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# BOOK REVIEWS

MARCY F. LAWTON, EDITOR

**Helping and communal breeding in birds.**—Jerram L. Brown. 1987. Princeton University Press, Princeton, NJ.

**Science as a process.**—David L. Hull. 1988. The University of Chicago Press, Chicago. $39.95, cloth.

> I freely acknowledge that Mr. Matthew has anticipated by many years the explanation which I have offered on the origin of species, under the name of natural selection. I think that no one will feel surprised that neither I, nor apparently any other naturalist, had heard of Mr. Matthew's views, considering how briefly they are given, and that they appeared in the appendix to a work on Naval Timber and Arboriculture. I can do no more than offer my apologies to Mr. Matthew for my entire ignorance of his publication.
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> Charles Darwin
> *Gardner's Chronicle,*
> 16:362, 1860

The reaction of ornithologists to *Helping and communal breeding in birds* must be fascinating to sociologists of science. On the one hand, the book met with favorable reviews from such general interest journals as *Science* (Ewald 1987), *Nature* (Orians 1987), and *American Scientists* (Curry 1988) and served as the occasion for Brown's receipt of the American Ornithologists' Union's prestigious Brewster Award. On the other, the public reception of the volume—or lack of it—by Brown's close conceptual colleagues, i.e., the score or so of scientists whose lifework is also the study of avian cooperative breeding, is curious, and suggests that the Brewster Award was presented in recognition of the lifetime contributions of an important thinker, rather than in celebration of this volume itself.

To date, the pages of the leading American ornithological journals are devoid of comment on *Helping and communal breeding in birds.* In the 2 years since the book appeared, I have tried to convince over a dozen experts in avian cooperative breeding to review it. Their reasons for turning me down made it clear that, by in large, those who should be most well-qualified to review this volume are confused and faintly embarrassed about just what kind of contribution *Helping and communal breeding in birds* represents.

The embarrassment derives, undoubtedly, from the fact that to a reader familiar with the literature of cooperative breeding, Brown's book is characterized by a near universal failure to grant credit to other workers for their part in the development of a research program that has spanned more than two decades and which today represents one of the most active areas of ornithological research. This is not to say that Brown does not cite other workers. He does. Indeed, the bibliography provides a good review of the literature. To someone outside the immediate field, nothing appears amiss. In what way, then, does *Helping and communal breeding in birds* fail to grant credit where credit is due?

David Hull may have the answer. In his rich, provocative volume, *Science as a process,* Hull develops what he calls a selection model for the evolution of science. His theory is based on his study of the science of systematics and is built upon what he has learned about science as a social and human process, rather than about science as a way of knowing.

In this volume, Hull traces the emergence of cladism as a dominant school of systematics. Combining historical and sociological approaches, Hull presents a detailed analysis of the professional pathways by which the people who developed cladism came to dominate the professional literature, the professional societies, and the professional academies of modern systematics.

Hull uses this sociological history in order to demonstrate that what he calls the "competetive cooperation" of scientists usually leaves a clear trail of ideas, expressed as sets of what Hull terms "conceptual lineages." Conceptual lineages are the result of a social process in which, in order for scientists to obtain credit for innovation, they must invoke the authority of their predecessors. In the scientific literature, this invocation takes the form of citations and results in "information being transmitted largely intact from physical vehicle to physical vehicle" (p. 436).

Tracing conceptual lineages depends heavily upon the assumption that scientists do indeed attribute credit or invoke support by citing the work of other scientists more or less as it first appeared in the literature. It is because most scientists do just this, Hull contends, that "ideas come to 'belong' to particular scientists . . ." (p. 447) and it becomes possible to trace the direct lineal descent of ideas.

The notion that one can trace conceptual evolution in scientific traditions is, of course, not new; and Hull's dedication to the faithful replication of ideas makes *Science as a process* a first-rate synthesis of recent thinking about evolutionary epistemology and cultural evolution. Moreover, while Hull may be a faithful replicator, he is also a fine interpreter. For those who never got around to working through Boyd and Richerson's tome on cultural evolution (1985, reviewed in *Condor* 88:123–125) or who are still confused about why most philosophers of science seem faintly contemptuous of Kuhn, Hull provides consistently lucid explanations.

Whether or not Hull's theory proves tenable, i.e., whether or not it is indeed possible to understand conceptual evolution by tracing lineages of "conceptual replicates." Hull's contention that the phenomenon of faithful conceptual replication is widespread is fascinating and, on the face of it, not the sort of idea one would expect from David Hull.

This is not Pollyanna we're dealing with. Hull is a cynical scholar, a man who once waved a fork in my face while asserting that any scientist not actively engaged in major conceptual controversies was a scien-

tific failure. (He ignored my suggestion that Skutch's [1954, 1960, 1969] *Life histories of Central American birds* would be a seminal work in neotropical ornithology long after Skutch's theoretical debates with Lack had been forgotten.)

Whether or not one buys Hull's assessment of the reasons for which scientists cite one another's work—he writes that they do so "because it is in their own self-interest" (p. 311)—the fact is, scientists almost always do cite one another and, as Hull demonstrates in his presentation of the history of cladism, they usually do so with surprising fidelity.

Which brings us back to Brown's book. Whatever other virtues this book may embody, faithful replication of the ideas of his predecessors is not one of them. Let us take, for example, Brown's treatment of the development of ecological constraints models for the evolution of cooperative breeding in birds.

The nature of ecological constraints in the evolution of cooperative breeding and the limits of such models to explain its maintenance is perhaps the most fertile and productive area in the field today (c.f., Koenig and Pitelka 1981, Emlen and Vehrencamp 1983, Woolfenden and Fitzpatrick 1984, Rabenold 1984, Zack and Ligon 1985, Koford et al. 1986, Stacey and Ligon 1987). Most people working and writing in this area are aware that these are ideas that have been developed by an increasing number of theoretical and empirical workers. This recognition is usually present in the literature.

For instance, in one of the early ecological constraints models, Emlen and Vehrencamp (1983) introduced their ideas by first presenting the results of Koenig's 1981 work and writing: "Koenig concluded that cooperative breeding birds live in groups because they are 'forced' to do so by severe ecological constraints" (p. 100). With respect to the development of this idea, Emlen and Vehrencamp present Koenig's data and his conclusions and go on to say that "The idea is not new. . .".

Then, in an exercise that would warm Hull's heart, Emlen and Vehrencamp document the ways in which the idea they are developing is not new, by tracing the conceptual lineage within which they are working. Their citations go back to Selander (1964), and mention Brown (1974, 1978), Woolfenden and Fitzpatrick (1978), Gaston (1978), Koenig and Pitelka (1981), and Emlen (1981, 1982) along the way.

How different is Brown's representation of the history of this idea! Brown begins his presentation with an unexceptionable statement:

> When such suitable habitat is fully occupied, thereby preventing additional individuals from breeding, these individuals may be referred to as surplus, and the breeding habitat may be said to be saturated (p. 71).

Brown then goes on to present his model as though he is the first worker to have developed such a construct. He tells us nothing of the 20-year history of empirical and theoretical work that led to the nearly simultaneous development of several habitat saturation models or of the data bases that supported those theories.

Instead, Brown cites a paper of his own (1969), a 25,000-word review of the question of the role of territoriality on population regulation. Far from concluding that habitat saturation constrains breeding behavior, this review argues that the "amount of reliable information is hardly sufficient for sweeping generalizations concerning the limiting effects of territorial behavior on reproduction . . ." (p. 305).

Careful reading of this paper reveals that, generously interpreted, a passage of about 300 words exists that can be said to edge up to the issue of habitat saturation. Nonetheless, the passage is, like Patrick Matthew's description of the principle of natural selection, brief, buried, and obscure. It hardly merits a claim of theoretical priority, nor does it justify Brown's failure to discuss the habitat saturation models that appeared between 1969 and 1987.

Now, this is not to say that Brown fails utterly to cite these works. He does cite them, but in ways that minimize or ignore their conceptual contributions. So for instance, Emlen and Vehrencamp's two major theoretical papers on habitat saturation are cited in passing in Brown's later discussion of the factors that influence the number of potential helpers in any given year. In this context, Brown writes:

> conditions that affect breeding success can influence the proportion of nonbreeding helpers in the population in two ways: (1) by same year effects on rate of food intake causing some *territories or foraging areas* (for colonial species) to be subthreshold for breeding as described by Orians (1977b) and Emlen (1982a, 1984; Emlen and Vehrencamp, 1983, 1985) . . . (p. 77).

This form of citation has two effects. It trivializes the contributions Emlen and Vehrencamp have made to the development of the first set of ecological constraints models for the evolution of cooperative breeding and it makes it impossible for the authors to claim they have been overlooked.

This sort of trivializing of the contributions of others is characteristic of the entire book and the distortions inherent in such a presentation give the knowledgeable reader (i.e., one with more than a passing familiarity with the development of work on cooperative breeding) a sense of being trapped in a hall of mirrors. Moreover, anyone familiar with the genuine contributions Brown has made to the field of cooperative breeding in birds must be baffled and saddened by the way he treats the work of others. This man is an award winning scientist, a man with a hard-won, international reputation. He has no need to co-opt ideas, and his apparent inability to see that this is what he does when he fails to recognize the ways in which his colleagues have helped this field to grow is the source of the embarrassed silence with which his immediate conceptual community has met *Helping and communal breeding in birds.*

It will be interesting to see how *Helping and communal breeding in birds* fares. It is not immediately clear what can be predicted from Hull's descriptions of science as a process. On the one hand, by claiming so many ideas as his own, Brown may raise what Hull terms his "conceptual inclusive fitness" enormously.

On the other hand, because Brown distorts so much of the development of the field as a conceptual framework for empirical study and because he fails to present the reader with a solid body of his own empirical data, this book may well be selected against.—MARCY F. LAWTON, Dept. Biological Sciences, The University of Alabama, in Huntsville, Huntsville, AL 35899.

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**Reproductive success: studies of individual variation in contrasting breeding systems.**—T. H. Clutton-Brock, ed. 1988. University of Chicago Press. ix + 538p. $75.00 cloth, $29.95 paper.

Variation in individual reproductive performance is the raw material upon which Darwinian selection must act, yet most models and theory in evolutionary biology concern themselves primarily with mean, or average, reproductive performance. This focus on mean performance, while useful from a theoretical point of view, may actually obscure useful patterns and information that could allow us to understand the action of selection, both natural and sexual, and the dynamics of populations. *Reproductive success* is the first book to collect and evaluate numerous studies of variation in reproductive performance over the lifetimes of recognizable individuals. Clutton-Brock has made an attempt to draw examples from as wide an array of taxonomic groups as available, yet the results come primarily from three groups: insects, birds, and mammals, with a single chapter on frogs. Even within these few groups, the quality of the data are highly variable. There is good news for ornithologists, however, since nine of the 10 best data sets are from long-term studies of birds.

Despite the variability in the quality of the data, a number of general trends and numerous useful insights can be discerned. First, male reproductive success (RS) generally varies more than female RS, but the variation in female performance is far greater than is traditionally assumed. Second, in most species where data exists, the best predictor of lifetime reproductive performance is survival. The major exception to this pattern may be in highly polygynous species where male mating success may be a better predictor, but the data supporting this argument are fairly weak (for reasons described below). Third, if the individuals with the longest lifespans also show the highest rates of reproduction, this calls into question the general concept of tradeoffs between survival and reproduction, especially for female organisms. This finally leads to the conclusion that in most populations, the bulk of successful reproduction may be performed by only a small per-

centage of the total population, and that these "superior" phenotypes show little or no cost of reproduction.

The putative existence of these superphenotypes has possible implications for both the study of selection and adaptation, especially if traits can be identified that contribute strongly to this high rate of RS. For this reason, one of the most stimulating chapters in the book is Grafen (chapter 28) "On the uses of data on lifetime reproductive success." At first, this chapter appears anomalous because Grafen's basic argument is that most of the data in this book are of limited use in studying adaptation, although they may be useful for examining selection in progress. Grafen is a disciple of the British "argument from design" school, and advocates the use of experiments that demonstrate current "function" as being the way to study adaptation. Despite Grafen's arguments, however, if variation in traits, either behavioral, morphological, or physiological, can be found that correlate with the variation in reproductive performance, they may well be useful in elucidating phenomena related to adaptation.

Grafen is correct, however, in pointing out that simply measuring RS tells us little or nothing about either selection or adaptation. One general weakness of most of the studies in this book is, in fact, that although they do an admirable job of describing variation in individual performance in some detail, they do little to examine the underlying factors that might contribute to this variation. Notable exceptions to this rule are chapters on *Polistes* wasps by Queller and Silk, on red deer by Clutton-Brock et al., and several of the chapters on birds.

One result that seems apparent from reading this book is that if you want to obtain a strong data set on lifetime RS, study birds, especially monogamous ones. Excellent results are provided by both van Noordwijk and van Balen, and McLeery and Perrins on Great Tits (*Parus major*), on Song Sparrows (*Melospiza melodia*) by J.N.M. Smith, on House Martins (*Progne* sp.) by Bryant, on sparrowhawks by Newton, on kittiwakes by Thomas and Coulson, on fulmars by Ollason and Dunnett, and on Florida Scrub Jays (*Aphelocoma coerulescens*) by Fitzpatrick and Woolfenden. The only weak chapter on birds is by Harvey et al. on Pied Flycatchers (*Ficedula hypoleuca*) which presents no data on individual variance in RS and little data on any other topic.

The mammalian studies are all on polygynous species and run the gamut from excellent to weak. The chapter on red deer by Clutton-Brock et al. presents an excellent data set combined with a thought provoking discussion of the factors that contribute to variation in individual RS. At the other extreme is a chapter on northern elephant seals by LeBoeuf and Reiter, which uses data from male and female cohorts born 10 years apart to compare male and female lifetime RS. Since the male cohort was part of an expanding population whereas the female cohort was part of a stable or declining population the results are not at all comparable, and in fact LeBoeuf and Reiter obtain the unlikely result that *mean* male RS (2.95) was more than three times that of *mean* female RS (0.75). This demonstrates why comparisons of male and female lifetime RS should be drawn from the same cohort.

Another general observation that one gathers from this book is that data on reproductive success, whether seasonal, annual, or lifetime, should always be presented as histograms or frequency distributions. Reproductive data presented as means, even with standard errors or deviations appended, obscure too much information and patterns that allow us to understand the dynamics of a cohort or population.

Overall, I regard *Reproductive success* to be a successful book. It would be an excellent text for a graduate seminar, since it covers a reasonable taxonomic array, discusses a number of salient issues in evolutionary biology, and even presents a very intriguing way of evaluating the contribution of various components to total variation in reproductive output by David Brown. Strengths and weaknesses of various approaches and viewpoints are presented in the chapters on general issues by Brown, Grafen, and Clutton-Brock. *Reproductive success* demonstrates that we have come a long way in our understanding of population biology and reproductive success, but perhaps even more important, it demonstrates that we still have a long way to go and points us firmly in the right direction.—RAYMOND PIEROTTI, Department of Biology, University of New Mexico, Albuquerque, NM 87131.