Research News

A sense of history

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Mating preferences for specific traits increase the fertility, fecundity or offspring fitness of choosy individuals. However, current fitness benefits offer an incomplete account of the relative influence of different signals on mate choice. The history of selection on sensory systems in a broader ecological context can provide many missing details. Recent innovative use of neural networks by Phelps and Ryan shows that modelling the chronological order in which past selective forces have acted predicts the actual mating preferences of túngara frogs.

Sensory exploitation is the wallflower in the endless dance of wits between competing adaptive explanations of mating preference evolution. Such adaptive explanations predict coevolution of female preferences and male traits and the build-up of genetic correlations between the two. Female choosiness is adaptive because females benefit directly, or because one or more components of offspring fitness (e.g. survival, mating success and disease resistance) are elevated[1,2]. The role of evolutionary history in shaping current female mating preferences is often acknowledged, occasionally ignored, but seldom investigated directly. It is very rarely considered a direct alternative to adaptive models (Box 1). Two genuinely innovative studies by Phelps and Ryan[3,4], one just published, do much to rectify this situation. They remind us that incorporating historic explanations in models provides a deeper insight than does restricting our inquiries to the current adaptive value of traits[5].

Phelps and Ryan[4] first trained a simple neural network (Box 2) to distinguish between the whine call of a male túngara frog (*Physalaemus pustulosus*) and a noise stimulus of the same duration and temporal changes in loudness (i.e. an identical sound amplitude envelope). The noise had the same frequency (pitch) components as the call of a male frog but these components were randomized within the sound envelope. The neural networks that are most familiar to behavioural ecologists consist of an input layer, a single 'hidden' layer and an output layer (e.g. Refs 6,7). Phelps and Ryan's neural network had an input layer with 15 neurons, each selectively sensitive to an 87 Hz range of sound frequencies. The total frequency range covered was, therefore, 1305 Hz (261–1565 Hz), which spans the range of natural calls. Each input neuron was connected to all 12 neurons in a feature detector layer. Each of these was, in turn, connected to all 12 neurons in a context layer. The context layer neurons were then connected back to each feature detection layer neuron, forming a feedback loop between the two layers. Finally, the feature detection neurons were connected to a single output neuron.

There are two 'hidden' layers in Phelps and Ryan's networks because sound has a temporal component. Rather than a network being played the sound directly, it was asked to discriminate between stimuli presented as spectrograms – visual representations of sound where frequency is plotted against time. The intensity of the sound at each time and/or frequency point was indicated by the shade of the image. The darker the image, the louder the signal. The test stimulus was placed at random within a time window divided into 70 slices. The network was then fed consecutive slices of the spectrogram one by one, starting with the first, until all 70 had been played. Feedback from the context layer to the feature detection layer changed the activity of the feature detection neurons, providing a form of memory because the response to later parts of a stimulus

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Box 1. Will history teach us nothing?

Students of animal behaviour treat history and current adaptive value as separate levels of explanation[a]. Why then do most researchers working on sexual selection only study the current fitness benefits of female mate choice? An implicit assumption is that identifying these benefits reveals the dominant forces that shaped the mating preference. What does history add? Whereas weak versions of sensory exploitation (closer to sensory drive or receiver bias models[b]) note that signals and preferences are predisposed to evolve in directions determined by the sensory capabilities of receivers in specific environments, they do not contradict the claim that preferences and traits coevolve because of fitness benefits of female choice. Weak versions of sensory exploitation only highlight the likely direction in which characters have evolved.

By contrast, stronger versions of sensory exploitation (closer to pre-existing bias[c] or sensory trap models[b]) present alternative evolutionary histories to those invoking current adaptiveness of mate choice. They are supported by phylogenetic evidence that the male trait was sexually selected by a female preference that had already evolved[b–d]. (Unfortunately, mapping characters onto phylogenies has its weaknesses. Specifically, when a preferred trait is gained in all descendants, the pre-existence of the preference is undetectable. Thus, male sensory exploitation of very strong preferences might not be detected.) The strength of Phelps and Ryan's modelling[e] is to show that historic accounts can do more than just identify the origin of female mating preferences, they also have the potential to explain many of the details.

References
a Tinbergen, N. (1963) On aims and methods of ethology. *Z. Tierpsychol.* 20, 410–433
b Endler, J.A. and Basolo, A.L. (1998) Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* 13, 415–420
c Basolo, A.L. (1995) Phylogenetic evidence for the role of a preexisting bias in sexual selection. *Proc. R. Soc. London. B Biol. Sci.* 259, 307–311
d Shaw, K. (1995) Phylogenetic tests of the sensory exploitation model of sexual selection. *Trends Ecol. Evol.* 10, 117–120
e Phelps, S.M. and Ryan, M.J. (2000) History influences signal recognition: neural network models of túngara frogs. *Proc. R. Soc. London B Biol. Sci.* 267, 1633–1639

Box 2. Neural networks

A neural network is a mathematical model, run on a computer, which learns to distinguish patterns[a–f]. It mimics a real neural system and consists of layers of highly interconnected cells (neurons). A simple network comprises an input layer where each neuron is or is not activated by the stimulus, a 'hidden' layer for processing and an output layer. The level of activation of a receiving neuron depends on the activity of the sender neuron and the weighting given to the connection between them. One training method uses a 'genetic algorithm' analogous to the process of natural selection[g]. To start, a set of networks is generated that differ only in the weighting given to various connections. One measure of fitness is the difference in the final output of each network when offered the target versus control stimuli. This is an index of the ability of a network to correctly identifying target stimuli. The fitness of a network determines the probability that it will enter the next generation. Networks can then be treated as chromosome-like strings of values representing specific neuron–neuron connection weights. A mutation process is run and small changes in the weightings are made at random points along the 'chromosome'. 'Swapping' whole sections between the 'chromosomes' of different networks simulates recombination. Once complete, the new generation of networks is re-assembled and their discrimination abilities (fitness) calculated again. The process is repeated for each generation until the desired degree of accuracy is achieved. It is known that both the training protocol[a] and the nature of the control stimuli[f] can influence the final outcome.

References

a Phelps, S.M. and Ryan, M.J. (2000) History influences signal recognition: neural network models of túngara frogs. *Proc. R. Soc. London B Biol. Sci.* 267, 1633–1639

b Phelps, S.M. and Ryan, M.J. (1998) Neural networks predict response biases of female túngara frogs. *Proc. R. Soc. London B Biol. Sci.* 265, 279–285

c Enquist, M. and Arak, A. (1993) Selection of exaggerated male traits by female aesthetic senses. *Nature* 361, 446–448

d Johnstone, R.A. (1994) Female preferences for symmetrical males as a by-product of selection for mate recognition. *Nature* 372, 172–175

e Cook, N.D. (1995) Artifact or network evolution? *Nature* 374, 313–314

f Kamo, M. *et al.* (1998) Neural network for female mate preference, trained by a genetic algorithm. *Philos. Trans. R. Soc. London Ser. B* 353, 399–406

g Michalewicz, Z. (1996) *Genetic Algorithms + Data Structures = Evolution Programs* (3rd edn), Springer-Verlag

depends on those stimuli that have preceded it.

In 20 selection simulations, each lasting on average 1000 generations, networks were trained to recognize the male túngara frog call (Box 2). Phelps and Ryan then tested the best network per simulation with a series of 34 stimuli that the network had not encountered before. These stimuli comprised the calls of other species in the *P. pustulosus* clade, as well as various hypothetical reconstructions of ancestral calls. Amazingly, the responses of the 20 artificial networks (the proportion of calls 'recognized') was strongly correlated with the proportion of live female *P. pustulosus* that approached the same stimuli in phonotaxis tests (in which the alternative was a white noise stimulus). The network response explained 65% of the variation in stimulus recognition by real female frogs.

This study is important for two reasons. First, actual female preferences for a wide range of novel stimuli emerged simply because of selection for mate recognition (discriminating between a conspecific call and noise). Earlier studies training neural networks for mate recognition also produced 'hidden preferences'. However, these studies used extremely simple training stimuli[6,7] and were not designed to be directly compared to real female responses. Second, the criticism that neural networks oversimplify reality[8,9] is now directly challenged: Phelps and Ryan were able to predict the behaviour of real females even when they used smaller networks with only eight neurons per 'hidden' layer[4]. In a broader context, the ability of neural networks to mimic real females can now be put to the test. Will networks trained using calls from other acoustically signalling taxa, such as crickets, birds and other frogs, also successfully predict female preferences? Such networks have already successfully predicted simple stimulus–response relationships[10].

Replaying evolutionary history

Using the uncanny ability of networks to emulate real female frogs, Phelps and Ryan[3] then tested whether the evolutionary history of mate recognition systems affects current preferences. Again, they selected networks to discriminate target frog calls from noise. This time, however, the networks were trained to learn four successive calls. Initially, the networks were trained to recognize the first call with a pre-specified degree of accuracy. Once done, the discrimination task was changed to the ability to recognize the second call with the same level of accuracy, and so on. This simulates the history of mate recognition evolution, with the caveat that female mate recognition is unlikely to have evolved by 'catching up' to instantaneous changes in male signals.

Phelps and Ryan imposed three different training histories on the networks, and then selected all networks to discriminate a modern *P. pustulosus* call from a noise stimulus with the same degree of accuracy. Thus, the recent history of the networks was identical, and it was only their deeper history that differed. In the 'mimetic' history, the network was trained in a sequence that matched the hypothetical evolution of male calls. The first call was the hypothetical ancestral call for the *P. pustulosus* species group. Thereafter, the reconstructed ancestral calls at nodes moving up the clade to the extant *P. pustulosus* call were used as the target stimuli. (If these calls are poor estimates of the true ancestral calls, the subsequent findings are even more impressive.) With a 'random' history, three randomly picked ancestral or extant calls from the *P. pustulosus* clade were used. Consistent differences in the behaviour of networks trained with a mimetic versus a random history could be taken to reveal the effect of history on receiver evolution. The only problem with this approach is that the random history networks are exposed to a greater range of sound stimuli. They might simply evolve greater permissiveness. What we really want to know is whether the history of a network matters while controlling for permissiveness. To do this, Phelps and Ryan used a third 'mirror' history training regime. Using principal component analysis, they obtained 12 independent variables that accounted for most of the

variation among calls. For each principle component, the difference between the ancestral call and the extant *P. pustulosus* call in the mimetic history was calculated. Mirror calls were created by reconstituting the call based on sign-reversed principle components. Each mirror and ancestral call was, therefore, equidistant from the extant *P. pustulosus* call in 12-dimensional space.

The effect of evolutionary history on mating preferences was tested by comparing the behaviour of networks with that of real female túngara frogs using the same set of 34 stimuli as in the earlier study[4]. The results were unequivocal. The mimetic history networks showed similar responses to real females ($r = 0.56$), whereas mirror and random history networks did less well ($r = 0.32$ and 0.20). The ability of the mimetic network to predict the responses of real females was significantly better than that of the other two networks. History did matter.

Historic and adaptive explanations are conceptually distinct, but that does not mean that one can be ignored while the other is studied (Box 1). There is no doubt that adaptive consequences of female choice could, if incorporated, affect the outcome of Phelps and Ryan's network models. Many of the observed differences between female túngara frog call preferences and those of the network models might then be explained. However, if the potential sources of error and artefact are considered, the fact that a simple network can fairly accurately predict the current responses of female túngara frogs to many stimuli without recourse to data on direct and indirect fitness benefits is impressive. It reminds us that the simple task of mate recognition (discriminating a conspecific call from noise), when combined with an evolutionary history, can tell us a great deal about female mating preferences and the likely direction in which sexually selected male traits evolve. With these new studies[3,4] tests of sensory exploitation hypotheses have moved far beyond the initial (and somewhat weak) generalization that the evolution of mating preferences might precede that of preferred traits[11–13]. Moreover, these studies restore some perspective to a field dominated by tests of hypotheses invoking current adaptive value. Neural networks provide an opportunity to determine whether specific, but historically deep-seated, discriminatory tasks (such as mate recognition or signal detection) have had a strong or weak influence on currently observable mating preferences.

References
1 Møller, A.P. and Alatalo, R.V. (1999) Good-genes effects in sexual selection. *Proc. R. Soc. London B Biol. Sci.* 266, 85–91
2 Wedell, N. and Tregenza, T. (1999) Successful fathers sire successful sons. *Evolution* 53, 620–625
3 Phelps, S.M. and Ryan, M.J. (2000) History influences signal recognition: neural network models of túngara frogs. *Proc. R. Soc. London B Biol. Sci.* 267, 1633–1639
4 Phelps, S.M. and Ryan, M.J. (1998) Neural networks predict response biases of female túngara frogs. *Proc. R. Soc. London B Biol. Sci.* 265, 279–285
5 Tinbergen, N. (1963) On aims and methods of ethology. *Z. Tierpsychol.* 20, 410–433
6 Enquist, M. and Arak, A. (1993) Selection of exaggerated male traits by female aesthetic senses. *Nature* 361, 446–448
7 Johnstone, R.A. (1994) Female preferences for symmetrical males as a by-product of selection for mate recognition. *Nature* 372, 172–175
8 Cook, N.D. (1995) Artifact or network evolution? *Nature* 374, 313–314
9 Dawkins, M.S. and Guilford, T. (1995) An exaggerated preference for simple neural network models of signal evolution. *Proc. R. Soc. London B Biol. Sci.* 261, 357–360
10 Ghirlanda, S. and Enquist, M. (1998) Artificial neural networks as models of stimulus control. *Anim. Behav.* 56, 1183–1189
11 Endler, J.A. and Basolo, A.L. (1998) Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* 13, 415–420
12 Shaw, K. (1995) Phylogenetic tests of the sensory exploitation model of sexual selection. *Trends Ecol. Evol.* 10, 117–120
13 Basolo, A.L. (1995) Phylogenetic evidence for the role of a preexisting bias in sexual selection. *Proc. R. Soc. London. B Biol. Sci.* 259, 307–311

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Mitochondrial mutations may decrease population viability

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It is ironic that an organelle that is pivotal for the function of male gametes is inherited by sons only from their mother. A recent study of human fertility has provided the first definitive evidence that mitochondrial DNA mutations can reduce male fertility but with little or no effect on females. These results present the possibility that the viability of small populations might be reduced by increases in the frequency of mtDNA genotypes that lower the fitness of males.

Mitochondria are generally transmitted maternally so that deleterious mutations that affect only males will not be subject to natural selection (Fig. 1)[1]. Sperm are powered by a group of mitochondria at the base of the flagellum, and even a modest reduction in power output by the mitochondria might reduce sperm mobility and male fertility[2]. It is, therefore, possible that mitochondrial DNA (mtDNA) mutations might reduce male fertility but have little effect on females.

In 1996, Frank and Hurst[1] pointed out that the maternal inheritance of mtDNA created a male–female asymmetry in the expected severity of mitochondrial mutations. They showed that the expected equilibrium frequency of a mitochondrial mutation in a large population is approximately $q = \mu / s_f$, where μ is mutation rate and $1 - s_f$ is the relative fitness of a female with the mutation[1]. For example, consider a mutation with a mutation rate of 10^{-4} that affects sperm mobility and reduces male fertility by