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References

1 Johnson, G.D. and Patterson, C. (1996) Relationships of lower euteleostean fishes. In *Interrelationships of Fishes* (Stiassny, M.L.J. *et al.*, eds), pp. 251–328, Academic Press
2 Myers, G.S. (1949) Usage of anadromous, catadromous and allied terms for migratory fishes. *Copeia*, 89–96
3 McDowall, R.M. (1988) *Diadromy in Fishes*, Croom Helm
4 Ishiguro, N.B. *et al.* (2003) Basal euteleostean relationships: a mitogenomic perspective on the phylogenetic reality of the Protacanthopterygii. *Mol. Phylogenet. Evol.* 27, 476–488
5 López *et al.* (2000) Phylogenetic relationships of esocoid fishes (Teleostei) based on partial Cytochrome *b* and 16S mitochondrial DNA sequences. *Copeia*, 420–431
6 Nelson, J. (1994) *Fishes of the World*, 3rd edn, John Wiley & Sons
7 McDowall, R.M. (2002) The origin of the salmonid fishes: marine, freshwater, or neither? *Rev. Fish Biol. Fish.* 11, 171–179
8 Madison, W.P. *et al.* (1984) Outgroup analysis and parsimony Syst. *Zool.* 33, 83–103
9 Schluter, D. *et al.* (1997) Likelihood of ancestor states in adaptive radiation. *Evolution* 51, 1699–1711
10 Margolis, L. (1965) Parasites as an auxiliary source of information about the biology of Pacific salmons (genus *Oncorhynchus*). *J. Fish. Res. Board. Can.* 22, 1387–1395
11 Tchernavin, V. (1939) The origin of salmon: Is its ancestry marine or fresh water? *Salm. Trout Mag.* 95, 120–140
12 Stearley, R.F. and Smith, G.R. (1993) Phylogeny of the Pacific trouts and salmon (*Oncorhynchus*) and genera of the family Salmonidae. *Trans Am. Fish. Soc* 122, 1–3336
13 Arratia, G. (1997) Basal teleosts and teleostean phylogeny. *Palaeo Ichthyol.* 7, 5–168
14 Müller-Schmidt, A. *et al.* (1993) Molecular analysis of ependymins from the cerebrospinal fluid of the orders Clupeiformes and Salmoniformes: no indication for the existence of an euteleost infradivision. *J. Mol. Evol.* 36, 578–585
15 Gross, M.R. *et al.* (1988) Aquatic productivity and the evolution of diadromous fish migration. *Science* 239, 1291–1293
16 Heape, W. (1931) *Emigration, Migration and Nomadism*, Heffer & Sons
17 Miya, M.H. *et al.* (2003) Basal actinopterygian relationships: a new perspective based on 100 complete mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* 26, 121–138
18 Inoue, J.G. *et al.* (2003) Basal actinopterygian relationships: a mitogenomic perspective on the phylogeny of the ancient fish. *Mol. Phylogenet. Evol.* 26, 110–120
19 Oakley, T.H. and Phillips, R.B. (1999) Phylogeny of Salmonine fishes based upon growth hormone introns: Atlantic (*Salmo*) and Pacific (*Oncorhynchus*) salmon are not sister taxa. *Mol. Phylogenet. Evol.* 11, 381–393
20 Wilson, M.V.H. and Williams, R.R.G. (1992) Phylogenetic, biogeographic, and ecological significance of early fossil records of North American freshwater teleostean fishes. In *Systematics and Historical Ecology and North American Freshwater Fishes* (Mayden, R.L., ed.), pp. 224–244, Stanford University Press

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Letters

In defence of the caring male

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Kokko and Jennions [1], when discussing the evolution of progeny-caring behaviour in a recent issue of *TREE*, assert that females are 'more likely than males to care for their offspring', citing Quellar [2]. But is this assertion, which is in danger of becoming 'conventional wisdom', actually true?

Besides, is knowing that more females than males care for their progeny heuristic about the adaptive ecology of parental care? If so, is it true when the ratio is 51:49%, or perhaps 60:40%? And, is progeny guarding less interesting if only, say, 42% of males do so? I doubt it, particularly as the adaptive benefits of parental care by either sex are widely diverse across taxa, making it seem more interesting to determine the adaptive costs and/or benefits for either parent and to seek general patterns (a bottom-up, rather than top-down, perspective).

Kokko and Jennions [1] (and Quellar [2]) present no numbers in support of their assertion, and do not specify the taxa being considered. Clearly, female mammals undertake most care – lactation is an exclusively female function. But, what about other groups?

Among fishes, parental caring is diverse in character and, contrary to Kokko and Jennions [1], more males than females care for progeny [3,4]. Because the number of fish species approximates that of all tetrapods [5], it is dubious that, among vertebrates, 'females are more likely than males to care for their offspring' [1].

Helfman *et al.* [4] argue that 'the most common caregiver in fishes is the male', and that they exhibit diverse forms of brood protection. The Gobiidae, in which many males undertake brood protection, has ~2000 species [5], so that one teleost family has about one third the number species of birds or mammals, giving males a head start in a 'global competition' for which sex most often guards its progeny.

Does brood guarding (at least in fishes) disadvantage the male, as Kokko and Jennions [1] assert? Arguing in an adaptationist circle, one might conclude that it does not or they would not do it. It becomes a question of whether the benefits exceed the costs. Some of the advantage for male gobies of staying at a site might derive not from guarding

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eggs, but by providing an optimal site for further spawning (some gobies are promiscuous, repeat spawners [6]). The advantage to the male of protecting earlier spawnings might thus be an indirect benefit of guarding his territory; females might prefer to deposit eggs where eggs are already being guarded by a male [3]. Overall, there is a multitude of explanations for why either sex cares for the offspring.

Where to now? Those arguing that more females than males guard their progeny should provide taxon-specific data. Exploring the context of one or other sex caring for offspring would be informative. Meanwhile, understanding the adaptive value of brood caring by either sex seems to me much more interesting than knowing how many of either sex care for their offspring. The statement that more females than males care for their offspring seems neither generally true nor meaningful.

References

1 Kokko, H. and Jennions, M. (2003) It takes two to tango. *Trends Ecol. Evol.* 18, 103–104
2 Quellar, D.C. (1997) Why do females care more than males? *Proc. R. Soc. Lond. Ser. B* 264, 1555–1557
3 Blumer, L.S. (1979) Male parental care in bony fishes. *Q. Rev. Biol.* 54, 149–161
4 Helfman, G. *et al.* (1997) *The Diversity of Fishes*, Blackwell Science
5 Nelson, J.S. (1994) *Fishes of the world*, 3rd edn, John Wiley & Sons
6 McDowall, R.M. and Eldon, G.A. (1997) Reproductive cycling and fecundity estimation in the upland bully. *J. Fish Biol.* 51, 164–179

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Letters Response

Response to McDowall: in defence of the caring male

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McDowall [1] takes issue with two points in our recent *TREE* article [2] about the prevalence of female versus male care. He states that it is not clear that females tend to provide more care than males, and that documenting such a general bias is unlikely to teach us anything of interest. A debate concerning these issues is definitely welcome, as we highlighted results that call earlier explanations into question [3,4].

Do females really care more? Undoubtedly 'yes', if one simply counts species. In terrestrial invertebrates, which account for most animal species, female-only care predominates (e.g. [5]). Greater female than male care is also observed in reptiles, birds and mammals. There are two groups where this trend is absent. In amphibians, male-only and female-only care are equally common and, in fishes, male care predominates. Perhaps more important than listing the exact number of species, however, is knowing how many phylogenetically independent evolutionary transitions there are from no care or biparental care to female-only or male-only care. For example, in cichlid fishes, transitions from biparental care to female-only care predominate [6], but, in teleost fishes in general, transitions from no care to male-only care are most common [7,8]. In frogs, transitions from no care to male-only or female-only care are equally common [8]. More work is needed on other taxa, especially those where female care predominates.

It is well known that teleost fishes do not show female-biased care. In 1975, G.C. William [9] suggested that this was because, in external fertilizers, guarding eggs does not preclude males from attracting mates. More recent studies show that female fish preferentially spawn with males who are guarding eggs [10]. McDowall discusses other plausible reasons why brood care might not compromise the ability of male fish to attract additional mates. We simply note that, if the balance of the care equations shifts towards male care in fishes owing to lower costs of caring, this only confirms the merit of seeking general principles that can be tested in a variety of taxa.

This brings us to the question of whether there is merit in explaining a general bias in nature. In our view, the most fundamental reason to be interested in sex differences of care is that nature has conveniently provided us with partially controlled experiments in the form of within-species comparisons between the sexes. In many cases, we can reasonably assume that care by either parent is equally beneficial to offspring. So, whenever one parent contributes more than the other, we can suspect that he or she derives greater net benefits from caring. This enables us to compare the absolute costs and benefits of parental care.

Queller [3] offered two theoretical arguments as to why males will benefit less from parental care than females: lower certainty of paternity and sexual selection leading to fewer males than females qualifying to mate. The merit of a top-down, theoretical approach is to help us detect cases where the general explanation does not work, and this is why taxa such as fish beg for closer inspection. Far from letting us ignore natural history, a top-down approach can often direct our attention to natural anomalies.

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