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Sex Allocation: L'Enfer C'est les Autres?

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Brine shrimp produce a maladaptive excess of sons when co-occurring with females from a related parthenogenetic species. Still, this sex ratio may be adaptive if, by mating with females of the other species, males miss out on mating with their own.

When Theodosius Dobzhansky stated his famous sentence: “Nothing makes sense in biology except in the light of evolution”, he was probably far from realizing that sex allocation — the study of how sexual organisms allocate resources into the number and quality of daughters and sons — would become one of the hallmarks of the explanatory power of evolutionary theory. Indeed, sex allocation is a classic illustration of scientific accomplishment, where elegant and intuitive theory is supported by a vast body of field and laboratory experiments [1]. Ronald Fisher predicted that, in panmictic (large, randomly mating) diploid populations, parents should allocate the same resources for the production of male and female offspring (often leading to an even sex ratio) [2]. However, in structured populations with few founding females, a female-biased sex ratio is

predicted, to minimize sons competing among themselves and to maximize the production of females that will found new patches [3]. This paradigmatic example, referred to as the ‘theory of local mate competition’, has been quantitatively tested and verified in comparative [4–7] and experimental evolution [8,9] studies. A new study in this issue of *Current Biology* by Lievens *et al.* [10], however, challenges the ubiquity of the predictive success of sex allocation theory.

In most studies, observed sex ratios are such that fitness is maximized. But in some rare cases, maladaptive sex allocation does occur. For instance, in parasitoid wasps of the genus *Melittobia* females produce a far more female-biased sex ratio than that predicted by local mate competition [11]. Also females of another parasitoid wasp, *Nasonia vitripennis*, produce sub-optimal sex ratios after

exposure to neonicotinoid insecticides [12]. In this case, females fail to adjust the proportion of female offspring to the number of founding females, entailing a significant fitness cost.

In the same way that a map is still a map even when held upside down, a good theory may still provide clues to the problem under analysis, even when observed facts do not match its predictions. This is nicely illustrated by the new study of Lievens *et al.* [10] showing (apparently) maladaptive sex allocation in the invasive brine shrimp *Artemia franciscana* (Figure 1). *A. franciscana*’s natural range spreads through the Americas, in particular saline lakes — most of the commercial production of brine shrimps comes from North America’s Great Salt Lake — and temporary ponds [13]. Commercially available worldwide, due to its extensive use in aquaculture,

A. franciscana is also a cosmopolitan species, with invasive populations in Europe, Asia, Madagascar, North Africa and Australia [14]. *A. franciscana* produces an even sex ratio in their native range, which is in agreement with the classical Fisherian prediction, given the high population sizes found in this species. However, in the Mediterranean region, *A. franciscana* shares its habitat with *A. parthenogenetica*, an old-world parthenogenetic brine shrimp composed exclusively of females that reproduce clonally without the need of fertilization by a male gamete.

In the populations present in this region, Lievens *et al.* [10] found that *A. franciscana* females produce a male-biased sex ratio. Moreover, there is a positive correlation between the proportion of sons produced by *A. franciscana* and the number of *A. parthenogenetica* (females) present in the population. The authors followed by experimentally exposing *A. franciscana* populations to an excess of females. Regardless of this excess being due to conspecific or *A. parthenogenetica* assexuals, the response was the same: an overproduction of male offspring. Those populations are still panmictic; hence, the optimal sex ratio expected is 50/50. This maladaptive sex allocation probably results from a lack of discrimination between conspecific and heterospecific females by *A. franciscana* males. Therefore, these results show reproductive interference — a reproductive interaction between different species that results in a fitness decrease for one of the species. In this case, the reproductive interaction affects sex allocation. Hence, this represents a form of reproductive interference [15] unreported so far.

But does such an excess of males have to be all that maladaptive? A closer look at the map provided by theory may shed light on this issue. Indeed, one has to consider that males that engage in reproductive interactions with females of another species will be unavailable to mate with females of their own species. This is particularly true in *A. franciscana*, which exhibits a complex mating behaviour. Males clasp females dorsally to get the female in amplexus — the embrace that precedes copulation [16,17]. The resulting mating pairs (Figure 1) may stick together

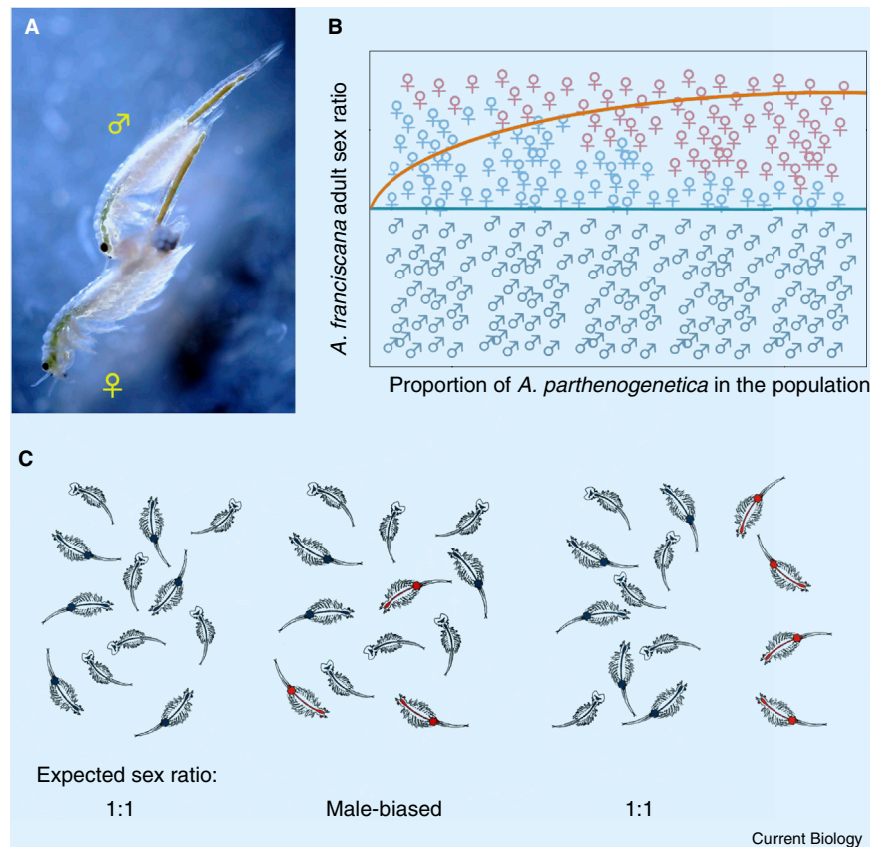


Figure 1. Sex allocation in brine shrimp.

(A) In Anacostran crustacea, such as *Artemia*, females are more receptive during the progressive maturation of the ovaries. To mate, a male approaches and touches the female's body with his clasper and attempts to grasp the female in amplexus. Males clasp females dorsally for periods of up to several days. Image: Thomas Lenormand. (B) Lievens *et al.* [10] show that the sex allocation of *A. franciscana* responds to the combined number of conspecific (blue) and heterospecific females (red) in an almost Fisherian mode (blue line). As a result, the sex ratio of *A. franciscana* becomes male-biased when accounting for conspecific males and females only (orange line). This is observed both in natural populations from the invasive range and in experimental manipulations. (C) In their natural range, *A. franciscana* produces an even sex ratio (C1). However, when in the presence of *A. parthenogenetica* females (red), *A. franciscana* males (grey) fail to distinguish them from conspecific females (blue). This excess of females is expected to select for a male-biased sex ratio (C2, cf. main text). Natural selection is also expected to favour males that preferentially mate with conspecific females. This mating assortment should result again in an unbiased sex ratio, as populations of the two species will effectively be separated (C3).

for several days [17,18]. As a consequence, males can remain unavailable for mating for long periods, and even more so in the presence of females of another species. Thus, a female producing an excess of sons actually increases the probability of transmitting her genes to future generations, as this increases the probability of having a son coupling with a female of his own species (Figure 1). Hence, at the individual level, *A. franciscana* sex allocation is probably close to optimal, assuming a high cost of mating with heterospecific females.

Still, males that mate with females of the other species are losing effective mating

opportunities, so one would expect strong selection for the male's ability to discriminate between females of the two species. In this system, *A. franciscana* males mate with *A. parthenogenetica* females, so mate choice, if present, will at best be incomplete. However, even if mate choice is weak, males may still invest less time in mating with heterospecific females, as recently observed in spider mites [19]. If so, sex allocation should reflect the average degree of conspecific preference observed in the population, such that high frequency of conspecific matings leads to an even sex ratio and high frequency of heterospecific matings to a male-biased

sex ratio (Figure 1). In order to understand whether this is the case, it is key to study the within population variability in mate choice and reproductive interactions between species. The comparison between mating preference and the degree of reproductive interference between native and invasive populations may also be an important piece of the puzzle.

In sum, Lievens et al. [10] show how contact with a parthenogenetic species during range expansion in the brine shrimp leads to a novel form of reproductive interference, by modifying sex allocation. Given the growing importance of biological invasions, this study may be the first of many. More generally, rather than testing and fitting populations to predictions given by equations, sex allocation theory can enlighten us on the particular ecological conditions experienced by populations. The two *Artemia* species studied by Lievens and colleagues [10] may actually provide a textbook example on how sex allocation works.

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Parental Care: When the Sex Has to Stop

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How is sexual conflict during reproduction resolved when parents collaborate to rear offspring? A new study shows that female burying beetles communicate their hormonal status to their male partners to avoid costly superfluous mating, using an anti-aphrodisiac pheromone.

Parental care is an altruistic trait [1,2]: it is beneficial to offspring because it increases fitness, but is costly to parents because providing care uses up resources that parents would otherwise allocate to future reproduction [3]. What mechanisms

determine how much care parents should provide in each breeding attempt and when they should invest in further breeding opportunities? A new study by Engel *et al.* [4] addresses this fundamental question and shows how this important trade-off is

hormonally regulated in an insect with extended parental care.

Across the animal kingdom, females typically provide more care than males. Even in species in which both sexes look after offspring, the amount of care