

important issue both theoretically and experimentally [5], researchers ignore how female reproductive traits intervene during fertilization. Once this is clarified, we can then ascribe female traits as 'resistant' or 'selective'. The second is to study the genetics of the female preference and associated male traits [5]. A genetic correlation is expected between both traits only if traditional female choice is occurring. The third and final approach is to track the rates of origin of female and male traits on phylogenies once resistance or selectivity has been determined. This will explain the prevalence of either process.

Studies of fruit flies and water striders have suggested that negative fitness outcomes for females are a widespread phenomenon, but it is premature to claim that sexual conflict is widespread based on data from relatively few taxa. Related to this, no discussion was made by Chapman *et al.* of recent studies showing how females control both their reproductive decisions and the fitness payoffs accrued by them (e.g. [6–10]). By omitting them, readers might not only believe that the dichotomy of sexual conflict and female choice does not exist, but, if it did, that it has been settled in favour of sexual conflict.

## References

- Holland, B. and Rice, W.R. (1997) Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* 52, 1–7
- Parker, G.A. (1979) Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects* (Blum, M.S. and Blum, N.A., eds), pp. 123–166, Academic Press
- Chapman, T. *et al.* (2003) Sexual conflict. *Trends Ecol. Evol.* 18, 41–47
- Cordero, C. and Eberhard, W.G. (2003) Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J. Evol. Biol.* 16, 1–6
- Simmons, L.W. (2001) *Sperm Competition and its Evolutionary Consequences in the Insects*, Princeton University Press
- Edvardsson, M. and Arnqvist, G. (2000) Copulatory courtship and cryptic female choice in the red flour beetles *Tribolium castaneum*. *Proc. R. Soc. Lond. Ser. B* 267, 559–563
- Elgar, M.A. *et al.* (2000) Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. *Proc. R. Soc. Lond. Ser. B* 267, 2439–2443
- Sakaluk, S.K. and Eggert, A.K. (1996) Female control of sperm transfer and intraspecific variation in sperm precedence: antecedents to the evolution of a courtship food gift. *Evolution* 50, 694–703
- Tallamy, D.W. *et al.* (2002) Male traits under cryptic female choice in the spotted cucumber beetle (Coleoptera: Chrysomelidae). *Behav. Ecol.* 13, 511–518
- Tallamy, D.W. *et al.* (2003) Copulatory courtship signals male genetic quality in cucumber beetles. *Proc. R. Soc. Lond. Ser. B* 270, 77–82

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doi:10.1016/S0169-5347(03)00182-4

## Letters Response

# Response to Eberhard and Cordero, and Córdoba-Aguilar and Contreras-Garduño: sexual conflict and female choice

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Eberhard and Cordero [1] begin with a claim that, in our recent *TREE* article [2], we are inconsistent in our use of an older, and new narrower definition of sexual conflict. For the former, we quoted the original views of Parker, Trivers, and Dawkins, and we stand by this usage. The 'narrow' definition noted by Eberhard and Cordero was not a definition at all, but rather an attempt to set recent models of sexual conflict into the broader context of sexual selection theory (direct versus indirect selection, and their signs). Córdoba-Aguilar and Contreras-Garduño [3] imply that we ignore difficulties in disentangling sexual conflict from 'traditional models'. In fact, we were clear that the 'boundary, if there is one, between traditional models of sexual selection and sexual conflict has not yet been carefully explored theoretically' [2]. Yet, we believe that there is much to learn along this road, and initial forays

have supported this view. Eberhard and Cordero consider this an overly optimistic viewpoint.

Eberhard and Cordero also appear to distrust the quantitative predictions of theory, citing, for example, conflicting conclusions about the feasibility of early handicap models. Although these conflicts were real, they did not result from an inherent lack of precision, but from differing underlying assumptions. We see little problem here. However, we do see persistent problems arising from errors in the interpretation and application of theory. For example, in spite of 20 years of contrary research, Córdoba-Aguilar and Contreras-Garduño assert that genetic correlations between female preference and preferred traits are only expected under 'traditional female choice'. This statement is false, a fact that is well known [2]. Such correlations result from assortative mating between males and females bearing alleles for the trait and preference. A hunt for such correlations, although destined for success, would be uninformative in

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distinguishing between these processes of coevolution. Similarly, both sets of authors suggest that direct fitness costs of manipulative males might be more than offset by benefits accrued through production of manipulative sons. This view echoes the earlier ‘sexy son’ hypothesis [4], which has neither theoretical nor empirical support (e.g. [5,6]). In the context of sexual conflict, the idea had been already been modeled in the 1970s [5]. More recently, sexy son effects were investigated in a genetic model of sexually antagonistic coevolution [8]. Although costly female resistance easily led to the exaggeration of manipulative male traits, the inclusion of sexy sons had no effect on the equilibrium values of either trait. This result has a long and consistent history [9].

Another form of indirect selection on female preference, the so-called ‘good genes’ effects, can shift equilibrium values of male and female traits, and has received little attention in analyses of sexually antagonistic coevolution [7,10]. We noted that these indirect effects are likely to occur, but that theory suggests they will be relatively weak [2]. We do agree with Eberhard and Cordero and with Córdoba-Aguilar and Contreras-Garduño that, in the end, their relative strength in nature will only be resolved by experiments, and that more experiments are required. We do not agree that attempts have not been made to assess indirect benefits in those species where direct costs have been assayed. One of us made an initial attempt at such an experiment (in the field) over ten years ago [11], and more recent experiments, by Holland, Rice, and Promislow [12–14], collectively do not make a strong case for substantial good gene effects. Future experiments might do so.

Córdoba-Aguilar and Contreras-Garduño make several claims that puzzle us. For example, in no place did we argue that males usually emerge at the ‘forefront’ in conflicts, or that males ‘take over’ the reproductive ‘decisions’ of females, or that such takeovers give rise to unending coevolution. The closest we came to this was a healthy distance, when we stated that ‘neither sex can be said to win a conflict’ [2]. Two of Córdoba-Aguilar and Contreras-Garduño’s prescriptions – studying female traits influencing fertilization, and mapping traits on phylogenies – are interesting but ill defined at best, and in

spite of their claims, both types have been conducted and were cited [2].

Eberhard and Cordero would like to see fitness assays of direct and indirect selection in wild populations. So would we; although we think that this is a tall order given the obstacles that Eberhard and Cordero note in assaying these same effects in the lab. Both sets of authors would also like to see more taxa included in sexual conflict research. We agree and therefore ended our review with ‘The taxonomic breadth and range of phenotypic traits that are involved in sexual conflict...remains unclear’ [2]. We hope that our optimism will encourage further theoretical analysis and careful empirical work in a diverse array of taxa.

#### References

- 1 Eberhard, W.G. and Cordero, C. (2003) Sexual conflict and female choice. *Trends Ecol. Evol.*, 18, doi:10.1016/S0169-5347(03)00180-0
- 2 Chapman, T. *et al.* (2003) Sexual conflict. *Trends Ecol. Evol.* 18, 41–47
- 3 Córdoba-Aguilar, A. and Contreras-Garduño, J. (2003) Sexual conflict. *Trends Ecol. Evol.*, 18, doi:10.1016/S0169-5347(03)00182-4
- 4 Weatherhead, P.J. and Robertson, R.J. (1979) Offspring quality and the polygyny threshold: ‘the sexy son hypothesis’. *Am. Nat.* 113, 201–208
- 5 Kirkpatrick, M. (1985) Evolution of female choice and male parental investment in polygynous species: the demise of the ‘sexy son’. *Am. Nat.* 125, 788–810
- 6 Ligon, J.D. (1999) *The Evolution of Avian Breeding Systems*, Oxford University Press
- 7 Parker, G.A. (1979) Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects* (Blum, M.S. and Blum, N.B., eds), pp. 123–166, Academic Press
- 8 Gavrillets, S. *et al.* (2001) The evolution of female mate choice by sexual conflict. *Proc. R. Soc. Lond. Ser. B* 268, 531–539
- 9 Cameron, E. *et al.* Sexual conflict and indirect benefits. *J. Evol. Biol.* (in press)
- 10 Kokko, H. *et al.* (2002) The sexual selection continuum. *Proc. R. Soc. Lond. Ser. B* 269, 1333–1340
- 11 Arnqvist, G. (1989) Multiple mating in a water strider: mutual benefits or intersexual conflict? *Anim. Behav.* 38, 749–756
- 12 Holland, B. and Rice, W.R. (1999) Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl. Acad. Sci. U. S. A.* 96, 5083–5088
- 13 Promislow, D.E.L. *et al.* (1998) Adult fitness consequences of sexual selection in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. U. S. A.* 95, 10687–10692
- 14 Holland, B. (2002) Sexual selection fails to promote adaptation to a new environment. *Evolution* 56, 721–730

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doi:10.1016/S0169-5347(03)00179-4

#### Letters

## ‘Big bang’ for Tertiary birds?

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I enjoyed Feduccia’s [1] recent article in *TREE* where he reiterates his hypothesis that the radiation of modern birds (Neornithes) occurred in an ‘explosive manner’ in the aftermath of the ‘Cretaceous–Tertiary (K–T) cataclysm’

[2]. I note, however, that this argument [1,2] is based primarily on counts of the number of fossil neornithine genera, before and after the K–T boundary. Feduccia’s ‘big bang’ hypothesis does not consider the fact that molecular clock studies are becoming increasingly less discordant with the fossil record as both calibration and rate

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