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Current Biology

Maladaptive Sex Ratio Adjustment in the Invasive Brine Shrimp *Artemia franciscana*

Highlights

- *Artemia franciscana* produce more sons when the adult sex ratio is female biased
- Invasive *A. franciscana* also respond to native asexual females
- Facultative sex ratio adjustment is maladaptive for invasive *A. franciscana*

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In Brief

Lievens et al. provide a rare example of maladaptive sex allocation. They show that the sex allocation strategy of the brine shrimp *Artemia franciscana* is information limited in its invasive range, causing its ancestral sex ratio adjustment trait to become maladaptive. Despite this, the trait persists unchanged ~500 generations after the invasion.

Maladaptive Sex Ratio Adjustment in the Invasive Brine Shrimp *Artemia franciscana*

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SUMMARY

Sex allocation theory is often hailed as the most successful area of evolutionary theory due to its striking success as a predictor of empirical observations [1]. Most naturally occurring sex ratios can be explained by the principle of equal investment in the sexes [2–4] or by cases of “extraordinary” sex allocation [5]. Deviations from the expected sex ratio are often correlated with weak selection or low environmental predictability (e.g., [6, 7]); true cases of aberrant sex allocation are surprisingly rare [8]. Here, we present a case of long-lasting maladaptive sex allocation, which we discovered in invasive populations of the exclusively sexual brine shrimp *Artemia franciscana*. *A. franciscana* was introduced to Southern France roughly 500 generations ago [9]; since then, it has coexisted with the native asexual species *Artemia parthenogenetica* [10]. Although we expect *A. franciscana* to produce balanced offspring sex ratios, we regularly observed extremely male-biased sex ratios in invasive *A. franciscana*, which were significantly correlated to the proportion of asexuals in the overall population. We experimentally proved that both invasive- and native-range *A. franciscana* overproduced sons when exposed to excess females, without distinguishing between conspecific and asexual females. We conclude that *A. franciscana* adjust their offspring sex ratio in function of the adult sex ratio but are information limited in the presence of asexual females. Their facultative adjustment trait, which is presumably adaptive in their native range, has thus become maladaptive in the invasive range where asexuals occur. Despite this, it has persisted unchanged for hundreds of generations.

RESULTS

Although we expect sexual *Artemia* to produce balanced offspring sex ratios (see the [Experimental Procedures](#)), we regularly observed extremely male-biased sex ratios in *Artemia franciscana* in Southern France, and these biases were strongly correlated with the proportion of *Artemia parthenogenetica* in

the sample ([Figure 1](#)). We collected demographic data from 56 samples of *Artemia* (over 7,000 adults sexed) taken from 12 sampling sites in two large salterns between the years 2010 and 2015 and analyzed the factors affecting the sex ratio of *A. franciscana* in each sample (sex ratio r = number of adult males / total number of adults). The proportion of *A. parthenogenetica* in the samples varied seasonally between 0 and 0.99 ([Figure S2](#)). The sex ratio of *A. franciscana* varied very strongly among samples and throughout the year ($0.4 \leq r \leq 1$), with the highest sex ratios occurring in December and the lowest in May ([Figure 1](#)). After controlling for the seasonal effect, the sex ratio of *A. franciscana* was positively and strongly correlated with the proportion of *A. parthenogenetica* ([Figure 1](#); [Table S1](#)).

Our field results suggested that the presence of *A. parthenogenetica* causes the adult sex ratio of *A. franciscana* to become male biased, and we designed an experiment to confirm this. We combined different numbers of lab-raised *A. franciscana* and *A. parthenogenetica* into parental groups ([Table 1](#); for a full explanation of the tested hypotheses, see the [Experimental Procedures](#)) and monitored their offspring sex ratio (3,820 offspring sexed; [Table S2](#)). First, we verified that *A. franciscana* from Southern France (the invasive range) produced balanced offspring sex ratios when placed in groups with balanced adult sex ratios. This was indeed the case, independently of the total size of the group ([Figure 2](#), “invasive range” and “invasive range*” groups). We then tested whether the biased sex ratios observed in the field could be induced by adding asexual females to the group and, if so, whether addition of conspecific females elicited the same response. We found that when the adult sex ratio was female biased, whether by the addition of *A. parthenogenetica* or *A. franciscana* females, *A. franciscana* females produced male-biased offspring sex ratios ([Figure 2](#), “invasive range + ♀” and “invasive range + P” groups). Finally, we investigated whether sex ratio adjustment in the presence of asexual females was a trait that *A. franciscana* had acquired in its invasive range, or whether it was an ancestral trait that could be observed in native populations. The latter was true: when we placed *A. franciscana* from a native-range population (Great Salt Lake, Utah) in groups with “excess” *A. parthenogenetica* females, they also produced biased offspring sex ratios ([Figure 2](#), “native range + P” group). Statistically, the three female-biased parental groups produced equivalent male-biased offspring sex ratios (0.60, 0.62, and 0.58, respectively; [Table S2](#)), which differed from the balanced offspring sex ratios produced by the equal sex ratio groups (0.51 and 0.48; [Table S2](#); statistical comparison in [Table S3](#)).

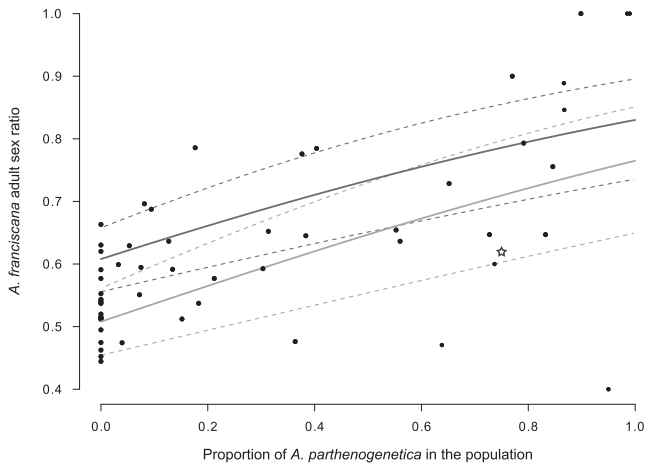


Figure 1. The Adult Sex Ratio of *A. franciscana* in Natural Populations Increases When Asexual *A. parthenogenetica* Are Present

The sex ratio also varies with month; the curves represent the predictions of the best model for December (highest sex ratios; shown in dark gray) and May (lowest sex ratios; shown in light gray), and the dashed lines represent the upper and lower binomial 95% CIs for the two curves. Small points represent the samples where fewer than 20 *A. franciscana* were counted. The star corresponds to our experimental result for the treatment “invasive range + P” (Figure 2). See also Figure S2.

DISCUSSION

The first conclusion that we draw from our experimental results is that *A. franciscana* can plastically adjust their offspring sex ratio in response to changes in the adult sex ratio (Figure 2, compare the first three treatments). This could be advantageous in their native range: Werren and Charnov [11] proposed that in species with overlapping generations, perturbations of the stable age distribution could select for facultative sex ratio adjustment; parents should then produce more offspring of the under-represented, more competitive sex. Although it is unclear to which extent *A. franciscana* generations overlap in nature [12], the native populations do regularly experience perturbations in the adult sex ratio (see Figure S1 and Table S4), and our results confirm their ability to respond to these perturbations. It is worth noting that females are the heterogametic sex in *A. franciscana* [13, 14] and that the sex-determining meiosis in oocytes is triggered by fertilization [15]; this provides females with the potential to adjust the primary sex ratio in real time [16–18]. This study pro-

vides the first evidence of facultative sex ratio adjustment in *Artemia*, which may become a useful model organism to resolve some of the empirical debate around Werren and Charnov’s model (e.g., [19, 20]).

Second, our experiment confirms the field data and shows that *A. franciscana* mistakenly adjust their offspring sex ratio in response to the presence of *A. parthenogenetica* females (Figure 2, compare the third and fourth treatments). It is likely that *A. franciscana* are unable to differentiate between con- and heterospecific females; this has already been noted with regards to male mate choice [21, 22] and is unsurprising because it is the only brine shrimp species in its native range [10]. In the invasive range, therefore, *A. franciscana* seem to be limited by information: they mistake parthenogenetic females for conspecifics. A handful of previous studies have described similar effects of information constraints on sex ratio adjustments [23–25], but these studies deal with spatially segregated patches (anhill, fly pupae) where information is not universally faulty and the population-wide impact of bad decisions may be limited. In contrast, where *A. franciscana* coexists with *A. parthenogenetica*, mistaken sex ratio adjustment occurs on a population scale. Interestingly, both *A. franciscana* and *Nasonia* [25] females make poor sex allocation decisions based on a failure to identify heterospecifics; such constraints, if looked for, may be more common than we think in sex-ratio-adjusting species.

Facultative sex ratio adjustment is thus maladaptive for *A. franciscana* in its invasive range. When *A. parthenogenetica* are present, the false sex allocation cue they cause overwhelms any relevant variation in *A. franciscana* sex ratio and causes a mass overproduction of males. Females will then become the more reproductively competitive sex, and parents mistakenly producing excess sons will be disadvantaged compared to any (hypothetical) parent producing fewer sons in favor of daughters [2, 11]. This disadvantage is unlikely to be compensated for by “correct” sex ratio adjustment at other points in the lifespan, as *A. parthenogenetica* are typically present from May until October, well above the life expectancy of *Artemia* [26].

Finally, and surprisingly, invasive *A. franciscana* in Southern France still display the exact same sex ratio adjustment response as naive populations, despite ~500 generations of exposure to an environment where this behavior is costly (Figure 2, compare the fourth and fifth treatments). This result contrasts sharply with previous experimental evolution studies on sex allocation, which show that populations can evolve to match predicted sex ratios within 2 to 54 generations [27–31] (though at least one natural

Table 1. Composition of the Experimental Treatments

Treatment	Parental Group Composition				Origin of <i>A. f.</i>	Parental Sex Ratio	
	<i>A. f.</i> Males	<i>A. f.</i> Females	<i>A. p.</i> Females	Total		“True”	“Perceived”
Invasive range	5	5	–	10	A-M, France	0.5	0.5
Invasive range*	20	20	–	40	A-M, France	0.5	0.5
Invasive range + ♀	5	35	–	40	A-M, France	0.125	0.125
Invasive range + P	5	5	30	40	A-M, France	0.5	0.125
Native range + P	5	5	30	40	GSL, USA	0.5	0.125

We formed parental groups out of different numbers of *A. franciscana* (*A. f.*) and *A. parthenogenetica* (*A. p.*), with different “true” and “perceived” parental sex ratios. “True” sex ratio, *A. franciscana* males / *A. franciscana* males and females; “perceived” sex ratio, *A. franciscana* males / (*A. franciscana* males and females + *A. parthenogenetica*). A-M, Aigues Mortes; GSL, Great Salt Lake.

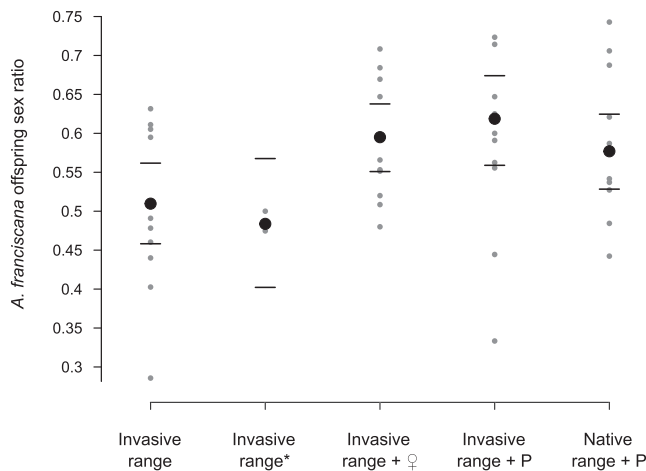


Figure 2. *A. franciscana* Produce Male-Biased Offspring Sex Ratios When Experimentally Exposed to Female-Biased Parental Sex Ratios

They do this independently of their geographical origin (“invasive range” versus “native range”) and of whether the female bias is caused by conspecific females (“+♀”) or by *A. parthenogenetica* asexuals (“+ P”). Small gray points are the results for each replicate, large black points are the mean, and horizontal bars represent the binomial 95% confidence intervals. See also Table S2.

population has not evolved within this timeframe [32]). Why is adaptation so much slower in invasive *A. franciscana*? Selection should be strong, so that even a loss-of-function mutation restoring fixed Mendelian segregation of the Z and W chromosomes to oocytes—and thus a Fisherian sex ratio—should generate a considerable net advantage. For example, based on our experimental treatment “invasive range + P,” we estimate that in a stable population containing 75% asexuals, the relative fitness of a mutant Fisherian parent would be $W = 1.06$ compared to a typical parent producing 62% males [3]. The occurrence of such a loss-of-function mutation is unlikely to be limiting because the Southern French *Artemia* population is very large (estimated on the order of 10^9 – 10^{10} in the Aigues-Mortes saltern alone by commercial exploiter F. Gout, Camargue Pêche, Grau-du-Roi, France; unpublished data), so that we expect Nu to be large. The persistence of maladaptation may be explained by the requirement of a more complex series of mutations; alternatively, and more plausibly, the necessary loss-of-function mutation may be present but (partially) recessive. Supporting the latter possibility, a recessive loss of plastic sex allocation has recently been shown in parasitoid *Asobara japonica* wasps [33]. If the mutation is recessive, the large population size of *A. franciscana* could slow its increase to a detectable frequency [34, 35].

The evolution of an optimal sex allocation in invasive *A. franciscana* has thus been limited by two factors. First, a previously beneficial sex ratio adjustment trait became informationally limited when the species found itself in a novel ecological situation (sympatry with *A. parthenogenetica*). Afterward, as discussed above, it is likely that genetic limitations slowed the loss of the now-maladaptive trait.

Hamilton famously said that the study of sex allocation “best proves [...] the Neodarwinism paradigm as a whole” [1], due to

its success in demonstrating adaptation. However, adaptation is only one side of the evolutionary coin: evolution proceeds locally by tinkering with the available variability and without foresight, so that maladaptation is also expected [36, 37]. Indeed, it is perhaps surprising that so few cases of maladaptation have been reported in this well-studied field. The extraordinary maladaptive sex ratios of invasive *A. franciscana*, perhaps along with other “inexplicable” sex ratios (e.g., [8]), show that like any other trait shaped by natural selection, sex allocation cannot always be optimal.

EXPERIMENTAL PROCEDURES

Biology of *Artemia* and the Invasion of *A. franciscana*

The brine shrimp *Artemia* (Branchiopoda: Anostraca) is a genus of small crustaceans present worldwide in hypersaline environments, notably salt lakes and salt pans. In general, *Artemia* mature within a few weeks and have a life expectancy of ± 3 months [26]. When under optimal conditions, females of most *Artemia* species produce a large clutch of ovoviparous offspring roughly every 5 days [26]. When stressed, *Artemia* produce diapausing eggs that can be stored for years [12].

Sexual *Artemia* populations can be expected to conform to the Fisherian prediction of a balanced sex ratio, since populations are enormous and lack spatial structure [12, 38]. The sex ratio of sexual *Artemia* hatched from diapausing eggs is indeed ~ 0.5 (Table S4), although the adult sex ratios in natural populations are often variable (Table S4), possibly due to differences in male and female tolerance of abiotic factors [39] or food quality [40].

A. franciscana is a bisexual species native to the New World, where it is not sympatric with any other *Artemia* species. The species has been widely introduced to the Old World for commercial purposes [10]. Although *A. franciscana* typically competitively excludes its native congeners, this is not the case in Southern France, where the invader still coexists with native parthenogenetic clades, traditionally called *A. parthenogenetica* [10, 41]. We estimate that this coexistence is roughly 500 generations old: the first introduction of *A. franciscana* occurred in 1970 [9], and as *A. franciscana* is present and reproductive during most of the year ([41] and unpublished data), as many as 12 (overlapping) generations may be produced over the course of a year. *A. franciscana* and *A. parthenogenetica* are genetically distinct and cannot interbreed [42].

Field Observations of *A. franciscana* Sex Ratios in the Native Range

To confirm the reportedly variable sex ratios of *A. franciscana* in its native range (see Table S4), we requested and obtained survey data of the adult sex ratio in the Great Salt Lake from the Great Salt Lake Ecosystem Program (Utah Division of Wildlife Resources). The Great Salt Lake population is one of the largest populations of *A. franciscana*’s native range [43]. The dataset contained adult sex ratios recorded from 453 field samples collected between 2000 and 2014. We excluded the years 2000–2002 from the dataset because contamination of the lake with parthenogenetic females has been reported for those years [43]; unfortunately, the proportion of the population that was parthenogenetic during this period is not known, so we were unable to calculate sex ratios. The data are represented visually in Figure S1 and have been included in Table S4.

Field Observations of *A. franciscana* Sex Ratios in the Invasive Range Sampling

We quantified the sex ratio of *A. franciscana* in its invasive range using 55 different samples from Southern France (Table S5). Samples were taken in Aigues-Mortes (43.53°N, 4.21°E; 53 samples from ten sites) and Gruissan (43.08°N, 3.09°E; two samples from two sites); some samples consisted of freshly sampled, live *Artemia*, and others had been conserved in 96% EtOH after sampling. The samples spanned the period 2010–2015 and included all seasons (March–May, 8; June–August, 19; September–November, 16; December–February, 12). For each sample, we counted the number of adult male *A. franciscana*, adult female *A. franciscana*, and adult female *A. parthenogenetica* in a representative subsample (average number

Table 2. Expectations of the Experiment under the Different Scenarios

Scenario	Expected Offspring Sex Ratio under Each Scenario			
	Invasive Range*	Invasive Range + ♀	Invasive Range + P	Native Range + P
Ancestral trait	0.5	male biased	male biased	male biased
Novel trait—discriminate trigger	0.5	0.5	male biased	0.5
Novel trait—indiscriminate trigger	0.5	male biased	male biased	0.5
Interference	0.5	0.5	male biased	male biased

Our experimental setup allowed us to distinguish between the four scenarios that explained our field results (male-biased sex ratios in the presence of *A. parthenogenetica* for invasive *A. franciscana*), as shown in the table. The scenarios and predictions are described in the [Experimental Procedures](#).

of individuals counted per sample = 132; minimum = 19; maximum = 428). *A. parthenogenetica* occasionally produce “rare” males, which may have been misclassified as male *A. franciscana*, but their frequencies are so low (almost exclusively <1% [44]) that this should not bias our estimation of the *A. franciscana* sex ratio. We calculated the sex ratio of *A. franciscana* as the proportion of males in that species; this is the tertiary or adult sex ratio.

Statistical Analysis

See the [Supplemental Experimental Procedures](#).

Experimental Test of Sex Ratio-Biasing in *A. franciscana*

Experimental Design

Based on the *A. franciscana* sex ratios that we observed in the invasive range, we hypothesized that the presence of *A. parthenogenetica* causes the adult sex ratio of *A. franciscana* to become male biased. We considered that one of three scenarios could be underlying this pattern. The first possibility was that native-range *A. franciscana* are facultative sex ratio adjusters, able to plastically adjust their offspring sex ratio in response to occasional perturbations in the adult sex ratio (as suggested by Werren and Charnov [11]). This trait would have been carried over to the invasive range, where the presence of *A. parthenogenetica* females could trigger the same response as an overabundance of conspecific females. We called this possibility the “ancestral trait” scenario. Second, in the “novel trait” scenario, invasive-range *A. franciscana* could have evolved to produce more sons in response to the presence of *A. parthenogenetica* for unknown reasons. Within this scenario, we considered that invasive-range *A. franciscana* could have evolved to react specifically to the presence of *A. parthenogenetica* (a “discriminate trigger” or to the presence of any females (an “indiscriminate trigger”). Finally, we considered the possibility that *A. parthenogenetica* manipulate their competitors into producing unnecessary males, which we called the “interference” scenario.

We tested our hypothesis and distinguished between the three underlying scenarios by tracking the offspring sex ratio produced by adult *A. franciscana* when placed in parental groups with varying sex ratios. The treatments were as follows (Table 1): “invasive range,” “invasive range + ♀,” and “invasive range + P” all used *A. franciscana* from the invasive range and had no bias, a “true” female bias caused by conspecific females, and a “false” female bias caused by parthenogenetic females, respectively. The treatment “native range + P” used *A. franciscana* from the native range and had a “false” female bias caused by parthenogenetic females. We expected different offspring sex ratios for these four treatments under the scenarios “ancestral trait,” “novel trait,” and “interference”; the predictions are shown in Table 2. Our baseline expectation was a balanced offspring sex ratio (see above). Where we expected male-biased offspring sex ratios, we were unable to predict the bias precisely: for the “ancestral trait” scenario, we would need to know to which extent generations overlap in the field [11], and we could not make theoretical predictions for the speculative “novel trait” and “interference” scenarios. Each treatment was replicated ten times. Although density was kept constant (see below), we accounted for the possibility that sex ratio might be affected by the absolute number of parental individuals by including two replicates of an additional control treatment “invasive range*,” with a higher number of individuals (Table 1).

Every 5 days over a period of 25 days, we harvested the live larvae (nauplii) produced by each parental group, counted them, and reared them in separate jars until maturity. When the nauplii reached sexual maturity, we determined their species and sex. We calculated the offspring sex ratio produced by

each parental group as the proportion of adult offspring in that group that were male (the tertiary offspring sex ratio). We calculated the offspring sex ratio produced by each parental group as the proportion of adult offspring in that group that were male (the tertiary offspring sex ratio). Some of the offspring sex ratio data were excluded due to errors during data collection.

Experimental Conditions

See the [Supplemental Experimental Procedures](#).

Statistical Analysis

See the [Supplemental Experimental Procedures](#).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, and five tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.03.074>.

AUTHOR CONTRIBUTIONS

Conceptualization, E.J.P.L., Y.M., and T.L.; Methodology, E.J.P.L., G.J.B.H., Y.M., and T.L.; Investigation, G.J.B.H., E.J.P.L., and T.L.; Formal Analysis, G.J.B.H.; Writing – Original Draft, E.J.P.L.; Writing – Review & Editing, E.J.P.L., Y.M., and T.L.; Supervision, Y.M. and T.L.; Funding Acquisition, T.L.

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