

Evolution: Informational Constraints on Adaptation

Dispatch

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Many species adaptively alter offspring sex ratios, yet little is known about how they obtain relevant environmental information. New work on the parasitoid wasp *Nasonia vitripennis* reveals that the presence of eggs on hosts provides a reliable cue allowing females to determine the degree of local mate competition and adaptively adjust offspring sex ratios.

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.

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.

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 [6]. 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 [6]. A new study by Shuker and West [7], 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.

The parasitoid wasp *Nasonia vitripennis* has been one of the primary model systems used to study the precision of sex ratio adjustment [8]. 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. 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 fulfils 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 [9].

To study how *N. vitripennis* females obtain relevant information from the environment to alter the sex ratio of their offspring, Shuker and West [7] simultaneously manipulated the cues they envisaged as being the most likely to provide information on the degree of local mate competition. They used unparasitized hosts and hosts parasitized during the 24 hours prior to the start of the experiment. They then provided three types of social environment: a focal female alone, a focal female plus four other females, and a focal female and four other females that were experimentally prevented from ovipositing. Hence, there were six treatments in total for determining whether females primarily alter their sex ratio in response to previous parasitism of hosts. In the multiple female experiments, all competing females were red-eye mutants so that the experimenters could identify the offspring of the focal female.

The results unambiguously revealed that the most important cue influencing sex ratio was the parasitization of hosts. When encountering parasitized hosts, focal females laid eggs with a sex ratio close to even, independently of the presence or absence of other females and whether they were fertile or not. By contrast, in the experiments with unparasitized hosts, the offspring sex ratio was significantly female-biased and the social environment significantly affected the sex ratio. When females were alone, the proportion of males was less than 20%. In the presence of four sterile females, however, the proportion of males increased to almost 30%. Finally, in the experiment where focal females were with four other reproductive females, the sex ratio was 43%. The higher proportion of males produced in presence of fertile females compared to sterile females most likely stemmed from the fact that some of the hosts were already parasitized when visited by the focal female.

How adaptive behavior is influenced by the information available to females was determined by comparing the observed sex ratio with the optimal sex ratio. Using Hamilton's equation [3,10], Shuker and West [7] calculated that the optimal sex ratio is 0.38 in the experiments where focal females compete with four other females. The observed sex ratio was 0.43 when focal females were with the four normal females, which is not significantly different from the predicted value. As a result, the mean fitness of females in this experiment was very high, 99.7% of that of an optimal female. By contrast, the observed sex ratio was lower (0.30) and significantly different from the predicted value when the focal female was in the presence of the four sterile females. In this experiment, the fitness of females was 99.4% of the optimal value. From

these data, Shuker and West [7] concluded that females behave less optimally when they are prevented from using information on whether or not hosts are parasitized, a cue normally available in nature. While this conclusion is probably correct, some caution is nevertheless required because the fitness difference between the two experiments was small and sample sizes were not sufficient to allow us to statistically compare the observed fitness values achieved under the two experimental conditions.

This study [7] has two important implications for our understanding of sex ratio and in a more general sense for adaptation as well. It first demonstrates the importance of carefully considering all the cues that organisms may use to alter their behavior. This problem is particularly acute for studies conducted in the laboratory, as it is almost impossible to provide an environment identical to the one experienced by organisms in the wild. Thus, the possibility that deviations from optimal behavior are laboratory artifacts stemming from organisms lacking important cues available under normal conditions can never be ruled out. Alternatively, field observations have also important limitations because they do not allow us to control for unwanted variables.

Fig wasps, the other group of organisms commonly used to study adaptive sex ratio variation in response to difference in LMC, provide a good example of this effect. All data on sex ratio and female number in the patch — in this case a fig — have been collected directly in the field with a resulting good fit between the expected and observed sex ratio values [5,11]. However, recent genetic work revealed that, contrary to general belief, figs are sometimes pollinated by two or more cryptic fig wasp species, thus leading to estimation errors of the degree of LMC based on the number of female per fig [12]. Incidentally, it was found that taking into account the presence of cryptic species has led to an even better fit between observed and expected sex ratio data [12].

The second message of this study [7] is that gauging the precision of adaptation is a daunting task. A qualitative approach requires a good understanding of mechanistic issues with correct theoretical predictions possible only if one knows the relevant environmental information used by females to determine the level of LMC. Moreover, there might be costs associated with information gathering, resulting in behavioral decisions being made on only limited information and hence being error-prone. Recent empirical and theoretical work on sex ratio in social insects has led to a similar conclusion on the importance of considering mechanisms and costs. The outcome of the queen-worker conflict on colony sex ratio in ants critically depends on the relative power of queens and workers to manipulate sex ratio to their advantage [13,14] and the cost associated with this manipulation [15].

One of the most fascinating challenges for studies of adaptation will be to determine the roles of the various ecological, genetic, physiological and developmental factors constraining the precision of adaptation. This will require the collaboration of scientists with different backgrounds and concentrated effort on

one or a few model organisms, as has been done previously by molecular biologists. While *N. vitripennis* has many of the characteristics to make it a model species, a formidable challenge with this organism will be to devise experimental conditions encompassing all the environmental factors that may have a role under natural conditions.

References

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