

Constraints on adaptation: explaining deviation from optimal sex ratio using artificial neural networks

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Abstract

Determining processes constraining adaptation is a major challenge facing evolutionary biology, and sex allocation has proved a useful model system for exploring different constraints. We investigate the evolution of suboptimal sex allocation in a solitary parasitoid wasp system by modelling information acquisition and processing using artificial neural networks (ANNs) evolving according to a genetic algorithm. Theory predicts an instantaneous switch from the production of male to female offspring with increasing host size, whereas data show gradual changes. We found that simple ANNs evolved towards producing sharp switches in sex ratio, but additional biologically reasonable assumptions of costs of synapse maintenance, and simplification of the ANNs, led to more gradual adjustment. Switch sharpness was robust to uncertainty in fitness consequences of host size, challenging interpretations of previous empirical findings. Our results also question some intuitive hypotheses concerning the evolution of threshold traits and confirm how neural processing may constrain adaptive behaviour.

Introduction

A central aim of evolutionary biology is to determine what limits the ability of natural selection to produce perfect adaptations (Gould & Lewontin, 1979; Williams, 1992; Barton & Partridge, 2000). Sex allocation, in particular the ratio of the sexes produced in dioecious species, has often been used as a focal process for studying such constraints. Theory predicting optimal behaviour in sex allocation is well developed, and empirical data are extensive, making investigation into general questions about constraints to adaptation possible (e.g. Herre, 1987; West & Herre, 1998; West & Sheldon, 2002; Boomsma *et al.*, 2003; Shuker & West, 2004; Burton-Chellew *et al.*, 2008; Pannebakker *et al.*, 2008). Theory predicts that individuals should adjust the sex of their offspring in response to changes in environ-

mental conditions such as resource availability (Trivers & Willard, 1973). There is considerable empirical evidence for such adjustments in many organisms (reviewed in West, 2009). Although data often provide qualitative fits to the predicted behaviour, deviations from optimal sex allocation strategies are often seen (e.g. Charnov *et al.*, 1981; Orzack, 1990; Orzack *et al.*, 1991; Herre *et al.*, 2001; Moore *et al.*, 2005). Suggestions have been made to explain such deviations, such as the presence of costs associated with altering the sex ratio (see Pen & Weissing, 2002), adaptive plasticity in highly variable (evolutionary) environments (Herre, 1987), differences in selective pressure (Griffin *et al.*, 2005) and restrictions on knowledge of the environment (Charnov *et al.*, 1981; Flanagan *et al.*, 1998; Shuker & West, 2004). Identifying the constraints that lead to these deviations is important if constraints on other life history traits are to be identified in the future (West *et al.*, 2002) and if evolutionary biology is to become even more 'predictive'. We investigated whether various aspects of neural processing restrictions are responsible for deviation from optimal sex ratios using artificial neural networks (ANNs) as models

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for neural processing in a simple system based on parasitoid wasps. Whereas our empirically led focus is on sex allocation in wasps, understanding how information is obtained and used by animals to make important behavioural and life history decisions remains an important challenge uniting cognition, behaviour and ecology (Dall *et al.*, 2005; Stephens, 2007).

Much of the work on sex allocation has been carried out using parasitoid wasps (Hymenoptera), where males develop from unfertilized eggs and females develop from fertilized eggs (Cook, 1993; Godfray, 1994). This allows females to control the sex of their offspring (Godfray, 1994). Solitary wasps, which lay a single egg per arthropod host, are predicted to lay males in small hosts (low resource availability for the developing offspring) and females in large hosts (high resource availability for the developing offspring). This occurs as the fitness of female wasps is expected to increase more with the size of the host from which it emerged than does the fitness of male wasps. This results from the correlation between adult body size and host size and because large females have a much larger egg load and host finding capability than smaller females, but the mating advantage of large males over smaller males is less pronounced (see Godfray, 1994). It is predicted that the shift from laying male to female offspring should be a sharp switch, at a specific host-size threshold (Charnov *et al.*, 1981), but the observed data show a gradual transition in many species (van den Assem, 1971; Charnov *et al.*, 1981; Simbolotti *et al.*, 1987; Godfray, 1994; West & Sheldon, 2002). Such gradual switches are also encountered in other organisms which show shifting sex allocation in response to environmental, social or maternal condition (e.g. West & Sheldon, 2002; Sheldon & West, 2004).

Recently, ANNs have proved informative tools for investigating a wide range of evolutionary phenomena that involve information and neural processing (e.g. Kamo *et al.*, 1998, 2002; Phelps & Ryan, 2000; Tosh & Ruxton, 2006; Tosh & Ruxton, 2008; Mannella & Baldassarre, 2007; Tosh *et al.*, 2009). ANNs are simple analogues of real neural processing networks which, although greatly simplified, maintain the fundamental element of neural processing (Tosh & Ruxton, 2008). Using ANNs allows us to combine an idealized form of neural processing with a well-characterized model of sex ratio, resulting in a more biologically explicit evolutionary model than is provided by current models. Combining ANNs with a genetic algorithm means that their evolutionary history can be easily manipulated, enabling investigations into the effects of events in the past on current responses to stimuli (Phelps & Ryan, 2000). ANNs can inform on how perceptual systems solve problems and can provide hypotheses to be tested empirically. In this study, we investigate not only whether the ANNs can solve the sex allocation problem, thus identifying whether the processes of information acquisition and neural processing are likely to prevent

evolution to the optimal threshold, but also when and how they fail and what the characteristics of the errors are.

We investigated whether gradual rather than sudden shifts in sex ratios of parasitic wasps in response to host size could be explained through incorporating ANNs into sex allocation theory. Populations of ANNs evolved according to a biologically inspired genetic algorithm where the fittest individuals go on to reproduce, with fitness determined from empirically observed relationships (see Methods). We tested four specific hypotheses, suggested by previous research, about the sharpness and position of the sex allocation switch. (i) If maintaining some aspect of a neural network is costly in fitness terms, the structure and function of the network will be affected (Laughlin *et al.*, 1998; Phelps, 2007) and its ability to process information could be damaged resulting in a more gradual switch being observed. (ii) If the underlying host-size distribution is changing through time, then the optimal switch point would not be fixed, which would result in a gradual shift in sex ratio with increasing host size (Charnov *et al.*, 1981). (iii) Smaller neural networks (brains, or parts of brains dealing with a focal behaviour) could constrain performance (Cole, 1985; Mares *et al.*, 2005; but see Chitka & Niven, 2009) resulting in suboptimal sex allocation. (iv) The unpredictability of future environmental conditions that will be experienced by offspring, or the unpredictability of environment quality from information available to a mother, constrains the ability to make correct decisions, resulting in suboptimal sex allocation (Charnov *et al.*, 1981; King, 1989; West & Sheldon, 2002; Sheldon & West, 2004).

Methods

We model the behaviour of solitary parasitoid wasps, basing parameters on the species *Lariophagus distinguendus* Förster (Hymenoptera, Pteromalidae) as necessary data for this species are abundant and show sex ratio shifts in the predicted direction. Data exist on how host size affects emerging wasp size (Charnov *et al.*, 1981), and how that in turn relates to fitness through the number of expected offspring (van den Assem *et al.*, 1989). Through these known relationships, we were able to build a genetic algorithm according to which the ANNs evolved. Additional analysis showed that the exact form of the relationships is not important, as the overall shape of the fitness landscape (fitness gains and losses because of different switch gradients and switch points) does not change for different parameters of the system if the marginal fitness gains with increasing host size are greater for females than for males. Therefore, our results should extend to any species where female offspring benefit more from larger hosts than do male offspring. For simplicity, we assumed in the model that wasps assess size using physical measurement as has

been shown in some species of parasitoid (e.g. Schmidt & Smith, 1987) and that host size represents host quality.

Fitness functions

To obtain a single relationship linking the fitness of a wasp to the size of the host it was produced in, we used previously published empirical studies that linked host size to adult body size (Charnov *et al.*, 1981) and subsequently body size to fitness (van den Assem *et al.*, 1989) for *L. distinguendus*. The estimate of the relative fitness of a son was taken from a male's ability to inseminate females over its lifetime, and the relative fitness of a daughter was based on a measure of egg production (Charnov *et al.*, 1981; van den Assem *et al.*, 1989). From empirical data, Charnov *et al.* (1981) found that male wasps emerging from a host of size x in the range 0.7–1.3 mm had head width y given by $y = 0.16 + 0.28x$. There was no further increase in male head width for males emerging from hosts larger than 1.3 mm. For females, emerging from hosts of size 0.7–1.3 mm, $y = 0.11 + 0.37x$, and for hosts of size 1.3–2.0 mm, $y = 0.54 + 0.044x$. For males, van den Assem *et al.* (1989) found that the number of full inseminations likely to be achieved by a male wasp with head width y (in mm) over its lifetime is given by $v = 24y - 3.5$. Similarly, they found that the egg production (in 130 h) of a female with head width y is given by $v = 59y - 17$. Combining the two functions for males means that male relative fitness v is a function of host size given by

$$\begin{aligned} v &= 6.72x + 0.34 & \text{if } 0.7 \leq x \leq 1.3 \\ &= 9.076 & \text{if } x > 1.3 \end{aligned} \quad (1)$$

Similarly for females,

$$\begin{aligned} v &= 21.83x - 10.51 & \text{if } 0.7 \leq x \leq 1.3 \\ &= 2.596x + 14.86 & \text{if } x > 1.3 \end{aligned} \quad (2)$$

Following Charnov *et al.* (1981) and using these relative fitness measures and assuming a uniform host-size distribution over the range 0.7–2.0 mm, numerical search shows that the optimal host size at which to switch from laying male to female offspring is 1.428 mm (to three decimal places; see Appendix S3 for details). In some of the later treatments, the fitnesses calculated from eqns (1) and (2) were adjusted as the wasps were subject to additional neural costs that affected fitness, or noise in the relationship between host size and offspring fitness (details given in the Treatments section).

Artificial neural networks

We used simple feed forward fully connected ANNs to represent the information processing systems of the wasps (see Fig. 1). The simple and generalized input

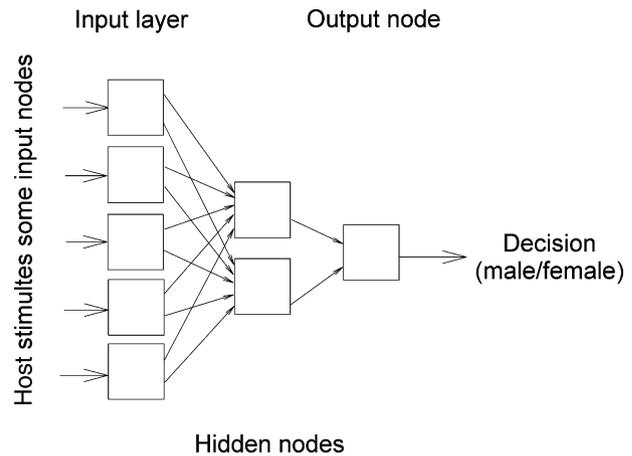


Fig. 1 Illustrative figure of a feed forward artificial neural network with five input nodes, two hidden nodes (in a single hidden layer) and one output node. The networks used consisted of an input layer of 200 sensing nodes arranged in a single row. Hosts were projected onto the centre of the input layer, stimulating between 70 and 200 of the sensing nodes. Each hidden node and the decision node also had a bias associated with it, i.e. a nonweighted input not associated with the sensing area.

layer could be interpreted as touch sensitive cells on the tip of an ovipositor sensing the size of the host (see van den Assem, 1971). The inputted information passes to a single layer of hidden nodes through weighted connections, where the weights control how information is passed through the network. The major results are presented for ANNs with five hidden nodes; however, this was varied between 1 and 7 nodes to investigate the effects of the number of hidden nodes as a proxy for the complexity of the nervous system or the size of the module in the brain dealing with this behaviour (referred to as brain size for simplicity, but see Chitka & Niven (2009) for a review of the meaning of brain size). Each hidden node outputted a sigmoidal function of the weighted sum of its inputs to a single decision node. The decision node output (decision) was probabilistic. A number between 0 and 1 was drawn at random from a uniform distribution, and if this value was less than the sigmoidal function of the weighted sum of the inputs (including the bias) to the decision node, then the output of the ANN was 1 (a male was laid), and if it was greater the output of the ANN was 0 (a female was laid). The sigmoidal function scales inputs to outputs between zero and one and is a simple transfer function frequently used in ANNs (Enquist & Ghirlanda, 2005). At the hidden node level, the function used was $1/(1 + \exp(-0.5x))$, and at the decision node the function used was $1/(1 + \exp(-x))$. Different functions were used at the different levels as the number of inputs to the hidden nodes was much larger, and therefore the input x was potentially much bigger, than the corresponding inputs to the output node.

Genetic algorithm

A population of wasps represented by these ANNs was allowed to evolve according to a genetic algorithm such that male and female wasps with the fittest ANNs passed on their weights to the next generation. All weights within each network were initialized from a standard normal distribution (mean = 0; standard deviation = 1). For each replicate, 250 females and 250 males were simulated initially. The population of wasps represented by the ANNs then evolved using a genetic algorithm. To form the next generation of wasps, for each host (fixed at 500 and representing the available host population), a female was chosen to reproduce (probabilistically) based on her fitness (rescaled between 0 and 1 relative to all females in the adult generation). In each case, a male was also chosen based on his fitness; however if the laying female's decision was to lay a male (unfertilized) egg, then none of the weights of the male ANN were used to produce the offspring (to replicate the haplodiploid genetic system). Fitness was determined from the size of the host that an individual emerged from [using eqns (1) and (2)], except during the first generation where all fitnesses were assumed to be equal. When a male offspring was produced, all weights were inherited from the mother, and when a female offspring was produced then approximately half of her weights were inherited from her mother and the remainder from her father (the set of weights inherited from each parent being chosen at random at each egg production step). The fitness of a given ANN can be interpreted as its ability to allow a female wasp with that ANN to allocate sons or daughters to hosts of the correct size range.

Fitness eqns (1) and (2) were derived from the potential egg production of females and the likely number of matings achievable for males; however within any generation of the genetic algorithm the fitness values were rescaled to obtain a fitness measure relative to other wasps of the same sex. This prevents population crashes, for example if only small (and therefore egg limited) females are produced at early stages of evolution, the fittest (largest) females will reproduce on all available hosts rather than being limited by egg load. The assumption that both a male and a female are chosen for any reproductive event, rather than a female mating with only one or two males during her lifetime as is usually the case (van den Assem, 1970; van den Assem *et al.*, 1989), speeds up the genetic algorithm and prevents premature reduction in 'genetic' (connection weight) diversity.

Random mutations in weights occurred at a rate of 0.01 per generation, and mutated weights were $\pm 5\%$ of their original value (plus or minus chosen at random). Biases were allowed to mutate in the same way.

For each generation, the 500 hosts were drawn at random from the set of discrete host sizes (0.7, 0.8, ...,

2.0). Increments of 0.1 mm were chosen as this is a small change, yet large enough to be detectable by real wasps (see Simbolotti *et al.*, 1987). This represents an unchanging host-size distribution across generations. We assumed a uniform host-size distribution, with hosts ranging from 0.7 to 2.0 mm, as this is the host-size range for *L. distinguendus* over which relationships between host larval size and emerging wasp size have been studied and theory developed (Charnov *et al.*, 1981; van den Assem *et al.*, 1989). A uniform host-size distribution was used as this is the simplest distribution and avoids problems associated with spread about the midpoint when midpoint is allowed to vary temporally.

Treatments

ANNs evolving according to the genetic algorithm described in the absence of additional costs were classified as being in treatment group A. We investigated the effects of including different costs to the network on the sex allocation switching behaviour in a number of ways to address hypothesis 1. The first costs were based on the number of active links within certain parts of the network. Although the system is greatly simplified from reality, this could represent costs associated with neurone maintenance (Phelps, 2007), although as the cost of each neurone is based on the number of active links with other neurones or sensing nodes, it could be interpreted as the cost of maintaining ionic gradients at synapses within the dendrites of the neurone (Magestratti, 2004). A link was considered active if the magnitude of its weight was greater than a threshold, taken to be 0.01. Fitness was calculated by multiplying the fitness that was determined from host size [from eqns (1) or (2)] by one minus the proportion of links in the network active above a threshold. These costs were implemented as treatments B and C. Treatment B included such costs only at the input nodes to hidden layer level (the cost of maintaining neurones associated with information gathering). Treatment C included the costs at the input nodes to hidden layer level and the hidden nodes to output node level (additionally including the cost of maintaining neurones associated with processing of the information).

The second types of costs were based on the size of the weights associated with each link within the network. This could represent costs associated with maintaining synapses (Phelps, 2007), for example the cost of reabsorption and recycling of neurotransmitter after excitation (Magestratti, 2004). Large weights represent synapses with large excitatory or inhibitory effects and hence would incur larger costs, and high costs could therefore limit the amount of information that can be passed across a synapse. For these costs, fitness was determined by multiplying the original fitness [calculated from eqns (1) or (2)] by a function $F(s)$, where s is the sum of the absolute values of the weights of the links in the network. For treatment D, this included only links

connecting the inputs to the hidden nodes, and for treatment E this included all links in the network. The function $F(s)$ was taken to be a sigmoid function $F(s) = 1 - 1 / (1 + \exp(-0.01(s - 450)))$. The imposition of both types of neural costs can affect the structure of the network to ensure that the required information is passed through the network at minimal cost (Phelps, 2007).

To address hypothesis 2, temporal variation in the distribution of host sizes was implemented as treatment F. Hosts were small (0.7–1.1 mm), medium (1.2–1.5 mm) or large (1.6–2.0 mm) in a particular generation (rather than fixed across all sizes for all generations). To address hypothesis 3, we tested the effect of the number of hidden nodes within an ANN on the ability to learn by comparing the outputs of ANNs with 1, 3, 5 and 7 hidden nodes evolving under treatment A (no costs).

To address hypothesis 4, we simulated the situation where offspring fitness is not entirely determined by host size but also by some additional stochastic factors, or by a degree of unpredictability in host size that results in unpredictability in offspring fitness. To do this, random noise was introduced to the fitness of each wasp after the initial calculation based on host size [from eqns (1) or (2)]. Three levels of noise were tested separately, drawn from uniform distributions: 0.85–1.15 (small random noise), 0.75–1.25 (intermediate random noise) and 0.5–1.5 (large random noise). Then, in each case the new fitness was calculated by multiplying the original fitness by noise. The three levels of random noise were implemented as treatments G (small random noise), H (intermediate random noise) and I (large random noise).

Replicates and sex ratio testing

For each treatment (summarised in Table 1), 12 independent replicate populations (cohorts) were simulated. Each was allowed to evolve under the genetic algorithm for 100 000 generations. After this time 20 ANNs (representing individual female wasps) were chosen at random from the population, and each was presented with 10 hosts of each host size, and the output (the decision to lay a male or female egg in the host as a 1 or 0) was recorded. The sex ratio profile (proportion of males laid in hosts with increasing host size) of each of the 20 ANNs was calculated and used for analysis. Sampling from the population was carried out as is likewise often carried out in empirical studies, because it would have been computationally expensive to test all female ANNs (around 250 per replicate) and carry out subsequent regressions.

Statistical analysis

To test for differences between switching behaviours in the ANNs that evolved under different treatments, we first fitted nonlinear regressions (using the method of least squares) of the form

$$r(x) = 1 / (1 + \exp(-ax - c)) \quad (3)$$

to the sex ratio profiles of each individual (using MATLAB's `nlfit` function). This was performed to extract parameters representing the behaviour of the ANNs that had an exact meaning, and although the method uses least squares fitting, the results are clearly reasonable based on raw data (see Fig. 4). The value of a determines the slope of $r(x)$, and the midpoint (the point at which $r(x) = 0.5$ for this value of a) is determined by c and is given by $-c/a$, which we label as parameter b (see Fig. 2). Parameter searches began at $a = -1$ (a value giving a slow sigmoidal decrease in sex ratio with increasing host size) and $c = 1.4$ (corresponding to a value of b near the optimal switch point). We then tested for differences in the values of the parameters a (steepness of switch) and b (location of switch) generated by the regressions for the individuals of the different treatments.

There were strong effects of cohort on the values fitted; therefore, an average (median) value for each parameter was taken for each cohort and used as independent data points. The median data were not normally distributed, and so nonparametric (Kruskal–Wallis) tests for group (treatment) differences were used. Post-hoc Mann–Whitney tests were used to determine pair-wise differences between treatments ($N_1 = N_2 = 12$ throughout). Interquartile ranges of the values of a and b generated within each cohort were also measured to indicate variability. The effects of treatment on this measure of variability were tested in the same way as differences in medians. The best-fit values of a and b generated by the nonlinear regressions were used. The maximum number of iterations of the fitting algorithm was set to 1000. In seven of the 2160 regressions, the iteration limit was reached and the parameter estimates from the final iteration were used.

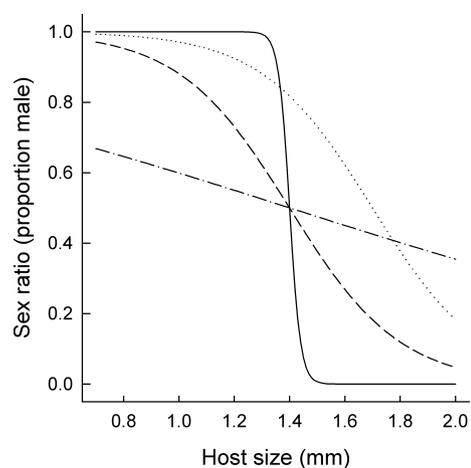


Fig. 2 The sex ratio of offspring laid in hosts of increasing size according to $1 / (1 + \exp(-a(x - b)))$ for several parameter sets. Parameters are (solid line) $a = -50$, $b = 1.4$, (dashed line) $a = -5$, $b = 1.4$, (dot-dash line) $a = -1$, $b = 1.4$, (dotted line) $a = -5$, $b = 1.7$.

Results

Fitness without costs

Populations (cohorts) of wasps with evolving ANNs evolve towards producing sharp switches, approaching the optimal exact switch (Fig. 3, and see supplementary Fig. S1.1 in Appendix S1). The overall sex ratio profile for all 12 cohorts evolving with no fitness costs is less steep (Fig. 3).

Effects of neural costs

Costs based on synapse maintenance or firing (treatments D and E) led to a significant reduction in the slope of the switching behaviour in ANNs (A–E group differences: $\chi^2_4 = 28.66$, $P < 0.001$; post-hoc A vs. D: $Z = -2.685$, $P = 0.007$, A vs. E: $Z = -3.551$, $P < 0.001$; Table 2; Fig. 4a). There was no effect on the slope of the switching behaviour of the alternative type of neural costs based on maintenance of neurones (treatments B and C) (A vs. B: $Z = 0.722$, $P = 0.471$, A vs. C: $Z = 0.549$, $P = 0.583$). There was no significant effect of any of the neural costs on the position of the switch point leant ($\chi^2_4 = 3.60$, $P = 0.462$; Table 2), and it is always near 1.4 (but see Table S2.1 for variation within individual cohorts).

There was an effect of the neural costs on the variability of the location of the switch point ($\chi^2_4 = 26.55$, $P < 0.001$) with ANNs evolving under costs based on neuronal firing (treatments D and E) producing cohorts which were more variable in switch point than

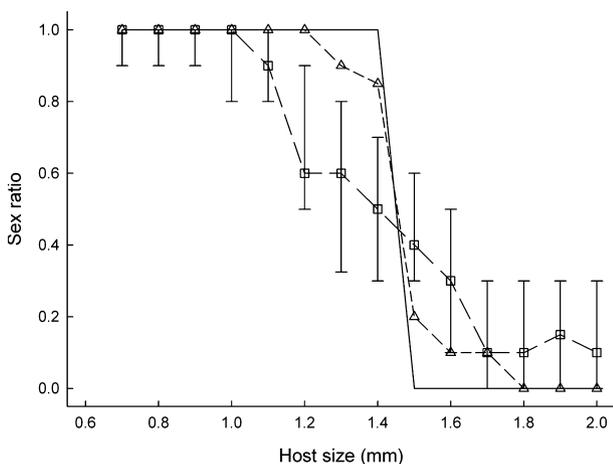


Fig. 3 Artificial neural networks (ANNs) can learn near-optimal sex ratio behaviour. The optimal sex ratio switching behaviour for the discrete system is shown (solid line), along with the sex ratio profile of a single cohort of ANNs (with the sharpest switch) evolving with no additional neural costs (short dashed line with triangle markers), and the sex ratio profile averaged over all 12 cohorts of ANNs evolving with no additional neural costs (long dashed line with square markers, error bars represent interquartile ranges).

those produced by ANNs evolving without costs (treatment A) (A vs. D, $Z = -3.031$, $P = 0.002$; A vs. E, $Z = -3.147$, $P = 0.002$). Similarly, there was an effect of the costs on the variability of the slope of the switch ($\chi^2_4 = 22.04$, $P < 0.001$), with ANNs evolving under most extreme costs based on neurone firing being less variable (A vs. E, $Z = 2.916$, $P = 0.004$). These ANNs generated shallower slopes and rarely exhibited rapid switches.

Temporal changes in host distribution

The evolution of the sex allocation switch point was influenced by the nature of the host distribution over time. There was a significant effect of a varying host-size distribution in shifting the switch point to a larger host size ($Z = -2.223$, $P = 0.026$; Table 2; Fig. 4b). However, there was no significant effect on the slope of the switch ($Z = 0.779$, $P = 0.436$). There was also no significant effect of the moving host-size distribution on the variability of the slope or switch point within each cohort (for a : $Z = -1.241$, $P = 0.215$; for b : $Z = 0.722$, $P = 0.471$; Table S2.2).

Effects of number of hidden nodes on learning

The structure of the neural network influenced the evolution of the switch point. There was a significant effect of the number of nodes in the hidden layer on the slope of the switch from male to female offspring ($\chi^2_3 = 16.79$, $P = 0.001$; Fig. 4c). ANNs with one hidden node displayed more gradual switches than ANNs with 3, 5 and 7 hidden nodes (1 vs. 3: $Z = 3.031$, $P = 0.002$; 1 vs. 5: $Z = -3.089$, $P = 0.002$; 1 vs. 7: $Z = 3.551$, $P < 0.001$; Fig. 4c). There were no differences between the slopes of the switches of ANNs with 3, 5 and 7 hidden nodes ($P > 0.05$ in all pair-wise comparisons). There were also differences in the within cohort variability (interquartile ranges of the values of a within each cohort) of the slopes across ANNs ($\chi^2_3 = 12.53$, $P = 0.006$), with ANNs with one hidden node being less variable than ANNs with 3, 5 and 7 hidden nodes (1 vs. 3: $Z = -2.165$, $P = 0.034$; 1 vs. 5: $Z = -2.685$, $P = 0.007$; 1 vs. 7: $Z = -3.147$, $P = 0.002$). There were no differences in the variability of the slopes of the switches of ANNs with 3, 5 and 7 hidden nodes ($P > 0.05$ in all pair-wise comparisons).

In contrast to the steepness of the switch, there was no significant effect of the number of hidden nodes on the location of the switch point ($\chi^2_3 = 1.85$, $P = 0.603$). However, there were differences in the variability of the locations of the switches within the cohorts across the treatments ($\chi^2_3 = 16.06$, $P = 0.001$), with the ANNs with one hidden node this time being more variable than ANNs with 3, 5 and 7 hidden nodes (1 vs. 3: $Z = 2.916$, $P = 0.004$; 1 vs. 5: $Z = 2.916$, $P = 0.004$; 1 vs. 7: $Z = 3.551$, $P < 0.001$; $P > 0.05$ in all other pair-wise comparisons). So although there was no difference in the location of the median of the switch point, it was a much

more variable in ANNs with only one hidden node (Table S2.3).

Effects of random noise

The addition of random noise to simulate unpredictability in offspring fitness did not affect the steepness of the switch ($\chi^2_3 = 1.20$, $P = 0.753$; Table 2; Fig. 4d). However, there was an effect on the location of the switch, with ANNs subject to the highest level of random noise (treatment I) switching sex allocation at a smaller host size than those evolving with no random noise ($\chi^2_3 = 9.95$, $P = 0.019$; post-hoc $Z = 2.454$, $P = 0.014$; Fig. 4d). There was no effect of the random noise on the variability of the slope or variability of the location of the switch within the cohorts across treatments (for a , $\chi^2_3 = 2.12$, $P = 0.548$; for b , $\chi^2_3 = 2.79$, $P = 0.425$; Table S2.4).

Discussion

This is the first model of sex allocation to explicitly include some form of the information processing system, which has allowed us to shed new light on a well-studied problem. We found that wasps modelled by ANNs can evolve towards producing abrupt switches from laying male to female offspring with increasing host size. The model uses fitness equations obtained from published

empirical studies, with no other rewards for making 'correct' decisions. However, the switches were in general less sudden than the immediate switch (exact threshold) predicted by optimality theory. Adding costs based on the neural weights (to simulate costs of synapse maintenance or firing) caused the switch to become significantly more gradual, thus moving further away from optimality, although there was no effect of including costs based on the number of active links (to replicate costs associated with maintaining neurones). Reducing the size of the ANNs to include only one hidden node resulted in a far more gradual switch when compared with those produced by ANNs with more hidden nodes, indicating that brain size could limit the ability to produce a threshold switch. We have therefore identified two constraints that could contribute to the suboptimal sex allocation behaviour observed in real parasitoid wasps.

Introducing random noise into offspring fitness, to simulate factors other than current host size affecting offspring fitness, affected only the location of the switch and not the slope as had previously been suggested (Charnov *et al.*, 1981; King, 1989; West & Sheldon, 2002; Sheldon & West, 2004). Similarly, a variable underlying host distribution, which had been proposed as a reason for gradual switching behaviour (Charnov *et al.*, 1981), also affected only the position of the switch and not its steepness. These differences in

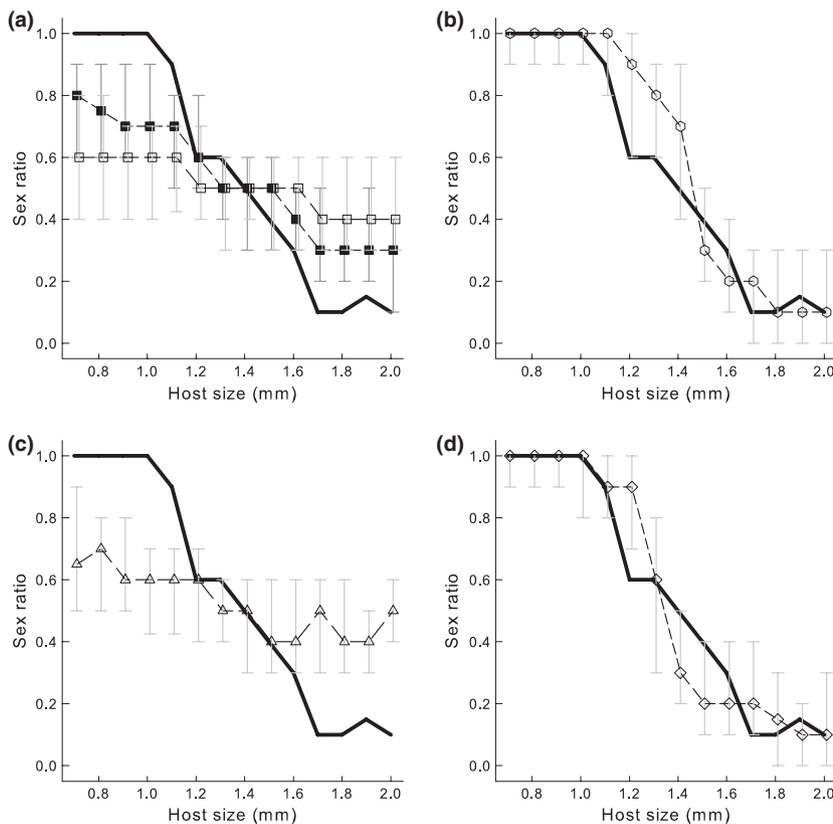


Fig. 4 The effects of treatments on the slopes and location of the sex ratio switch point. Solid line represents baseline data in all cases with no costs, no random noise, five hidden nodes and no temporal variation in the host-size distribution (given with interquartile ranges in Fig. 3). (a) Costs of synapse maintenance, at the input to hidden node level (solid squares and short dashed line) and both levels (open squares and dashed line). (b) Temporal variation in the host-size distribution (open hexagons and dashed line) affects location but not the steepness of the switch. (c) Artificial neural network structure influences the steepness but not the location of the switch (artificial neural networks with one hidden node shown by open face triangles and dashed line). (d) The largest level of random noise (open diamonds and dashed line) affects the switch point but not the slope. Symbols represent median values across all individuals in all cohorts, error bars represent interquartile ranges. Symbols and error bars are slightly offset for clarity. Not all treatments are shown.

switch point are of a very small size (approximately 0.05 mm), which are smaller than is likely to be measurable by real wasps (see Simbolotti *et al.*, 1987).

Why was an immediate switch not always observed?

Some individuals and some entire cohorts, evolving under the genetic algorithm with no costs and no random noise, generated very steep, almost instantaneous switches as predicted by theory (see Fig. 3 and supplementary Fig. S1.1 in Appendix S1). The overall sex ratio profile obtained from combining all of the replicates

within this treatment is less steep, because of the variability between cohorts (Fig. 3). It has been suggested that thresholds are not observed at population levels because although individuals display threshold behaviours, there is a continuous distribution of threshold value within the population (Hazel *et al.*, 1990). Our results show that the differences in switch point between the cohorts are small in comparison with the differences in slope (Table S2.1), indicating that the suggestion of Hazel *et al.* (1990) does not apply in this situation.

We suggest that not all of the ANNs (evolving with no additional costs) produced offspring sex ratio profiles with a sharp switch from male to female offspring because there is greater selection to evolve the optimal switch-point location than there is for the switch to have a steep slope. This can be seen in Fig. S3.1 in Appendix S3 of the online appendices which shows the relative fitnesses resulting from steep and gradual switches over the range of switch points. Although the threshold switch is optimal, there are not large fitness gains from a small increase in how quickly the switch occurs when the

Table 1 Summary of treatments and hypotheses they address.

Treatment	Summary	Hypothesis
A	No neural costs Constant host-size distribution 5 hidden nodes No random noise in fitness	Control treatment in all hypotheses
B	Neural costs based on: Number of active links In input nodes to hidden layer level Constant host-size distribution 5 hidden nodes No random noise in fitness	1
C	Neural costs based on: Number of active links In both levels Constant host-size distribution 5 hidden nodes No random noise in fitness	1
D	Neural costs based on: Size of weights In input nodes to hidden layer level Constant host-size distribution 5 hidden nodes No random noise in fitness	1
E	Neural costs based on: Size of weights In both levels Constant host-size distribution 5 hidden nodes No random noise in fitness	1
F	No neural costs Host-size distribution changing in time 5 hidden nodes No random noise in fitness	2
G	No neural costs Constant host-size distribution 5 hidden nodes Small random noise in fitness	4
H	No neural costs Constant host-size distribution 5 hidden nodes Intermediate random noise in fitness	4
I	No neural costs Constant host-size distribution 5 hidden nodes High random noise in fitness	4

Table 2 Summary data for the two parameters fit by nonlinear regressions, and measures of variability within cohorts.

Treatment	Median values			
	<i>a</i> (IQR)	<i>a</i> IQR (IQR)	<i>b</i> (IQR)	<i>b</i> IQR (IQR)
A	-4.55 (4.40)	1.36 (0.10)	1.43 (0.04)	0.10 (0.05)
B	-6.76 (3.70)	1.47 (2.77)	1.41 (0.07)	0.08 (0.05)
C	-7.21 (4.22)	3.06 (4.05)	1.40 (0.05)	0.07 (0.04)
D	-1.93 (2.52)**	0.75 (0.50)	1.38 (0.11)	0.18 (0.27)**
E	-0.20 (0.83)***	0.48 (0.22)**	1.38 (1.26)	1.24 (1.59)**
A	-4.55 (4.40)	1.36 (0.10)	1.43 (0.04)	0.10 (0.05)
F	-8.44 (16.72)	4.42 (23.19)	1.47 (0.05)*	0.08 (0.07)
1 hn	-0.46 (1.36) ^{abc}	0.56 (0.24) ^{abc}	1.38 (0.20)	0.43 (1.00) ^{abc}
3 hn	-4.06 (9.48) ^a	1.32 (27.70) ^a	1.40 (0.12)	0.11 (0.09) ^a
5 hn (A)	-4.55 (4.40)^b	1.36 (0.10)^b	1.43 (0.04)	0.10 (0.05)^b
7 hn	-5.11 (12.93) ^c	2.22 (11.01) ^c	1.41 (0.08)	0.09 (0.06) ^c
A	-4.55 (4.40)	1.36 (0.10)	1.43 (0.04)	0.10 (0.05)
G	-5.38 (13.83)	4.58 (15.31)	1.42 (0.06)	0.12 (0.12)
H	-3.85 (9.52)	1.73 (6.90)	1.44 (0.05)	0.12 (0.15)
I	-6.82 (8.60)	7.11 (16.11)	1.38 (0.09)*	0.07 (0.04)

Given are median values of parameter *a* (slope) and *b* (switch point) over 12 replicate cohorts, and the interquartile range of the median over the 12 replicate cohorts (in brackets). *Parameter* IQR refers to the median value of the within cohort interquartile range for each parameter across the 12 cohorts, the interquartile range of this measure is also given across the 12 cohorts (in brackets). Significant differences are indicated in each block of the table. Asterisks denote significant differences from the control treatment (A, given in bold) with no costs/random noise/moving host distribution; * denotes $P < 0.05$, ** denotes $P < 0.01$, *** denotes $P < 0.001$. When comparing between artificial neural networks with variable numbers of hidden nodes, all pairwise comparisons were made; median values with the same superscript (within the column) are significantly different.

switch point has evolved to be located in the optimal place. Therefore, evolution to a threshold switch could be very slow. A similar result was found by Bach *et al.* (2007) in the context of the evolution of dispersal behaviour. It was shown that threshold dispersal (dispersal of an individual from a patch only after a threshold value of population density) is optimal (and evolutionarily stable) but did not evolve within the simulated populations. Bach *et al.* (2007) concluded that the threshold behaviour is unlikely to be achievable as selection near this point is weak and drift takes over. Similarly, we found that selection was weak as behaviour approached an exact switch (see Appendix S3). With such weak selection around the threshold, we would expect a reasonable degree of variation in switch-point slope at mutation-selection balance (see Pannebakker *et al.*, 2008 for such a study of sex ratio variation). Weak selection around the optimum is a classic feature of sex ratio as a trait, because of its frequency-dependent nature and the weakly stable equilibrium generated (Charnov, 1982). Our results have implications to the evolution of other threshold traits, especially in terms of constraints that may underlie the accuracy of the threshold itself. We have identified two mechanisms which will promote variation about a threshold: weak selection around the threshold and likely constraints on information processing that limit ability to produce a perfect threshold.

Neural costs and brain size effects

Brain size (as correlated with body size) has previously been shown to limit the behaviour of other Hymenopteran species including the workers of some ant and bee species (Cole, 1985; Mares *et al.*, 2005), but whether neural network size is predictive of cognitive ability remains controversial (Chitka & Niven, 2009). We found that our proxy for brain size (or at least processing power) in this system (the number of hidden nodes and therefore also the number of potential links within the network) was associated with the accuracy of decision-making (see Fig. 4c). This is apparent as ANNs with one hidden node produced offspring sex ratio profiles with significantly shallower slopes than those produced by ANNs with 3, 5 or 7 hidden nodes and were therefore further away from their optimal behaviour. Furthermore, two of the 12 cohorts of the ANNs with only one hidden node did not produce a sex ratio that declined with host size, thus failing to learn the correct behavioural response to host size. There was no overall effect on the midpoint position of the switch, although it was more variable in ANNs with only one hidden node. This variability is associated with the shallower slope and reflects only that the sex ratios produced by the smaller ANNs were either male biased or female biased over the host range, but this is a further indicator of the poor behaviour of the smallest ANNs. An ANN with one hidden node is effectively a single layer network, which is inherently

less powerful than a two layer network, and so the inability of an ANN with 1 hidden node to learn the optimal behaviour is not unexpected.

It is initially surprising that the costs associated with neurone maintenance (treatments B and C; Table 2) did not affect the speed of the switching behaviour, as such costs can limit the number of active links within a network and therefore limit the effective size of the network. However, there appears to be redundancy within the ANNs with five hidden nodes. This is clear from Table 2 (and Table S2.3) as ANNs with only three hidden nodes can evolve a switch as steep as those with five hidden nodes but have fewer potential links. Costs that reduced the number of active links (those with weights above a small threshold) did not damage the ability of the ANNs to evolve the correct behaviour, as presumably redundant links were lost. There was a clear effect of costs associated with synapse maintenance or firing (treatments D and E). The sigmoidal costs that were included were strong, to reflect that the cost of passing information at a high capacity chemical synapse (large weight) is more than proportionally greater than the cost of passing information at a low capacity synapse (small weight) (Laughlin *et al.*, 1998). The costs resulted in many active synapses within the networks, but with smaller weights. Even with the redundancy of links in ANNs with five hidden nodes, the ANNs were unable to overcome these information processing constraints. We investigated the effects of only two types of potential costs that could occur in neural networks but found that they had different impacts on the deviation from optimal behaviour, highlighting that the nature of the costs incurred in maintaining neural networks might be very important. Synapse maintenance costs also affected the variability of the switching behaviour of the ANNs. The slopes became less variable when the most extreme costs were included, as the slope of the switch was usually very shallow. As with the smallest ANNs, this resulted in more variability in the midpoint but did not affect the overall position.

Effects of randomness in fitness

Gradual transitions in sex ratio with some environmental variable have been attributed to unpredictability in environment quality. For example, idiobiont wasps, which paralyse the host at parasitism, display more precise sex allocation shifts with host quality than koinobiont wasps, which allow the host to continue to grow after parasitism (King, 1989; West & Sheldon, 2002). A similar phenomenon is found in mammals, where variation in sex ratio is less closely correlated with maternal condition in species with long gestation periods (Sheldon & West, 2004). This study found that the incorporation of random noise into offspring fitness, reflecting unpredictability in environmental (host) quality, did not affect the decision accuracy of the ANNs, with the exception of the highest level of random noise, which

did then affect the midpoint of the switch, but the slope of the switch was not affected.

This result challenges the idea that it is unpredictability itself that causes gradual changes in sex allocation behaviour. Instead, it could be the nature of the unpredictability that is important; King (1989) argued that it is not the ability of an ovipositing female to predict future resource availability that is important to maintain the relationship between host size and offspring sex, but it is rather the existence of a consistent relationship between host size and resource availability in the first place. The random noise in fitness introduced in the simulations of treatments G, H and I does not change the underlying pattern of fitness with host size, instead it increases the variance around it, more so for larger hosts (which produce fitter individuals and fitness is perturbed by a proportion of its original value). Therefore, in the ANN system simulated, host size remains the best predictor of offspring fitness. This result also questions the more general suggestion of Charnov *et al.* (1981) that the presence of factors unknown to an ovipositing female that affect offspring fitness would result in a more gradual shift in sex ratio. Unsurprisingly, the relationship between host size and offspring sex is lost when fitness becomes completely random (results not shown). Similar results have been found for models of information sampling where an environmental variable changed through time, making the environment more or less predictable; too much variability means the information is of little value making a fixed strategy best, regardless of the state of the variable sampled (reviewed by Stephens, 2007). We have shown there is no *a priori* reason for unknown factors to influence to slope of the switch and suggest that this may prove to be a facet of environment-dependent thresholds more generally, despite the intuitive appeal of the 'confusing' effect of noise on threshold accuracy and precision.

The effects of a temporally changing host-size distribution

Charnov *et al.* (1981) predicted that a nonstationary distribution of host sizes would cause a more gradual switch in sex ratio with increasing host size. In particular, it was suggested that in such a situation, wasps would produce switches with different midpoints, resulting overall in a gradual switch. A similar point has been made regarding general threshold traits at the population level (Hazel *et al.*, 1990). The results of this study do not entirely support this prediction, as all ANNs within a cohort adjusted their switches in the same direction, resulting in a change in the switch point but not the slope of the switch. Also, the switch points produced by the ANNs evolving with varying host-size distributions were no more variable than those produced when the host-size distribution was constant, either within cohorts or across cohorts within the treatments (Tables 2 and S2).

The movement in switch point is likely to be due to the fact that the optimal threshold was actually shifted by the treatment itself. The optimal switch is calculated based on the distribution of the host sizes and hence if this changes the switch point can change (see Appendix S3 and Charnov *et al.*, 1981). The only other treatment to affect switch point was the highest level of random noise. Random noise in fitness affects the relative fitness of male and female offspring, which also affects the optimal switch point (see Appendix S3 for details). The lack of an effect of any of the other treatments on the midpoint of the switch is attributed to the stronger selection on the ANNs to evolve to produce a switch at the optimal point (Fig. S3.1 in Appendix S3).

Conclusions

Our study has more general implications for the evolution of threshold traits which depend on assessing one or more aspects of environmental quality (Roff, 1996). We have shown that threshold switches from one type of behaviour to another can evolve under reasonable assumptions; however a sharp threshold itself is rarely seen, and some aspects of neural processing and structure can limit threshold behaviour. Threshold traits are common and include other aspects of sex allocation (see Charnov, 1982; Hardy, 2002 and West, 2009), host choice (Plantegenest *et al.*, 2004), foraging (Stephens & Krebs, 1986) and oviposition decisions (e.g. Santiago Lastra *et al.*, 2006), as well as a range of phenotypic and behavioural plasticities (Stearns, 1992). Extending a similar modelling framework to these areas could therefore be potentially very informative.

This study is a first step towards incorporating details of neural structure (and associated costs) and evolutionary history into evolutionary models to predict optimal sex allocation behaviour. Similar approaches have been taken elsewhere (e.g. Phelps & Ryan, 2000; Tosh *et al.*, 2009), highlighting the benefits of modelling behaviour using ANNs and addressing the structure of information processing systems. We used a biologically plausible genetic algorithm to evolve ANNs capable of sex ratio adjustments in response to environmental conditions. We showed that including some types of potential neural costs or limiting the size of the ANNs increases deviations from optimal behaviour, but that the presence of random noise is not sufficient to cause such a shift. Generally, our results show how limitations of neural network size and costs of neural processing can constrain adaptation, leading to behaviours that are not adjusted perfectly in response to environmental variation.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Extended treatment A results.

Figure S1.1 Sex ratio profile of the 12 cohorts evolving under treatment A (control).

Appendix S2 Cohort median values of fitted parameters for ANNs evolving under various treatments.

Table S2.1 Treatments A–E.

Table S2.2 Treatments A and F.

Table S2.3 Treatment A with a varying number of hidden nodes.

Table S2.4 Treatments A and G–I.

Appendix S3 Details of estimating fitness.

Figure S3.1 The fitness gained by a female wasp through laying a sex ratio of varying slope and switch point.

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