

Avital, E. & Jablonka, E. 2000: *Animal Traditions: Behavioural Inheritance in Evolution*. Cambridge University Press, Cambridge. 431 pp., Hb US\$ 80.00, £50.00, ISBN 0-521-66273-7.

Reviewed by Bennett G. Galef, Jr., McMaster University. E-mail: galef@mcmaster.ca

Animal Traditions provides a well-written, handsomely bound, multiply indexed, though idiosyncratic, introduction to behavioural ecology. The authors' basic argument is that attention should be paid to the role of social learning when discussing the development of adaptive behavioural repertoires of animals. They provide a wealth of references to material consistent with their view, as well as a number of proposals for experiments that should interest professionals.

In the view of Avital and Jablonka, natural selection acting on genetic differences between individuals is often not a sufficient explanation for the adaptive behaviours of higher animals. The authors suggest that social learning is an important agent of evolutionary change in animals, underlying behaviours as diverse as speciation and pair-bond formation, and deserving of a far more prominent place in evolutionary thinking than it presently enjoys.

The literature review is broad, covering much basic behavioural ecology and selected aspects of animal learning. However, familiar material is often interpreted in unfamiliar ways. Avital and Jablonka consistently stress the role of information transmission by non-genetic means and gene-culture interaction in every aspect of animal life. They identify numerous instances where genetic differences need not underlie heritable differences in behaviour, and offer learning-based explanations for many behavioural differences between species or sexes that are usually assumed to be genetically based, but may, of course, have other causes.

Sometimes, the authors interpret the literature differently than would I. For example, in two discussions of the broader ramifications of sweet-potato washing and wheat placer mining on the 'culture' of Japanese macaques, Avital and Jablonka assert that because sweet-potato washing and wheat placer mining eventually led Imo and his fellows to wash potatoes in the sea, it also led them to bathe there. In the authors' words (p. 98) 'the two food washing traditions...triggered the tradition of using the sea for swimming and cooling in summer.' The authors fail to mention that 'in the summer of 1959 Mrs. Mito, [one of the provisioners of the Koshima monkeys] attracted the monkeys to go into the water of Otamari Bay by throwing peanuts in the sea' (Kawai 1965, p. 16). Human agency, rather than socially learned familiarity with the sea, seems to me to have promoted bathing.

In conceptually related passages, Avital and Jablonka (p. 134) suggest that the pine-cone stripping behaviour of black rats studied by Terkel and his associates in Israel was perfected over generations, whereas the literature indicates that, in one generation, a small percentage of adult rats (and many juveniles that interact with them) are able to develop the most efficient method of pine-cone stripping.

Such relatively minor lapses may be nothing more than poetic licence in the interest of good story telling. On the other hand, both interpretations are used by Avital and Jablonka's to support their hypothesis that animal 'culture', like human culture, shows increasing elaboration of traditional behaviours over generations, a process often referred to as 'ratcheting' in the literature on animal tradition.

Given the eclectic literature the volume explores, much material will be unfamiliar to any reader. It is therefore important to feel confident that the authors' scholarship is precise and unbiased. The few facts that I did check (out of hundreds in the volume) left me with the feeling that more may have been read into the results of some studies than would leave those who conducted them feeling truly comfortable.

My main problem with the monograph, and one I could not solve, concerned the audience for which the book is intended or appropriate. Both the writing style, which is clear and engaging, and the material covered seemed suitable for students new to behavioural ecology and even to evolutionary biology. There are fine descriptions of everything from DNA transcription to the Baldwin effect. However, 370 pages of text unrelieved by a single figure or illustration, a theoretical stance relatively idiosyncratic to the authors, and occasional failure clearly to distinguish what is known from what is speculative but possible, would make the text difficult to use in the classroom. Further, neophytes would be unlikely to have the expertise either to recognize the iconoclastic nature of many of the interpretations the authors propose or to evaluate the relative merits of the alternative hypotheses presented.

On the other hand, extensive presentation of introductory materials, the level of argument, and the use of footnotes instead of in-text citations make the book less than ideal for professionals. I was particularly put off by the need to mark the footnote section of each chapter with a 'Post-it' to facilitate the constant flipping back and forth from text to footnotes to references at the end of the volume necessary to know exactly what papers were being referred to by the superscripted numbers. *Animal Traditions* seemed to me a volume without an obvious audience.

Still, the authors suggest a number of potentially interesting experiments that could provide support for their sometimes intriguing, social-learning-based interpretations of everything from the fitness consequences of ecological compatibility among mating birds to the food preferences of cockroaches. I was also pleasantly surprised by the number of references to possible animal traditions that Avital and Jablonka had uncovered that I had not previously encountered in 30 years of reading the social-learning literature. Consequently, although few may have the necessary persistence, the volume should be of use to those interested in social learning and prepared to read through considerable introductory material to find useful nuggets.

Reference

Kawai, M. 1965: Newly-acquired sub-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates* **6**, 1–30.

Houston, A. I. & McNamara, J. 1999: *Models of Adaptive Behaviour*. Cambridge University Press, Cambridge. 378 pp., numerous figs and tables, Hb £65.00, US\$ 95.00, ISBN 0-521-38480-X. Pb £22.95, US\$ 34.95, ISBN 0-521-65539-0.

Clark, C. W. & Mangel, M. 2000: *Dynamic State Variable Models in Ecology*. Oxford Series in Ecology and Evolution, 289 pp., numerous figs and tables, program code (BASIC), web site, Hb £45.00, US\$ 65.00, ISBN 0-19-52266-6; Pb £22.50, US\$ 35.00, ISBN 0-19-512267-4.

Reviewed by Esa Ranta, University of Helsinki. E-mail: esa.ranta@helsinki.fi

Two books on stochastic dynamic modelling in behavioural ecology have appeared in less than 12 months from two major publishers in ecology. Is this a response to the demand, or is this an indication that behavioural ecologists are struggling with problems of how to model (and hence also to organize) the multitude of animal behaviour they are documenting? It might be just a coincidence, as the two teams have been rather productive in using dynamic modelling during the past few years and perhaps felt that it was time for a synthesis.

In science, the paramount question is to phrase research problems in theoretical terms. The theory of evolution by natural selection has also been the theory underlining research in behavioural ecology. The focus is on fitness differences among competing or alternative traits. This is precisely the scope of the two books. Or rather, the two books introduce a numeric technique for addressing which of the feasible traits gives the best fitness advantage for an individual. The method used is dynamic modelling, where a state variable (in behavioural modelling often the condition of an individual) affects the trade-off between different options faced. For example, is a hungry forager more prone to taking higher risks in getting food than a satiated individual?

The scope in stochastic dynamic modelling is to price the future – ‘a good animal is a living animal’ – only the strategies or traits that survive are of value. The technique in the modelling is to start from the finish and to end up with the beginning. The model includes a set of decision rules. At the penultimate time step available, behavioural options are compared against this set of rules and the behaviour yielding the highest fitness payoff is selected. The same is repeated at the time step before the penultimate step, and the system is backward iterated till the beginning is reached. By using this technique the best survival strategy is found. This technique also limits the branching points to a number that can be mastered with modern computing facilities.

Stochastic dynamic modelling is old hat in solving problems in other disciplines; it is not a newcomer in behavioural ecology either (Mangel, M. & Clark, C. W. 1988. *Dynamic Modeling in Behavioral Ecology*. Monographs in Behavior and Ecology, Princeton University Press, Princeton). A natural question arises: is there a need for new text book(s) on this subject? My answer is yes! A mere glance at behavioural journals gives the impression that the past 10 years or so have resulted in a rich selection of articles successfully using the stochastic dynamic modelling technique. It is also no surprise that the authors of the two books have been major players in producing these papers.

The two books obviously have much in common. All the major examples are the same in both treatments, and much of the structure in the two books is similar. Yet there are subtle differences between the two treatises. The Britons begin by discussing at length the philosophy of carrying out