

HISTORICAL PERSPECTIVES

HISTORICAL PATTERNS IN THE STUDY OF AVIAN SOCIAL BEHAVIOR¹

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The songs, calls, plumages and other behaviors of birds typically reflect their social relations. The study of social behavior, therefore, is basic to our understanding of the most conspicuous and endearing features of birds. Our knowledge of these behaviors has expanded considerably in the hundred-plus years since Darwin, but his books on the origin of species, sexual selection, and the expression of emotions still provide the base to which most modern studies can be traced (Darwin 1859, 1871, 1872). This review provides a historical perspective on some of the ways by which natural selection in the broadest sense has been thought to influence social behavior in birds. The first section of this paper reviews the major trends and events from 1859 to 1992. In the second section I look more closely at one aspect of social behavior and analyze the logical processes that led to scientific progress in a period that is familiar to me as a participant, namely from 1952-1992. I then contrast the two perspectives.

I have tried to be neutral and objective, but because I have been involved in some of the issues and controversies during the period I make no claim to have been completely successful. I draw heavily on my own experiences because I know them best; it could hardly be otherwise. The completely neutral participant in this field, in my opinion, does not exist.

THE FISSION-FUSION PATTERN

In Darwin's era disciplines that we now recognize as distinctly different from each other, such as ethology and ecology, had not split off from the vaguely defined area of natural history, and other disciplines were much less specialized (Benson 1988). The recognition of ecology and ethology in the 1950s, neuro-ethology in the 1960s, behavioral ecology in the 1970s and molecular ecology in the 1990s illustrates the continuing fissioning process. At the same time that fission by specialization was progressing, isolation among the fissioning fields increased and bridges between the emerging specialties became rarer. When bridges did occur, however, they were likely to be important and influential. The overall pattern is one of fission by specialization followed by selective fusion and cross-fertilization. Similar conclusions have been reached for ecology (Moore 1920, Brooks and McLennan 1991) and prob-

ably for many disciplines. I call this the fission-fusion pattern of history.

THE "MODERN SYNTHESIS"

A well-known example of the fission-fusion pattern is the fission of evolutionary biology in the early part of this century into the specialties of population genetics, systematics, and paleontology, followed by their fusion as the "modern synthesis," as it was termed by Huxley (1942). This interpretation of evolution reaffirmed the Darwinian view of evolution by selection of small variations among individuals, and it strongly influenced virtually all of the senior evolutionary biologists (including bird behaviorists) of today. Its major agents of influence were synthetic books in genetics (Dobzhansky 1937), systematics (Mayr 1942), and paleontology (Simpson 1944). This period of taking stock, mainly in the 1940s, has been acclaimed as a major epoch in evolutionary biology (Mayr and Provine 1980, Mayr 1993); but no synthesis or consensus lasts forever, and many changes have taken place that result in a different and more controversial evolutionary biology today (Antonovics 1987).

Perhaps the most important legacy of this period for social behavior was the consensus that was reached on the subject of speciation and the origin of behavioral isolating mechanisms. This view was fully described by Mayr (1963) for evolutionists generally. Its last appearance as a major part of a behavior text may have been as a chapter in Brown (1975). Closely related to the study of speciation is the study of geographical variation in behavior, with avian vocal dialects being a good example. Sociobiologists and behavioral ecologists in the 1980s largely ignored the relationship between behavior and speciation, but the modern focus on sexual selection has revived some interest in the subject (West-Eberhard 1983).

THE MACRO-EVOLUTIONARY PERSPECTIVE OF CLASSICAL ETHOLOGY

Beginning with Whitman's (1899, 1919) comparative studies of species of Columbidae and Heinroth's (1911) studies of various birds in zoos, ornithologists were impressed by behaviors that lacked conspicuous susceptibility to environmental influence during development ("innate"). In the same period, ornithologists began experiments that would elucidate the learning of behaviors such as vocalizations and social preferences (e.g., imprinting) in some species. These studies confirmed the early impressions that some behavior patterns were useful in classification because they re-

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vealed phylogenetic relationships. Thus behavior became an aid to systematics and the construction of phylogenies (Brooks and McLennan 1991), Lorenz's (1941) study of the Anatidae being a classic example. Although popular in the immediate post-Lorenzian era (Mayr 1958), when as a graduate student I indulged in it myself in a trivial way (Brown 1959), this application of social behavior to taxonomy gradually declined in the 1960s and 1970s to near extinction. Systematics looked elsewhere for inspiration and controversy, namely to molecular biology.

We have now reversed this relationship. Molecular systematics has become an exciting new tool to study the evolution of behavior, instead of behavior being used to study systematics. This is an example of fusion across a bridge between two separate specializations. The construction of a phylogeny based on presumably neutral genetic variation is now used to study the age and branching patterns of avian behaviors, such as brood parasitism (Lanyon 1992), helping (Edwards and Naem 1993), and foraging specializations (Richman and Price 1992).

Ethology in its early days guided by Lorenz was a Germanic discipline. One had to learn German to read the famous Kumpan paper (Lorenz 1937, 1970), and most of the important literature was in the German language. To become an ethologist one had to visit Germany, as did Margaret Morse Nice, author of a landmark behavioral study of the Song Sparrow (*Melospiza melodia*; Nice 1943), in 1938. All this changed when Tinbergen, a multilingual Dutch ethologist, accepted a chair at Oxford, England and began an important series of publications in English. For Americans, it happened just in time; for his subsequent books, "The Study of Instinct" and "The Social Life of Animals," were extremely influential for ornithologists in the 1950s, leading to establishment of animal behavior with an avian emphasis in the curriculum of many American universities. (It was not taught at Cornell University, where I was a student, until about 1955 or at Berkeley until 1957.) A history of the study of animal behavior in North America has been written by Dewsbury (1989). Tinbergen, besides being one of the kindest and most likable persons I have ever met, was an expert field naturalist and loved to work on the social behavior of gulls (Tinbergen 1953a, 1959). Tinbergen, Lorenz, and von Frisch were honored by a Nobel Prize in 1973 (Marler and Griffin 1973). Festschriften for Lorenz (Schleidt 1988) and Tinbergen (Baerends et al. 1976; Dawkins, M. S. et al. 1990) and brief autobiographies (Dewsbury 1985) provide further details on their lives and scientific contributions. The history of ethology has been described by Klopfer and Hailman (1967), Thorpe (1979), Beer (1963) and Barlow (1989, 1991). Some early papers in ethology are reprinted in the collection of Burghardt (1985).

While ethologists deserved their honors, I was personally disappointed at the time by two great gaps in the ethology of those years. As a naive graduate student I chose as a subject for my Ph.D. research a topic along the lines of students of Tinbergen, namely the analysis of the "motivation" of the displays and vocalizations of an avian species (Brown 1964b). This allowed me to realize that the analysis according to conflict of drives

that characterized ethology then ignored the brain, which was the source of the behavioral phenomena the ethologists were trying to study. To begin to fill this gap I attempted to bring together what was then known about "motivation" of displays with what was known about their neural basis, in the process introducing the term neuro-ethology (Brown and Hunsperger 1963). In the next decade I tried to develop this new field using birds (Brown 1969b, 1969c; Ingle and Crews 1985). My own efforts were not influential (Brown 1971, 1973), but exciting papers would later emerge by Nottebohm and colleagues (reviewed in Konishi 1985) and by others on invertebrate nervous systems. The study of "instinct" and social behavior in birds and other animals became neuro-ethological, illustrating again the pattern of fission followed by fusion.

THE POPULATION BIOLOGY OF BEHAVIOR

The second major gap in ethology at the time, as reflected in Tinbergen's books (1951, 1953b), was the lack of a population biology of behavior, which developed rapidly later in the 1960s (see below). No doubt Tinbergen and his students were early contributors in this area (Dawkins, M. S. et al. 1990), but in my opinion the principal impetus in this area among American students, such as Orians, Fretwell and myself, came from population biology, not from ethology.

In 1975, three books appeared that emphasized a new perspective among textbooks on behavior, that of natural selection. Previous texts had emphasized the developmental and physiological "Mechanisms of Animal Behavior" (Marler and Hamilton 1966) or had attempted a "synthesis of ethology and comparative psychology" (Hinde 1966, 1970). In contrast, the "central unifying theme of *biological evolution*" characterizes Brown (1975:xv), who wrote that "the central concepts in this book are concerned with populations." Similarly, although the primary message of "Sociobiology" (Wilson 1975) was interpreted by social scientists to mean an emphasis on nature rather than nurture (Barlow 1989, 1991), for behaviorists it was a heavy dose of population biology. Alcock (1975 and later editions) has also emphasized natural selection rather than physiological or developmental mechanisms. The 1970s were a period of major synthesis in which bridges between behavior study and population biology were built, at some cost to the study of mechanisms and development.

Although these three books had some influence of their own, they clearly reflected a trend that was already substantial. Even without these textbooks the trend toward fusion of population ecology, genetics, and behavior was booming and would have continued. The unprecedented front-page promotion of "Sociobiology" in the *New York Times* (May 28, 1975) before the book had even been seen by most "sociobiologists" and the Sunday-supplement treatment by the *Times* (Oct. 12, 1975) made this scholarly book a media event and consequently a political issue (see Barlow 1991). Nevertheless, anthropology had already absorbed lessons from the fusion of ethology and ecology (Tiger 1969, Tiger and Fox 1971). The animal nature of "the naked ape" had intrigued the common man (Lorenz 1963, Morris 1967) well before Wilson's tome.

What then were the origins of these trends, if we cannot attribute them to textbook writers? I would nominate two sources, the population ecology of David Lack and the population genetics of W. D. Hamilton. Certainly these writers influenced many ornithologists for decades. Two continuing themes in Lack's writings were the ecology of populations of birds (Lack 1954b, 1966) and the evolution of clutch size (Lack 1947, 1948a, 1948b, 1954a, 1968) by individual rather than "group" selection (an idea with a long history before Lack—see Burbridge 1992). Although Lack had already convinced most ornithological readers of the supremacy of individual selection, the opposing view favoring population- or deme-level selection was presented conspicuously by Wynne-Edwards (1962). The theme was not original with Wynne-Edwards (see Kalela 1954), but he published a lavish and ponderous elaboration of it. Squid-like this book propelled the population biology of social behavior backward in a cloud of black ink.

Reaction was strong and immediate. Although some sophisticates chose to ignore the crude reasoning of Wynne-Edwards because it was so obviously wrong as a general explanation, others attempted to refute his arguments (Wiens 1966). Still others felt that this was the time to elaborate the ways by which social behavior could be influenced by individual selection. For example, territoriality was Wynne-Edwards' prime example of a population-limiting behavior, but Brown (1964a) presented a general model that showed how various kinds of territorial behavior could evolve by individual selection, without the need for population-level selection. Similarly, Orians (1969) advanced a graphical model to explain the evolution of mating systems based on individual selection. Similar arguments on behalf of individual selection were made by Crook (1965) for a variety of avian social systems. Many of the papers of this era were concerned with spacing behavior and its effects on populations (Brown and Orians 1970). Together these led to a comparative ecology of social systems, still a popular field today (Lott 1991). An even more global approach was taken by Williams (1966), who attempted to outline how adaptations in general could evolve by individual selection. These works and many others established a consensus position on the side of individual selection. They created an atmosphere that was hostile to any mechanism that seemed to differ from old-fashioned individual selection. This conservative view proved to be an impediment to the acceptance of some exciting new ideas.

The most influential new idea in the realm of selection thinking was the theory of inclusive fitness launched by Hamilton (1963, 1964). To prevent this kind of selection from being confused with "group selection," Maynard Smith (1964) coined the term "kin selection," including both direct and indirect components of inclusive fitness (as they were later recognized by Brown 1980). While it was not spelled out explicitly, confusion of group and kin selection was implicit in some of the early literature attacking the use of inclusive fitness theory as part of an explanation of helping behavior in birds. Whether for this reason or for others, such as recoiling from the term altruism, inclusive-fitness thinking met a hostile reception among ornithologists that was based partly on misunderstanding of the concept, as shown by Dawkins (1979), and partly on old-fashioned conservatism. It would take three decades for facts and reason to overcome this resistance.

Returning to the theme of fission and fusion, I suggest that the principal origins of what we now know as sociobiology were on the one hand from the tremendous impetus that Hamilton's theory gave to the study of social insects and sociality in general and, on the other hand, from what I have termed the *comparative ecology of social systems* that developed in the 1960s among ornithologists. This fusion of population genetics and the work of avian field ecologists in the tradition of David Lack provided at least part of the wave of interest that resulted in the syntheses of 1975 (Alcock 1975, Brown 1975, Wilson 1975) and certainly was a strong stimulus to the study of avian social behavior in the 1970s.

BEHAVIORAL ECOLOGY EMERGES

Add optimal foraging theory to sociobiology and you have behavioral ecology—or close to it. Optimal foraging theory arose from theories of niche exploitation written by the messiah of American ecology and one of his prominent students (MacArthur and Pianka 1966) and by J. M. Emlen (1966). MacArthur's followers were influential, and they quickly expanded this approach into a flourishing field. The early period was reviewed by Pyke, Pulliam and Charnov (1977) at the time and by Schoener (1987) retrospectively. Although it may be argued that foraging is usually not considered to be social behavior, ideas from optimal foraging theory constituted the best developed applications of optimality methods to behavior, and these methods came to be applied also to conventional social behavior (Caraco 1979a, 1979b). Caraco showed how the transition between flocking and territoriality in juncos could be predicted on the basis of foraging and predation hazard. Caraco and Wolf's (1975) paper on optimal group size in lions spawned a series of papers on optimal group size in birds (reviewed in Pulliam and Caraco 1984, and Mangel and Clarke 1988), including one on group-territorial defense in birds (Brown 1982b). Optimality theory has been highly developed for the social insects (Oster and Wilson 1978), and it was even applied to helping behavior in birds (Brown and Pimm 1985); but in general it has been more useful for foraging than for social behavior. Perhaps this was because foraging behavior is more susceptible to simple models and experiments.

BEHAVIORAL ECOLOGY EMERGES

The combination of optimal foraging theory and the population biology of behavior into behavioral ecology has proven to be more viable than its separate parts. The field first became visible with two books by Peter Klopfer (1962, 1970). Its first journal, *Behavioral Ecology and Sociobiology*, began in 1976; and its second, *Behavioral Ecology*, in 1990. The field attracted its own "official textbook writers" (Krebs and Davies 1978, 1984, 1987, 1991) and founded its own society in 1986 in Albany, NY. Other recent surveys include Morse (1980) and Sibly and Smith (1985). The social behavior of birds received much attention in all these books, especially since most of the authors and editors had worked on birds to some extent.

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evance to population stability, a subject that had been considered at length by both Lack (1954b) and Wynne-Edwards (1962), the territorial behavior of birds received considerable attention in the 1960s (reviewed by Brown 1964d, Klomp 1972, Watson and Moss 1970). With the focus of interest turned to cost/benefit theories (Brown 1964a), however, attention shifted to the energetic consequences of territorial behavior (Carpenter and MacMillen 1976). An influential study of costs and benefits of territorial behavior in nectar-feeding birds in Africa (Gill and Wolf 1975, Pyke 1979) was the culmination of a productive research program on nectar-feeding birds in North America (e.g., Wolf and Hainsworth 1971). These studies generally agreed with the expectations raised by cost/benefit theories (Brown 1964a).

Studies on the transition between territorial and flocking behavior in the non-breeding season were pursued in a variety of species (reviewed by Milinski and Parker 1991, Davies and Houston 1981, Davies 1983). Both experimental and optimality methods were employed. Many predictions of a cost/benefit nature were tested and the theory was further elaborated with respect to avian social behavior.

The ideal free distribution and resources. When territories are compressible, increasing density of breeders may depress reproductive success. This depression lowers the value of a territory in a good habitat so that a newly arriving bird might have better success by breeding in a poorer habitat with lower density than a better habitat with a higher density. This trade-off between habitat quality and density was first formalized into an optimality model and tested with data by Brown (1969a). A similar trade-off, although complicated by additional factors, is inherent for females in the model of Orians (1969). A year later the density-habitat trade-off was again formalized using very elementary algebra by Fretwell and Lucas (1970), who described what they named the ideal free distribution (IFD) of competitors. Fretwell, an ornithologist, promoted the global applicability of this concept in a book (1972). Ornithologists at first paid little attention to the IFD but after a convincing experimental demonstration of it in fishes (Milinski 1979), it became a popular topic for modelers and lab tests in behavioral ecology (reviewed in Milinski and Parker 1991). A study of "ideal free ducks" demonstrated the tradeoff in free-living birds (Harper 1982). Its relevance to community ecology has been developed at length by Rosenzweig's group using hummingbirds among their test animals (reviewed in Rosenzweig 1991).

Mating systems. As cost/benefit modeling became popular in the 1960s attention turned to mating systems. Early work done on North American Icteridae (Orians 1961) led to a graphical polygyny threshold model (Verner and Willson 1966, Orians 1969). In it a decisive role was assigned to evaluation by females of territory quality and other conditions that affect female reproductive success. The classification of Emlen and Oring (1977), in contrast, named and explained avian mating systems on the basis of the male's behavioral response to various kinds of environment. More recently, research on avian mating systems has focused on the role of sexual conflict and the variability of mating systems (Davies 1985; Hatchwell and Davies

1992a, 1992b; Davies 1992). This topic will be covered in detail in a later essay in this series.

Sexual selection. A major change in the way ornithologists view sexual selection has occurred in recent years. An anecdote from my own experience illustrates it. In 1975 I gave modest space in a chapter on sexual selection to Fisher's (1930) ideas and raised the possibility of the importance of female choice in birds. In 1978 at a meeting of behavioral ecologists at Ann Arbor this passage was cited in a negative way; for the dogma then among ornithologists was that sexual selection in birds was caused only by aggressive competition among males, which could be easily seen (as in LeCroy's, 1981, explanation of sexual selection in birds of paradise), and not at all by competition among males through attraction and persuasion of females. Note that in sexual selection, competition is always between the members of one sex (i.e., "intrasexual" and never between members of different sexes ("intersexual"). The jargon that distinguishes between these concepts as inter- vs. intra-sexual selection is, therefore, nonsensical (Brown 1983b). Its continued usage depends on the sheeplike nature of some authors who use the terms simply because some others do so, regardless of their real meaning.

The landmark study in this area and one that killed the old dogma with a single blow was a carefully controlled field experiment on the Long-tailed Widow (*Steganura paradisaea*; Andersson 1982a). The data allowed the hypothesis of aggressive competition to be rejected, leaving competition by persuasion and attraction as the remaining alternative. This empirical study together with Zahavi's (1975) reshuffling of Fisher's and J. M. Emlen's (1973:51) ideas into the "handicap" theory stimulated much work on mate choice in birds.

Accepting that female choice had to be taken seriously for birds, modelers turned their attention to the reasons why females preferred particular traits under conditions where resources were not at stake. Did females prefer males with exaggerated signals because they identified genes that would make sons superior at attracting females, or did females prefer such males because they identified genes that would make both sons and daughters more viable (Andersson 1982b, 1986) or both? Models of the former situation allowed the initial stage of the male trait "before" selection to be entirely neutral (Lande 1980, Kirkpatrick 1982). Fisher (1915, 1930), however, thought that the process would begin with traits that were correlated with general good condition and that females would choose on the basis of male condition. In other words, he combined the two processes. Many authors have chosen to present these theories as alternatives, thus polarizing the field and tending to delay compromises. It seems possible to me that many sexual signals in birds identify males whose progeny will be both more viable and more sexually attractive. There should be a continual tendency for selection to carry condition-sensitive traits "too far," with their "dishonest" character only being selected against after some delay.

THE LOGIC OF SCIENCE HISTORY

Selected parts of the history of any field of science can be viewed as a progression in which events lead logi-

cally to new hypotheses, which lead to new predictions, new tests, and new discoveries in a cycle that tends to continue indefinitely. I do not think that the origin of a major theory can be explained easily in this way, but after such a theory has appeared many of its testable predictions and tests do follow logically from the theory. Several aspects of avian social behavior could be treated in this way, but space permits only one. The history of study of helpers-at-the-nest well illustrates this approach.

DISCOVERY AND RECOGNITION OF HELPERS-AT-THE-NEST

The term helpers-at-the-nest was coined by Skutch (1935), who first recognized the inherent interest of the subject and drew attention to it in a series of original observations and reviews (1953, 1959, 1961, 1987). A few earlier workers had noticed the phenomenon (Myers 1915) without drawing much attention to it, and some of Skutch's contemporaries may well have made their observations while unaware of Skutch's work (e.g., Ritter 1938, Yamashina 1938), but it was Skutch's early work that initiated historical continuity of interest in the subject. Helping attracted little interest at first, however, although a few species with helpers were subsequently studied without awareness of inclusive fitness theory (e.g., Davis 1942, Rowley 1965, Yamashina 1938, Brown 1963). Thus, although helping was known, it was essentially ignored in spite of Skutch and a few others for over 35 years.

THE ROLE OF THEORY

A nice demonstration of the importance of theory in stimulating research is the effect of inclusive-fitness theory on the study of helping. My own work on helping dates from the day in 1963 when I first read Hamilton's (1963) original paper on the evolution of altruism in the biology library at the University of Rochester. Surely, I thought then, many ornithologists will rush to test some of the predictions about helping that could be generated using Hamilton's rule. I was wrong. Although a non-ornithologist saw the connection (Williams 1966), it was not until I presented quantitative observations on helping in the Mexican Jay (*Aphelocoma ultramarina*) in the context of altruism seven years later (Brown 1970) that widespread interest in the relevance of Hamilton's rule to helping was aroused.

Theories not requiring kinship were also developed as alternatives (Trivers 1971, Axelrod and Hamilton 1981); and these too were considered in relation to helping (Brown 1975, 1978a; Brown and Brown 1980; Caraco and Brown 1986; Ligon and Ligon 1978, 1983; Ligon 1983). It is difficult to prove, but there is general agreement that the exponential increase in the number of publications on helping that is illustrated in Figure 1.1 of Brown (1987b) was due to interest generated by inclusive fitness theory and its alternatives. Regardless of which theory one favors, if any, it seems fair to say that the study of avian helping was theory-driven in the period 1970–1990. In this sense the study of helping may be said to have advanced logically.

THE DANGER OF DICHOTOMIES: POLARIZATION

The first reaction by many in the early 1970s to my position that it was useful to view helping in the context

of inclusive fitness theory was a mixture of disbelief of my observations, skepticism of any theoretical interpretation, and hostility based mainly, in my opinion, on misunderstanding and conservatism. I experienced them all personally. Misunderstanding of inclusive fitness theory in the 1960s and 1970s was rampant. Maynard Smith (1964) attempted to separate kin selection from the stigma of "group selection" using the placenta as an example of a kin-selected trait. Later Dawkins (1979) felt compelled to describe "Twelve misunderstandings of inclusive fitness theory."

In my own earliest theorizing about helping I attempted to combine ecological thinking from the study of avian social systems with the new insights of Hamilton (Brown 1969a). The principal vehicle for this synthesis was my three-phase theory, which viewed ecological factors, such as shortage of females or suitable territories, as "setting the stage" for helping by causing delayed breeding and delayed dispersal (Brown 1974). This theory was expanded and updated by Orians et al. (1977), Koenig and Pitelka (1981) and Emlen (1982). The common denominator was that ecological factors favoring delayed dispersal were viewed as "setting the stage" for helping.

Despite these efforts to integrate the ecological and genetic aspects of the subject, polarization occurred. Ecology and genetics came to be viewed by some as alternative explanations of helping. This interpretation arose from the argument that nonbreeding Scrub Jays stay home not for the indirect fitness advantages of helping but because they could not find suitable territories (Woolfenden and Fitzpatrick 1978). The possibility that both factors operated sequentially and together, which I had proposed earlier, was forgotten for awhile. The resulting polarization of the field based on such misunderstandings was extensive; and its effects are still felt. I have analyzed the detailed origins of this situation elsewhere (1978b, 1987a, 1987b). Polarizations are common in other fields too and often arise from oversimplified dichotomies, for example, over innate vs. learned behavior, sympatric vs. allopatric speciation, punctuated equilibria vs. gradual change. The literature of this period cannot be fully understood without appreciating the influence of polarization.

EVALUATION OF COSTS AND BENEFITS: RULES AND CURRENCIES

It was not at first realized that Hamilton's rule was incorrect for plugging in data from field studies on helping. Hamilton's rule was unsuitable because it was phrased in terms of fitness of members of the same generation rather than reproductive success of members of different generations. Although not widely appreciated, a turning point in studies of delayed breeding and helping came when a simple model was formulated that made possible a reasonably correct accounting procedure for ecological costs and benefits estimated across generations from natural populations. This procedure was based on what I have called the offspring rule (Brown 1987b) to distinguish it from Hamilton's rule.

Before I published the offspring rule I wrote to Hamilton suggesting that his rule was wrong for field studies. He very kindly wrote back and mathematically derived my version for field studies, the offspring rule, from

his version. Both rules were correct; Hamilton's rule was designed for fitness effects in the same generation principally among siblings, which facilitated theoretical models; the offspring rule was designed for effects on lifetime reproductive success across two generations, especially from offspring-helpers to parent-recipients. He urged me to publish the offspring rule separately (pers. comm.), but I opted to publish it as an appendix to my forthcoming book (Brown 1975), where it was soon noticed by one perceptive reader, S. Emlen.

Mathematical theorists were rightly unimpressed with the simple algebra that led to the offspring rule (they never mention it); nevertheless, the offspring rule was not published until 12 years after Hamilton's rule so it was not trivial. With Hamilton's idea now expressed in a form suitable for field studies, empiricists began to use it. It was soon applied to answer the question of whether or not delays in breeding were justified by increments to indirect fitness through helping (Brown 1978a; Emlen, S. T., 1978). Both authors agreed that delays in order to help were not justified by the gain in indirect fitness in several species, a conclusion that was consistent with the ecological theories of delayed breeding held by Selander (1964), Brown (1969d), Woolfenden and Fitzpatrick (1978), Koenig and Pitelka (1981), Emlen (1982) and most later authors. This result suggested that helping was not altruistic but was a strategy of "last resort" (Brown 1969d) or one of "making the best of a bad situation" (Marzluff and Balda 1990). At least two later studies, however, made a good case for helping being altruistic in some cases (Reyer 1984; Emlen, S. T., and Wrege 1989).

THE ROLE OF LONG-TERM STUDIES

It has been implied and even stated that Brown and Emlen's result is a consequence of long-term studies (Stacey and Koenig 1990, Koenig et al. 1992). This view is incorrect. None of the data selected by Brown and Emlen came from studies that at the time had been carried out more than five years (e.g., Rowley 1965, Parry 1973, Woolfenden 1975). The required data can be gathered in only one reasonably typical year (e.g., Brown and Brown 1981) or in five years (Emlen, S. T., and Wrege 1989).

Long-term studies are valuable for many reasons, but the major conceptual and empirical advances in this field came well before the first long-term study was published (Woolfenden and Fitzpatrick 1984) or the studies were based on experiments. Long-term studies provided a firmer base for the early findings and ultimately led to other discoveries (Stacey and Koenig 1990).

FIELD EXPERIMENTS

More important than long-term studies for results that are relatively free of alternative explanations are field experiments. The data utilized by Brown and Emlen were subject to a criticism that had been raised by Lack (1968) on theoretical grounds and by Brown and Balda (1977) and Gaston (1978) on the basis of their field data. These authors pointed out that when groups with more helpers outproduced groups with fewer helpers this result could have been caused by correlated differences in territory quality or other factors, such as

parental age. This reservation stimulated tests by means of helper-removal experiments. These showed that the helper-associated increment to breeding success expected under inclusive-fitness theory persisted even under controlled conditions (Brown et al. 1982), at least in the more typical cases. Similar and more robust results with a passerine bird were obtained much later with the Scrub Jay (*Aphelocoma coerulescens*) in Florida (Mumme 1992). Recent field experiments on other questions have also provided decisive tests of theory (Pruett-Jones and Lewis 1990, Komdeur 1992).

FUTURE EFFECTS

As more data became available it was possible to examine future effects on fitness. The logic of habitat-saturation arguments (Selander 1964; Brown 1969d, 1974; Woolfenden and Fitzpatrick 1978; Emlen, S. T., 1978) predicted that a future direct benefit of staying home as a nonbreeder could be the acquisition of a breeding position at home or nearby. Thus, I cannot agree with authors who claim that this possibility was overlooked. In their advocacy of future direct effects, however, these authors overlooked future *indirect* effects. The possibility of future indirect effects was first raised by Brown (1980), and the first estimates of them from field data were made by Reyer (1984) and Rabenold (1985). Later papers further formalized the calculation of future indirect effects and raised some controversy about accounting methods (Mumme et al. 1989; Creel 1990a, 1990b). Thus, a more complete and accurate account of costs and benefits was stimulated by the theoretical concept of future indirect fitness.

DIRECT BENEFITS OF HELPING

By causing so much attention to be given to indirect kin selection Hamilton also caused reactions that emphasized its alternative, namely direct selection. This first appeared in the form of the concept of reciprocal altruism, which was based on a simple application of game theory embodied in the Prisoner's Dilemma game (Trivers 1971). Cooperation or mutualism based on direct benefit can take two forms, one that is dependent on the behavior of the potential cooperator, as in the Prisoner's Dilemma (in general called score-keeping mutualism) and one that is not (byproduct mutualism; Brown 1983a). The first case to be analyzed in this way was the sharing of feedings of mixed broods by two or more sets of parents (Brown and Brown 1980, Caraco and Brown 1986). A clear rejection of either hypothesis was difficult, but the authors favored byproduct mutualism.

Another attempt to explain helping without indirect selection by invoking Trivers was described by Ligon and Ligon (1978, 1983) to explain helping by nonbreeding Green Woodhoopoes (*Phoeniculus purpureus*) and helping generally (Ligon 1983). The woodhoopoe case has been interpreted differently (Brown 1987b), and Ligon's general argument has found little support (Emlen, S. T. 1991).

FLEXIBLE STRATEGIES AND HELPING

Behavioral ecologists often use the adaptationist program (Gould and Lewontin 1979), as it should be used (Brown 1982a), to generate hypotheses for testing. Their predictions, however, are typically limited to consid-

erations of cost and benefit. These alone are insufficient to establish that the behavior of interest has resulted from natural selection (Endler 1986). Thus, although cost/benefit studies may test predictions of selectionist models, even if the results agree with the predictions they can often be caused by factors other than natural selection acting in the manner of the model. Textbooks of behavioral ecology (Krebs and Davies 1978, 1984, 1987, 1991) typically assume natural selection rather than trying to prove it. With this attitude by behavioral ecologists it is not surprising that Endler (1986) lists no examples of behavioral phenotypes that have been established by reasonable criteria to be caused by natural selection. One can think of a few candidate examples, but in any case this approach has not been fashionable and has been little used.

It was only a matter of time, therefore, before behaviorists began to realize that many seemingly adaptive behavioral differences between species or populations could also be caused environmentally, i.e., without genetic change. Helping behavior was a prime subject for this "new" approach. As usual, entomologists led the way. West-Eberhard (1987, 1989) developed the idea of flexible strategies to explain how simply changing the environment could be enough to induce greater sociality; and Sakagami and Maeta's (1987) elegant experiments on bees provided evidence that greatly strengthened the argument.

Similar arguments were developed for helping behavior in birds. The idea that helping might be a "neutral trait" was first raised by Woolfenden and Fitzpatrick (Woolfenden and Fitzpatrick 1984). In response I argued that the ability of helpers in colonial species to recognize kin with high consistency (while helpers in noncolonial species did not) argued in favor of adaptation because it was not explained by the "unselected hypothesis" (Brown 1987c). This exchange was ignored by most readers, but the same ideas were picked up soon by other authors. The neutral-trait idea surfaced as the unselected hypothesis (Jamieson and Craig 1987; Jamieson 1989, 1991) and my counter-argument was developed also by others (Emlen, S. T., et al. 1991). Although the flexible strategy approach has been used in the past to explain plural breeding in communally breeding birds (Brown and Brown 1980, 1990) it was not presented in a controversial way and so did not attract attention. Jamieson's papers have now drawn much attention to the problem, and it should receive more attention.

FUTURE TRENDS

Looking beyond the current concentration of studies on mate choice and the use of phylogenetic trees based on molecular data to study the phylogeny of behavior, I can see at least one neglected area that deserves attention. The study of social behavior needs to move from cost/benefit thinking to what can be called selectionist thinking (Charnov 1982) and beyond that to genetically based selectionist thinking. It is not enough to use the adaptationist program and optimality methods; we must think in terms of how selection actually moves a phenotype from one stage to another; and we must do this in a realistic genetic framework. Game theory is not enough.

The present gap in this area is reflected in the various

textbooks of Krebs and Davies. Quite unnecessarily they have simply assumed the operation of natural selection in a vague way and neglected nearly all genetic "details." I believe that it is better to emphasize the null hypothesis that selection is *not* directly responsible. This position stimulates us to try to reject the null hypothesis by studying whether or not selection is importantly involved, using the formal methods reviewed by Endler (1986). The failure of behavioral ecologists in the past to deal explicitly with the details of selection has strengthened the hand of those who claim that the diversity in social behavior among species of insects and birds is due entirely to phenotypic plasticity in a range of environments (West-Eberhard 1987, 1989; Jamieson and Craig 1987; Jamieson 1991). When genetic markers are available in studies of mate choice they reveal inadequacies in the currently popular theories of the evolution of mate choice (a theme that is too long to review here).

If selection is involved, then our attention shifts to the question of what developmental and physiological mechanisms mediate between the genes and the behavior. In the case of helping, when is kin recognition learned and what cues are used? Is there evidence that selection has elaborated the kin-recognition cues in colonial species more than non-colonial species, as implied by Brown (1987c)? Have endocrine mechanisms been specially selected in species with helpers? What are the hormonal correlates of feeding nestlings in breeders and non-breeders of species with and without non-breeding helpers (Vleck et al. 1991)? Are such correlates heritable?

Finally, if physical condition and health are important in competition for resources, perhaps the immune system is involved to a greater extent than is currently appreciated. Much evidence suggests that mammals sometimes choose mates using genes of the major histocompatibility complex (Brown and Eklund 1994). Perhaps birds do too by some unknown mechanism.

DISCUSSION

The first section of this review presents a broad view that identifies major trends and patterns and gives credit mainly to conventional and frequently cited sources. In contrast, the second section adopts a different approach, namely one that emphasizes the logical progression of the subject. In the broad perspective, major synthetic works are cited to document trends and patterns; but in the focused view of a participant, credit goes less to reviews and oft-cited papers, which characterize the later development of a field, and more to works that made a difference in the early history. Sometimes the relevant passages were short. Often they were presented quietly, without fanfare. Not uncommonly, only one or a few people were initially influenced by these passages. Thus, the papers credited in the second section are often not the most frequently cited papers or those written by authors with a high profile. They are influential not in the sense that they were popular or widely read but in the sense of leading logically to future steps. I hope I have shown that the two approaches used in this paper, one based on widely cited "landmarks" and the other based on cause and effect, can be quite different.

After writing this article I came across Ernst Mayr's

"How to Write History of Biology" (Mayr 1982). In defense of my frankly subjective treatment above I can do no better than to quote a passage from it:

Subjectivity enters at every stage of history writing, especially when one is seeking explanations and asks why, as is necessary in problematic history. One cannot arrive at explanations without using one's personal judgment, and this is inevitably subjective. A subjective treatment is usually far more stimulating than a coldly objective one because it has a greater heuristic value.

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