Inter-sexual selection and choice

12 February 2019

Why are individuals of the resource-limited sex choosy?

- Males hold territories, but territory quality and size are unrelated to feather length[1]
- Red-collard widowbird body condition is positivey correlated with tail length[1]
- Male body condition declines more slowly when tails are shortened
- More females nested in the territories of males with long tails (‘control’)
- Females prefer long-tailed males

[1] Pryke, S R, & S Andersson (2005). Biol. J. Linnean. Soc. 86:35-43.
[2] **Image:** *Euplectes ardens* Nigel Voaden.

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- **Mate-limited**: For the sex limited by access to mates, sexual selection expected for traits increasing competitive ability

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- In most species, females are resource-limited, & males are mate-limited

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Direct benefits: resource provisioning

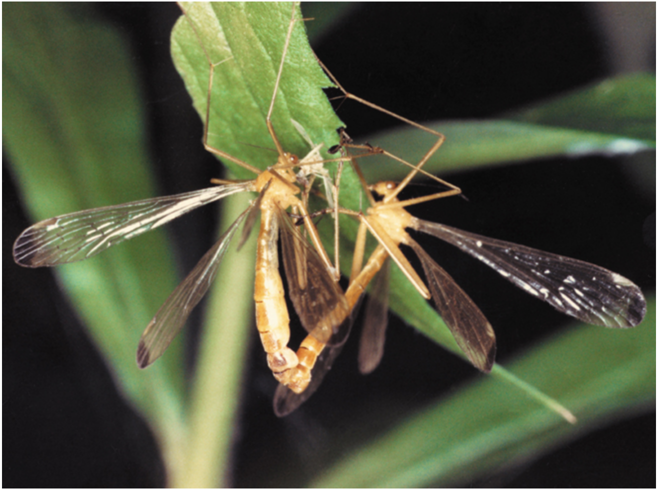

Figure 1: Copulating hangingflies

[1]**Image:** Byers, G W. (2002). Kansas School Naturalist. 48:0022-877X

Direct benefits: resource provisioning

- Thornhill[1] studied *Bittacus apicalis* in Michigan, USA
- Males catch prey, then use pheremones to attract females
- If females accept prey, copulation ensues while female eats
- Female gets food from the male, and does not need to risk predation hunting for herself

[1] Thornhill, R (1976). Am. Nat. 110:529-548

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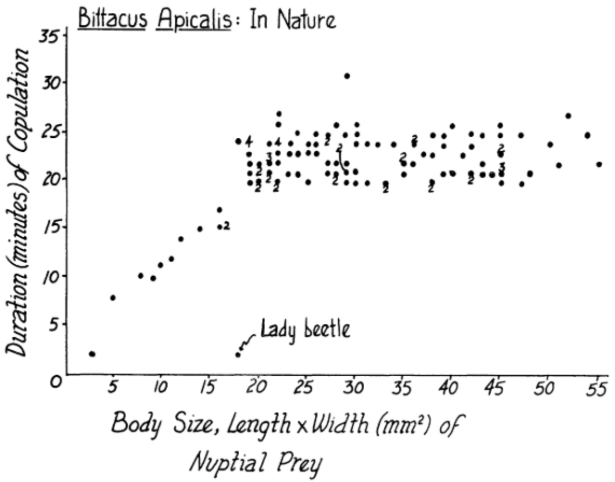

FIG. 3.—The relationship between the duration of copulation and nuptial prey size and palatability in *Bittacus apicalis* in nature. The numbers above the dots indicate more than one observation for a prey size. $N = 118$.

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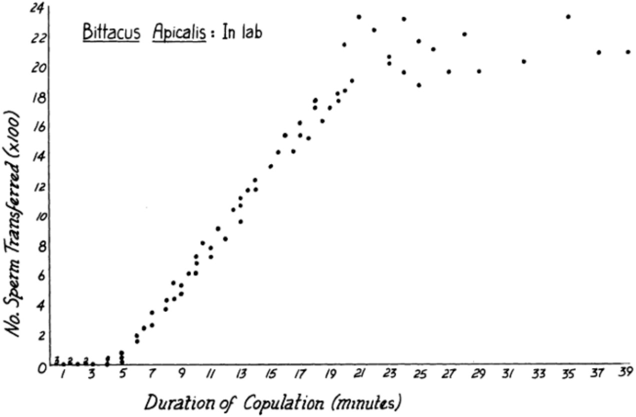

FIG. 4.—The number of sperm transferred as a function of the duration of copulation in *Bittacus apicalis*. $N = 71$.

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Pleiotropy: Choosiness as a side-effect of a trait

- Proctor[1] studied the water mite *Neumania papillator* in Ontario, Canada

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- Males attract females by trembling their legs, then transfer spermatophores
- **Proctor hypothesised that female choice for trembling behaviour evolved because it mimics vibrations of prey**

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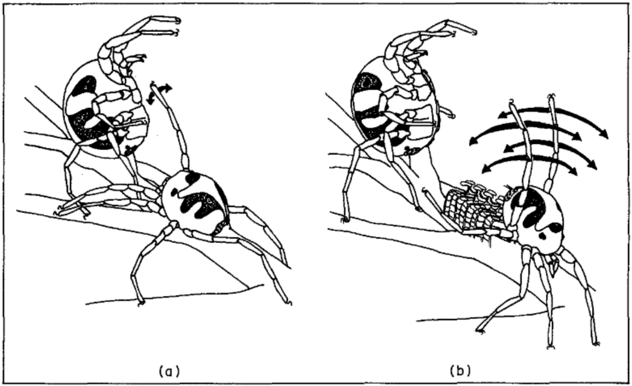

Figure 1. Courtship in *N. papillator*: (a) the male vibrates his foreleg in front of the female, which is in net-stance; (b) the female has turned slightly in response to the trembling, and the male fans his fourth legs over the spermatophores he has just deposited. Sausage-shaped objects on top of spermatophore stalks are sperm packets.

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Pleiotropy: Choosiness as a side-effect of a trait

Key results

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- Less well fed females responded to males more readily than well fed females
- Males tremble to determine female direction, and deposit spermatophores in front of them more often than expected by chance

Pleiotropy: Choosiness as a side-effect of a trait

- **But did female predatory behaviour evolve before male mating behaviour?**

[1] Proctor, H. (1992). Anim. Behav. 44:745-752

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- Proctor[1] investigated mite phylogeny to see which behaviour evolved first

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- **But did female predatory behaviour evolve before male mating behaviour?**
- Proctor[1] investigated mite phylogeny to see which behaviour evolved first
- Two evolutionary histories appear most likely (left)
  - Insufficient evidence for predatory behaviour evolving first (top)
  - Predatory behaviour evolved first, male mating behaviour independently evolved twice (bottom)

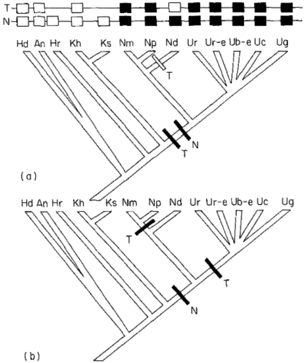

Figure 4. Behavioural character states overlaid on the cladogram, showing two equally parsimonious evolutionary scenarios (T = male courtship trembling; N = netstance). Presence of the behaviour in a species is indicated by a filled box above the species abbreviation and absence by an empty box. Blank lines indicate unknown character states.

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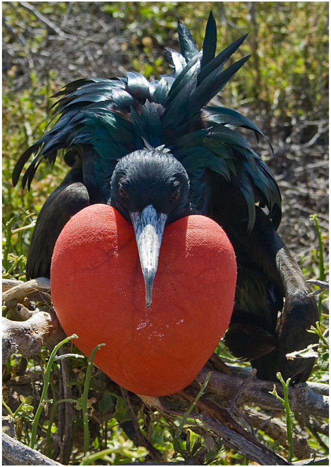
[1] Zahavi, A. (1975). J. Theor. Biol. 53:205-214

[2] Grafen, A. (1990). J. Theor. Biol. 144:517–546.

Good genes: Choosiness to increase offspring fitness

- Individuals of the mate-limited sex (usually males) are chosen by members of the resource limited sex (usually females) based on traits that are indicators of high fitness
- Chosen traits are often elaborate ornaments or behaviours



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[3] **Image:** *Fregata magnificens* Julian Hammer. CC 3.0

Good genes: Female choosiness in grey tree frogs

- Grey tree frogs (*Hyla chrysoscelis* & *H. versicolor*) endemic to North American woodlands
- During breeding season, males make pulsed calls to females ('trills')
- Males vary in **call rate (CR)** & **pulse number (PN)**
- Gerhardt et al.[1] hypothesised that females prefer higher CR & PR

[1] Gerhardt, H C, et al. (1996). Behav. Ecol. 7:7-18

[2] **Image:** *Hyla versicolor* Trisha Shears.

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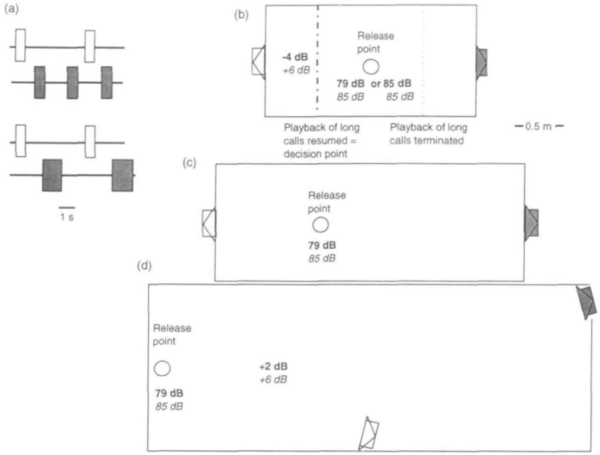

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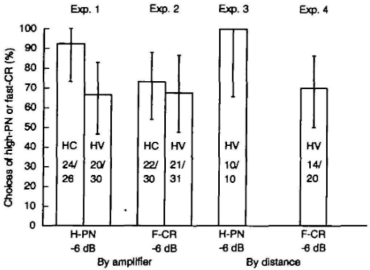

Figure 5
Percentage of female choices (one per female; HV = *H. versicolor*, HC = *H. chrysoscelis*) for high-PN (H-PN) or fast-CR (F-CR) calls over low-PN (L-PN) or slow-CR (S-CR) calls. In Experiments 1 and 2, a difference in SPL of 6 dB at the release point in favor of low-PN or slow-CR calls relative to high-PN and fast-CR calls was created by differential amplification; females were released midway between the speakers as in Figure 2b. In Experiments 3 and 4, the 6-dB difference was created by distance as shown in Figure 2c. Error bars represent 95% confidence limits on the proportions of females that responded to the preferred stimulus; raw data are also presented in each bar as the number of females choosing the preferred stimulus divided by the number of responding females. *p*-values for two-tailed binomial tests of the null hypothesis of no preference: Experiment 1—HC (<.001); HV (.099); Experiment 2—HC (.016); HV (.07); Experiment 3—HV (<.01); Experiment 4—HV (.12).

Gerhardt et al.'s[1] hypothesis supported; in experiments, females prefer:

- Higher call rates (CR)
- Higher pulse number (PN)

Preferences significant despite higher CR & PN speakers played more softly, or placed farther away from choosing female

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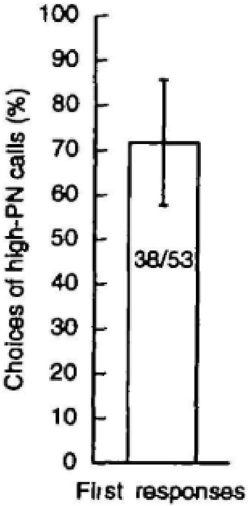

Further, when a loudspeaker playing a call with a relatively high pulse number (PN) was placed in the same direction but farther away from a loudspeaker with a short PN call, females tended to bypass the latter entirely and go to the farther high PN call.

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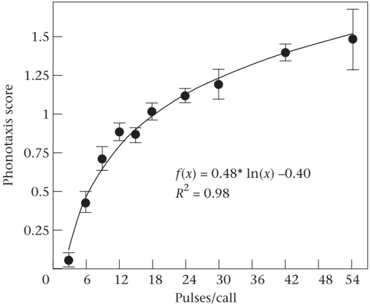

Figure 5. Phonotaxis scores of *H. versicolor* females to song models varying in pulse number. Each point represents the mean (±SE) of 10 females. A logarithmic curve is fitted to the data. The standard song model used in the control trials had 18 pulses/call.

- Bush et al.[1] further quantified *H. versicolor* response to PN.
- Calculated a phonotaxis score: ratio of time to reach loudspeaker during control trial to test trial ($t_{control}/t_{test}$)
- Control trial set to be as attractive as typically observed calls

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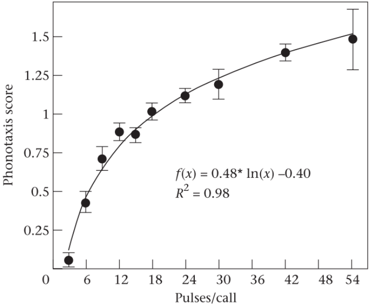

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- **Do males with higher call rates and pulse numbers have better genes?**

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Good genes: Female choosiness in grey tree frogs

- Welch et al.[1] collected unfertilised eggs from wild female tree frogs
- Fertilised some of a female's eggs with sperm of males with high pulse number, and some with sperm of males with low pulse number
- Measured fitness related traits of offspring from each type of male on a low and high food diet

[1] Welch, A M, et al. (1998). Science 280:1928-1930

Tree frog table

Welch et al.[1] found that offspring of males with higher pulse numbers had higher fitness, or no difference in fitness, across all measures of fitness

Fitness measure	High food diet	Low food diet
Larval growth	No difference	**Long-call better**
Time to metamorphosis	**Long-call better**	No difference
Mass at metamorphosis	No difference	**Long-call better**
Larval survival	**Long-call better**	No difference

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If the choosing sex is always selecting for ornamentation, why is there still variation in fitness?

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The lek paradox, and one potential resolution

The lek paradox: Given many generations of sustained selection for ornamentation (i.e., choice), genetic variation for ornamentation should erode, followed by variation for choosiness[1]

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Marlene Zuk and Bill Hamilton[2] suggest that female choice for ornamentation is related to signalling for parasite resistance by males

- Males that are genetically resistant to common parasites will have *good genes*
- Males that are not genetically resistant will have *bad genes*
- Selection should favour females who choose males with good genes for passing parasite resistance to offspring

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The lek paradox, and one potential resolution

Bright ornaments (e.g., bird plumage), might serve as a reliable indicator of good health due to parasite resistance.

Males ornamentation	Susceptible to parasites	Parasite resistant
None	Appears healthy	Appears healthy
Costly ornament	Appears unhealthy	Appears healthy

Host-parasite coevolution will cause alleles underlying parasite resistance to change over time, maintaining genetic variation[2]

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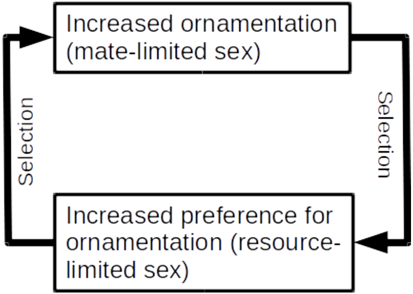
Runaway sexual selection: a positive feedback loop



- The 'runaway' of selection is a positive feedback loop between ornamentation and preference
- Feedback loop generates linkage disequilibrium between alleles for ornamentation and preference for ornamentation

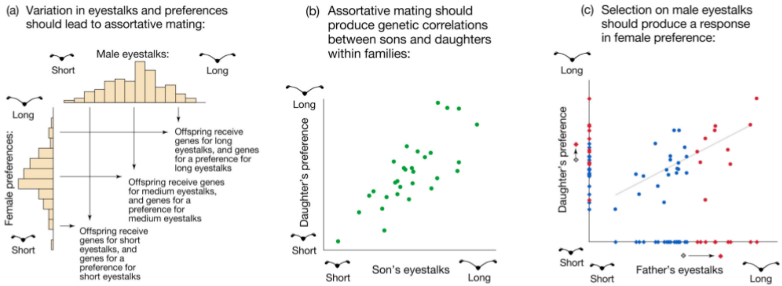
Runaway sexual selection: stalk-eyed flies

- Multiple species across the globe
- Roost at dawn and dusk on root hairs, and mate
- Males have longer eye stalks that females
- Some evidence male-male combat selects for longer eye stalks[1]

[1] Panhuis, T M & Wilkinson, G S. (1999). Behav. Ecol. Sociobiol. 46:221-227

[2] **Image:** Diopsidae Guido Bohne. CC 2.0

Runaway sexual selection: stalk-eyed flies



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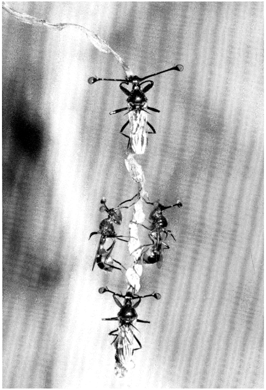

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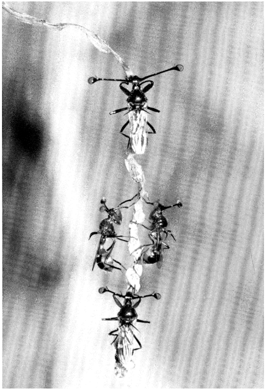

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- Established 3 laboratory populations
    - Control line with females and males picked at random
    - Long-selected line with females picked at random, but males with longest eye stalks
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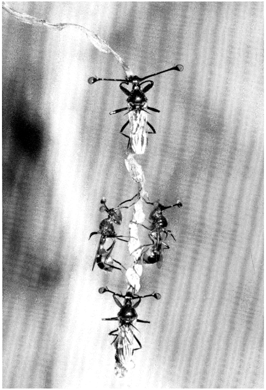

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- After 13 generations, male eye stalk length evolved

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Runaway sexual selection: stalk-eyed flies

- Females from each line placed in a cage between a long-stalk and short-stalk[1] (separated by a clear barrier with a hole small enough for females to pass)

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- Females from each line placed in a cage between a long-stalk and short-stalk[1] (separated by a clear barrier with a hole small enough for females to pass)
- Observed preferences of females from each line of male eye stalk selection

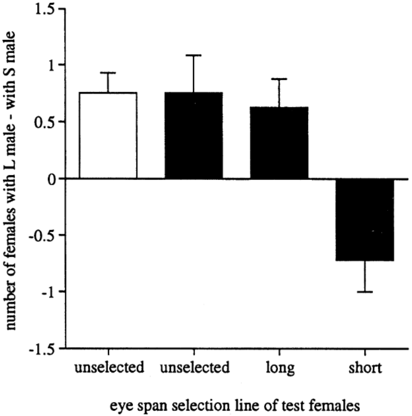

Figure 4. Difference between the number of females (mean ± s.e.) roosting either with an L or S male in the four mate choice experiments referred to in the text. Unfilled bar indicates experiment 1 where males could interact. Filled bars indicate, from left to right, experiments 2–4 in which a transparent perforated partition separated L and S males in each cage.

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- Both male eye stalk length and *female preference* for eye stalk length are heritable
- Sexual selection on the trait of one sex can cause an evolutionary response in the trait of the other sex
- Genetic correlation between male eye stalk length and female preference for eye stalk length[1,2]

[1] Wilkinson, G S & Reillo, P R. (1994). Proc. B. Soc. B. 255:1-6

[2] Freeman, S, & Herron, J C. (2007). Evolutionary analysis. Upper Saddle River, NJ: Pearson Prentice Hall.