BEHAVIOURAL ECOLOGY

Design for living

Manfred Milinski hails the long-awaited update of a classic on the optimal design of behaviour.

Natural selection produces impressive physical adaptations, but it is equally powerful in fashioning behaviour, given that it favours the individuals best able to avoid predators, choose mates, find food, and more. Ecology is the stage on which selection of the fittest occurs, and the discipline of behavioural ecology deals with the optimal design of behaviour.

The long-awaited update to a classic in this field is now here, presenting new directions in thinking and addressing burning questions. Richly informed by progress in many other disciplines, such as sensory physiology, genetics and evolutionary theory, it marks the emergence of behavioural ecology as a fully fledged discipline.

In 1981, John Krebs and Nick Davies's *An Introduction to Behavioural Ecology* (Blackwell Scientific Publications) boosted a flourishing new area of thought. It became fashionable to use economic theory to understand animal behaviour — for instance, the trade-off between the need to forage efficiently and to avoid being eaten.

That first edition was a masterpiece of scientific writing, embraced by behavioural ecologists worldwide. After two further successful editions at six-yearly intervals, we now have the fourth, co-authored by Stuart West and carefully updated throughout.

Among the elements appearing for the first time is a fascinating chapter on cognition, which looks at the ability of birds to plan for the future, and to behave as if they are able to interpret the knowledge of individuals that they observe. Another section shows that in evolutionary 'arms races' between, say, hosts and parasites, each invention by the parasite selects for a counter-invention by the host, which would otherwise lose the race. The result is much like the Red Queen's race in Lewis Carroll's *Through the Looking Glass*, where the pace must be kept up simply to stay in the same place. This is beautifully demonstrated using the coevolution of cuckoos and their hosts.

Studying animal personalities is trendy, but why is it advantageous for one individual to have personality A and another to have B? Related questions addressed in the book are whether animal groups such as packs or herds have leaders, or whether it is better for the group members to 'vote' on a course of action.

An Introduction to Behavioural Ecology (Fourth Edition)
NICHOLAS B. DAVIES, JOHN R. KREBS & STUART A. WEST
Wiley-Blackwell: 2012. 520 pp. £34.99, $149.95

The current bandwagon in behavioural ecology is sexual selection — which Charles Darwin wrote about but did not solve. This concept has produced a plethora of findings and ideas, which Davies *et al.* describe and discuss. They note that the 'runaway process', proposed by evolutionary biologist R. A. Fisher in the early twentieth century to explain why females such as peahens prefer ornamented and thus handicapped males, still awaits rigorous testing. However, the 'good genes for resistance' explanation, put forward by Bill Hamilton and Marlene Zuk in the 1980s, seems now to be confirmed. The Hamilton–Zuk mechanism posits that sexual ornaments such as the peacock's tail signal genetic resistance against the prevalent disease affecting that species, on the grounds that ill individuals could not produce such ornaments. Choosy females therefore obtain this resistance for their offspring.

In vertebrates, as the book describes, these 'good genes' are now known to be alleles of the polymorphic genes of the major histocompatibility complex (MHC), which direct the immune response to new infections. MHC genotypes can be detected through odour and are chosen before ornament. So a female will choose males whose odour indicates that their MHC alleles provide the optimal complement to her own. Among these, say the authors, she will prefer the most ornamented males, whose alleles include those for disease resistance. But this explanation still leaves many questions unanswered. For example, how does a Hamilton–Zuk mechanism work in insects, which lack MHC genes?

Sexual conflict also drives sperm competition, the evolution of behaviour that maximize the chances of sperm from a particular male fertilizing the egg. Will males that produce more sperm win out, or do eggs 'choose' spermatozoa with good genes? Today's science fiction is tomorrow's textbook wisdom.

The book also delves into the evolution of cooperation and altruism. Why invest resources to increase another individual's fitness? One explanation, kin selection, is that the individual helps only close relatives, which share copies of its genes. The conditions for altruistic behaviour by kin selection are given by Hamilton's rule: the benefit-to-cost ratio must be greater than one divided by the relatedness of the altruist to the recipient. So for full siblings, which have a relatedness of one-half, the benefit must be at least twice the cost. As discussed in the book, this rule seems to explain numerous phenomena, such as the social insects with their sterile worker castes, and also why we prefer to raise our own children.

There is overwhelming evidence for kin selection, but not all researchers agree with the theory behind Hamilton's rule, as a recent critique shows (M. A. Nowak *et al. Nature* **466,** 1057–1062; 2010). That Davies *et al.* do not discuss this dramatic development, which has great potential for new insight, is a pity.

Nevertheless, there is much here to inspire. An intriguing chapter on communication, for instance, discusses the major problem of signalling between animals — what keeps signals reliable and honest? Future discoveries will undoubtedly show why smiles and other signals of emotion are not faked often enough to be ignored.

This is a marvellous book, written in a lucid style. A must-read for those in the field, it is also a cornucopia of new thinking for anyone interested in evolution and behaviour. ■

DIGITAL VISION/DIGITAL ZOO/GETTY

The peacock's tail attracts mates — at a cost.

Manfred Milinski *is a director of the Max Planck Institute for Evolutionary Biology in Plön, Germany.*
e-mail: milinski@evolbio.mpg.de