Quick guide

Sex ratios

Michael Jennions[1,2,*], Tamás Székely[1,3], Steven R. Beissinger[1,4], and Peter M. Kappeler[1,5]

Isn't the birth sex ratio always 1:1 in animals? Yes, but there are some notable exceptions, like fig wasps and mites, with very biased birth sex ratios. The mathematics of the 1:1 birth sex ratio was first described by Carl Düsing. The principle, now referred to as the 'Fisher Condition' after Ronald Fisher, is deceptively simple: in diploid, sexually reproducing species, everyone has one mother and one father. The total reproductive output of males and females is, therefore, identical. If fewer individuals of one sex are produced, then their mean success must be higher than that of the other sex (Figure 1A).

Why? Because the same reproductive contribution to the next generation is apportioned among fewer individuals. Parents should then make more of the rarer sex, who would provide them with more grandchildren. A son and a daughter only become equally valuable when parents produce them in equal numbers in the population. In that situation, parents should be indifferent to the sex of their offspring. The 'Fisher Condition' has been used to explain the evolution of sex differences in traits ranging from parental care to breeding ornamentation. But sometimes people forget to consider this condition — even famous theoretical biologists like John Maynard Smith have made this mistake.

Okay, but what about those notable exceptions? Well, a 1:1 birth sex ratio is predicted when sons and daughters impose the same costs on parents. But if sons are cheaper, we expect parents to produce more of them (Figure 1A). But, if males become more common in the population, their mean reproductive success will decline due to the Fisher condition. The optimal parental strategy is to invest resources evenly into each sex.

If, say, sons cost a third as much as daughters, make three times as many sons.

Why thrice as many? Because a son's success is expected to be lower (on average he is one-third as successful as a daughter) but this drawback is balanced by his costing one-third as much to make. Thus, the return per unit of investment is the same for sons and daughters. Fisher actually concluded that parents should invest equally in sons and daughters, rather than make the same numbers of each. This statement is the bedrock of sex allocation theory. There are other deviations from the baseline that predict a biased sex ratio at conception: for example, when offspring of one sex compete more intensely with each other (as happens when, due to limited dispersal, sons compete with each other for matings, as occurs in pollinating fig wasps); or when one sex imposes greater costs on, or provides more help to, their parents than the other sex. But in most species the baseline scenario holds true, and the sex ratio at conception is close to 1:1.

But what if more individuals of one sex survive to sexual maturity? Do parents make more of the sex that dies sooner? No! The optimal parental decision is based on the cost to a parent's own ability to breed versus the benefit gained through grandchildren. For example, if the death of offspring imposes no costs on a parent (e.g., if it occurs after independence), then all that matters are the benefits. It might seem that the benefits of making a son decline if he is less likely to survive to breed. But remember the Fisher condition: the few surviving sons will be more successful on average per individual than the better surviving, hence more numerous, females. If only a third as many males as females reach maturity, then maturing sons will, on average, be three times as successful as maturing daughters. The reduction in the number of males is balanced by their resultant increase in mean breeding success.

So you can end up with really biased sex ratios at maturation?

Yes! There is no selection to prevent this. Sex differences in growth rates or susceptibility to parasites or predators could produce a strong sex bias (Figure 1B). In some shorebirds, for example, the adult sex ratio can be as high as six males per female! And in antelope, like kudu, where larger males are favoured by sexual selection, males often delay sexual maturation to reach a greater size: consequently, far more sons than daughters die.

But surely if a mother knows her sons will die more often she should make more daughters? We need to distinguish between what happens on average, and what happens when a mother has additional information about the likelihood that her sons will die compared to those of other mothers. Theory predicts that mothers should adjust the birth sex ratio in response to contingent factors, such as her body condition, food availability or the genes that her offspring will inherit from their father (Figure 1C).

So the adult sex ratio could be biased because parents make more of one sex and/or the sexes differ in their survival to adulthood. Yes. We can end up with very biased adult sex ratio for the two reasons you mention. In addition, adult mortality can differ between the sexes. For example, females tend to survive better than males in mammals, which, even if the sex ratio at maturation is close to 1:1, generates a female-biased adult sex ratio, as in humans (Figure 1D).

But why is the adult sex ratio typically female-biased in mammals and male-biased in birds? We don't know. The bias is unrelated to the birth sex ratio. The answer must lie with males and females having different life-styles, which has knock on effects on their survival. Males and females can differ in the resources they invest in a strong immune system or in their exposure to parasites, predation and diseases. One plausible explanation for the adult sex ratio difference between birds and mammals is that their natal dispersal patterns differ. In mammals, males tend to leave home, while in birds, females tend to leave.

CrossMark

Dispersal is risky and likely to elevate the risk of death.

So what are the implications of a biased adult sex ratio? The adult sex ratio might predict breeding systems and associated sex-specific behaviour. For example, in shorebird species where the adult sex ratio is male-biased, males tend to care for offspring while females breed polyandrously with several males; in species with a female-biased adult sex ratio, however, males desert their offspring in search of other mating opportunities, leaving females to care for young on their own (Figure 1E, F). In other taxa, however, including reptiles and mammals, there is evidence that bias in the adult sex ratio predicts the intensity of mating competition, not care patterns.

I thought a male-biased sex ratio always favours male investment in competition, not in caring! The operational sex ratio, the ratio of males to females in the mating pool, is a measure of the intensity of competition for mates. If the operational sex ratio is male-biased then male–male competition is high. All else being equal, the adult sex ratio and the operational sex ratio should be closely positively related, but there is a catch. The operational sex ratio is determined by the adult sex ratio and by how long each sex spends out of the mating pool. For example, if females spend less time caring for offspring than do males, then the operational sex ratio could still be female-biased (despite a male-biased adult sex ratio), which decreases selection on males to compete. But even if the operational sex ratio and adult sex ratio are biased in the same direction, selection to provide parental care due to a male-biased adult sex ratio could still be stronger than selection to invest in being competitive.

But why would males care more just because the adult sex ratio is male-biased? There is on-going debate, but recent theory suggests that it is instructive to focus on the sex ratio at maturation and then invoke the Fisher condition. If the sex ratio at maturation is male-biased then a male has a lower expectation than a female as to
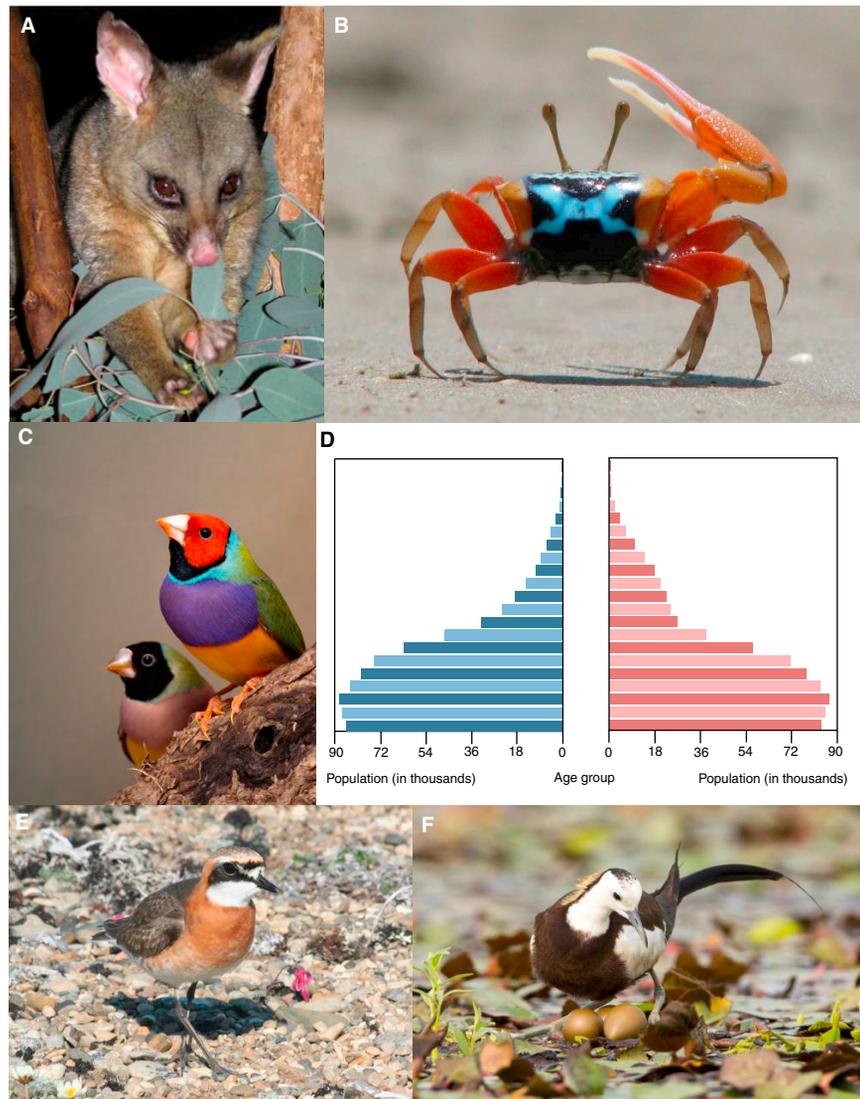
Figure 1. Sex ratio variation.
(A) A difference in the cost to a parent of making a son or daughter favours greater production of the cheaper sex. For example, in Australian brushtail possums, mothers share dens with daughters. This seems to be costly as mothers produce fewer daughters in populations where suitable tree holes are scarce (photo: Karen Ford). (B) In fiddler crabs, such as *Uca capricornis*, there is evidence that the adult sex ratio is often strongly male-biased (photo: Tanya Detto). (C) In some species mothers skew the sex ratio in response to contingent information. For example, in Gouldian finch, which has genetically determined red and black head colour morphs, females produce far more sons than daughters when they are paired with a male of the opposite head colour (and sons survive better than daughters when their parents are of different morphs) (photo: Sarah Pryke). (D) Adult male mortality is higher than that of females in many mammals, including humans. For example, in Swaziland females outnumber males in older age classes (image: CIA World Factbook). Finally, in shorebird species the adult sex ratio predicts the breeding system. (E) When the adult sex ratio is female-biased they tend to have conventional sex roles with female care (e.g. lesser sand pipers) (photo: Pavel Tomkovich) and (F) when it is male-biased they are 'sex role reversed' with male care (e.g. pheasant-tailed jacana; photo: Ghulam Rasool).

how many offspring he will produce over his lifetime (i.e. males have lower reproductive value). He has less to lose when there is a risk of dying while caring, so a father is prepared to pay more (risk death by caring) than a mother to increase the survival of a given set of offspring.

But why did you refer to the sex ratio at maturation and not the adult sex ratio? The Fisher condition does

not apply to the adult sex ratio when it comes to lifetime offspring production. For example, if the sex ratio at maturation is 1:1 then at ,maturity males and females have the same expected mean number of offspring, even if the sexes differ in adult mortality rates so that the adult sex ratio becomes very biased. The reason why the adult sex ratio predicts the breeding system in shorebirds might simply be because it is correlated with the sex ratio at maturation. Also, if the sexes differ in their mortality rates while caring for young (i.e., a different cost of reproduction), then the sex that has a lower cost of reproduction can afford to invest more in care because it is cheaper. All else being equal, however, a sex difference in mortality means that the adult sex ratio will be biased towards the sex with the lower cost of reproduction.

Where can I find out more?

Fairbairn, D.J. (2013). Odd Couples: Extraordinary Differences between the Sexes in the Animal Kingdom (Princeton: Princeton University Press).
Fritzsche, K., Booksmythe, I., and Arnqvist, G. (2016). Sex ratio bias leads to the evolution of sex role reversal in honey locust beetles. Curr. Biol. *26*, 2522–2526.
Hamilton, W.D. (1967). Extraordinary sex ratios. Science *156*, 477–488.
Jennions, M.D., and Fromhage, L. (2017). Not all sex ratios are equal: the Fisher condition, parental care and sexual selection. Phil. Trans. R. Soc. B (in press).
Kahn, A.T., Jennions, M.D., and Kokko, H. (2015). Sex allocation, juvenile mortality and the costs imposed by offspring on parents and siblings. J. Evol. Biol. *28*, 428–437.
Liker, A., Freckleton, R.P., and Szekely, T. (2013). The evolution of sex roles in birds is related to adult sex ratio. Nat. Comm. *4*, 1587.
McNamara, J. M., Székely, T., Webb, J.N., and Houston, A.I. (2000). A dynamic game-theoretic model of parental care. J. Theor. Biol. *205*, 605–623.
Queller, D.C. (1997). Why do females care more than males? Proc. R. Soc. B *264*, 1555–1557.
Schacht, R., Rauch, K.L., and Borgerhoff Mulder, M. (2014). Too many men: the violence problem? Trends Ecol. Evol. *29*, 214–222.
Székely, T., Weissing, F. J., and Komdeur, J. (2014). Adult sex ratio variation: implications for breeding system evolution. J. Evol. Biol. *27*, 1500–1512.
West, S.A. (2009). Sex Allocation (Princeton: Princeton University Press).

[1]Wissenschaftkolleg zu Berlin, Wallotstrasse 19, Berlin, Germany. [2]Evolution and Ecology, Australian National University, Canberra, Australia. [3]Department of Biology and Biochemistry, University of Bath, Bath, UK. [4]Department of Environmental Science, Policy and Management, Division of Ecosystem Sciences, University of California, Berkeley, USA. [5]Behavioral Ecology and Sociobiology Unit, German Primate Centre, Göttingen, Germany.
*E-mail: michael.jennions@anu.edu.au

Correspondence

Evidence from amber for the origins of termitophily

Shûhei Yamamoto[1,4], Munetoshi Maruyama[1], and Joseph Parker [2,3,4,*]

Fossil morphology is often used to infer the ecology of extinct species. In a recent report in *Current Biology*, Cai and colleagues [1] described an extinct rove beetle, *Cretotrichopsenius burmiticus*, from two specimens in mid-Cretaceous Burmese amber (~99 million years old). Based on morphology and the taxonomic group to which the specimens belong, the authors proposed that *Cretotrichopsenius* was a termitophile — a socially parasitic symbiont of termite colonies. Moreover, the new taxon was claimed to represent the oldest "unequivocal" termitophile so far discovered, pushing back the known evolutionary history of termitophily by ~80 million years, close to the origin of termite eusociality. *Cretotrichopsenius* is certainly an important discovery for understanding the evolutionary steps leading to this type of social insect symbiosis. However, we issue a caveat here concerning the authors' assertion that *Cretotrichopsenius* was truly termitophilous. Additionally, we question the authors' representation of a previously published, likely-termitophilous rove beetle in Burmese amber [2].

Cretotrichopsenius belongs to the staphylinid subfamily Aleocharinae, a speciose group with numerous termitophilous lineages [3]. The morphology of *Cretotrichopsenius* indicates membership of the tribe Trichopseniini. This tribe, together with its putative sister tribe Mesoporini [4], contains many termitophiles: all species of Trichopseniini are termitophilous, whereas multiple species of Mesoporini have independently evolved termitophily (the remainder of Mesoporini are presumed to be free-living) [2]. That the Trichopseniini–Mesoporini clade is an early-diverging branch of the aleocharine phylogeny [4] made it likely, *a priori*,

that extinct members of these tribes could have been evolutionarily ancient termitophiles. Importantly, beetles in both tribes have a limuloid (horseshoe crab-like) body shape, with a hood-like thorax that protects the head. Such limuloid anatomy is seen in a diversity of social parasite groups in Aleocharinae, attesting to its functional utility for survival inside ant and termite nests [3].

Cai and colleagues' assertion that *Cretotrichopsenius* was definitively termitophilous rests on its systematic placement in Trichopseniini and limuloid body shape [1]. However, in the case of the Trichopseniini–Mesoporini clade, limuloid morphology, though adaptive for termitophily, may not be *per se* an adaptation for this way of life. Rather, the defensive limuloid body shape likely arose in a free-living common ancestor of the two tribes [2,4,5]. This body plan is seen in all trichopseniine and mesoporine species (including free-living taxa), and is present to varying degrees in members of the earlier-diverging, entirely free-living aleocharine tribes Gymnusini and Deinopsini, as well as in members of predominantly free-living subfamilies closely related to Aleocharinae, the Tachyporinae, Habrocerinae and Trichophyinae. In other words, the limuloid shape arose prior to the convergent evolution of termitophily in multiple lineages of Mesoporini and in crown-group Trichopseniini (Figure 1A). Consequently, free-living, stem-group trichopseniines with limuloid anatomy once existed. For this reason, the authors' assertion that *Cretotrichopsenius* represents an "unequivocal" termitophile based on its limuloid body shape and membership of Trichopseniini is questionable. Critically, the authors failed to conduct a phylogenetic analysis to evaluate the placement of *Cretotrichopsenius*, so a position outside of termitophilous crown-group Trichopseniini remains possible (Figure 1A). Indeed, the authors note that unlike extant limuloid trichopseniines, which have short, compact antennae, *Cretotrichopsenius* has long, thin antennae with exposed pedicels, resembling those of free-living out-group Aleocharinae [1]. Moreover, based on the data in the paper, it is unclear if *Cretotrichopsenius* possesses any overt anatomical adaptations for termitophily: the additional characters

CrossMark