

different. Close up it is less so. And for environmentalists of a certain persuasion, Gould can seem eerily indifferent to the language of crisis and denudation, and to the cries of exhausted nature and scared humanity. Nature's may be a darker story than Gould thinks, more 'cruelly' darwinian.

*Bully for Brontosaurus* is the book that answers these doubts. In the face of many distresses (not least his own), Gould has allowed himself a good old-fashioned response to the world he sees, not least in the achievement of *Voyager* in photographing Neptune. He feels wonder. It may be an irony

that having often reminded us that we make up our own values, independent of nature (which will survive us, having long lived without us), he should allow himself such a fulsome reaction as that of permanent wonder. But these fine essays show that he entirely deserves so to do. Treasure your exceptions. □

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## Weighing up the costs

Darryl T. Gwynne

**The Evolution of Parental Care.** By T. H. Clutton-Brock. Princeton University Press. 1991. Pp.352. Hbk \$49.50, pbk \$19.95.

A MALE stickleback guarding eggs in a nest; a dying female mite exhibiting an extreme form of 'live birth' as she is devoured by her own progeny from the inside; and a male blister beetle inseminating his mate with Spanish fly, a chemical transferred to and conferring protection on eggs. Such diverse forms of reproductive effort all represent parental care in a broad and descriptive sense. From this concept of parenting, common themes can emerge, in particular the similar influence of ecological variables on the parental aspects of life histories.

Studies of parental expenditure may deal with its adaptive significance or its effect on sexual competition (mating systems). Clutton-Brock is almost exclusively concerned with the former topic and outlines five main areas for examination: the costs and benefits of parental care; interspecific variation in the extent of care; variation in the sex assuming the role of direct care of the progeny; how care is adjusted in its benefits to offspring and cost to parents; and how parents divide investment between sons and daughters. But the scope of his book is much broader than these areas may indicate and includes topics as disparate as egg size and interspecific variation in the composition of mammalian milk. The book is a good reference for the diverse forms of parental expenditure in animals, although the short subject index tends to limit this function. Many groups are considered and a quick glance through the excellent illustrations by Dafila Scott gives a flavour of the diversity of taxa covered. An obvious omission is plants; with such a broad concept of parental care, botanical information would have been useful to topics such as female gamete size and sex allocation.

Clutton-Brock discusses both problems encountered in answering certain questions

and where further investigation is needed. But more could have been done to point out how particular past studies have answered questions. An example concerns a question Clutton-Brock considers among the most fascinating: what factors determine the extent to which males and females are involved in direct (behavioural) care of progeny? One area of interest stems from the fact that in most animal groups, exclusive male care tends to occur when there is external fertilization of eggs. Several hypotheses have been advanced to explain this association; the fishes represent a key testing ground because of the diversity of fertilization modes and direct parental-care states within this group. Although Clutton-Brock outlines these hypotheses, he does not point

at least one other explanation, one that involves the influence of social environment. Models of the evolution of female mating preferences predict that populations with similar ecologies can evolve very different forms of male secondary sexual traits. A history of female preference for nurturant males in a population should perhaps be considered as a possible cause of sexual dimorphism in parental-care roles. It is known that male care can attract mates; male sticklebacks with eggs in the nest are preferred by females. Such males are even known to steal eggs from other nests, an act reminiscent of male bower birds stealing 'secondary sexual' attractive ornaments from the bowers of rivals.

One of the benefits of a review of a large subject is the clarification of questions for future research. In his concluding chapter, Clutton-Brock points to several such areas, including the need for improved measures of the costs and benefits of parental care and for certain theoretical analyses. Investigation of these areas would presumably involve the use of experimental and modelling methodologies. In addition to these, there is a need for phylogenetically controlled comparative approaches which would be particularly useful in understanding the diversity of parental-care strategies in animals. Such approaches rely on the reconstruction of phylogenies to determine both evolutionary

IMAGE  
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REASONS

Sticking around — why do male sticklebacks guard the eggs in the nest?

out that published studies report (statistical) separation not only of certain hypotheses that explain the association between care states and modes of fertilization but also of hypotheses that predict the direction of change of these states in evolutionary time.

As Clutton-Brock points out, exceptions to these trends, such as cases of exclusive male care in internally fertilizing species, also need explaining. He suggests that paternal care is retained in such cases because of ancestry or ecological pressures such as high costs of egg production that emancipate females from direct-care duties. But there is

changes in parental characters and the associations of these characters with other variables. It is this aspect, the extent to which further research is stimulated, that is perhaps the best measure of the success of a book such as this. This volume generates many avenues for future study and thus should be required reading for all behavioural and evolutionary ecologists. □

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