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### EVOLUTIONARY BIOLOGY: ON CONSTRAINTS ON ADAPTATION

The following points are made by Laurent Keller (Current Biology 2004 14:R757):

- 1) A long-standing question in evolutionary biology is how well organisms adapt to their environment. Providing a quantitative response to this question has proven to be a formidable task [1], because there are few systems where it is possible to make clear predictions about what constitutes an "optimal" phenotype in a given environment and to quantify how living organisms differ from this phenotype.
- 2) Sex ratio studies, particularly in species where there is local mate competition (LMC) with males competing to mate with their sisters, have been the most successful for testing the precision of adaptation [2-5]. Hamilton's LMC model [3] predicts that females should produce a female-biased sex ratio when male dispersal is restricted and matings occur between the offspring of one or few females in the natal patch. The degree of female bias should increase when the probability of sib-mating increases. When only one female contributes offspring to a patch, her best sex ratio strategy is to produce only enough sons to mate with the daughters that are produced.
- 3) Numerous studies have shown that LMC theory can explain variation in the sex ratio across populations and species, as well as the facultative adjustment of offspring sex ratio by individuals in response to local conditions. These studies usually assume that the primary cue used by females to determine the level of local mate competition is the density of other females in a patch. A new study by Shuker and West, however, reveals that the shift in offspring sex ratio is primarily caused by the presence of eggs laid by other females on the host and to a lesser extent by the presence or absence of other females in the patch.
- 4) The parasitoid wasp *Nasonia vitripennis* has been one of the primary model systems used to study the precision of sex ratio adjustment. This small wasp oviposits up to 40 eggs on the pupae of numerous dipteran species. More than one female may oviposit on a single host, although they prefer unused hosts.





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Males have reduced wings and do not disperse from the natal patch, while females have wings and disperse after mating to find new patches of hosts. This mating system fulfills the assumptions of LMC and a large body of experimental work shows that females produce a sex ratio which is broadly in line with theoretical predictions, making *N. vitripennis* a textbook example of species that adaptively shifts the sex ratio of its offspring.

References (abridged):

1. Orzack, S.H. and Sober, E. (2001). *Adaptationism and Optimality*. (Cambridge: Cambridge University Press)
2. Hardy, I.C.W. (2002). *Sex Ratios: Concepts and Research Methods*. (Cambridge: Cambridge University Press)
3. Hamilton, W.D. (1967). Extraordinary sex ratios. *Science* 156, 477-488
4. West, S.A., Herre, E.A. and Sheldon, B.C. (2000). The benefits of allocating sex. *Science* 290, 288-290
5. Herre, E.A. (1987). Optimality, plasticity and selective regime in fig wasp sex ratio. *Nature* 329, 627-629

Current Biology <http://www.current-biology.com>

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Related Material:

#### THE RHYTHM OF MICROBIAL ADAPTATION

The following points are made by Philip Gerrish (*Nature* 2001 413:299):

- 1) Populations of organisms adapt to their environment through the production of beneficial mutations and the subsequent spread of these mutations to predominance in the population via natural selection, a process known as "fixation". The fixation of a given beneficial mutation often takes a long time, and during this time it is possible and likely, in large microbial populations, that one or more alternative beneficial mutations will appear in the still-prevalent parental lineage in which the given beneficial mutation appeared. The result is the simultaneous presence in the population of several new lineages that each carry a selective advantage over their common progenitor.
- 2) Quoting Ernst Mayr, the evolutionary biologist "studies the steps by which the miraculous adaptations so characteristic of every aspect of the organic world have evolved." But the general nature of such adaptive steps is still unclear. Evolution is often thought to be random and dependent on unpredictable events. In this light, one might expect the steps taken by adaptation to be completely random, both biologically and temporally.
- 3) The author presents a mathematical derivation to demonstrate that, on the contrary, adaptive steps can have fairly strong rhythm. The author reports that the strength of the adaptive rhythm, i.e., its relative temporal regularity, is equal to a constant that is the same for all microbial populations. As a consequence, numbers of accumulated adaptations are predicted to have a universal variance/mean ratio. The author suggests the derived theory is potentially applicable to the study of molecular evolution.

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**Related Material:**

**ON THE CONTROL OF SEX RATIOS IN ANT COLONIES**

**The following points are made by L. Passera et al (Science 2001 293:1308):**

**1) Social insects provide some of the most striking examples of elaborate cooperative behavior, yet life within colonies also entails conflicts. In ants, the most strident conflict concerns sex ratio, with workers favoring a more female-biased sex investment ratio than queens. This conflict arises because of the hymenopteran haplodiploid system of sex determination, whereby unfertilized eggs develop into males and fertilized eggs develop into females. As a result, workers in colonies headed by a single once-mated queen are three times more related to sisters than to brothers.**

**2) Because of this asymmetry in relatedness, the population-wide sex allocation ratio should equilibrate at 3:1 (female:male) if workers control the colony's investment in reproductive offspring. In contrast, because queens are equally related to their daughters and sons, an equal investment in male and female reproductives is expected if the colony's allocation of resources is under the control of the queen. Because they control brood rearing and food flow in the colony, workers can bias sex allocation, for example, by selectively eliminating males and/or preferentially feeding females, and workers have indeed been demonstrated to manipulate colony sex ratios in this way.**

**3) The authors report a study in which they exchanged queens between male- and female-specialist colonies of the fire ant *Solenopsis invicta*. These exchanges quickly reversed the sex-ratio biases of adopting colonies. The sex ratio of queen-laid eggs differed strongly between male- and female-specialist colonies. The authors suggest that these findings indicate that queens can force workers to raise male sexuals by limiting the number of female brood, and that the findings help to explain why sex investment ratios lie between the queen and worker equilibria in this and many other ant species.**

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