Individuals and Populations

Behavioural Ecology. Ecological Consequences of Adaptive Behaviour. R. M. SIBLY and R. H. SMITH, Eds. Blackwell Scientific, Palo Alto, Calif., 1985. x, 620 pp., illus. $96; paper, $39. From a symposium, Reading, England, April 1984.

This book, the outcome of a symposium organized by the British Ecological Society, focuses on the relationship between behavioral ecology and population dynamics. This is reflected by the question posed on the cover: "If evolution is a fitness-maximizing process in which optimal behaviour strategies are selected for, what are the consequences for populations?" Though the answers suggested by the authors are many and varied, several themes emerge. First, an understanding of population dynamics requires some knowledge of whether the population in question is made up of discrete groups. Such subdivision cannot be discerned without knowledge of the behavioral dynamics underlying individual dispersal. For example, T. Clutton-Brock and S. Albon show that red deer live in cohesive matrilineal groups and that it is the groups, not the population, whose numbers are directly regulated by selection. Similar subgroups are found in insects (M. Hassell and R. May) and carnivores (H. Kruuk and D. MacDonald), suggesting that the issue of population dynamics cannot often be understood without studies of animal dispersion.

Second, natural selection usually operates at the level of the individual. Consequently, behaviors favoring individual fitness will predominate even if they have a negative impact on the population. These effects can be severe and may have resulted in extinctions of species as well as many of the fluctuations that characterize some species. K. Mann, for example, reports extreme population fluctuations in sea urchins resulting from adaptive changes in individual foraging behavior. The population cycles described by R. Moss and A. Watson in red grouse and by C. Krebs in voles can be ascribed, in part, to adaptive changes in individual spacing behavior. D. Cowan and P. Garson describe great differences in competitive behavior in the European wild rabbit depending upon the availability of burrows. These studies of the behavior underlying individual foraging, spacing, and competition provide a basis for predicting the population dynamics of these species.

Third, individual variation attributable to behavior is not noise at the population level. It is often an evolved trait in its own right. Almost every animal population is composed of individuals occupying different phenotypic classes—adult or juvenile, breeder or non-breeder, fighter or sneaker, mimic or model. Behavioral ecology provides the means by which the fitness of these subgroups can be measured and subsequently used for predicting population dynamics. In an interesting paper on the breeding behavior of a bird called the dunnock, A. Houston and N. Davies show that polyandrous females lay larger clutches than do monogamously paired females. By studying these two mating types, Houston and Davies were able to measure the fitness consequences of the clutch size adjustment to show how it maximizes individual success and to provide the means for calculating population dynamics under different mating systems. R. Dunbar, in a review of the social behavior of mammals, finds that the subordinate females are often non-breeders. This may be adaptive behavior, since the progeny of subordinate mothers would probably not survive. However, a consequence is that the effective population size is smaller than would be predicted from the number of "mature" females. Population biologists studying recruitment in mammalian populations should therefore be aware of adaptive variation in female fecundity.

These findings, along with others, suggest that the field of population biology should include behavior along with population dynamics and evolutionary genetics in explaining population phenomena.

Readers of the volume will find a diversity of papers that go beyond the topic of population dynamics. For example, the significance to behavioral ecology research of long-term studies with individually marked animals is highlighted by the work of R. McCleery and C. Perrins. Using 37 years of data on individually marked birds, the authors show that the key factor limiting the numbers of great tits is probably over-winter mortality, not breeding success as suggested by shorter term studies. The data accumulated by following individuals are also sufficiently sensitive to distinguish cause from effect in measuring components of lifetime reproductive success. Such sensitivity cannot be provided by correlational data. An equally impressive long-term study with individually tagged animals is that of J. Coulsen, C. Thomas, and colleagues on reproductive success in kittiwake gulls.

The importance of individual variation is illustrated by Coulsen and Thomas's paper. These authors conclude that the most important factor influencing breeding success in kittiwakes is the quality of the individuals. From 25% to 33% of the variation in breeding success is attributed to consistent, lifetime differences among parents. Interestingly, it appears that these differences are not heritable. Similarly, I. Hanski shows that body size greatly influences feeding behavior in shrews. For example, during a short-term energy crisis, it pays large individuals to rest, whereas slightly smaller individuals benefit by entering a feeding frenzy. L. Partridge and P. Green argue that since optimal foraging theory is focused on "typical individuals" it has missed widespread feeding specializations among individuals, including changes in gut morphology, digestive abilities, and sampling behavior. A theoretical treatment of how individual differences in competitive ability may influence migration behavior, individual dispersal, and even the carrying capacity of the environment is provided by W. Sutherland and G. Parker. They suggest that to understand carrying capacity one must focus on factors affecting the feeding of the poorest rather than the average individual.

Individual variation is also of importance to research concerned with frequency-dependent biological games. Here the analysis is done with game theory, and John Maynard Smith's concept of evolutionarily stable strategies emerges as a major theoretical contribution. The paper by G. Parker, probably his clearest concerning ESS analysis, will go a long way toward bringing this concept into behavioral ecology. Partridge and Green's paper on foraging theory, Sutherland and Parker's on dispersion patterns, and R. Smith and C. Lessells's on larval competition in granivorous insects are the few in this volume to include game-theoretic analysis.

Another important development in behavioral ecology has been the recognition that natural selection can act at several levels: the gene itself, the individual, deme, or group (both kin and otherwise), and the population, species, or community. However most authors, following the debate during the 1960's and early 1970's over individual versus group selection, in which group selection was overridden, have ignored selection beyond the individual. I was therefore glad to see P. Harvey's "enlightened" paper on group selection. Unfortunately, it is the only paper that considers a level of selection above the individual. A selection model that incorporates all possible levels of phenotypic expression into a single mathematical function should be a major goal of evolutionary biology.

Life history theory emerges as one of the

weakest areas in behavioral ecology. This is borne out by R. Sibly and P. Calow, who attempt to reduce the complexity of selection generated from habitats to two dimensions: juvenile growth rate and survivorship. This approach ignores the contributions of life history theorists such as Brian Charlesworth, Eric Charnov, William Schaffer, and Steven Stearns, who base their models on relationships in age-specific survival probabilities and fecundities. Since its incorporation into behavioral ecology is surely one of the most important future directions for the field, it is unfortunate that life history theory is not better represented.

The book lacks a balanced international authorship (over 80% of the 55 authors are British), and most of the papers are based on studies of birds or mammals (there are only two papers on insects, both on parasitic wasps; one on a marine invertebrate; one on a crustacean; and one on a fish, studied in the laboratory). The papers it contains are generally well written and of high quality, however. Its ecological approach and emphasis on population dynamics complements the evolutionary approach of the collective volume *Behavioural Ecology* edited by John Krebs and Nicholas Davies (Sinauer; second edition, 1984).

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The Fishing Problem

Exploitation of Marine Communities. R. M. MAY, Ed. Springer-Verlag, New York, 1984. x, 367 pp., illus. $20. Dahlem Workshop Reports; Life Sciences Research Report 32. From a workshop, Berlin, April 1984.

The basic premise of traditional fishery management has been that fish populations can be exploited to produce a maximum sustainable yield in a naturally persistent equilibrium condition. Single-species population models based on mortality, growth, and reproduction (recruitment) and data on size-selective mortality induced by a fishery are combined to prescribe fishing tactics intended to maximize and stabilize the yield over time. This approach developed, in part, from observations of how individual fish populations and catches responded to increases or decreases in fishing effort. However, with its general application, fish populations are typically overexploited and yields decline or even cease. In short, "fisheries are not being managed well."

May and his 47 distinguished co-authors primarily address the idea that the "fishing problem" has been too narrowly defined, that we are exploiting not a single species but communities of interacting species, usually in multispecies fisheries. They also point out that equilibrium fishing may be undermined by genetic changes in populations induced by fishing, by changes in external factors such as climate, and by the inability of our institutions to implement the appropriate management measures because fish are treated as a common-property resource. They make it clear that application of fishery science is always in an arena filled with uncertainty that requires decision-makers to be ready to react and adapt to change or to the unpredicted.

To me the exciting feature of this excellent book is that the authors raise many questions and make many insightful suggestions about how fishery science should proceed now that we realize that the issues to be addressed have to do with the exploitation of communities rather than populations per se. The book does not present a consensus but rather the sometimes contradictory ideas of individual authors or working groups. Yet even with its contradictions the book signals a significant change in perspective: fishery scientists and marine ecologists are attempting to cope with the broader causes of uncertainty and to develop new approaches that incorporate uncertainty into management recommendations. Development of more predictive models that incorporate the complexities discussed is one of the major challenges to fishery science and its application in the decades ahead.

Exploitation of Marine Communities is full of quotable statements for consideration in courses in fisheries or to provoke thought or action. A selection follows:

R. J. H. Beverton et al.: "Clear and unambiguous evidence of interspecific interaction in major marine ecosystems, which could be used directly to achieve a significant improvement in single-species assessments, as yet hardly exists."

G. Sugihara et al.: "Exploited fish populations are embedded within a complex web of interactions involving species from many different taxa existing together in a variable environment." The task at hand is "how to best characterize and simplify complex systems to highlight change and to understand structure in marine communities."

J. H. Steele: "Historical evidence suggests that regional fish stocks can change very markedly and very rapidly between high and very low levels of abundance at intervals of about 50 years." "Principles of fishery management, which assume a single underlying long-term equilibrium, were developed during a period (1920–1970) when there was a relatively stable situation." "We should replace the single equilibrium assumption by the recognition of possible multiple states, each markedly different from the others, with the changes between them occurring rapidly, and with the frequency of change increasing with increased predatory fishing pressure."

J. A. Gulland: "The simple single-species models that have been the basic tools of the fishery scientists for the past twenty years can be used to give advice with only a small number of unpleasant surprises (e.g., the collapse of the Peruvian anchovy), and advice given now, based on these single-species models, is much more useful to the manager than a situation in which he gets no advice until more sophisticated models are developed."

The editor sees the book as "essentially a tentative statement—often by several dissonant voices—about directions in which we may be heading" and represents it as "intended to stimulate, not to codify." I agree and appreciated the stimulation it provides.

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Influences in Psychology

Points of View in the Modern History of Psychology. CLAUDE E. BUXTON, Ed. Academic Press, Orlando, FL, 1985. xiv, 468 pp. $58; paper, $29.95.

Points of View in the Modern History of Psychology offers a significant departure from the usual ways in which psychologists assess their past. Histories of modern psychology typically have been Whiggish: charts of scientific progress illuminated with great men, great discoveries, and great currents of thought. One form these histories have taken is exemplified by E. G. Boring's chronicle of the experimental approach, a work that is nearly as revealing for what it omits as for what it recounts. Another form is what has come to be called the "schools and systems" approach, where competing theories are each analyzed in terms of their premises and historical roots and sometimes traced back to pre-Socratic thought. *Points of View* is an attempt to transcend these tropes of history, offering students a treatment of psychology's past not as a progressive march but as an assemblage of variegated points of view that have been constructed during the modern era. Also, rather than offering only internalist history (dealing solely with intellectual issues within the field) the editor urged externalist accounts that would enable read-