We examine the proposal that the high levels of ecological specialization seen in many animals has been driven by benefits in decision accuracy that accrue from this resource-use strategy. Using artificial analogs of real neural processing (artificial neural networks), we examine the relationship between decision accuracy, level of ecological specialization/generalization, and the punishment/reward for selecting non-host resources. We demonstrate that specialists make more accurate resource-use decisions than generalists when the consequences of using a non-host are neutral or positive but not very positive. Pronounced unsuitability of non-host resources in fact promotes higher decision accuracy in generalists. These unusual predictions can be explained by the special properties of neural processing systems and are entirely consistent with patterns of performance of many specialists in nature, where non-used resources are, curiously, often quite suitable for growth and reproduction. They potentially reconcile the long-observed discrepancy between the presence of high levels of ecological specialization in many animal groups and the absence of strong negative fitness correlations across resources. The strong theoretical support obtained here, and the equally good support in experimental studies elsewhere, should bring the “neural limitations” hypothesis to the forefront of research on the evolutionary determinants of ecological range.

Results

The predictions of the model are shown in Fig. 1 and can be summarized very succinctly. Extreme specialists outperform extreme generalists cognitively when, and only when, the fitness consequences of using a non-host resource are neutral or slightly positive (specialist advantage has all but disappeared when non-host choice is approximately equal to half of the reward for host choice). If choosing a non-host resource has negative fitness consequences, generalists always outperform specialists. Additional analyses to test the robustness of these central predictions in response to differently shaped resources, different densities of resources during evolutionary training, and different search costs (punishment for choosing “empty space”) as well as analyses to determine the statistical significance of key effects are presented in the supporting information (SI). To summarize, predictions are generally robust to changes in these parameters. Shape (use of bilaterally symmetric resources) has no appreciable impact on the central predictions outlined above. Presentation of resources at low density during training restricts the range of specialist advantage when use of non-hosts is rewarded positively; however, this effect is nullified at high densities, where the range of specialist advantage when use of non-hosts is rewarded positively is extended and where specialists enjoy a cognitive advantage at all but the most positive reward values.

Ecological range of the organism can be defined as the number of different resources used by an organism to feed, reproduce, and survive. Ecological range directly impacts on many of the most pressing environmental concerns to humans, including the response of species to manmade or natural environmental perturbation, establishment of invasive organisms, extinction risk, and biodiversity levels (1–4). Ecological range as a research determinant of ecological range.
The main effect of introducing search costs is to overextend the range that specialists enjoy a cognitive advantage into the region where use of non-hosts has a negative impact on fitness (very negative impacts of using non-hosts, as usual, promote cognitive advantage in generalists).

Discussion

The central results of this study (that extreme specialists outperform extreme generalists cognitively when, and only when, the fitness consequences of using a non-host resource are neutral or slightly positive) are important, following as they do a succession of theoretical models that essentially indicate increased suitability of non-host resources inhibits specialization and attendant speciation (19–23). Although some models have indicated that specialization can be promoted despite nonnegative fitness correlations of different resources (24–26), to our knowledge, this is the first study to have some degree of suitability of non-hosts as a necessary central component. The results presented are entirely consistent with observed patterns of performance of specialist organisms in nature and provide strong support for the neural limitations hypothesis.

Why is specialization promoted only when non-host resources are neutral or useful and not when they are harmful? The answer probably lies in antagonism between the processes of acceptance and rejection in a shared neural apparatus. Most resources that a specialist encounters are non-host resources, and, if these are harmful, fitness can be maximized by concentrating the neural apparatus on the process of rejection at the expense of acceptance. The opposite is true, of course, of generalists. Increasing the benefits of non-host resources presumably “liberates” the process of acceptance in specialists (all resources can now be accepted without serious fitness consequences) and discrimination of a single resource from the rest is probably a simpler task than discrimination of a group of different resources from the rest. Although not directly informing on neural processing mechanisms within our model, the main model predictions can also be interpreted from an information theoretic perspective (27). Stephens (28) has shown that the value of information increases as the marginal costs of failing to use it increases. Failing to use information in this context is the same as behaving the same way in all environments and not utilizing the information available to make appropriate decisions. Failure to use information can be seen as analogous to selecting inappropriate

Fig. 1. The relationship between decision accuracy, level of specialization/generalization, and punishment/reward for choosing non-host resource items during training in an artificial neural network. When networks are punished (negative values) for choosing non-hosts, extreme specialists never outperform extreme generalists in terms of standardized decision accuracy (ability to choose appropriate host resources from mixed projections of hosts and non-hosts). Specialists only outperform generalists when choosing a non-host resource has neutral or slightly positive consequences. Because many specialized organisms in nature can use non-host resources well, these predictions provide strong theoretical evidence that decision accuracy could play an important role in the evolution of specialization in nature. The measure “network decision accuracy” is the number of resource projections from 250 in which a host resource was chosen from a mixture of hosts and non-host in a standardized test. The “level of specialization” measurement is simply the number of asymmetric host resources that networks were trained to select during training.

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non-hosts in our study. From this perspective, one could interpret our results in the following way: there is a minimum value of information required to evolve precision for any one-host resource, and so very high information value is required for generalists to evolve precision across a wide range of hosts. Therefore, generalists can only evolve high precision when the costs of failing to exclude non-hosts are extreme, and specialists are most accurate when these costs are minimal to moderate. When there is no real cost to choosing a non-host over a host, there is little difference in precision of generalists and specialists. These are essentially the main results of our study. Some extremely interesting information theoretic perspectives on neural network functioning have been proposed, where one function of the neural processing system is thought to be reduction of information redundancy between neural layers (29). It may be that the dynamics of decision accuracy seen in our study is somehow correlated with efficiency of redundancy reduction, induced by ecological conditions (value of non-host resources).

There are good reasons why we believe significance should be attached to the predictions of our model. First, we used the connectionist approach, in which simple neural network models are used to explain behavioral processes in human and non-human animals, and this approach has a long and distinguished history of application in psychology and animal behavior. Organization of information processing into networks of neurons was a fundamental step in the evolution of behavior, and it seems that this step promoted many of the animal behaviors that we still see today. Second, our model has fewer user-defined parameters than many simulation models, and because of the complexity of information transfer processes within the network, it is very difficult to predict model output before running simulations. In no sense, then, can it be said that the model was set up to output a specific region of “output space.” The fact that the interesting and important predictions we have produced have arisen as an unexpected, emergent property of the model imbues predictions with particular significance.

Of course, there are several notes of caution to be sounded. We have only considered one part of the decision-making process, decision accuracy, and an equally important aspect of decision making is decision speed. Decision speed is important in an ecological context because an increase in foraging time can result in increased predation (9). In many animals there is a negative relationship between decision accuracy and decision speed (see ref. 30 and references therein). However, this relationship cannot be universally assumed because detailed studies of human cognition indicate that the nature of the decision accuracy–speed relationship can vary depending on the type of tasks undertaken (31). Some progress has been made in understanding the neural basis of decision speed in primates, and it appears to be underpinned by a growth of activity in certain brain regions consequent of accumulated evidence for and against alternative outcomes (32). This mechanism suggests that models based on sequential sampling and random walks (31) are particularly suited to modeling decision speed, and such models can be easily integrated within the modeling framework of the present report. Obtaining a clear picture of the dynamics of all aspects of decision making, as we have done for decision accuracy, is particularly important because it is likely that the importance of different components of decision making will vary according to the ecology of different organisms.

Another important issue is search costs. We designed the main part of our study with two groups of organisms in mind: plant-eating insects and certain parasite species, to which the neural limitations hypothesis has been applied (9). These organisms typically disperse by flight to locate resources, and the energetic costs of continuing search within a short time frame are negligible in comparison to the benefits and detriments of locating suitable and unsuitable resources, respectively, in the same short time frame. Hence, we have assumed within our model that search costs are negligible in comparison to these other activities. However, as we have mentioned above, searching for resources can in some circumstances have high costs, such as increased predation risk (9). Our analysis of variable search costs described in the SI indicates that when high search costs are included specialists enjoy a higher decision accuracy that generalists across an even wider range of ecological conditions (punishment/reward value for choosing a non-host resource) than without search costs. Thus, the inclusion of significant search costs within our model further support the neural limitations hypothesis, indicating that it could under some circumstances operate largely independently of major ecological variables such as the value of non-host resources.

Another point of emphasis is that we do not consider the neural limitations hypothesis a completely independent mechanism for the evolution of ecological specialization. Rather, as we have shown here, if organisms are already being selected for specialization for other reasons they can expect an additional cognitive advantage under realistic ecological conditions that will further promote specialization. Demonstration of how this cognitive advantage actually affects the readiness that organisms evolve specialist behavior will require integration of the neural limitations hypothesis into conventional mathematical models of ecological specialization. The present model is fundamentally allied to visual processing and we need to develop the model to consider the olfactory and gustatory cues used by most specialist organisms. Nevertheless, it is exciting to speculate on the implications of this additional cognitive boost for the ecology of organisms. The specialization process may only require a modest initialization such as through temporary local abundance of a resource before the neural limitations mechanism takes over and moves the specialization process to completion. These results could also help to resolve the continued controversy surrounding the plausibility of sympatric speciation. Implications of the neural limitations mechanism for speciation will depend on details of the system under consideration; however, it is conceivable that the increased resource fidelity resulting from this mechanism could further restrict gene flow and be just the boost diverging biotypes need.

**Materials and Methods**

We direct readers who wish to examine the modeling procedures in full detail to the SI.

We used a simple 2-layer artificial neural network to represent sensory processing of the consumer. The network consisted of an input layer of 200 receptor cells that were arranged into eight 25-cell sections (Fig. 2). Resource items were projected onto a number of these sections; each section could contain at most, 1 resource item. Information was propagated to a layer of 3 neurons that output a binary code specifying which of the 8 sections and, by extension, which resource item should be selected from those simultaneously available. The basic input–output mapping is not unlike certain systems of visuospatial processing in higher animals (33); however, the model is stripped of all but the most fundamental elements of neural processing (namely parallel distributed processing). Although this aspect of the model makes it a more simplified representation of real, organic information processing systems, it also makes it a potentially very wide application across the animal kingdom.

We constructed 40 different artificial resource items (Fig. 3), each of which could be projected onto the sensory surface of the consumer. The number of pixels in each resource/projection was sampled from the same statistical distribution. These 40 items could be split into 4 types: those with bilateral symmetry (e.g., most animals), those with radial symmetry (e.g., cnidarians, echinoderms, and many flowers), those that were asymmetric (e.g., sponges and many plants in gross morphology), and those that were completely random in conformation. The former 3 categories were, moreover, all designated “cohesive” in body plan in that no pieces of body tissue (no activated pixels) were spatially isolated from the rest.
Each neural network could output 3 decisions: select a section of the sensory surface onto which a host resource is projected, select a section of the sensory surface onto which a non-host resource is projected, or select an empty section of the sensory surface (analogous to “continue search”). We trained neural networks with a genetic algorithm in which they increased or decreased their fitness with choice of host or non-host resource items projected onto them (choice of an empty section was considered neutral), and the highest scoring networks were selected, mutated, and moved into the next generation of training. Multiple projections containing 1 or more resource items randomly selected from the 40 were input into the neural network (Fig. 2). We trained networks to select asymmetric resource items from each of these projections and to avoid all others (i.e., asymmetric resources were designated hosts and all other resources were non-hosts), but the number of asymmetric resources that the network was trained to select was also varied. At one extreme, there was a generalist treatment where the network was rewarded for selecting any of the 10 asymmetric resources (i.e., there were 10 resource types designated as host, and the 30 remaining resources were non-hosts). At the other extreme, there was a specialist treatment where only 1 specific asymmetric item was rewarded (only 1 host, and the remaining 39 resources were designated non-hosts). We varied the score for choosing a non-host resource within the genetic algorithm. The reward for choosing a host resource was fixed at $+5$, but punishment/reward for choosing a non-host was sampled as follows: $-5$, $-2.5$, $-1$, $-0.5$, $0$, $+0.5$, $+1$, $+2.5$, and $+5$. The last value ($+5$) was a control; the selection of hosts and non-hosts was equally valuable, and thus differential range has not been selected.

After training (see SI for details) we created a standard set of input projections that allowed us to produce an equivalent measure of “decision accuracy” of networks that were trained to different levels of ecological range (generalist or specialist) and with different punishment/reward values. Briefly (see SI), each projection contained host sections and non-host sections into which appropriate hosts (rewarded during training) and non-hosts (punished/rewarded from $-5$ to $5$ during training, see above) from each training treatment were inserted at random. The ability of trained networks to discriminate hosts from non-host resources in their particular standard set (a standardized

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**Fig. 2.** A neural network that selects particular resource items projected onto its input surface. Resource items are projected onto particular input sections and the neural network outputs a binary code that indicates the section selected. During training of the network, if a host resource item is projected onto the selected section, the neural network is rewarded. If a non-host item is projected onto the selected section, the network is punished or rewarded at a lower rate. High-scoring neural networks are chosen for mutation and movement into the next generation of training. In this way the neural network evolves to recognize and select certain resource items and avoid others. We trained neural networks to be generalist and specialist on asymmetric resource items in a larger ecosystem of various resource body shapes, keeping the reward for choosing asymmetric host resources constant but varying the punishment for choosing the remaining non-hosts. Using standardized input sets, we then tested the decision accuracy (ability to choose host resources from mixed projections of hosts and non-hosts) of networks across levels of specialization and punishment.

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**Fig. 3.** Projections of the body plans of resource items. We trained neural networks to be generalists or specialists on the asymmetric items, rejecting all others. Punishment for choosing a non-host resource item was varied along with level of specialization/generalization. Using standardized input sets, we then tested the decision accuracy (ability to choose appropriate host resources from mixed projections of hosts and non-hosts) of networks across levels of specialization and punishment.
measure of cognitive accuracy) was plotted against ecological range and reward/punishment for choosing a non-host resource. In effect, to test the decision accuracy of neural networks, each network (regardless of training experience) was presented with an artificial community of resource items, all of which had the same number of host resources at exactly the same spatial position within the community. Because the number and position of host and non-host resources offered to each network was identical and the set of host resources trained on and presented during measurement of cognitive accuracy were the same for each network, any differences in accuracy can only be induced by differences in the training regime (in terms of ecological range or punishment/reward).

ACKNOWLEDGMENTS. This work was supported by United Kingdom Natural Environment Resource Council Grant NE/D011035/1.

Supporting Information

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SI Text

The Neural Network and Training Procedures. We used a 2-layer neural network with 200 input units and 3 output units (Fig. 1). The network was “fully connected” in that there was a connection between all input and output units. Output units were binary stochastic elements (1, 2) with \( p_i \), the probability of firing of the \( i \)th unit, defined by

\[
p_i = g \left( \sum_{j=1}^{M} w_{ij} x_j \right)
\]

where \( g(x) \) is the binary sigmoid function \( g(x) = \frac{1}{1 + \exp(-x)} \), the \( j \)th input layer unit provides input \( x_j \) to the \( i \)th unit via the connection \( w_{ij} \), and \( M \) is the number of inputs to the unit. Input units were stimulated by artificial resource items (Fig. 2), outputting “1” where part of the body of the resources was projected onto a unit and “0” where there was no resource item projected. In implementing the neural network we divided the input layer into \( 8 \times 5 \times 5 \) unit sections and resource items could only be projected within sections and not between. Depending on the stimulation pattern of the input surface, the network could output 1 of 8, 3-digit binary codes. Each of these codes represented selection of a particular input section. Input sections ran clockwise from 1 to 8, with segment 1 in the top left corner of the input layer (Fig. 1), and output firing patterns for each segment were as follows: (1, 1, 1) = section 1, (1, 1, 0) = 2, (1, 0, 0) = 3, (0, 0, 0) = 4, (0, 0, 1) = 5, (0, 1, 1) = 6, (1, 0, 1) = 7, (0, 1, 0) = 8.

We trained the neural network using a genetic algorithm (3). Fifty networks were created in each generation of training, with initial weight values for each selected at random between 1 and \(-1\), and the 600 synaptic weights in each encoded in a vector. Within each of these vectors representing weights between different layers of the neural network, the linear position of a weight was given by

\[
S = ((l-1)d3)(d2)(d1) + (k-1)(d2)(d1) + (j-1)(d1) + i
\]

where \((i,j,k,l)\) index a position in a 4-dimensional array with dimensions \([d1, d2, d3, d4]\); in this case \((10 20 13)\). A single set of 250 resource projections was input into each neural network. In all cases a resource projection consisted of a random number of resources between 1 and 8, chosen at random from the pool of 40 (Fig. 2), simultaneously projected at random onto sections of the input layer. Only the task of training varied between treatments (see the Training Treatments section below) not the nature of input sets. Selection of an input section by the network onto which a host resource was projected was rewarded a value of 5, selection of a section onto which an non-host resource was projected was punished/rewarded a range of values (see below) and selection of an empty section was given a score of \(0\) (considered equivalent to “continue search,” in itself a fairly neutral contributor to organismal fitness). Overall scores of each of the 50 neural networks after presentation of the 250 projections were calculated, and the top scoring 10% of networks were chosen for mutation and recombination. Networks were paired at random from this 10% to produce 25 pairs, and while a pairing could occur more than once, no network could mate with itself. Pairs were recombined with a probability of 0.6 and during the recombination event sections of the paired weight vectors were swapped at a recombination point chosen at random between 0 and 600. After recombination, or if a recombination event did not occur, vectors were mutated. This occurred with a probability of 0.1 at each vector element, with the amount to be added or subtracted to the present value sampled at random from a normal distribution with mean 0 and variance 3. After recombination and mutation, the 50 networks were passed to the next generation of training, and the same projection set used in the last generation was presented to each network. The average score of networks had invariably settled to a stable value after training was run for 300 generations.

Training Treatments. Training treatments refers to resource items that were considered hosts (rewarded) and non-hosts (punished/rewarded) in the above section, and also the reward/punishment values given within the genetic algorithm for choosing a non-host resource item. Projections of resources are shown in the text, Fig. 2. Number of pixels in each resource projection was rounded from random samples of the normal distribution with mean of 11.8 and variance 3.1. We rewarded asymmetric resources selected by the network and punished all others selected, and varied the level of specialization/generalization of networks. In the extreme generalist treatment we rewarded selection of all 10 asymmetric items, then removed 2 resources at random from the list of rewarded types, now rewarding selection of only 8 asymmetric resources and punishing selection of all other resources. This removal process was repeated, removing 2 resources (or only 1 if 2 remained) each time until we arrived at the extreme specialist treatment where only 1 asymmetric resource was rewarded. We thus created a series of networks training on a specific set of resources and varied their level of specialization. This process of training and removal was repeated 10 times to obtain 10 replicates representing unique sets of resources that networks varied in ecological range. Each one of these replicates was in turn represented by 10 stochastic repeats of training procedures. These procedures were repeated for various values of reward/punishment for choosing a non-host resource. Reward for choosing a host resource remained static at +5 but punishment/reward for choosing a non-host was tested at the following values: \(-5, -2.5, -1, -0.5, 0, +0.5, +1, +2.5, \) and +5. In all cases but 1 (the last, the control), punishment/reward for choosing a non-host item was less than the reward for choosing a host one. We, therefore, in all cases but the control, induced some degree of specialization on the host resources (we term these “hosts” because the networks evolve to preferentially select them) but the difference between reward and punishment for choosing host and non-host items varied. In effect we induced ecological range through differential reward and then analyzed the resultant consequences for decision accuracy.

Quantifying Network “Decision Accuracy.” We required a set of input projections that would give us an equivalent, standardized measure of decision accuracy (the ability of networks to select host resources, those rewarded with +5 during training from projections containing hosts and non-hosts, those punished/rewarded during training) of networks regardless of training experience. A set of 250 projections was created exactly as described above in the The Neural Network and Training Method section. In each projection we then selected the sections on which resources of 1 of the 4 shape types were projected (this choice was arbitrary as allocation of resources from the 40 to projections...
is random) and designated these “host locations.” All other locations where resources were projected were designated “non-host locations.” We then modified this template set of projections for each set of networks that were trained to a particular ecological range, and obtained this ecological range on a specific set of resources, inserting appropriate hosts for each treatment randomly into host locations and non-hosts into non-host locations. Take for example the treatment in which networks were trained to recognize the 2 asymmetric resources second and eighth from the left in the main text, Fig. 2 and reject all other items (a quite specialized network). These 2 resources were inserted at random into the host locations of the template projections, and all other 36 resources items inserted at random into the non-host locations. Consider now a slightly more generalized treatment that included 4 asymmetric resources (first, second, sixth, and eighth, from the left). These resources were inserted at random for insertion into host locations of the template projections and the remaining 36 resources items inserted at random in the non-host sections, and so on. Thus, regardless of training experience, decision accuracy of networks was gauged by their ability to select hosts resources from input projections containing the same number of hosts and non-host, at exactly the same positions of the neural network input.

Robustness of Predictions to Parameter Variation. Resource shape. We repeated all modeling procedures described in the main text and SI but instead of selecting from the pool of asymmetric resources as in the main text (Fig. 2), we selected from the bilaterally symmetric resources. The results are displayed (Fig. S1). The use of bilaterally symmetric resources had no appreciable effect on the central predictions of the model. Extreme specialists outperform extreme generalists cognitively when, and only when, the fitness consequences of using a non-host resource are neutral or slightly positive, and generalists always outperform specialists if selecting a non-host resource has negative fitness consequences.

Resource density during evolutionary training. We repeated all modeling procedures described in the main text and SI except we varied the density of resources presented in each projection during training. In the low density treatment the number of resources in each projection was selected at random between 1 and 4 and in the high density treatment resources were randomly selected between 5 and 8. Training at low density had the effect of restricting the range over which specialists enjoy a cognitive advantage when selection of a non-host resource has positive fitness consequences (Fig. S2). Extreme specialists outperformed extreme generalists (the means were higher and confidence intervals did not overlap) only when reward for selecting a non-host resource was +0.5. Training at high density had the opposite effect and appeared to extend the range over which specialists enjoy a cognitive advantage when selection of a non-host resources has positive fitness consequences (Fig. S3). Here specialists had a clear cognitive advantage over generalist within the range of rewards for selecting reward for selecting a non-host resource, 0 to +2.5.

Search costs. We added costs (−1 and −2.5) to the selection of “empty space” during training, that is equivalent to “continue search.” This simulation applies to organisms that the cost of continuing search (rather than selecting a resource) is appreciable relative to the reward they would enjoy if they selected a suitable resource. The principle effect of introducing search costs was to extend the range over which specialists enjoy a cognitive advantage into the region where selection of a non-host resources has negative fitness consequences. The range was extended further, the greater the costs, however, even for a search cost punishment of −2.5, at an extremely negative cost for selecting a non-host, generalists still enjoyed a cognitive advantage over specialists (Figs. S4 and S5).

Statistical Significance of Effects. It is clearly important to establish that the effects we describe above are greater in magnitude than would be expected due to random variation. We conducted a detailed statistical analysis for one key effect from the main set of predictions (Fig. 1), namely the transition from generalist to specialist advantage when networks were punished −0.5 for selecting a non-host resource vs a neutral value for selecting a non-host resource. This is equivalent to demonstrating that the slope of cognitive performance from specialist to generalist at −0.5 is positive, whereas the slope at 0 is negative and that these differences in slope are statistically significant. We fitted linear models to both datasets (the linear model fitted well, both P < 0.001) and demonstrated: (i) the slope parameter is positive at a punishment value of −0.5 and negative at a neutral value for selecting a non-host resource, and (ii) there is no overlap in confidence intervals for these 2 slope parameters (Fig. S6). We further conducted an ANCOVA with value of choosing a non-host resource (−0.5 or 0) as a main effect and ecological range (i.e., the number of resources designated hosts) as a covariate (the test included main effect, covariate, and main effect × covariate terms) and demonstrated a highly significant main effect × covariate interaction term (F1,116 = 37.0, P < 0.001) indicating that the slopes of the 2 datasets significantly differ.

Fig. S1. Model predictions when all modeling procedures are repeated using bilaterally symmetric resource items instead of asymmetric ones.
Fig. S2. Model predictions when resources are selected at low density during training procedures. Otherwise all modeling procedures are unchanged.
Fig. S3. Model predictions when resources are selected at high density during training procedures. Otherwise all modeling procedures are unchanged.
Fig. S4. Model predictions when a “search cost” (punishment for choosing empty space) of −1 is introduced during training procedures. Otherwise all modeling procedures are unchanged.
Fig. S5. Model predictions when a search cost (punishment for choosing empty space) of $-2.5$ is introduced during training procedures. Otherwise all modeling procedures are unchanged.
Fig. S6. Linear models fitted to data in Fig. 1 for the punishment/reward for choosing a non-host resource set to $-0.5$ and $0$. Slope parameters are positive at $-0.5$ and negative at $0$ and there is no overlap between confidence intervals of these parameters.