Digest: What keeps sexual signals honest? A general new explanation

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One of the most tantalizing phenomena in evolutionary biology has just received a new, elegant mathematical explanation. Rather than relying on the much-contested handicap principle, Fromhage and Henshaw's simple new model is based on resource trade-offs and explains why keeping costly sexual signals honest is evolutionarily optimal. Complications such as the supposed inherent wastefulness of the handicap principle, or social punishment of dishonest cheaters, are no longer needed to explain honesty in sexual signaling.

Secondary sexual traits, that is, traits that are not related to the reproductive systems, but rather function to attract, court, or gain access to a mate, include unforgettable visual displays such as the tail of the peacock, cumbersome weaponry such as antlers and horns, and the extravagantly decorated bowers of bowerbirds. How can such costly and seemingly wasteful displays, and the preference for them in the opposite sex, be evolutionarily stable? Surely a choosy animal should prefer a mating partner that does not waste resources on ridiculous displays? Although these displays and preferences might be favorable if displays provide reliable signals of quality to the chooser, it is unclear what prevents lower-quality individuals from displaying exaggerated signals that lie about their quality? In other words, what keeps sexually selected signals honest?

For decades, heated debate has surrounded a potential explanation for this conundrum. Zahavi (1975) proposed that if such signals are costly, better-quality individuals might be better able to cope with the costs and would therefore be able to signal more strongly—they can afford to play with a handicap. From the very beginning, the logic of this "handicap principle" received strong criticism, but through a history of timely defenses from some of the previous century's influential evolutionary biologists (Grafen 1990; Maynard Smith 1991), it stands as a fascinating example of a fallacy that has remained a well-known and mostly accepted theory (Penn and Számadó 2020). Although the current century's biologists are demonstrating a seemingly ever decreasing range of validity for the handicap principle (e.g., Johnstone et al. 2009), this loss of explanatory power has not been compensated for by a rise of other general explanations for how honesty is maintained in costly sexual signals. In a new study, Fromhage and Henshaw (2022) show that trade-offs between multiplicatively acting fitness components (such as mating success and survival probabilities) produce positive correlations between signal strength and individual quality under a broad range of conditions.

Although previous influential models of the handicap principle assumed that quality is some abstract property each individual possesses (and then assume a specific fitness function for each quality individual), Fromhage and Henshaw (2022) base quality on differences in available amounts of a limiting resource. Fitness components are then functions (a and b) of the amounts of resources allocated to them. It has long been known that if these fitness components trade off additively, the optimal resource allocation to each fitness component is simply where the marginal fitness change in investing more in one component over the other is equal ($da = db$). Fromhage and Henshaw (2022) next show that under a multiplicative trade-off between the fitness
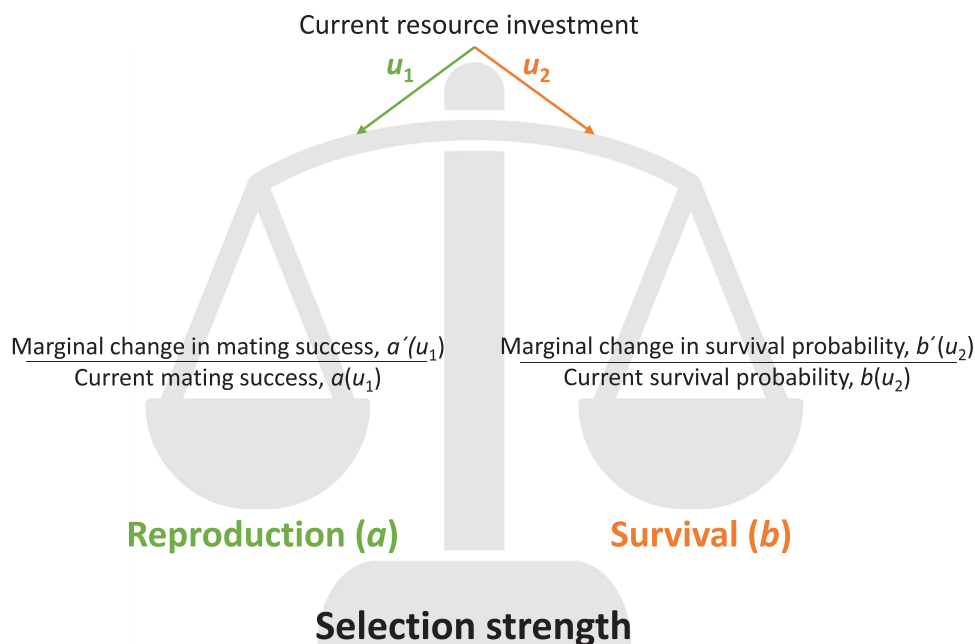
Figure 1. Selection strength is expected to balance investments of a common limited resource *u* into fitness components in a multiplicative trade-off, as the one shown here between reproduction (*a*) and survival (*b*). For a given split of resources u_1 and u_2 into reproduction and survival, respectively, the balance depends on the ratio between the marginal change in each component and its current value. Thus, an increase, for example, in reproductive investment without a concurrent increase in the marginal change in mating success, shifts the balance away from investing in reproduction—that is, selection strength for increasing mating success is weakened. Balance illustration by Iyi Kon, Vecteezy.com.

components, it is the marginal *proportional* (rather than absolute) change in fitness components that is balanced at the optimum (Fig. 1). These translate mathematically to selection gradients (eqs. 6–8, Fromhage and Henshaw 2022): if investment in one fitness component (e.g., signal strength to increase mating success) is increased, without its marginal fitness change also increasing, selection for investing in signal strength becomes weaker. Thus, a *balanced* (although not necessarily equal) investment across multiplicative fitness components ensures signal honesty without invoking the "wastefulness" inherent in the handicap principle.

Fromhage and Henshaw (2022) go on to show certain cases (shapes of fitness components as functions of investments) in which these trade-offs do not lead to a positive correlation between sexual signals and individual quality. However, in contrast with models defending the handicap principle, it is now the exceptions to the main result that rely on specific, limiting assumptions.

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Associate Editor: K. Moore