parasite-mediated sexual selection

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What causes sexual ornaments and behavior (**secondary sexual characteristics**): primary are the gonads and reproductive equipment themselves)? Peacock's tail, bird song repertoires, conspicuous color patterns, sexual displays

This is a conspicuous problem: occurred to Darwin

Two possibilities for sexual selection are (1) male-male competition (horns etc.) or (2) female choice. (Competition is usually among males, and choice usually by females, because females usually invest more in offspring.) We will focus on female choice.

Fisherian "runaway" model ("sexy son")

- trait initially advantageous
- preference and trait become genetically correlated (trait expressed in males, preference in females)
- *Requirements*: heritability of trait and preference. trait not too expensive (no requirement that the trait should be expensive)
- *Tests/predictions:*
  - negative or zero correlation between male quality and trait
  - genetic correlation between trait and preference (Houde and Endler compared guppy populations in different streams)
  - high variability among populations in ornaments?

Zahavi "handicap" principle

The **handicap principle** says that traits are not chosen despite their being costly, but *because* they are costly. **Good genes** model. Ornaments are a signal of good genes: they must be costly, otherwise you can't rely on the honesty of the signal.

- revealing traits: indicate male condition/quality
- conditional traits: only expressed by high-quality males
- viability ("Zahavi") traits: expressed by everyone, but kill off low-quality males

The handicap principle seems paradoxical, but models and observation have suggested that it actually works (in part because traits are only expressed in males)

Problem with handicap principle: what maintains genetic variation for "goodness"? Under normal conditions (directional selection), one would expect that soon everyone would have good genes and there would be no variability (nothing for females to choose from

except luck). Constant mutation could lead to a *mutation-selection balance*, or a variable environment could keep changing what genes are "good". Of course (as we know), parasites represent a strong driver of variability in the biotic environment.

Hamilton-Zuk hypothesis

(the Red Queen returns)
a subset of the handicap principle
requirements (Combes (2005) p. 185)

- females prefer resistant (showy) males (also required by Fisher)
- correlation between quality (resistance) and trait (*not* required by Fisher), or negative correlation between parasite load and trait
- (genetic) heritable variation in resistance (the hardest one to prove)
- Parasite load decreases host viability (otherwise there is no point in selecting resistant males)
- (genetic) heritable variation in trait

Evidence for H-Z: between-species

If H-Z is operating, we expect a **positive** correlation between parasite load and showiness across species. This correlation has been found, for example, in Hamilton and Zuk's original study which correlated human judgements of species brightness with information on ectoparasite load. Other studies have been more equivocal.

There are some problems with between-species comparisons, though:

- reverse causality: showiness could cause parasitism (e.g. brighter species could attract more ectoparasites, or species that invest more in showiness could have less to invest in parasite resistance)
- ecological correlates: showiness and parasitism could both be driven by other factors (hole-nesting, polygyny)
- falsifiability: when a correlation is not found, how do you decide whether the data are really good enough to reject?
- phylogenetic controls
- dynamics: how do we know that parasite-driven sexual selection couldn't be so effective that it would drive parasite loads to *lower* levels in showy species?

Evidence for H-Z: within species

Guppies (Martin & Johnsen, 2007):

- *Gyrodactylus turbulli* infestation lowers brightness of parasitized males

- it also reduces the number of sexual displays
- females prefer brighter males
- we don't know whether resistance is heritable
- we can't rule out transmission avoidance (see below)

Barn swallows (Møller, 1990):

- females prefer males with longer tails (manipulative experiments, shortening and lengthening male tails)
- males with longer tails have fewer mites (field observation)
- chicks with heavy mite loads are smaller at fledging, leading to lower survivorship/fecundity/fitness
- *heritable variation in resistance*: cross-fostering offspring of long-tailed males in the nests of short-tailed males (and vice versa) shows that offspring of long-tailed fathers inherit their fathers' low mite loads. This rules out the hypotheses that
  - long-tailed males have just avoided parasitism by luck
  - females are selecting males for paternal care (**direct benefits**) [and offspring are less parasitized, e.g., because they're better nourished]
  - offspring benefit by avoiding direct transmission of mites from fathers (also **direct benefits**)

Meta-analysis (Poulin & Hamilton, 1997)

- negative relationship between parasite load & expression of secondary sex characters (more in experiments)
- no difference with/without parental care
- no difference between behavioral and morphological traits
- direct measures of immune function give stronger results than measures of parasite load
- stronger for ectoparasites (transmission avoidance?)

Alternatives

Alternatives to H-Z: both can be tested (with some difficulty) by manipulative cross-fostering experiments

- selection for parental care (direct benefits) [can be ruled out in species without parental care]
- selection for parasite avoidance.
  - e.g.: sage grouse & red ink hematomas (Spurrier et al. in Clayton (1991)) [can be ruled out for non-directly transmitted parasites; stronger evidence for ectoparasites suggests parasite avoidance]
- selection for female fecundity (pipefish, Combes (2005) p. 180)

Immunocompetence handicap hypothesis

Why is testoterone immunosuppressive?

Folstad & Karter (1992): turning off your immune system is the ultimate "handicap''. Thus, it is not a coincidence that females prefer traits that are linked to (temporary) immunosuppression; males that can afford to turn off their immune systems during the mating season must have good genes ...

Good links between androgens and secondary sex characteristics. Some support for the link between testosterone (and other androgens) and immunosuppression, but high variable results in different experiments. Immunoredistribution rather than immunosuppression?

Other axes of signalling and immune function: carotenoid, melanin, androgen (testosterone) systems.

Balenger & Zuk (2014)

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