

## Testing hypotheses in the historical sciences

In ecology and evolution, not all hypotheses are susceptible to experimentation: the system might be too large or complex; the events might have occurred in the past; or the process might be slow. Because we cannot devise an experiment to test them, such 'historical' hypotheses are commonly pooh-poohed as subjective and unscientific cousins to experimentation.

Philosopher Carol Cleland [1] now challenges this bias by contrasting the philosophy and practice of experimental and historical science. The experimental approach poses a single hypothesis, which gives rise to a prediction. An experiment either confirms or denies the hypothesis by comparing results to predictions. By contrast, the historical method begins with many

working hypotheses, which are confirmed or denied by 'traces' or clues. Cleland argues that, although the manner of inquiry differs, neither experiment nor historical inference has greater power to test hypotheses.

The myth of experimental superiority arises from its apparent monopoly on falsification, which requires that hypotheses be put to 'risky tests' that are likely to result in rejection of the hypotheses. Cleland asserts that experimental scientists seldom take such risks. Instead, they falsify auxiliary assumptions that are likely to produce non-confirming results.

Thus, the scientist's vantage point in time determines what constitutes proof. Predicting a future event (experimental outcome) requires a firm grasp on all contingencies. In

experiments, a result contrary to prediction does not necessarily mean that the central hypothesis is wrong. By contrast, hypotheses about past events might require only a few key clues. Cleland asserts that such 'smoking guns' offer inferences of equal strength to that of confirmatory experiments.

In a day when research dollars and journal pages are subject to fierce competition, Cleland encourages us to rethink the limits of experimentation and the value of the historical perspective.

1 Cleland, C.E. (2001) Historical science, experimental science, and the scientific method. *Geology* 29, 987–990

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## Can good genes explain the peacock's tail?

Whether the choice for good genes can drive both the evolution of elaborate displays in one sex (usually males) and the preference for them in the other (usually females) has remained controversial since Zahavi proposed the good-genes handicap model. First, female preference should deplete genetic variance in the population, eliminating the benefit to the preference. Second, the potential benefit could be counteracted easily by natural selection if there was a cost to the female preference. In a new paper, Houle and Kondrashov [1] develop a model of good-genes choice that reveals the conditions required for the coevolution of costly mate choice and exaggerated displays.

The model considers the evolution of (1) overall genome quality; (2) a display function expressed only in males; and (3) a female mate-choice function based on the display trait. A male's (genomic) quality decreases linearly with the number of mutations, usually assumed to occur with a conservative rate of 0.5 per genome per generation. The optimal display based on viability selection decreases with increasing mutational load, and viability is assumed to decline exponentially or as a Gaussian curve from this optimum. The model includes assessment errors by females when evaluating the state of the display, which can contribute to the maintenance of genetic

variation in quality. It also assumes that, although the display correlates with male quality, it explains only part of the variance. Any possibility of a Fisherian runaway process is excluded because selection gradients on the display and preference are calculated separately assuming only variation between genetic quality and either the display or preference. The model focuses purely on good-genes sexual selection and, to my knowledge, is the first



quantitative genetics model to do so. Under one parameterization, which includes a coefficient of variation in display of 5% and a cost to females of rejecting a male of 1%, the model predicts an increase in mean male display of 45% or eight phenotypic standard deviations (in some bird families, it can be as much as 30%). Of particular importance, the model makes assumptions and predictions that can be realistically tested in natural biological systems.

The crux of the model involves the parameterization of the costs and benefits of choice. The benefits involve quantifying the variance in genetic quality and the relationship between quality and fitness. The costs are both direct, such as reduced survivorship through rejecting a male, and indirect, such as the cognitive machinery required to assess the display reliably. Little is known about either. The direct cost of mate rejection was assumed to be 1%, which might not be appropriate for all mating systems. Previous researchers have argued that the machinery required to assess the display might have pleiotropic costs, which are not explicitly considered in the current model. However, evidence showing that display assessment might involve pre-existing, naturally selected sensory systems (e.g. sensory bias), such as a female guppy's preference for orange colouration in males and the importance of orange carotenoid in their diet, suggests that pleiotropic costs might be minimal or even beneficial.

1 Houle, D. and Kondrashov, A.S. (2002) Coevolution of costly mate choice and condition-dependent display of good genes. *Proc. R. Soc. London B Biol. Sci.* 269, 97–104

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