

Evolutionary biology

# Sex change and relative body size in animals

Arising from: Allsop, D. J. & West, S. A. *Nature* **425**, 783–784 (2003)

Organisms that change sex during their lifetime use a variety of strategies — they may be female first<sup>1</sup>, male first<sup>2</sup> or even repetitive sex changers<sup>3</sup>. Natural selection should favour those individuals that change sex at a time when it increases their reproductive value<sup>4–6</sup>. Allsop and West<sup>7</sup> claim that the relative timing of sex change is invariant across all animals, with individuals changing sex at 72% of their maximum body size, and infer that natural selection for sex change must therefore be fundamentally similar across animals. Here we explain why we believe that Allsop and West's claims are not supported by their analysis or by their empirical data<sup>7</sup>.

Inspection of the data underlying Allsop and West's results<sup>7,8</sup> reveals that relative size at sex change ( $L_{50}/L_{max}$ ) is highly variable (Fig. 1a). The basis for their claim of invariance is a tight relationship and a slope of unity when the average size at sex change ( $L_{50}$ ) is plotted against maximum size ( $L_{max}$ )<sup>7</sup>. We suggest that the same relationship would hold if the average size at sex change were randomly distributed between  $L_{mat}$

the size at maturity, and maximum size.

To test this idea, we developed a null model. Species were randomly assigned a maximum size (between 2 mm and 1.5 m)<sup>7</sup>, a size at maturity (assumed for simplicity to be 50% of their maximum size)<sup>9</sup>, and an average size at sex change between maturation and maximum size. We used this null model to generate 10 data sets with 77 species in each (Fig. 1b). This null model excludes only the factor of interest (the real distribution of size at sex change) while incorporating other realistic factors (such as a non-zero size at maturity) that might confound the results<sup>10</sup>.

Our regressions of  $\log(L_{50})$  against  $\log(L_{max})$  were indistinguishable from the regression found by Allsop and West<sup>7</sup>. Our analyses gave significant slopes ranging between 0.96 and 1.04, and explained 95–97% of the variation in size at sex change (Fig. 1c). Our results satisfy the criteria used to claim that the relative size at sex change is invariant<sup>7</sup>, even though the relative size at sex change is randomly distributed.

We repeated our analyses with a more realistic null model<sup>10</sup> in which each species was

randomly assigned a size at maturity of between 40% and 80% of its maximum size<sup>11</sup>, and found that this did not alter our conclusions. In this model, relative size at sex change develops a left skew like that seen in Fig. 1a. Furthermore, the variance in  $L_{50}/L_{max}$  (mean  $\pm$  s.d. =  $0.018 \pm 0.003$ ;  $n = 10$  data sets) is indistinguishable from the variance found in the real data. The results of the null model of Gardner *et al.* (A. Gardner, E. Charnov, D. J. Allsop and S. A. West, manuscript in preparation) depend on the questionable assumption that size at maturity can range over 0–100% of maximum size. We conclude that Allsop and West's results<sup>7</sup> do not demonstrate that relative size at sex change is invariant, and therefore that they offer no insight into natural selection for sex change.

These problems arise because size at maturity and maximum size constrain the set of possible values that average size at sex change may take (Fig. 1d). When the relationship between  $L_{max}$  and  $L_{50}$  is plotted on a log–log scale, these constraints cause apparent invariance in  $L_{50}$  and a restriction in the range of possible slopes to values near 1.0 (Fig. 1e). As constraints on the attribute of interest become more stringent, it will generally become harder to reject the null hypothesis that the attribute is randomly distributed between the constraints.

Empirical data demonstrate that individuals change sex over a large range of sizes<sup>1–3</sup>. The timing of and size at sex change are often precisely linked to changes in relative condition and group membership<sup>1–3</sup>, suggesting that natural selection has shaped flexible sex-change strategies that are contingent on social context. To advance our understanding further we need to attend to the great variation in sex-change strategies within and among species.

Peter M. Buston\*, Philip L. Munday†, Robert R. Warner‡

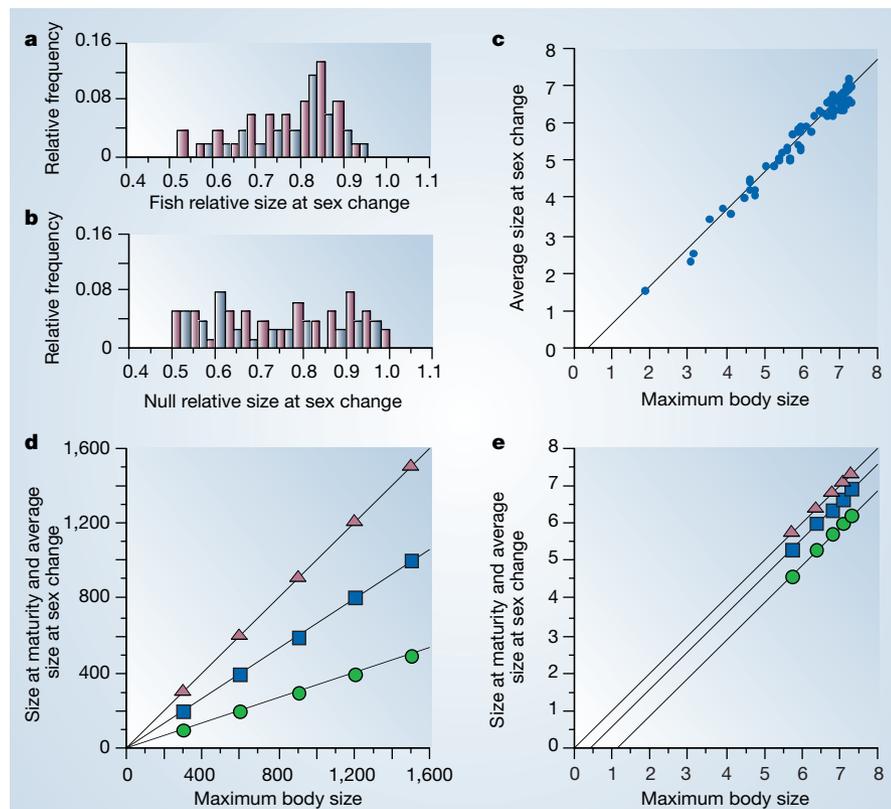
\*National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, California 93101, USA

e-mail: [buston@nceas.ucsb.edu](mailto:buston@nceas.ucsb.edu)

†School of Marine Biology and Aquaculture, James Cook University, Townsville, Queensland 4811, Australia

‡Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106, USA

doi:10.1038/nature02512



**Figure 1** Relative size at sex change varies widely among animals. **a**, Distribution of relative size at sex change ( $L_{50}/L_{max}$ ) for 52 species of fish used by Allsop and West<sup>7,8</sup>. **b**, Distribution of relative size at sex change for 77 hypothetical species generated by our null model. **c**, Log–log plot of average size at sex change ( $L_{50}$ ) against maximum size ( $L_{max}$ ) for 77 hypothetical species. The null data generate apparent invariance in relative size at sex change (**b, c**). **d**, Size at maturity ( $L_{mat}$ ) plotted against maximum size: green circles,  $L_{mat} = 33\% L_{max}$ ; blue squares,  $L_{mat} = 66\% L_{max}$ ; red triangles,  $L_{mat} = 100\% L_{max}$ . Average size at sex change must fall within these constraints. **e**, Log–log plot of the data shown in **d**. From **d, e**, it is evident that more stringent constraints generate more apparent invariance.

- Warner, R. R. & Robertson, D. R. *Smithson. Contr. Zool.* **254**, 1–27 (1978).
- Buston, P. M. *Nature* **424**, 145–146 (2003).
- Munday, P. L., Caley, M. J. & Jones, G. P. *Behav. Ecol. Sociobiol.* **43**, 371–377 (1998).
- Ghiselin, M. T. Q. *Rev. Biol.* **44**, 189–208 (1969).
- Warner, R. R. *Am. Nat.* **109**, 61–82 (1975).
- Charnov, E. L. *The Theory of Sex Allocation* (Princeton University Press, Princeton, 1982).
- Allsop, D. J. & West, S. A. *Nature* **425**, 783–784 (2003).
- Allsop, D. J. & West, S. A. *J. Evol. Biol.* **16**, 921–929 (2003).
- Charnov, E. L. *Life History Invariants* (Oxford University Press, Oxford, 1993).
- Gotelli, N. J. & Graves, G. R. *Null Models in Ecology* (Smithsonian Institution Press, Washington DC, 1996).
- Beverton, R. J. H. *J. Fish Biol.* **B41**, 137–160 (1992).

Allsop & West reply — Buston *et al.*<sup>1</sup> criticize our<sup>2</sup> use of standard methodology<sup>3–5</sup> to test for an invariant relative size at sex change, and propose instead a null model based on randomization techniques: however, their *ad hoc* model is not null.

The main problem is that it assumes an invariant relative size at maturity, which follows from two of the dimensionless invariants assumed by Charnov's model<sup>6</sup>:  $\alpha \cdot M$  and  $k/M$  (where  $\alpha$  is the age at first breeding;  $M$  is the adult mortality rate; and  $k$  is the relative growth rate, or Bertalanffy coefficient). If these are invariant, then their product  $\alpha \cdot k$  is invariant, and so the relative size at maturity ( $L_{\text{mat}}/L_{\text{max}} = 1 - \exp(-\alpha \cdot k)$ ) is also invariant. These are the crucial invariants for Charnov's model, so we would expect the null model of Buston *et al.* to produce an invariant relative size at sex change, and hence to fit our data. If an invariant relative size at maturity is not assumed, then more appropriate null models can be developed (for example,  $L_{\text{mat}}/L_{\text{max}} \sim U[0,1]$ ,  $L_{50}/L_{\text{max}} \sim U[L_{\text{mat}}/L_{\text{max}}, 1]$ ) and the predictions of these differ significantly from the observed data (A. Gardner, E. Charnov, D.J.A. and S.A.W., manuscript in preparation; simulation results,  $P < 0.0001$ ).

There are other problems with the model of Buston *et al.* First, the distribution of relative size at sex change in the actual data is significantly different from the uniform distribution they assume (for fish:  $P = 0.000001$ ; for all species:  $P = 0.02$ ). More generally, invariance is statistical — it does not imply that all individuals do exactly the same thing<sup>3,4</sup>.

Second, they arbitrarily assign a size at maturity of 50% of maximum body size. This forces their model to fit the data, giving an average size at sex change of 75% of maximum body size (observed is 72%). Their citation<sup>4</sup> actually suggests that 50% is a lower

bound, with an average value of 65%, which would give a mean size at sex change of 83%, far from the observed.

Third, the assumption of a uniform distribution in relative size at sex change assumes no selection on size at sex change, which is not the case<sup>4,7,8</sup>. Fourth, the model of Buston *et al.* and our version are both unrealistic 'straw men', easily knocked down, as shown here.

A more powerful and informative approach is to carry out a sensitivity analysis of Charnov's model<sup>6</sup> and test how variation in different parameters influences the relative size at sex change and its variation. We are doing this (A. Gardner, E. Charnov, D.J.A. and S.A.W., manuscript in preparation) and have found that the prediction of an invariant size at sex change relies primarily on invariance in  $\alpha \cdot M$  and  $k/M$ , with variation in  $\delta$  — the coefficient relating male fertility to size — having little effect. This explains the results of the null model of Buston *et al.* (which does not assume an invariant  $\delta$ ) and explains why breeding system and taxa do not significantly influence the relative size at sex change<sup>2</sup>.

Buston *et al.* suggest that variation within species provides problems for our invariant result. However, this criticism misses the purpose of cross-species comparative studies<sup>5,9,10</sup>. The aim is to look for general patterns across species — this does not imply that there is no within-species variation. For example,  $\alpha$  is often facultatively adjusted within species<sup>11</sup>, but this does not disrupt the  $\alpha \cdot M$  invariant<sup>4</sup>. The study of variation across and within species should be seen as complementary approaches, not alternatives. Our results<sup>2</sup> indicate that Charnov's model<sup>6</sup> efficiently encapsulates the crucial aspects of the underlying biology.

We agree that relative size and social con-

text will influence the advantage and timing of sex change for specific individuals, and that the importance of this varies across species (in contrast to the assumptions made by Buston *et al.* in their model)<sup>7,8</sup>. However, our results indicate that these effects may average out, so the relationship between size and fitness can be approximated extremely well by a single positive relationship for each sex. It is a statistical fact that biological details matter for the timing of when individuals change sex, but not for explaining the average pattern across species.

Our approach is based on fundamental assumptions and evolutionary theory developed over the past 30 years<sup>4,7–9</sup>. The novelty lies in the predictions of these models being phrased in terms of dimensionless qualities that are invariant and determining the consequences for general patterns of sex change<sup>2,4,6</sup>.

**David J. Allsop, Stuart A. West**

*Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh EH9 3JT, UK*  
e-mail: david.allsop@ed.ac.uk

doi:10.1038/nature02513

1. Buston, P. M., Munday, P. L. & Warner, R. R. *Nature* doi:10.1038/nature02512 (2004).
2. Allsop, D. J. & West, S. A. *Nature* **425**, 783–784 (2003).
3. Brown, J. H., West, G. B. & Enquist, B. J. in *Scaling in Biology* (eds Brown, J. H. & West, G. B.) 1–24 (Oxford University Press, Oxford, 2000).
4. Charnov, E. L. *Life History Invariants* (Oxford University Press, Oxford, 1993).
5. Harvey, P. H. & Pagel, M. D. *The Comparative Method in Evolutionary Biology* (eds May, R. M. & Harvey, P. H.) (Oxford University Press, Oxford, 1991).
6. Charnov, E. L. & Skuladottir, U. *Evol. Ecol. Res.* **2**, 1067–1071 (2000).
7. Charnov, E. L. *The Theory of Sex Allocation* (Princeton University Press, Princeton, 1982).
8. Leigh, E. G., Charnov, E. L. & Warner, R. R. *Proc. Natl Acad. Sci.* **73**, 3655–3660 (1976).
9. Frank, S. A. *Foundations of Social Evolution* (Princeton University Press, Princeton, 1998).
10. Allsop, D. J. & West, S. A. *Evolution* (in the press).
11. Stearns, S. C. *The Evolution of Life Histories* (Oxford University Press, Oxford, 1992).