years 1848–1852 in South America collecting zoological specimens. Brooks argues that from the beginning his real purpose was to investigate the appearance of new species through a study of the geographical distribution of related forms. Wallace's first paper on this topic was written soon after he set out for Southeast Asia and appeared in 1855 under the title "On the law which has regulated the introduction of new species." Brooks describes at length the development of Wallace's ideas through to the writing of the 1855 and 1858 papers. In his conclusion, Brooks goes on to claim that Wallace's views on branching evolution played a key role in stimulating Darwin to develop his own principle of divergence. This is not a new idea. It was advanced by Arnold Brackman in 1980 (*A Delicate Arrangement: The Strange Case of Charles Darwin and Alfred Russel Wallace*, Times Books). David Kohn refuted Brackman's claim at some length in these columns (*Science* **213**, 1105–1108 [1981]), but Brooks believes that his own more sophisticated interpretation of Wallace's early views will allow it to be revived.

Brooks argues that the image of a "branching tree" of natural relationships in Wallace's 1855 paper forced Darwin to begin thinking about divergence. This ignores all the other influences that were driving Darwin in the same direction in the 1850's (see Dov Ospovat, *The Development of Darwin's Theory*, Cambridge University Press, 1981). According to Brooks, though, Darwin did not complete his theory of divergence through ecological specialization until Wallace's 1858 paper led him to reread the earlier one. A major addition to Darwin's "Natural Selection" manuscript, known to have been written in May or early June 1858, is seen as a new insight on divergence inspired by Wallace. To give Darwin time for this burst of activity, Wallace's 1858 paper must have arrived earlier than the normally accepted date of 12 June. Brackman suggested that the paper arrived on 3 June, but on the basis of a study of British and Dutch postal records Brooks argues that it could have been in Darwin's hands by 28 or 29 May. He finds, however, that an earlier letter from Wallace to another contact in Britain did not arrive until 3 June. The postal evidence is thus unreliable, and the case for Wallace's influence on Darwin must rest on a comparison of what the two men wrote.

Brooks acknowledges (p. 243) that Wallace did not have a theory of how divergence occurs, yet he insists that Darwin was not able to complete his own solution to this problem until he reread Wallace's 1855 suggestion that the gaps in the "tree" of relationships are caused by the extinction of parent forms. The plausibility of this claim is undermined by the fact that both the tree analogy and the idea that parent forms are exterminated by their more specialized descendants are contained in the 1857 letter to Asa Gray used by Darwin in the presentation to the Linnean Society. On this basis, most Darwin scholars see the 1858 material on divergence as a natural extension of Darwin's earlier ideas. I do not think they will be convinced by Brooks's assertion that this was a new initiative inspired by Wallace. Indeed, given the lack of attention paid to divergence in Wallace's 1858 paper, it is difficult to see why it should have prompted Darwin to check the very brief reference to the same topic in the 1855 paper.

The question of divergence may distract attention from Brooks's valid insistence that Darwin and Wallace had very different concepts of natural selection in 1858. He argues that Wallace did not believe that varieties within a species might occupy different ecological niches. They all get their living in the same way, although some will be more efficient than others. The struggle for existence ensures that less efficient varieties have a limited population size, but Wallace did not claim that they are driven to extinction by the superior variety. Only at a time of unusual environmental stress will the less efficient varieties become extinct, leaving the fittest one as the sole representative of the species. This is a plausible reading of the 1858 paper, which would imply that Wallace's original form of natural selection was much less ruthless than Darwin's. Curiously, Brooks asserts (p. 222) that Wallace explained the formation of varieties through the natural selection of individual differences. But if the less efficient varieties could survive except in a time of unusual stress, how could Wallace have supposed the struggle for existence to be powerful enough to act on mere individual differences? In fact, as Brooks's own summary of the 1858 paper reveals (pp. 189–190), Wallace simply assumes that a species will split into varieties and scarcely mentions the action of selection on individual differences. His real interest was the interaction between varieties, not between individuals (see P. J. Bowler, "Alfred Russel Wallace's concepts of variation," *J. Hist. Med.* **31**, 17–29 [1976]). The two men were certainly arguing along different lines: Wallace did not deal with selection of individual differences, postulated only an episodic selection of varieties, and had no concept of divergence through ecological specialization. One can only conclude that it was quite reasonable for Darwin's friends to give Wallace's paper a subordinate position in the joint presentation to the Linnean Society.

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Avian Population Biology

The Arctic Skua. A Study of the Ecology and Evolution of a Seabird. PETER O'DONALD. Illustrated by Robert Gillmor. Cambridge University Press, New York, 1983. xvi, 324 pp. $49.50.

In recent years it has been increasingly realized that for the study of wild populations of organisms in field conditions the skills and knowledge of the geneticist are just as important as those of the ecologist or ethologist. Peter O'Donald's latest book, *The Arctic Skua*, is an excellent example of the value of this approach. The author applies his expertise as a population geneticist to the long-term study of a wild population of birds. This monograph of the Arctic skua (parasitic jaeger in North America) is thus unlike most avian monographs in subject matter. In addition to distribution, feeding, and breeding ecology, O'Donald covers the topics of genetics, sexual selection, demography and selection, genetic models of sexual selection, and mating preference.

A unique feature of the Arctic skua is its plumage polymorphism. Like Kettlewell's famous peppered moth, the skuas may be melanic or non-melanic. The melanism has a genetic basis and appears to be a stable polymorphism with a clinal distribution. Although O'Donald's genetic analyses include measures of heritability of some continuously variable traits, his major concern is to understand the plumage polymorphism. The questions he poses are: What is the genetics of the polymorphism? Is the polymorphism stable? How are the gene frequencies spatially and temporally distributed? What selective forces are acting on the morphs, and are they sufficient to "protect" the polymorphism against extinction of alleles? The answers to these questions must be considered as the unique contribution of the book, and the quality of the book rests largely on the author's success in handling them. In my opinion, this success is mixed. O'Donald certainly is to be complimented on writing the first comprehensive book dealing with an ecological genetic investigation of a bird population. His large data base collected over several years and in two locations has allowed him to write many scientific papers. Now that the population study is terminated it is fitting that it be brought together into a single volume. Often, theories and concepts developed early in a study have to be rejected as more data accumulate, and O'Donald critically appraises and frequently rejects hypotheses he himself had proposed earlier. He is often as critical of his own work as he is of that of others.

O'Donald states in the concluding section of the book that to a population geneticist the most important question is: Is the polymorphism "protected"? To oversimplify his argument, he finds that the non-melanic form gains a selective advantage in that it reaches reproductive maturity at a younger age than the melanic form. Since the two morphs have no detectable differences in annual survival or longevity, this should give a fitness advantage to the non-melanic form. Selection at another stage of the life cycle favors the melanic form. Newly mated melanic males nest earlier and produce more fledglings than the nonmelanic forms. These are the only obvious differences in the measured components of fitness, and O'Donald builds them into various models to see if they can account for the "protection" of the polymorphism. In general they cannot, and additional mechanisms such as nonrandom mating, heterozygote advantage, and gene flow must be invoked. One is left with the feeling that there are too many explanations available, and perhaps this will often be the case in real-world populations.

One criticism I have of this book relates to O'Donald's interpretation of the enhanced fecundity of the melanic forms. He concludes that this is an example of sexual selection with females choosing melanic males preferentially and thereby nesting earlier in the season with higher reproductive success. O'Donald admits that he has no direct evidence of female choice or sexual selection and must rely on indirect approaches. He implies that some quality of the melanic males makes them more attractive, perhaps through some pleiotropic relationship between melanism and hormone levels. A simpler alternative would be that breeding melanics are on average more successful simply because they are on average older. This follows from the fact that pale morphs nest at an earlier age than non-melanics yet have similar annual adult survival rates. Nowhere in the book does O'Donald address this plausible explanation. Whenever age is investigated, it is in terms of years of breeding experience, not actual age.

A second, but minor, negative comment relates to O'Donald's superficial treatment of the North American segment of the species. This is particularly evident in his range maps, which are grossly inaccurate for the New World.

Overall, I found this a stimulating and provocative book. To those evolutionary ecologists who have not previously looked at populations from a geneticist's viewpoint it will be particularly valuable.

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Marine Communities

Biotic Interactions in Recent and Fossil Benthic Communities. MICHAEL J. S. TEVESZ and PETER L. MCCALL, Eds. Plenum, New York, 1983. xviii, 837 pp., illus. $95. Topics in Geobiology, vol. 3.

Biotic interactions are in. Witness the number of books on coevolution published recently. The present book clearly documents that paleontologists (contrary to the title, the perspective is purely paleontologic) actively participate in the trend. The editors and the authors can take pride in this endeavor.

Underlying the contributions in this volume is recognition of the obvious but too rarely cited phenomenon that a wide variety of biotic interactions occur in modern benthic communities and play a part in controlling the composition and distribution of the communities. It is obvious also that such interactions occurred and played a role in the geologic past, but it is something else to identify effects of any interaction in a particular fossil assemblage. Paleontologic data are static, showing patterns, not processes. Fortunately, there are many independent lines of evidence that may be used in deciphering the interplay of biotic and abiotic factors that gave rise to the patterns. In their contribution to this book Kidwell and Jablonski lucidly discuss paleoecologic and stratigraphic criteria for identifying the operation of taphonomic feedback, or the effects of accumulating dead shells on the distribution of benthic organisms. There is also functional morphology, that unsung hero of any paleontologic inference; and often traces of biotic interactions are left directly on the skeletons of benthic organisms. That much more than merely anecdotal evidence can be derived from the fossil record is best demonstrated by the research of Jennifer Kitchell and her collaborators on shell-drilling gastropods and their prey. For some reason this topic has been left out of the book, but a review by Kitchell of biotic interactions in siliceous phytoplankton is included. This paper exemplifies the potential and also the limitations of paleontologic inference about directed biotic interactions.

The importance of paleontology with respect to biotic interactions does not, however, rest on particular kinds of research such as are represented in this book. Rather, it rests on the unique accessibility to paleontologists of the evolutionary time scale. It is the time scale that is claimed to separate microevolution from macroevolution and to allow for distinction between short-term biotic interactions and community evolution. On the macroevolutionary scale, individual species, lineages, and even clades are no longer of particular interest. It is functional groups, or guilds, that are of concern. Consequently, community evolution is defined by reference to patterns of relative significance of various guilds. The widely but ambiguously used, and often misused, concept of community may thus regain its significance. It no longer refers to a superorganism consisting of strongly integrated species controlled largely by directed interactions, but rather to an association of guilds in which weak, diffuse interactions play a predominant role. Community ecologic organization may still come to be recognized as a, perhaps the, controlling factor in the evolution of species, but this is no longer an assumption.

This shift in conceptual framework is made explicit by Thayer. His bulldozing hypothesis (that the rate of sediment bioturbation by deposit feeders and predators has considerably increased through geologic time, thus contributing to the decline of immobile benthos living on soft substrates) is well supported by a variety of lines of biologic and paleontologic evidence; additional sedimentologic evidence is provided by Larson and Rhoads. A similar approach is taken by Vermeij with respect to durophagous predation.

The concluding part of the book is even more ambitious, for the aim is to put forth new (macro)evolutionary prin-