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Behavioural Ecology: Natural History as Science

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Abstract

Behavioural ecology emerged from ethology, ecology, and population genetics as the result of a scientific revolution in the late 1960s and the 1970s; this could be seen as the coming of age of natural history as science. With the aid of a straw poll from 25 practising behavioural ecologists, I attempt to review the main components of this revolution in terms of the history of its main subdisciplines and to identify the scientists perceived as having the major influences.

Introduction

This essay is a perspective on the events in the late 1960s and 1970s that led natural history to blossom into a formal science. Although I have obtained views from other behavioural ecologists, it is necessarily a personal overview. Others will see it differently—but I have tried to present a balanced account, with informed postgraduates and post-docs as intended readers. This essay is for them. The difficulty has been to decide what to leave out.

In the beginning—let's start with ethology, the science of animal behaviour as consolidated by the three Nobel laureates, Tinbergen, Lorenz, and von Frisch. It was in the context of ethology that the major animal behaviour journals began: *Zeitschrift für Tierpsychologie* (1937; *Ethology* from 1986), *Behaviour* (1947), and *Animal Behaviour* (1958; starting as the *British Journal for Animal Behaviour* in 1953), which serves the two societies, the Association for the Study of Animal Behaviour (Europe based), and the Animal Behavior Society (North America based). Ethology had (and still has) a wide remit: to understand animal behaviour in terms of its causation, development, and evolution (in the sense of phylogeny) as well as function (adaptive significance). This last area (i.e., understanding the selective forces that have shaped behaviour) exploded in the 1970s, leading to the formation of a new discipline: behavioural ecology (or sociobiology). To cope with this surge, new journals began: *Behavioral Ecology and Sociobiology* (1976), *Ethology and Sociobiology* (1979; *Evolution and Human Behavior* from 1997), and *Behavioral Ecology* (1990), after the founding of the International Society for Behavioral Ecology in 1986. The older journals continue to flourish, publishing increasing numbers of articles on behavioural ecology as well as all other aspects of animal behaviour.

Much has been written about sociobiology, its implications for human nature, and the controversy after the publication of Wilson's (1975) *Sociobiology: The New Synthesis* (e.g., Segerstråle 2000). Unfortunately, this political controversy obscured what was being achieved in the 1970s: a revolution in the way we study and understand animal behaviour. I shall avoid the politics and concentrate on the science (see also Alcock 2001a).

The distinction between natural history and biology is blurred: though its exact remit is debatable (Arnold 2003; Greene 2005), natural history represents a suite of activities, ranging from hobbyist interests in wildlife and nature to subsets of biological science related to evolution, ecology, behaviour, phylogeny, and taxonomy. The best naturalists had always been scientists in the sense of research inquiry. But perhaps the most explicit melding of natural history and biology is the area of behavioural and evolutionary ecology. These disciplines represent the scientific coming-of-age of the best traditions of natural history; this essay celebrates the scientific revolution associated with their genesis.

What's in a Name?

Many would see the first announcement of this revolution as the publication of Wilson's monograph. The term "sociobiology" is still used, but possibly because it lays stress on social behaviour, many have preferred "behavioural ecology," which more naturally includes all aspects of behavioural adaptation. The distinction between behavioural ecology and sociobiology was never clear, and many see them as synonyms or, at most, that sociobiology is a subset of behavioural ecology. In the late 1970s, sociobiology was used much more, and I spent a year in 1978–1979 in a research group in King's College, Cambridge, on their sociobiology (not behavioural ecology) project. After Wilson's book, and the resulting political clamour, there was a push in the States towards its impact on human behaviour. For whatever reason, Wilson himself was driven in this direction (his 1979 book *On Human Nature* won a Pulitzer Prize). In contrast, Krebs and Davies defined the field more widely in their highly influential edited volumes *Behavioural Ecology: An Evolutionary Approach* (1978, 1984, 1991, 1997) and their student text *An Introduction to Behavioural Ecology* (first edition 1981).

There was perhaps a degree of North American–European rivalry involved here. One colleague, a respondent for *Influences and Influencers*, remarked that:

> *[B]ehavioral ecology arose largely as a tactical alternative to sociobiology in the mid-70s. . . . whatever we call this field it was (and largely still is) a US/UK mixed-marriage. . . . John Krebs spearhead[ed] a hostile takeover of E. O. Wilson's "new synthesis" almost before the paint could dry, successfully usurping and greatly improving the emerging field we now perceive.*

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The terms probably had some reflection on the interests of the protagonists. Wilson is a world authority on ants, a notably social group of insects, and sociobiology must have seemed an ideal emphasis. Much of Krebs's early interests lay in food foraging, for which the term sociobiology must have seemed less than ideal. But influences are a complex fusion: Krebs began foraging work in Canada under the influence of Charnov, who, at the time, was Orians's student; Orians began his career in the late 1950s, supervised by Lack at Oxford!

The boundary between evolutionary and behavioural ecology is muddy. One respondent for *Influences and Influencers* saw behavioural ecology as a subdiscipline of evolutionary ecology; others saw them as related disciplines, one dealing with behaviour and the other with growth, timing of maturity, sex allocation, and so on. Thus, foraging and mate searching are typically seen as behavioural ecology and life history strategy as evolutionary ecology, but in reality, the distinction is blurred. The evolution of switches from juvenile to adult or from one strategy to another during growth cannot be understood without consideration of the behaviour and fitness options associated with each life history stage.

The terms behavioural ecology and evolutionary ecology are themselves perhaps less than ideal—both have much less to do with classical ecology than with evolution and adaptive value, something that ecology (which typically seeks to explain population numbers, succession, community and ecosystem structure, distribution, and energy flow) has never really espoused. For instance, classical ecology sought to explain distributions among habitats at a proximate level, in terms of tolerance of features such as temperature and salinity. Behavioural ecology sought ultimate explanations, in terms of selective forces shaping the decisions about *where* to search for food or mates. There was also a difference in practical approach: classical ecologists typically ventured into the field to obtain samples for lab analysis. Early behavioural ecologists, like naturalists, tended to do most of their work in the field. They often still do, but most now use more lab technology.

Ideally, a term was needed that would describe the study of the ecological aspects of strategic adaptation in all aspects of behaviour and in the allocation of expenditures by individuals. To my knowledge, no simple general term exists for this, and our "scientific natural history" has become known as behavioural–evolutionary ecology. Most of us are more than happy that the Krebs and Davies texts have led the revolution, defined the field, and guided its development to maturity.

So What Was the Revolution?

In a very real sense, Darwin was the founder of the discipline. Behavioural ecology can be seen as a return to Darwinian principles after most researchers in behaviour and ecology had abandoned them for decades. The revolution resulted from increased awareness of selection mechanisms, application of predictive Darwinian models, and an understanding of inherent underlying conflicts of interests.

Tinbergen's (1963) celebrated "four questions" had made ethologists aware of the different types of explanations for biological features, one of which concerned why it is favoured by selection. This was to be the new dimension: interpreting behaviour in terms of underlying evolutionary mechanisms. Ethology bequeathed little grounding in what was needed here, and in retrospect ecological–evolutionary biologists such as Lack, Crook, MacArthur, Williams, and Orians were pioneers of the 1960s. Population genetics offered rigorous, but strategically simple genetic models; their expansion to complex multilocus and multiallele cases often became problematic. Behavioural ecologists needed more strategic richness to cope with phenotypic problems in behaviour or resource allocation; a merger was impossible and so phenotype modellers threw out diploid genetics, implicitly or explicitly assuming haploidy

or asexuality (now often called the "phenotypic gambit"; Grafen 1984). Population geneticists involved in the attack on sociobiology used this simplification as part of their armoury. Critiques were also levied against the concepts of optimality, and another line of attack branded the "adaptationist programme" as "Panglossian" (e.g., Gould & Lewontin 1979), in the sense that every feature is seen as a perfect adaptation (see Segerstråle 2000). It is true that behavioural ecologists necessarily start by *assuming* adaptation because their mission is to understand the nature of the selective forces that have shaped a given character. But they also assume that there are trade-offs and other nonadaptive constraints on adaptation. Insight is achieved by correctly deducing what adaptation is and what constraint is.

Individual Selection and the Selfish Gene

Two stages stand out in ethology's metamorphosis into behavioural ecology. The first was the attack on implicit or explicit assumptions that the unit of selection is the group or species. Despite believing that they were following Darwinian principles, most ethologists and ecologists in the 1960s typically explained function in terms of "advantage to the species." This verbal shorthand was misguided, leading to error if individual and group (or species) interests differ. In his book *Animal Dispersion in Relation to Social Behaviour*, Wynne-Edwards (1962) argued that social displays were "epideictic" mechanisms evolved to convey information about population density, predicting that reproduction should be reduced at high density to avoid population crashes through overexploitation. Seeing that a non-Darwinian mechanism was required (variants that switched off reproduction could hardly be favoured by natural selection; Darwin had similarly agonised over sterile castes in social insects), he invoked the group as the unit of selection, and thus made group selection explicit for explanations of behaviour (the original concept was due to Carr Saunders, 1922).

A groundswell of rebellion began, crystallised by Williams's seminal book *Adaptation and Natural Selection* (1966a), restating Darwinian principles and stressing that an advantage must be sought at the level of the individual ("individual selection") or the gene. This rebellion had many instigators—the avian ecologist David Lack was notable in the United Kingdom. Wynne-Edwards's proposition had been opposed from the start by such people as Maynard Smith (1964), who analysed the difficulties faced by a gene causing its bearer to act against its own (Darwinian) interests, but in the interests of the group as a whole. Crook pioneered the study of social organisation in an ecological context in weaver birds (1964) and in primates (Crook & Gartlan 1965). One respondent for *Influences and Influencers* wrote:

*George Williams' 1966 book dealing with Wynne-Edwards' 1962 group selection tome . . .
like Crook's argument that ecology might be a stronger determinant of social structure than
phylogeny, had an enormous effect on those of us entering animal behavior. It focused atten-
tion on the individual, on conflict and competition, and set the scene well for papers that fol-
lowed pursuing the individual selection line of thinking.*

Another respondent pointed out that Williams's book had actually been
written before he read Wynne-Edwards's (1962): it was in response to
Emerson considering a termite colony as an individual and was extensively
reworked to counter Wynne-Edwards.

"Advantage to the species" is still seen or heard today, mostly through
naïvety as a prerevolution legacy. It is still defended by those who argue, in
view of the relentless extinctions of animal species over geological time, that
the species is the unit of selection (see Segerstråle 2000), but few behavioural
ecologists see it as a mechanism that shapes phenotypic adaptation.

The three great pioneers of population genetics, Fisher, Haldane, and
Wright, were clearly aware of the distinction between group and individual
selection. Group selection now has a more rigorous framework than it had
in the 1960s and 1970s: it can be argued to work under some conditions (e.g.,
D. S. Wilson 1980). The general consensus, implicit or explicit, is that
Darwinian selection should be the first line of enquiry for understanding
adaptation unless there are special reasons for not doing so (e.g., strong
group, kin, or reciprocity effects, which require expanded notions of fitness).
Dawkins (1976) stressed that the unit of selection is strictly the gene, rather
than the individual, an issue that has attracted considerable debate
(Segerstråle 2000). His "selfish gene" metaphor has nevertheless had much
force in promoting the philosophy of behavioural ecology, and the typical
assumption of the phenotypic gambit (Grafen 1984) has some equivalence to
Dawkins's premise.

Conflicts of Interest

The second step was the growing awareness of the underlying conflicts of
evolutionary interest between individuals. By now, this is seen more explicitly
as conflicts at the genetic level within and between genomes. For many adap-
tations, particularly those that involve conflicts of interest, the fitness "pay
off" to a given individual depends not only on its own strategy, but also on
the strategies played by individuals with which it interacts or competes. For
analysing such situations, Maynard Smith and Price (1973) borrowed ideas
from game theory in mathematics (von Neumann & Morgenstern 1944) to
produce the crucial concept of the evolutionarily stable strategy (ESS),
which, when played by most of the population, cannot be invaded by any rare
alternative strategy. In terms of game theory, an ESS is a "best reply" to itself.

Thus, ESS philosophy seeks to explain a current evolutionary state but not evolutionary dynamics that may lead to it. There are two formal stability conditions for a strategy to be an ESS, such that rare individuals deviating from the ESS population cannot invade (Maynard Smith & Price 1973; Maynard Smith 1982). Game theorists later identified the first ESS condition as a Nash equilibrium in game theory (Nash 1951).

ESS theory had several rather specific precursors. Examples are the sex ratio (Fisher 1930) and its distortion from unity (Hamilton 1967), animal distributions (Orians 1966; Fretwell & Lucas 1969; Parker 1970a), and contest behaviour (Maynard Smith & Price 1973; Maynard Smith 1974; Parker 1974). Trivers (1971) explicitly referred to the Prisoner's dilemma, a much-analysed scenario in game theory, while discussing reciprocal altruism, and his seminal papers on parental investment (1972) and parent–offspring conflict (1974) stressed that pay offs depended on the behaviour of other family members in a way that very few had previously envisaged.

Game theory has probably been more successful in its application to evolutionary biology than in its original contexts (economics and the social sciences). Evolutionary game theory has continued to develop since its inception. ESS is a stability concept. A strategy may satisfy Maynard Smith's conditions but may never converge to the ESS: one needs to ensure that a population deviating slightly from the ESS will actually converge back to it rather than spin away chaotically, cycle, or move towards a different equilibrium. One ideally now requires additional extra conditions for convergence, ensuring that an ESS is also *continuously stable* (Eshel 1983).

Associated with ESS is the concept of optimality. Optimality models make assumptions about selective forces and biological constraints (such as known trade-offs). The possible strategies (plausible possibilities that might be generated by mutation) and their "fitness pay offs" are defined. The optimal solution is that which maximises Darwinian (or inclusive) fitness. There may be more than one local optimum. ESS is simply competitive optimisation: one seeks a strategy that when played by most of the population is stable against invasion by rare mutant strategies (Maynard Smith 1982). Optimisation, without this frequency dependence, is used widely for some problems, such as life histories (Stearns 1976) and foraging behaviour (Stephens & Krebs 1986). David McFarland and his coworkers in Oxford pioneered the application of state-dependent optimisation to motivational decision making in the 1970s (e.g., Sibly & McFarland 1976; MacFarland & Houston 1981). This "state–space" approach was analytical, though explicit solutions were not always possible. It developed into the more accessible, computer-based, dynamic programming approach that has by now been applied to many problems in behavioural ecology (Houston & McNamara 1985; Mangel & Clark 1988). One major change was that numeric solution of dynamic programming equations allowed the incorporation of stochastic

effects. Dynamic programming techniques have more recently been developed to solve state-dependent ESS problems or "dynamic games" (Houston & McNamara 1999; Clark & Mangel 2000).

ESS–optimality models are best seen not as tests of whether animals behave optimally but as a means of testing our insight into the moulding of an adaptation (Parker & Maynard Smith 1990). A fit between model predictions and empirical observations indicates that we may have correctly identified the selective forces and the biological constraints against which they are operating. Models have typically two functions. General models make simple assumptions and generate wide-ranging conclusions (e.g., what forms of solution might be possible). Specific models make quantitative predictions for a given species, are usually more complex, and have parameters specifically relating to that species.

The value of formal modelling has been that assumptions about selection, constraints, and underlying conflicts could be used to make testable predictions. Behavioural ecology's triumph has been to allow much more rigorous evaluation of how behaviour is shaped by selection.

The Influences and the Influencers

In an attempt to get a balanced view of the major influences, I e-mailed 31 well-known behavioural ecologists, most (but not all) between 50 and 60 years of age. Each was asked to list: (1) the 12 papers (not books) that have had the biggest influence on behavioural ecology's development (series such as Hamilton's two 1964 papers counted as one paper), and (2) the 10 people who have most influenced behavioural ecology. I explained that although many of the authorities in the two lists would overlap, (2) gave an opportunity to include, say, the author of a highly influential book, or body of research papers, none of which individually may qualify for (1). Self-citations were not allowed in either list. Any part of evolutionary biology or ecology was eligible for inclusion if it had had an impact on behavioural ecology. I received 25 responses (5 U.S.A., 16 U.K., 4 elsewhere) for list (1) and 22 (3 U.S.A., 15 U.K., 4 elsewhere) for list (2).

Obviously, this could never be a rigorous exercise; it is flawed in several ways. Selections were made from my e-mail list, which imposed immediate bias, though I attempted a spread across gender, continents, and areas of interest. Both lists would probably have had more bias towards U.S. nominations if there had been more U.S. respondents. There was an understandable and expected tendency for respondents to nominate preferentially within their own areas. I did not define a time period (e.g., post-1950): several respondents mentioned that legendary names, such as Darwin, Fisher, Haldane, Lack, and Bateman, should be included but were omitted because

they were considered too early. Finally, my request inevitably put respondents in an embarrassing position: nominations to myself must be heavily discounted. What began as a simple, ingenuous attempt to strive for balance and fairness quickly became an absorbing exercise in data analysis, only a part of which is given here.

With these caveats in mind, there is nevertheless considerable uniformity in opinions about influencers and influential papers; 35 influencers and 70 influential papers were nominated. I took a vote score as the number of nominations for a person or paper divided by n (the number of respondents), or n-1 if the respondent was a candidate.

For influencers, 11 names had a vote score greater than 0.4 (9 or more votes): after this the score dropped below 0.2 (Fig. 3-1a). Table 3-1 shows the
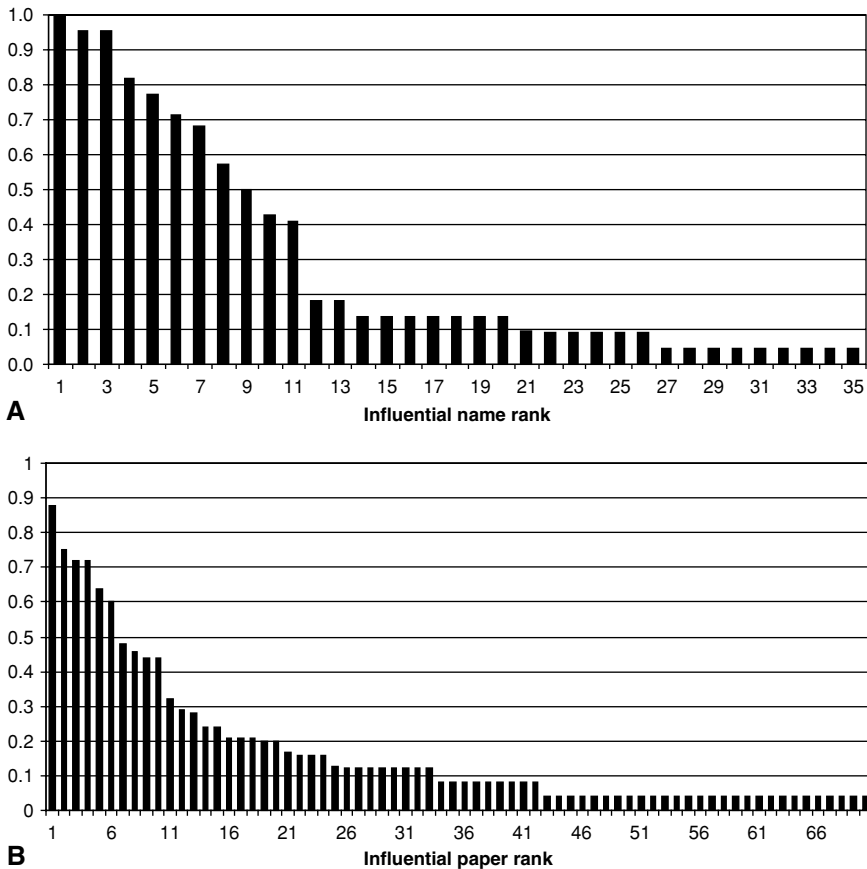

A **Influential name rank**

B **Influential paper rank**

Figure 3-1
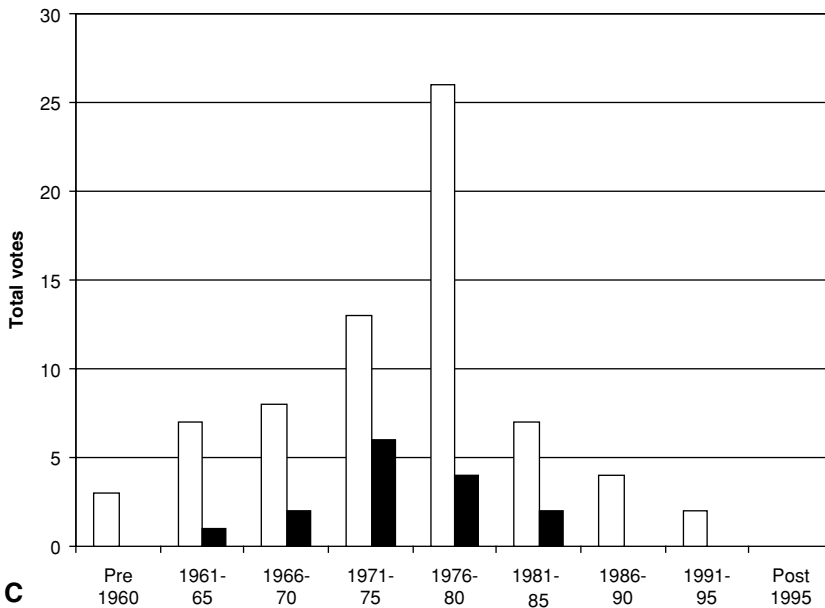
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Figure 3-1   *Continued*

top 10 influencers by vote score (relegating myself to an arbitrary 11th place), with three other measures for each influencer: (1) the number of their papers nominated, (2) the summed votes for their nominated papers, and (3) a "textbook score" (sum of total first-author references listed, or number of pages on which that author is listed in the index, for eight texts in the general areas of animal behaviour or behavioural ecology; see Table 3-1). Each influencer's rank (out of 35) is shown in brackets. It is notable that influencers are a mix of theorists and empiricists. Whereas theorists (e.g., Hamilton, Trivers, and Maynard Smith) were ranked higher in paper nominations, empiricists (e.g., Krebs, Davies, and Clutton-Brock) ranked higher in the textbook score (the top textbook scorer [83] was S. T. Emlen). Names in Table 3-1 account for 77% of total votes; the remaining 24 names each gained between 1 and 4 votes.

For influential papers, the distribution of scores (Fig. 3-1b) showed a typical decay curve with a maximum of 0.88 for Hamilton (1964), to 27 papers each with just one vote. Fifteen papers were nominated by about a quarter of the respondents or more (gaining a score of 0.24 or more), representing 62% of the total votes. The remaining 54 nominated papers gained between 1 (28 papers) and 5 (5 papers) votes each. In the spirit of the original request, Table 3-2 lists the top 12 papers (two had a score of 0.24, counting as tied at

Table 3-1 Nominations for top 10 influencers.

	Influential name	Vote score	Number of nominated papers	Summed votes for nominated papers	Text book score
1	J. R. Krebs	1.00	3 (6=)	6 (8)	81 (2)
2	J. Maynard Smith	0.96	6 (3)	34 (4)	71 (6)
3	W. D. Hamilton	0.82	7 (2)	60 (1)	61 (8)
4	R. L. Trivers	0.77	5 (4=)	59 (2)	45 (12)
5	N. B. Davies	0.71	2 (8=)	2 (19=)	79 (3)
6	E. O. Wilson	0.68	0	0	41 (14)
7	E. L. Charnov	0.57	5 (4=)	20 (5)	35 (15)
8	R. Dawkins	0.50	2 (8=)	4 (12)	58 (10)
9	T. H. Clutton-Brock	0.43	1 (11=)	1 (21=)	73 (5)
10	G. C. Williams	0.31	2 (8=)	4 (11)	23 (22)
	[G. A. Parker]	0.95	8 (1)	44 (3)	76 (4)

Rank (out of the 35 nominations) for measures other than vote score is given in parenthesis. Text book scores were derived from: counting indexed page citations—Dugatkin (2004), Krebs & Davies (1991); counting first author references—Alcock (2001b), Barnard (2004), Goodenough, McGuire & Wallace (2001), Krebs & Davies (1997), McFarland (1999), Manning & Dawkins (1998).

12th), after deleting two of my own (relegated arbitrarily to 14th and 15th places in Table 3-2). Table 3-2 also includes ISI cumulative citations for each paper.

The 70 nominated papers showed a marked peak in the second half of the 1970s: after this the fall-off is steep, and no nominations are later than 1992 (Fig. 3-1c). In contrast, the 12 most influential papers (see Table 3-2) peaked in the first half of the 1970s. The results may be sensitive to the respondents' age distribution, though there was no obvious tendency for younger respondents to nominate more recent papers. The distribution (see Fig. 3-1c) concurs with the genesis of behavioural ecology in the 1970s.

Papers nominated as most influential tend to be theoretical; no empirical works are included in Table 3-2. Reviews tended to be excluded, exceptions being Trivers (1971 *Q. Rev. Biol.*) and Parker (1970b *Biol. Rev.*); arguably these both proposed new ideas rather than just syntheses.

The survey generated a basis for the following brief outline of the areas that were most influential in the development of behavioural ecology. All nominated papers are mentioned. The superscripts before each citation give the number of votes for that paper (e.g., Hamilton ([22]1964) indicates that 22 out of 25 respondents included this in their list of the 12 most influential papers).

Table 3-2 Papers nominated most influential.

	Influential paper	Subject area	Vote score	ISI citations
1	Hamilton (1964) J. *Theor. Biol.*	Altruism—inclusive fitness	0.88	4451
2	Trivers (1971) *Q. Rev. Biol.*	Altruism—reciprocal	0.72	1594
3	Trivers (1972) chapter in *Sexual Selection and the Descent of Man*	Sexual selection— parental investment	0.72	4090
4	Maynard Smith and Price (1973) *Nature*	Fighting and ESS	0.64	1008
5	Trivers (1974) *Amer. Zool.*	Parent-offspring conflict	0.60	1135
6	Hamilton & Zuk (1982) *Science*	Sex and sexual selection—role of parasites	0.48	1210
7	Charnov (1976) *Theor. Pop. Biol.*	Optimal foraging— marginal value theorem	0.46	1267
8	Emlen & Oring (1977) *Science*	Sexual selection— mating systems	0.44	2078
9	Hamilton (1967) *Science*	Sex ratio	0.40	1272
10	Zahavi (1975) J. *Theor. Biol.*	Handicaps and signals	0.32	958
11	Axelrod & Hamilton (1981) *Science*	Altruism—reciprocal, cooperation	0.28	1082
12=	Hamilton (1971). *J. Theor. Biol.*	Grouping—selfish herd theory	0.24	1128
12=	Maynard Smith (1977) *Anim. Behav.*	Parental investment	0.24	448
	[Parker (1970) *Biol. Rev*.]	Sexual selection— sperm competition	0.75	1127
	[Parker (1974) *J.Ttheor. Biol*.]	Fighting and assessment	0.29	648

Cumulative ISI citations were counted at the end of January 2005.

The Areas

A few areas (e.g., kin recognition and fluctuating asymmetry) were not nominated by respondents. Surprisingly, mainstream life history theory (e.g., Stearns[1]1976) was not perceived as having had a major influence in behavioural ecology despite often being well cited), presumably being seen by respondents as evolutionary ecology.

Altruism, Sociality, and Cooperation

Hamilton's ([22]1964) remarkable insights into the evolution of altruism and sociality through relatedness have justifiably become legendary and are subject of interest outside the field of behavioural ecology. Hamilton's proposition to replace Darwinian (i.e., "self's") fitness with inclusive fitness is justifiably famous: his equation $rb > c$ (Hamilton's Rule) was to become the $E = mc^2$ of behavioural ecology. Grafen (2004) presents a sensitive and penetrating account of Hamilton's life and Segerstråle (2005), a comprehensive biography. A fascinating autobiographical account is found in *Narrow Roads of Gene Land* (Hamilton 1996, 2001, 2004).

In addition to being a top influencer (Table 3-1), Hamilton produced several seminal papers (Table 3-2). The [22]1964 papers in the *Journal of Theoretical Biology* (preceded by a note in *American Naturalist* in [1]1963) attracted the highest vote score and had the highest ISI citation of the entire survey (see Table 3-2). The idea for this work was stimulated by his contact with Fisher (and with Fisher's pioneering 1930 book) as a student at Cambridge and became (at his own proposal) the subject of his postgraduate research at the London School of Economics. Haldane was then at University College, London, and had earlier published verbal statements relating to kin selection (cited by Hamilton [1]1963). Maynard Smith (then also at University College) had similar interests: the now ubiquitous term "kin selection" derived from a paper by Maynard Smith ([3]1964). Hamilton ([22]1964 and elsewhere) used the term "inclusive fitness."

Hamilton's proposition that selection maximises an individual's inclusive fitness has been one of the most studied principles in behavioural ecology; kin-selected altruism enjoys a vast literature. It initially received only gradual attention, mainly in relation to the evolution of sociality in the Hymenoptera due to the high coefficient of relatedness between sisters under haplodiploidy. Later, and probably due to its attention from Wilson (1975), a torrent of research in social behaviour in diverse groups meant that it became hailed as a major triumph. Sherman's ([2]1977) important early study showed that individuals were more likely to perform alarm calls if close relatives were nearby. Hamiltonian principles are now routinely used in all analyses of behaviour involving kin.

Although kin selection was still gaining momentum, Robert Trivers (a top influencer, see Table 3-1; producer of several major papers, see Table 3-2) had begun work on reciprocal altruism, an alternative mechanism for the evolution of altruistic behaviour (Trivers [18]1971). His proposal that individuals that interact repeatedly can achieve an overall gain by cooperation was not opposed to kin selection but an alternative mechanism that may apply when beneficiary and donor are unrelated. This idea has also attracted much attention; most notably, Axelrod and Hamilton ([7]1981, see Table 3-2) proposed the

simple "tit-for-tat" rule of thumb for reciprocal interactions. One of the first claims for reciprocal altruism in nature concerned consortships of the same two males guarding receptive female olive baboons (Packer 1977): at a given consortship, one tended to guard against rivals while one mated; roles were reversed in other consortships. Reciprocal food sharing in vampire bats (Wilkinson 1984) remains a convincing example.

Optimal Foraging

The study of food foraging was one of the first topics to be developed. Prerevolution pioneers were MacArthur and Pianka ([3]1966), Emlen (1966), and Schoener (1969, [2]1971). Eric Charnov (a top influencer, see Table 3-1) quickly became the leading theorist of the early phase. He had worked on optimal foraging as his doctorate of philosophy topic under the supervision of Gordon Orians. Charnov has generated many original and fundamental insights, particularly in sex allocation (1982) and life history theory (1993), and most notably (for behavioural ecology), he was the originator of the Marginal Value Theorem, a citation classic (Charnov [11]1976a, see Table 3-2). Parker and Stuart ([1]1976) developed the same theorem independently, but Charnov's paper has received almost eight times the number of citations. Charnov gave the principle a name (from economics) and framed it in terms of food foraging, which was at that time one of the areas of greatest movement. Parker and Stuart's paper, though general, was set in terms of mate searching and was more diffuse, including a model of competitive foraging. Charnov ([5]1976b) also developed and tested optimal diet models and coauthored an early review of optimal foraging (Pyke *et al*. [1]1977). He had a major influence on John Krebs (also a top influencer, Table 3-1), with whom he collaborated at that time (Krebs *et al*. [2]1974).

Most early foraging models assumed gain rate maximisation. Only later did predation risk become seen as an important parameter: Milinski and Heller ([1]1978) were first to show that sticklebacks shift their foraging behaviour to balance feeding benefits against predation risk. "Risk-minimisation" models typically asked a different question: should foragers avoid variance in gains to reduce their risk of starvation? They are an alternative to gain maximisation (see Stephens & Krebs 1986).

A possible reason for the early boom in optimal foraging was that simple experiments (sometimes adapted from operant psychology) were easily set up (most animals eat more readily than they mate or give alarm calls), generating results that could be compared *quantitatively* with theoretical predictions. The psychology link may have been one impetus for the statistical sophistication in behavioural ecology. John Krebs did much to establish behavioural ecology as a rigorous discipline by pioneering the meticulous empirical testing

of models in optimal foraging. He achieved the highest of all scores as an influencer (nominated by all respondents): his name has become synonymous with behavioural ecology and his role as a top influencer relates both to his research and to the classic Krebs and Davies text and edited volumes.

An early hope of MacArthur and Schoener was that optimal foraging theory would help in the understanding of broader ecological questions about community structure. This remains unfulfilled. But there have been many triumphs (see Stephens & Krebs 1986): optimal diet models and Marginal Value Theorem have found hundreds of uses and continue to do so.

Animal Contests and Evolutionarily Stable Strategy

Darwin had seen the evolution of horns, antlers, and so on, in terms of male–male competition for females (intrasexual selection). Later, in the ethology era, implicit group selection arguments repeatedly proposed that contests should be settled without undue harm to contestants.

The beginnings of contest models and ESS theory were intimately entwined. John Maynard Smith and George Price realised that a logic for contest rules remained unformulated. Their paper (Maynard Smith & Price [16]1973) centred on "symmetric contests" (i.e., between identical opponents), and is usually cited as the origin of the ESS concept. My own interest in contests came from observing struggles between male dung flies for females but was stimulated by the same question: how should individual fitness be maximised in a contest? It centred on asymmetries between opponents: (1) in "resource holding potential" (RHP; roughly equivalent to fighting ability), and (2) in the value of the contested resource (Parker [7]1974). Although not deduced by ESS logic (the manuscript was completed before the Maynard Smith and Price paper), it proposed a rule for asymmetric contests that was later vindicated by ESS analysis (Hammerstein & Parker 1982). Simultaneously, Maynard Smith ([4]1974, [2]1976) showed that a purely arbitrary asymmetry (i.e., unrelated to RHP or to resource value) could be used to settle contests. I first met John Maynard Smith in 1974, and our subsequent collaboration (Maynard Smith & Parker [3]1976) concerned the role of pay off–related asymmetries and became an ISI citation classic. John was one of the most delightful of people, but I was so fearful of his intellectual abilities that I cannot claim to have contributed much directly to this paper. One credit I could perhaps take relates to proposing the "information acquired during a contest" model, which John (rarely for him) decided to approach by simulation rather than analysis. Later, Enquist and Leimar (1983) took this idea much further in their "sequential assessment game"; it has much greater biological reality than earlier models.

Animal fighting had long been the subject of empirical research, but the ESS models quickly spawned studies that were interpreted within the new framework. A notable early example was Nick Davies's ([1]1978) study of territoriality in speckled wood butterflies, where an arbitrary asymmetry (prior residence) appeared to be used to settle contests conventionally (i.e., without escalation or damage to either contestant). Though the arbitrary asymmetry rule may not explain why residents win in the butterflies (Stutt & Willmer 1998), Davies's study was nevertheless very influential in stimulating a combination of experiments and game theory in field studies of animal contests.

Though contest behaviour still attracts both theoretical and detailed empirical research (e.g., Elwood & Briffa 2001), it is now less popular. Its greatest contribution to behaviour ecology probably relates to its role in the development of ESS.

Sexual Selection

A third of all nominated papers related to sexual selection; the three decades of behavioural ecology have probably seen more research in this field than any other.

Darwin's first brief account of sexual selection is in *The Origin of Species* (1859); he formulated the principles extensively later in *The Descent of Man and Selection in Relation to Sex* (1871). Many earlier papers supported his ideas (e.g., Richards 1927). However, probably due to Huxley's (1938) influence, it lost ground to the ubiquitous impact of implicit group selectionism. To comply with "advantage to the species," male–male combat was seen as an adaptation to purge weakness from the population (stronger males fathered progeny that survived predation, thus "the species" benefited). Thus, Huxley, although accepting that males competed for females, denigrated intrasexual selection as an explanation and entirely dismissed Darwin's second mechanism, intersexual selection (female choice). From 1930 to 1970, sexual selection received little support. Notably, Bateman's ([3]1948) seminal paper stood against the tide: it was to become very influential later, but at the time was largely ignored, especially by ethologists and ecologists.

Against this background, the early 1970s saw dramatic changes that reasserted sexual selection as a powerful adaptive explanation. Bob Trivers's paper ([18]1972) had a huge influence: it has been cited almost as often as Hamilton's 1964 classic, see Table 3-2). My own field studies of dung flies began in 1965, supervised by the late Howard Hinton, a leading entomologist. Robin Baker (then a fellow postgraduate studying butterfly migration) and I had settled on what would later be termed individual selection as the logic for adaptive interpretation (I first encountered Williams's book in Liverpool around 1970). Perhaps fortunately, Hinton did not read my thesis.

Though liked and admired by his postgraduates, he supervised by example but did not delve deeply into what they actually did. I recall a conversation where he criticised my intrasexual selection interpretation of mate guarding by male dung flies, urging me to seek advantages to the female and the offspring. My Ph.D. thesis, completed in 1968 and published in 1970–1974, was an attempt to vindicate intrasexual selection (see Parker 2001). I calculated expected gain rates (fertilised eggs per minute) to males, adopting various strategies to predict the male's optimal: (1) copula duration, (2) locality to search for females, (3) locality for copulate (dung or surrounding grass), and (4) strategy for guarding or not guarding his female after copulation. Most calculations were early ESS analyses—they depended on the current strategy played in the population. The predictions matched the field observations and perhaps provided the first detailed quantitative evidence that intrasexual selection shapes adaptation (see Parker [5]1978 for a summary). They also generated my interests in sperm competition (Parker [18]1970b), animal fighting (Parker [7]1974), animal distributions (Parker [5]1978), and sexual conflict (Parker [4]1979).

AU: Ph.D. thesis OK?

Author: or "copulation"?

By the late 1970s, intrasexual selection had regained widespread acceptance as an explanation of much of male combat and competitive searching. The notion that it could also shape postcopulatory adaptations to reduce sperm (interejaculate) competition (Parker [18]1970b, see Table 3-2) took longer to attract interest. Bob Smith, a sperm competition pioneer (1979), organised a symposium at the 1980 Annual Meeting of American Society of Naturalists and the Society for Study of Evolution in Tucson, Arizona, which generated the first edited volume on sperm competition (Smith 1984). Interest subsequently soared; now there are six research books, a fascinating popular science book (Birkhead 2000), and a best-seller (Baker 1996).

It was quickly appreciated that female choice for direct benefits (Orians [5]1969; Verner & Willson 1966; Thornhill 1983) posed less difficulty than when benefits are purely genetic. For the latter, R. A. Fisher (1930) had formulated a theory, leading to his celebrated "runaway" process, and his last Ph.D. student, Peter O'Donald, had modelled the population genetics of female choice (see 1982 for summary). Zahavi ([8]1975) saw male ornaments as handicaps, arguing that females should choose handicapped males, because they must carry "good genes" for condition (having survived the costs). This notion attracted considerable controversy until Grafen ([3]1990) claimed it to be vindicated in his pioneering work on biological signalling. Lande ([2]1981) pointed out that Fisher's runaway depended on genetic covariance between the female preference and the preferred character and discovered his famous line of equilibrium between the magnitude of the male ornament and that of the female preference. His work catalysed a wave of interest, and new theoretical developments followed swiftly (e.g., Kirkpatrick 1982, Pomiankowski

et al. [1]1991, Iwasa and Pomiankowski [1]1991). The renewed interest in intersexual selection stimulated an important conference (the "porno-Dahlem"; Bradbury & Andersson 1987).

A problem is that additive genetic variance associated with the male trait should diminish through selection by female choice, unless recurrent mutation is very high. Hamilton and Zuk ([12]1982, see Table 3-2) suggested that genetic cycles in host resistance and parasite virulence could sustain heritable variation in fitness, allowing continued selection for female choice if male ornaments reflect male condition (and hence true fitness). They found a correlation between brightness of ornaments and reduced parasite burdens (Hamilton & Zuk [12]1982). Some tests (e.g., Møller [1]1990) and proposed mechanisms (e.g., Folstad & Karter [1]1992) for the Hamilton and Zuk theory are persuasive. Additional ways to avoid the problem of diminishing genetic variance have been proposed more recently (Pomiankowski & Møller 1995; Rowe and Houle 1996).

The 1980s developments in female choice were not purely theoretical. Partridge ([1]1980) showed that *Drosophila* females allowed to choose their mate produced larvae with higher competitive ability than females randomly allocated a mate, suggesting female choice of "good genes" (though male–male competition could not be ruled out). Andersson's ([3]1982) beautiful field experiment showed that female widow birds prefer males with long tails, suggesting that the tail had evolved through female choice. Bateson ([1]1982) found that both sexes of Japanese quail preferred cousins when offered siblings, cousins, or unrelated individuals as potential mates and proposed that mate choice had evolved to generate "optimal outbreeding."

Interest in the cause of sexual selection began with Darwin (1871), who argued that it arose from the gamete size difference between males and females (anisogamy). Parker and colleagues ([5]1972) showed how anisogamy could arise by disruptive selection on an isogamous, externally fertilising, marine ancestor. Trivers ([18]1972) proposed that sexual selection was fuelled by sex differences in parental investment (PI = the cost of an offspring to the parent measured in terms of lost future offspring), allowing role reversal if male care sufficiently exceeds female care. Gwynne and Simmons (1990) induced role reversals experimentally in a bush cricket, and Simmons (1992) confirmed that these followed reversals in relative PI. Clutton-Brock and Vincent (1991) proposed that the intensity and direction of sexual selection related to potential rates of reproduction of the two sexes. In a classic, highly cited paper, Emlen and Oring ([11]1977, see Table 3-2) outlined how ecology and mating systems shape the "operational sex ratio" (OSR) and proposed that OSR determined the intensity of sexual selection. Bateman ([3]1948) had argued that sexual selection arises out of a higher variance in

male than female fitness, using *Drosophila* as a demonstration. Sutherland (1985) pointed out that although variance in reproductive success indicates a potential for sexual selection, it does not actually demonstrate it: Bateman's result could be explained by chance due to sex differences arising from the OSR.

The definitive synthesis of sexual selection by Malte Anderson (1994) relates mainly to precopulatory adaptations; any deficit in terms of postcopulatory adaptations is redressed by the several books on sperm competition and the two books by Eberhard (1985, 1996), developing the idea that females may operate various forms of sperm selection ("cryptic female choice") over acceptance or use of given ejaculates, generating a suite of postcopulatory adaptations arising through intersexual selection.

Sexual Conflict

The "battle of the sexes"—long a concept of human life—was nevertheless slow to invade evolutionary biology. Trivers ([18]1972) described conflict between the sexes over parental investment in his classic model of mate desertion. My dung fly work (Parker 1970a, [51]1978), examined the different fitness interests of male and female, and stimulated a series of general sexual conflict models (Parker [4]1979) in work completed in 1976 but that languished long in press. I stressed that male behaviour may often serve male interests but be deleterious to females. One model analysed when it is favourable or unfavourable for a female to mate with a male with a mating advantage trait that reduces her own immediate reproductive success (see also Andrés & Morrow 2003). Another, a male–female arms race game, generated "unresolvable evolutionary chases" between the sexes. Something rather similar has recently been proposed as "chase away" by Holland and Rice (1998). Charnov (1979) developed ideas of sexual conflict for hermaphrodites and applied it to some features of plant reproduction (e.g., double fertilisation in angiosperms).

Sexual conflict has been studied empirically in many species. One of the earliest studies was that of Downhower and Armitage (1971) on conflict over the mating system in yellow-bellied marmots. A powerful example occurs in *Drosophila*, where males ejaculate an agent in the seminal fluid that increases male success in sperm competition but reduces the female's longevity (Chapman *et al.* 1995). Other notable studies concern infanticide and rape in langurs (Hrdy 1977), mate guarding in water striders (Arnqvist 1989), and dunnock mating systems (Davies 1992). Sexual conflict is currently one of the fastest moving areas in behavioural ecology, and remains controversial (e.g., Eberhard 2004).

Sex Ratio and Sex Allocation

Many great triumphs in understanding adaptation have occurred in the area of sex ratio and sex allocation (Charnov 1982). The relatively low number of nominations in this area by respondents probably relates to its perception as evolutionary ecology. Fisher solved the unity sex ratio problem in a cryptic verbal account in his famous 1930 monograph. In a paper far ahead of its time, Shaw and Mohler (1953) formulated Fisher's argument game theoretically and showed that the ESS (as it would later become called) was the unity ratio (see also Shaw 1958). Similarly, Hamilton's classic paper ([11]1967, see Table 3-2) used game theory to find "unbeatable strategies" (a precursor of ESS) that deviated from unity. He examined intragenomic conflict (the ESS ratio depended on whether sex-determining genes were on sex chromosomes or autosomes) and population-biased sex ratios. For example, if matings are between progeny of N females (local mate competition), then under autosomal sex determination at low N the sex ratio will be female-biased. Such skews occur in parasitoid wasps. Trivers and Willard ([3]1973) first proposed the notion of individual-based sex ratio "decisions," arguing that if offspring size or condition, or both, is more important to one sex than the other, the offspring's sex should depend on the mother's condition. There have been many investigations of this idea, some giving remarkable support (e.g., Burley [1]1986; Clutton-Brock *et al.* 1986).

Eric Charnov (see Table 3-1) has been highly influential in sex allocation theory, especially in showing how sex ratio decisions should be tuned to the local environment (e.g., Charnov & Bull 1977). Decisions in specific conditions should relate to the distribution of conditions across the breeding population, an idea supported by data on parasitoid wasps (Charnov *et al.* 1981). He also made seminal advances in modelling hermaphroditic systems (e.g., Charnov 1979a). His highly cited monograph (Charnov 1982) reviewing the evidence for prediction–observation concurrence in sex allocation studies by the early 1980s is a remarkable testament to the force of Darwinian selection.

Life-History Switches and Alternative Strategies

Life history strategy also received relatively few nominations: the most attractive areas related to reproduction and sexual selection (Hamilton [11]1967; Trivers & Hare [5]1976; Trivers & Willard [3]1973; Williams [2]1966b; Burley [1]1986; Charnov [1]1979b), though two concerned senescence (Williams [2]1957; Hamilton [1]1966).

<AU: Prevalently cited Ok?> The most prevalently cited area has been alternative mating strategies (or tactics), where males show more than one mating pattern, often associated with their phenotype. Typically, males play opportunistic "sneak" strategies

Parker   43

when smaller, switching to "guarder" when larger and able to defend females
or territories. The pioneering study was that of Alcock and colleagues ([1]1977)
in the bee *Centris pallida*, where adult male size varies greatly due to larval
nutrition.

Environmentally determined alternative strategies whose frequencies are
not moderated by selection, and hence may differ in fitness, were termed
"best of a bad job" strategies (Maynard Smith 1982). Commonly, fitness of
alternative strategies is frequency-dependent. Gadgil (1972) proposed that
sexual selection might generate polymorphism with fitness of two male
morphs equalised at their ESS frequencies. Evidence soon followed for equal
fitness of the two male morphs (fighting, winged) in fig wasps (Hamilton
1979) and for the two alternative male life histories in bluegill sunfish (Gross
and Charnov 1980).

Alternative strategies need not be restricted to male mating behaviour.
Brockmann and colleagues (1979) showed the two strategies for gaining a
burrow (digging and entering) shown by female digger wasps were frequency-
dependent and had similar fitnesses. Barnard and Sibly's (1981) "producer–
scrounger" concept was an early general formulation of alternative strategies
maintained by frequency-dependence.

If pay offs are frequency-dependent, and phenotypes show continuous
variation (e.g., size), selection should generate an ESS switch point (e.g.,
switch size) at which it pays to change from one strategy to another. This idea
had its origin in Ghiselin's (1969) "size advantage" hypothesis for sequential
hermaphroditism—individuals should first occupy the sex where size
increases fitness less, so that size benefits occur where it counts most (see
Warner *et al*. 1975). The ESS rules (West-Eberhard 1979; Charnov *et al*.
1978; Parker 1982, 1984; Repka & Gross 1995) are that: (1) the switch point
phenotype must have equal fitness in the two strategies that it separates, and
(2) no phenotype must be able to profit by switching to any alternative strat-
egy. These rules apply generally to continuous phenotypes, (e.g., strategies
may be alternative patches in a habitat) (Parker & Sutherland 1985). Charnov
and colleagues (1978) first provided evidence that age of sex change in a pan-
dalid shrimp fits this "equal fitness at the switch point" principle.

It was quickly realised that alternative male mating strategies were ubiqui-
tous and diverse (Dunbar 1983); several such strategies may occur in just one
species (Taborsky 1994). By now a large literature exists.

Biological Signals

Zahavi's ([8]1975) handicap idea (see the section Sexual Selection) was highly
controversial until supported theoretically (Pomiankowski 1987; Grafen
[3]1990). The papers by Dawkins and Krebs ([3]1978) and Krebs and Dawkins

([3]1984) were probably more attractive to behavioural ecologists at the time. Nevertheless, the Zahavi controversy stimulated interest in the evolution of biological signals. Enquist (1985) first brought game theory and signalling together, but it was Grafen ([3]1990a, b) who incisively defined biological sig-nalling as an area. Grafen's model requires that signals are costly, which is why it appears to vindicate Zahavi. One respondent wrote, "This paper not only reinstated Zahavi's idea, it finally brought animal communication, game theory, and sexual selection together."

<AU: "are" or "be"?>

So much depends on the interpretation of Zahavi's ([8]1975) writing that Grafen could possibly (in my view) have avoided stressing Zahavi's paper; Grafen's model is a continuous strategy game involving female preference and costly male advertisement, where increasing advertisement yields increas-ing benefits. Godfray (1991) applied Grafen's model to interpret offspring begging as an honest signal of need; an alternative is that begging represents scramble competition among offspring (Macnair & Parker [1]1979).

Recent discussion has centred on whether signals must always be costly. Maynard Smith's (1991) discrete strategy "Sir Philip Sidney game" shows that for a cost-free signal to be reliable, signaller and receiver must place the possible outcomes of the interaction in the same rank order of preference. Animal signals and communication are the subjects of several books and reviews, the most recent being that of Maynard Smith and Harper (2003) stressing the diversity of ways signal reliability might be maintained, depend-ing on the system.

Animal Distributions

Habitat choice and spatial distribution have arguably been the developments of greatest importance to mainstream ecologists. Fretwell and Lucas ([4]1969; Fretwell 1972) deduced the evolution of distributions in patchy habitats, under various assumptions about territoriality or its absence. The "ideal free" distribution (unconstrained animals distribute such that no individual can profit by moving elsewhere) later became a much-studied concept (Milinski 1979 was the first direct test).

Others had foreshadowed Fretwell's visionary insights, but less generally. I developed my own version (the "equilibrium position") of "ideal free" in my Ph.D. thesis (1968) to explain the distribution of male dung flies (Parker 1970a, [5]1978). Orians's ([5]1969) "polygyny threshold" model (see also Verner & Willson 1966) predicted how successive females should settle when faced with a choice of male territories. One respondent wrote:

> *[Orians's model] was for me the first clear example of how good theoretical models were useful in our field. . . . [Fretwell's] notion of ideal free settlement was critical at the time it came out by providing some feasible mechanisms for how Crook-type processes might arise*

by simply mapping animals down on heterogeneous landscapes. It built on Orians's [model], but also generalized it.

The concept developed in many ways (see Tregenza 1995). Sutherland (1983) showed how "ideal free" applies under interference competition, and Sutherland and Parker (1985; Parker & Sutherland 1986) investigated effects of competitive asymmetries between individuals.

Comparative Approach

Major advances in comparative analysis techniques accompanied the behavioural ecology revolution. Traditional ethology had tended to focus on phylogenetic constraints on behaviour. John Crook pioneered a comparative approach that stressed ecological influences. He sought correlations across species and between types of social behaviour and ecological variables, first in his weaver bird monograph ([1]1964) and later in overviews of avian ([1]1965) and primate (Crook & Gartlan [2]1966) social organisation. Crook's approach was soon extended to avian breeding biology (Lack 1968) and antelope social organisation (Jarman [1]1974).

A seminal development came when Clutton-Brock and Harvey ([1]1977) measured adaptations and ecological variables on a continuous scale and applied multivariate statistics to seek correlations. Initially, each species was used as a data point, which posed problems: methods quickly developed using contrasts between independent evolutionary events as data (pioneers were Ridley 1983, for discrete comparisons; Felsenstein 1985, for continuous characters). By 1990, comparative methods had become powerful tools for studying biological adaptations (Harvey & Pagel 1991; Harvey & Purvis 1991) and are now used extensively.

Predation, Flocking, and Vigilance

With typical originality, Hamilton ([6]1971) proposed flocking to be the result of each individual's reducing its "domain of danger" to predators by moving closer to others ("selfish herd" theory). For a flock of size N, individual risk dilutes to $1/N$.

Lazarus (1978) argued that an individual's domain of danger is reflected by its vigilance against predators. Competition may reduce food intake: flocking and vigilance soon became seen as resulting from trade-offs between feeding and predation. Caraco and colleagues ([1]1980) demonstrated that both flock size and vigilance increase in the presence of a predator. Vigilance was seen as a second advantage in flocking—in addition to Hamilton's dilution effect,

"many eyes" reduced the predator's chance of success. Bertram (1980) showed that although individual vigilance levels decreased with flock size, the summed vigilance does increase, supporting "many eyes" predictions, and numerous subsequent studies have shown similar trends. But theoretically, the ESS vigilance per individual declines so steeply with flock size that the summed vigilance generally also declines (Parker & Hammerstein 1985). Counter to "many eyes" predictions, predators should be more successful with bigger flocks, leaving Hamilton's dilution effect the main reason for aggregation. This theoretical prediction is counter to observations and remains something of a mystery, unless the effective flock is smaller than the total flock.

Alexander's seminal paper ([4]1974) built on Hamilton ([6]1971) by stimulating a more general approach to the advantages and disadvantages of group living and reinforcing the interpretation that sociality requires a net benefit to the individual rather than to the group.

Mating Systems, Reproductive Skew, and Social Groups

Sexual selection, ecological constraints, and patterns of dispersion of the sexes all interact and thus influence the structure of the mating system (Emlen & Oring [11]1977; Clutton-Brock 1989; Davies 1992). Given that males and females will be under selection to maximise their own interests, there can be considerable sexual conflict over the mating system (Davies 1992). Early landmarks were Orians's [5](1969) study of New World blackbirds and Bradbury and Vehrencamp's ([1]1977) study of bats.

Alexander's ([4]1974) analysis of individual costs–benefits of social grouping acted as a catalyst for many new developments. In social breeders, dominance and priority over access to resources leads to reproductive skew: the reproductive success differential between dominants and subordinates. The first skew model was developed by Sandy Vehrencamp ([1]1983) to analyse, in relation to group size, how much bias a dominant can enforce before it benefits a subordinate to leave to breed independently. Her model spawned a series of skew models, and its basic approach is still applied for understanding dynamics within groups. Social breeding now represents a huge area in behavioural ecology.

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Intrafamilial Conflict

Lack ([1]1947) applied a pioneering optimality approach to the problem of clutch size: the optimal clutch size maximised the product of offspring number and fitness, implicitly assuming that selection maximises the caring

parent's fitness. Hamilton's inclusive fitness classic ([22]1964) had hinted that parent and offspring interests were not identical. But it was Trivers's revolutionary paper on parent–offspring conflict ([15]1974, see Table 3-2) that laid bare the notion of the family as a harmonious unit. Trivers predicted that in sexually reproducing species, a current offspring gains by receiving more PI than is optimal for the parent to give. He later (Trivers & Hare [5]1976) showed that investment in progeny in social insects matched offspring interests, rather than those of queens. In contrast, Alexander's widely cited paper on evolution of social behaviour ([4]1974) developed the idea of "parental manipulation," (i.e., that parents can manipulate offspring into the outcome best for the parent), supporting Lack's ([1]1947) original emphasis. Such an outcome is likely in some instances; for example, hatching asynchrony in birds is something that parents determine long before offspring can exert any influence. (It is set by the start of incubation.)

Alexander's (1974) paper also disputed the theoretical basis of parent–offspring conflict, something he later retracted (Alexander 1979) after an analysis by Blick (1977). Mark Macnair and I (Parker & Macnair [1]1978; Macnair & Parker [1]1978) applied a combination of population genetics and ESS approaches, confirming that Trivers was correct and examining the effect of different mating systems and types of conflict. Haig (1992) extended our approach to allow for genomic imprinting, suggesting that the conflict was not only between mother and offspring, but between the genes (determining how much PI the offspring takes) inherited from the male and female parents. O'Connor ([1]1978) showed that in birds, where death of offspring is common if food is scarce, there are three different thresholds (reflecting the different interests of the players) as food supply diminishes: (1) one for fratricide (now generally called siblicide), (2) one for infanticide, (3) and one for suicide.

Since 1980, much empirical and theoretical work has been directed towards intrafamilial conflict. The family is now perceived as a cauldron of conflict, with each of the players having different interests: resolution must satisfy sexual conflict, parent–offspring conflict, and sib-competition simultaneously (see Mock & Parker 1997 for review).

The Future

Mercifully, the political feuds about human nature and criticisms that the adaptationist approach was "Panglossian" (Gould & Lewontin [1]1979) proved to be only diversions that obscured what was happening: the explosion of one of Tinbergen's ([3]1963) celebrated "four questions" (see Alcock 2001a).

I write this essay exactly 40 years after starting work in behavioural ecology. My travel with this obsession has been immense fun: my only sadness is that I shall not see how our understanding will have developed after the next

40 years. I might like to conclude that behavioural ecology has now matured, is now safe, secure, and forever will be so. I would probably be wrong. The generation of ethologists working before the behavioural ecology revolution probably felt secure about ethology. Perhaps ethology did not actually die, but rather was revolutionised by concepts from population biology and economics. If the ethologists could be criticised, it is only for taking their eyes off the Darwinian ball—and if this was refocused by Williams, Maynard Smith, Hamilton, Trivers, and others, they may have argued that it was difficult to be an expert in behaviour and evolutionary biology at the same time. But it all felt more like a revolution than a gentle, gradual metamorphosis. Sooner or later, behavioural ecology may be similarly assaulted, as the future in science is about as predictable as the stock markets.

At the moment, I see the main changes as involving technology. Advances in molecular biology such as fingerprinting (Jeffries *et al.* [1]1985) have revolutionised how we can study paternity (the first application being that of Burke *et al.* [2]1989), sperm competition, kinship, and so on. Modern comparative methods and computer technology have revolutionised how we can analyse comparative or other data. These advances have extended existing insights rather than changed the philosophy: we are still integrating the conceptual advances from the revolution. Deeper understanding of mechanisms is eroding the view of the animal as a "black box," a necessary approach of the 1970s. By this more broadly zoological approach (genes to physiology to behaviour), the constraints underlying each suite of adaptations are gradually becoming better understood. With deeper understanding of constraints, we can develop more realistic evolutionary models and predictions for the adaptations.

Revolution or gradual changes are not the only possibilities. My bet is that each area of behavioural ecology will each become a discipline in its own right, with coverage spanning the molecular to the evolutionary. That is the current trend: natural historians are simply becoming much more enlightened.

Finally, to the new colleagues for whom this essay might serve a purpose, I sincerely wish you as much joy from behavioural ecology as it has given me. Science is about seeing questions and discovering how to answer them. Hopefully, your generation will not only be able to answer some of the questions we failed to answer but will also see some of the questions we failed to see.

Acknowledgments

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