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. 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 Ryan3,4, one just published, do much to rectify this situation. They remind us that incorporating historical explanations in models provides a deeper insight than does restricting our inquiries to the current adaptive value of traits5.

Phelps and Ryan4 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 network that is most familiar to behavioural ecologists consists 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

Box 1. Will history teach us nothing?

Students of animal behaviour treat history and current adaptive value as separate levels of explanation. 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) 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 or sensory trap models) 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 evolved6–8. 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 modelling9 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

Box 2. Phelps and Ryan’s memory sound network

The neural network was trained to recognize the whine call of a túngara frog (Physalaemus pustulosus). An input neuron was connected to all 12 neurons in the feature detection layer, each of which 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. This network was able to distinguish the whine call from a noise stimulus of the same duration and temporal changes in loudness (i.e. an identical sound amplitude envelope). 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.
Box 2. Neural networks

A neural network is a mathematical model, run on a computer, which learns to distinguish patterns. 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. 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 and the nature of the control stimuli can influence the final outcome.

References


Replaying evolutionary history

Using the uncanny ability of networks to emulate real female frogs, Phelps and Ryan 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 used 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

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Mitochondrial mutations may decrease population viability

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Mitochondria are generally transmitted maternally so that deleterious mutations that affect only males will not be subject to natural selection (Fig. 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. It is, therefore, possible that mitochondrial DNA (mtDNA) mutations might reduce male fertility but have little effect on females.

In 1996, Frank and Hurst 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 \( q = \mu / s \), where \( \mu \) is mutation rate and \( s \) is the relative fitness of a female with the mutation. For example, consider a mutation with a mutation rate of \( 10^{-4} \) that affects sperm mobility and reduces male fertility by

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 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 test 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. 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