trends in ECOLOGY & EVOLUTION
October 1994 Vol. 9, No. 10 [100] pp. 358–360

The evolution of behavioural ecology

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As recently as 1986, the International Society for Behavioural Ecology (ISBE) was little more than groups of individuals standing in isolated corridors bemoaning the fact that to meet with colleagues in their field they had to attend three different conferences (Ecology, Evolution and Animal Behaviour), none of which focused on their specific interests. Today, the ISBE has over 1150 members and meets every two years in international locations. It publishes its own journal, *Behavioral Ecology*, and is recognized as one of the fastest growing disciplines in biology.

Behavioural ecologists strive to understand why behaviour is adaptive. To do so, they study how behaviour, ecology and occasionally genetics interact to determine fitness. Ideally they would arrive at a fitness function describing how fitness varies with degree of behavioural expression. In knowing this fitness function, the behavioural ecologist can not only explain the adaptiveness of the behaviour but also predict its expression over a broad range of environments and organismal types. Behavioural ecologists apply their search for fitness functions to all aspects of what animals and plants do with their bodies. This includes behavioural mechanisms, reproductive strategies, survival strategies, social behaviour, life history strategies and population interactions. Behavioural ecologists believe that by understanding how the actions of an organism affect its fitness, the organism as an entity can be explained. To a behavioural ecologist, therefore, the term 'behaviour' means much more than 'response to a stimulus' – behaviour is everything an organism does.

History of behavioural ecology

Behavioural ecology had its beginnings in 1960s schools of thought in behaviour (e.g. J.H. Crook, N. Tinbergen), ecology (e.g. D. Lack, R.H. MacArthur) and evolution (e.g. W.D. Hamilton, J. Maynard Smith, G.C. Williams). In the 1970s, although unrecognized as a distinct field, it was generating new concepts

in reproduction (e.g. Refs 1,2), survival[3,4] and social interactions[5,6]. The 1980s saw rapid growth, the formation of research groups at universities, and the first international meeting. In 1986, the highly successful International Behavioural Ecology Meeting held in Albany, NY, USA (organizers J.L. Brown, T. Caraco, C. Barkan and D. Steadman) was the catalyst for a new society (ISBE) to recognize behavioural ecology as a distinct discipline. Now, although only eight years old, behavioural ecology has matured into an internationally established discipline with faculty positions, university courses and its own journal.

Where we've been

The field of behavioural ecology may be divided into seven subject areas. These areas vary greatly in intensity of research activity (Box 1). Using conference presentations as a measure of activity, 33% of work is in Reproductive Strategies; about 14% in each of Survival Strategies, Social Behaviour, Population Biology and Life Histories; 7% in Behavioural Mechanisms; and 3% in Applied Topics. One notable trend is that the proportion of research activity in Reproductive Strategies has increased while that in Survival Strategies has decreased. This trend is due, at least in part, to an increasing interest in sexual selection, and a decreasing interest in foraging studies.

Today's hot topics

Sexual selection is hot. Eight years ago, in 1986, the inaugural issue of *TREE* ran sexual selection as its cover article. Today, more than 20% of all behavioural ecology research is on sexual selection and interest is still growing. Many researchers are using new DNA fingerprinting technology to measure paternity, identify its behavioural, morphological and ecological correlates, and study the likelihood that females, rather than males, are in control of sperm competition[7]. Those studying mate choice are measuring the fluctuating asymmetry of display characters as a reliable indicator of phenotypic and thus genotypic quality (Ref. 8, but see Ref. 9). The influence of parasites on sexual selection[10] remains a popular hypothesis, with some researchers suggesting that parasite load may be related to fluctuating asymmetry in insects, birds and humans[11]. Another hot topic within Reproductive Strategies is parental care[12], especially the role of paternity[13], parent–offspring conflict[14], and present and future trade-offs.

Interest in foraging research has clearly waned (Box 1), perhaps because it has become difficult to expand beyond the successes of 'classical' foraging theory[15]. However, Survival Strategies is far from dead, as evidenced by the many foraging papers in current issues of *Behavioral Ecology*. Popular topics are currencies[16,17], social interactions[18], learning and memory, and life history theory[19].

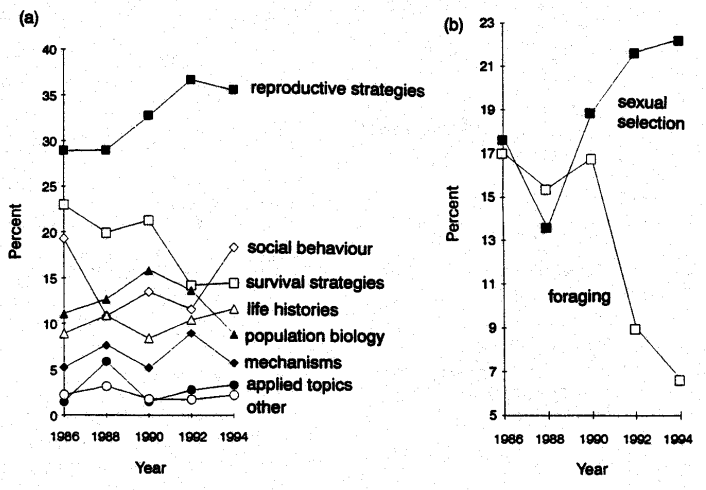
The enigma of cooperation in a selfish gene environment keeps researchers producing new theoretical[20–22] and empirical[23,24] studies of Social Behaviour. The concept of phenotypic plasticity, in which individuals adjust their phenotype in response to the environment, has stimulated new questions for Population and Life History studies, such as: do predator–prey cycles arise from prey adjusting their reproductive effort, is age of maturity adjustable, and what stimulates the choice between cannibalistic and omnivorous life histories (e.g. Ref. 25)?

Research in Behavioural Mechanisms is being fuelled by the need to understand how the machinery that gives rise to behaviour also controls it. Research in foraging has stimulated new questions about learning and memory mechanisms[26,27], while studies in sexual selection have given rise to questions about

Box 1. Trends in behavioural ecology research

The International Society of Behavioural Ecology holds conferences every two years. Its past conferences and total presentations are: 1986 Albany, USA, 135 presentations; 1988 Vancouver, Canada, 221; 1990 Uppsala, Sweden, 334; 1992 Princeton, USA, 578; 1994 Nottingham, England, about 450 (a few months before this conference I have a confirmed list of 180 talks, and an estimate of 270 posters). I've reviewed the abstracts (in the case of Nottingham the titles of talks) and assigned each presentation to one of seven subject areas: Behavioural Mechanisms (including research on such topics as learning and memory, hormones, genetics, chemical and other signals, and methods for assessment); Reproductive Strategies (mating systems and mating, sexual selection, alternative breeding tactics, parental care); Survival Strategies (foraging, access to resources, predator–prey relationships, exploitation and parasitism, territoriality); Social Behaviour (cooperation, selfishness and aggression, kinship and nepotism, altruism, helpers, dominance relationships, communication); Life Histories (sex, sex allocation, cost of reproduction, reproductive effort, trade-offs, age at maturity, fecundity, lifespan, correlated responses, development); Population Biology (population size, dynamics, predation, use of space, migration and movement, co-evolution, interspecific interactions, hybrids); Applied Topics (conservation, animal welfare, studies of humans). The few presentations that do not seem to fit the above seven are assigned to the category Other (about 2%).

The representation of each subject area at each conference is shown in (a). The average ranking across the five conferences is: (1) Reproductive Strategies (average 33%); (2) Survival Strategies (19%); (3) Social Behaviour (15%); (4) Population Biology (12%); (5) Life History (10%); (6) Mechanism (7%); (7) Applied Topics (3%). The category Other averaged only 2% of presentations. This ranking was statistically consistent across the five conferences (Chi-square 33.1; df = 7; $P < 0.001$) although some changes occur. Significant differences in the proportion of presentations exist between Reproductive and Survival Strategies, between Life Histories and Mechanisms, and between Mechanisms and Applied Topics (*t*-tests, $P < 0.05$).



Over the five conferences there was a significant increase in presentations in Reproductive Strategies ($r = 0.92$, $P = 0.027$), and a significant decrease in Survival Strategies ($r = -0.90$, $P = 0.040$). Reproductive and Survival Strategies were negatively correlated ($r = -0.88$, $P = 0.049$). As seen in (b), this pattern is largely due to a change in interest in two topics: sexual selection (Reproductive Strategies) increasing and foraging (Survival Strategies) decreasing. In 1986, sexual selection and foraging both represented about one out of six presentations; by 1994, sexual selection had risen to one out of 4.5 and foraging had dropped to one out of 15. It will be interesting to track these topics in the future.

female mechanisms for controlling sperm competition[7,28]. The application of behavioural ecology theory to humans is beginning to raise interesting questions about medicine[29,30]. Are current medical practices such as treating the fever response with aspirin or using gene therapy on what may be pleiotropic genes, hindering our health?

What are today's hot tools? If you need DNA fingerprinting for your studies of reproductive strategies, investigate the new single-locus technique of microsatellites[31]. Dynamic programming with a computer can place your fitness calculations into a life history context[19]. And, phylogenetic systematics[32,33] can improve your use of the 'comparative method' for identifying adaptations.

Where next?

While the future is difficult to predict, there are some paths that appear inevitable. We need a new theory of mating systems. Recent paternity studies using DNA fingerprinting have negated mating system classifications based on male control. We now need a theory that incorporates the conflicting interests of males and females, and the factors determining which sex is in control, in order to predict patterns of male–female pairing.

Population ecologists will increasingly knock on behavioural ecologists' doors as individual-based models become a major tool for understanding population dynamics and community structure. Similarly, population geneticists will need the fitness functions developed by behavioural ecologists to continue their progress from a descriptive to a predictive field[34].

We will increasingly embrace life history theory as we evolve from asking 'is this behaviour optimal?' to 'what is the fitness consequence of this behaviour?'. One of the most significant contributions of behavioural ecologists is that their use of life history theory led to the recognition that individual variation is often adaptive, as in the case of individual optimization of clutch size. In the future, life history theory may help us to penetrate developmental biology and build a theory of ontogeny that links individual cell lineages to fitness consequences, as well as addressing intra-genomic conflict.

Behavioural ecology of plants and the other Kingdoms is vastly understudied. Many biologists seem to think that only animals 'behave' – plants just 'hold tight and take their punishment'. But roots and sunshine are simply constraints. Plants have reproductive strategies, survival strategies and social interactions. Moreover, their reduced mobility may make them easier to study. It will be illuminating to see how theories of behavioural ecology explain plant behaviour.

As behavioural ecologists grow to recognize that they, more than anyone, are specialists at understanding the adaptations organisms need to survive and reproduce, they will turn to solving problems in conservation biology.

In North America, the Human Behaviour and Evolution Society meetings have many interesting presentations on human behavioural ecology, but currently most apply behavioural ecology to identify patterns already known in other animals. The future will see the ISBE combining human data with that of other organisms to develop basic behavioural ecology theory. The Human Behaviour and Evolution Society, using this theory, will build a field of applied human behaviour.

Two factors will drive an increasing interest in investigating the psychological, physiological and genetic mechanisms underlying adaptations. First, these proximate mechanisms can be shown to influence the fitness functions of behaviour, as in the case of female mechanisms of sperm storage that determine male mating success, and the genetic relatedness among individuals that determines who benefits from altruism. Second, we will have the ability to predict new mechanisms such as those needed for the 'conflict' between mother and foetus (see Bateson, this issue), for manipulation of sex ratio, and for holding specific items of information in the brain.

Concluding remarks

Founded in 1986, the discipline of behavioural ecology has in its first decade established itself as the premier field for understanding why organisms behave as they do. It unites nature's sources of selection – ecology and genetics – with the organism's response – behaviour – and therefore occupies a significant position in evolutionary biology. Moreover, it gives theoretical justification to mechanisms of causation and development on the reductionist side, and population dynamics and genetics on the holistic side. The next decade will be a dynamic phase in the evolution of behavioural ecology. There are new ideas, new technologies and the possibility of integrating across many different disciplines.

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