such as primates). Birds display sufficient diversity and complexity in their social systems to make them valuable as models for understanding the social behavior of other, higher forms; yet they retain sufficient simplicity to make quantitative data collection relatively easy. For these reasons I expect that avian examples will provide many of the model systems used in the critical future testing of sociobiological theory.

In summary, the historical interactions between ornithology and sociobiology have always been mutualistic. Ornithological concepts provided one of the original impetuses for sociobiology, and the quantity of the avian literature helped speed the early growth of the new field. But, as genetic theory advanced, ornithology became a major beneficiary as well as contributor. Ornithologists are now better able to see and understand patterns in the diverse array of avian social organizations, and they are better able to ask more meaningful and testable questions about their subjects. As ornithologists make use of these newlyfound, interpretative skills, they will, in turn, be building the empirical data base that will lead to the refutation of some, and the modification and ultimate verification of other, sociobiological hypotheses. This feedback between empirical data and theoretical ideas is the very foundation of the scientific method. The fields of ornithology and sociobiology are deeply interwoven, and each has benefited tremendously from the activities of the other. Let us hope that the mutualistic cross-benefits continue into the decades ahead.

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SOCIOBIOLOGY IN RELATION TO ORNITHOLOGY

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I do not see sociobiology and ornithology as separate subjects that "relate" to one another, but as fields of interest with a wide area of overlap. Thus there are some areas of pure ornithology, such as communal nesting or alarm calls, that are at the heart of sociobiological interest, whereas there are other important areas, such as bird physiology or navigation, that are outside and uninfluenced by sociobiology.

In my view bird studies were one of the most important spawning grounds of sociobiology. In particular, and rather paradoxically, the fundamental disagreement between Wynne-Edwards (1962) and Lack (1966) over the mechanisms of population

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regulation stimulated detailed consideration of the level at which natural selection can act. Lack's ornithological data were vital in arguing the case for individual selection rather than group- or species-level selection. The resulting general appreciation of individual selection made the acceptance of selection at the level of the gene much easier; gene selection is basic to kin selection, Hamilton's (1964) powerful concept that did so much to launch sociobiology.

At a less general level, bird studies provided some of the best early examples of phenomena of particular sociobiological interest. Such examples include bird alarm calls (Maynard Smith 1965; Trivers 1971), needing explanations of such altruistic behavior; co-operative breeding (Maynard Smith and Ridpath 1972, Woolfenden 1976, Emlen and Oring 1977) and the interaction of altruistic and selfish behavior; and the reversal of sexual roles (Jenni 1974). In addition, birds have provided, in the peacock's tail, the paradigm for theoretical discussion of sexual selection and Zahavi's (1975) infuriating Handicap Principle. Ornithology would no doubt have produced more numerous sociobiologically important findings if its subjects were both more socially organised and less annoyingly mobile.

The advent of sociobiology or of its associated way of thinking has clearly given ornithology not a rude jolt, in the sense of disturbing ornithology, but rather a huge nudge in one direction—namely concentrating on individuals. It is only a short time ago that we focussed on how birds recognised their own species and avoided mating with members of another species. In a sense this has been completely superseded; when we are examining whether and how individual birds can recognise their own mates or relatives, and investigating which particular mate they choose, to ask how they can recognise their own species seems to have little relevance. It is as a result of concentrating on individuals that some of the functional questions of only a decade or two ago are no longer worth asking. For example, few ornithologists (I hope) would now ask themselves "What is the function of a pecking order in chickens?," for such an interaction between individuals can have a "function" only at the species level, whereas how each individual behaves is presumably determined by natural selection at the individual level. We would now ask "Why does Chicken A accept domination by Chicken B?," and as a result we can in principle quantify the answer in terms of that chicken's reproductive success if it does or does not accept B's domination. Similarly, questions on the functions of, for example, dialects or pair bonds, both being relationships between individuals, would now usually be phrased and answered in terms of the selective advantages to each individual in the relationship.

Concentrating on individuals rather than on the species brings with it consideration of possible conflict, assessment, and deceit. We were familiar with the evolutionary conflict between cuckoos and their hosts, but clearly similar conflicts occur in nests without nest parasites—a chick is probably selected to try to get more than its share from its parents, and a parent is probably selected to be able to detect and counteract such deceit (Trivers 1974). Courtship displays may provide a means by which a bird both enables a potential mate to assess its qualities and attempts to deceive it as to those qualities. Certainly, animals' lives appear to get more complex when those animals are not just acting for the good of the species as they used to do! For example, we now have to ask not just "How do quail chicks synchronise their hatching?," but "Why do the early ones help the slower ones in this way?"

Has sociobiology's input into ornithology been positive and fruitful? I believe the

answer is that it has been, and that it has also been highly stimulating. I would have to add, though, that we cannot tell with absolute certainty, because it is possible that it has attracted attention and research away from other areas that might have been even more beneficial.

And where should we go in the future? Clearly some lines of ornithological research will and should continue on their way regardless of sociobiology's impact. Kin selection or reciprocal altruism have little to do with the aerodynamics of flight. At least, they have little to do with it directly, but they may well influence a bird's methods of competing, which influence its size and shape, which influence its flying performance. We have not yet managed satisfactorily to incorporate physical and ecological aspects of a bird's life with the more purely sociobiological aspects. We need to know what birds are capable of, what discriminations they can achieve, how much information they can extract from their environment, and what calculations they can perform with that information. We need more long-term field studies of more individual birds, and this will require better ways of tracking them and observing or recording what they are doing. We need field-oriented work on their reproductive physiology, especially on aspects of sperm competition—it may be in the oviduct that the major battles between males, between male and female, and between female and offspring are taking place. We need field experiments to go with theories such as the Handicap Principle (Zahavi 1975) for the evolution of sexual adornments, or the Beau Geste Theory (Krebs 1977) for the existence of song repertoires, to show *whether* they can work before we spend too much time considering why they *might* work. And we still need that good field study of peafowl to show that the marvellous tail is really used for something different that none of us had ever thought of!

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