose numerous forms of DDS on artificial prey groups.

The study provides an empirically testable framework.

It could allow prediction of the forms of natural selection imposed by predators on prey groups.