

The Evolutionary Biology of the Threespine Stickleback

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MICHAEL A. BELL and SUSAN A. FOSTER, Eds. Oxford University Press, New York, 1994. xii, 571 pp., illus. \$98 or 65[pounds].

Because the study of variability lies at the heart of evolutionary biology, species that exhibit considerable variation across their geographic range are of special interest to comparative biologists interested in understanding evolutionary patterns and processes at the species level. Few vertebrates match threespine sticklebacks (*Gasterosteus aculeatus*) in the extent of geographic variation in morphology, behavior, and ecology, and the nature of this variation makes this species an especially well-suited model for many types of evolutionary studies. Threespine sticklebacks have been recognized for years as a species particularly amenable to biological study, and the scientific literature analyzing sticklebacks extends from the 1750s through the dawn of modern behavioral biology (in which the threespine stickleback featured prominently) to recent populational and morphological studies of variation. Even since the publication of this book, threespine sticklebacks have been featured in *Science* (4 November 1994, p. 798, and 6 January 1995, pp. 30-31) for their utility as a model system for studying the evolutionary process of character displacement.

Threespine sticklebacks are generally held to be a species complex composed of many distinct populations (some of which actually may be separate species) distributed in the Northern Hemisphere in coastal marine and associated freshwater habitats. Within these areas, stickleback populations may be exclusively marine, be restricted to freshwater, or may migrate from marine to freshwater habitats during their lives. Threespine sticklebacks are not naturally found in the central continental areas of North America, Europe, or Asia. Many stickleback populations, especially in northern freshwaters, are small, isolated groups that may have invaded these habitats at various times following the last glaciation during the past 15,000 years. As this geographic pattern would suggest, many freshwater stickleback populations are highly fragmented, and this pattern is likely to have resulted from multiple freshwater invasions from the ancestral marine population. The fragmentation of stickleback populations has resulted in considerable divergence in many aspects of behavior, ecology, and morphology. For example, among populations breeding season varies between 50 days and one year, lateral bony plates and fin spines range from being well developed to absent, and there is extensive variation in body coloration.

Variation among threespine-stickleback populations is nicely introduced by Bell and Foster in their introductory chapter to this book, and they use this chapter to provide a useful overview of stickleback biology. The topic of variability is also explored in detail in several other chapters, and an especially complete treatment of life history variation among populations is provided by J. A. Baker, who draws on a synthesis of many studies worldwide in an attempt to draw general conclusions about the patterns and causes of variation. This chapter will be of special interest to workers on life-history theory, as many features of reproductive biology are examined in relation to geography and ecology. Baker's chapter also is the most successful in its effort to synthesize data and extract general patterns of variation. McPhail's chapter highlights several Canadian populations that have been used as a model system for the study of morphological divergence and speciation and documents the remarkable distinctions between lake and stream populations and between benthic and limnetic sticklebacks.

One major theme that emerges from this book is the complex history of stickleback evolution and our lack of knowledge about this history. Because the divergence among populations is relatively recent, the phylogenetic history of populational differentiation has been difficult to elucidate. This is a severe handicap to future progress, as the interpretation of so many patterns of ecological and behavioral differentiation depends on phylogenetic data. Indeed, with even basic questions as to the number of species represented within the threespine-stickleback complex unresolved, Buth and Haglund's admonition (p. 84) that phylogenetic research could "end our application of the vague concept of 'complex' to this taxon" is well taken. Indeed, several chapters suffer considerably from attempts to discuss the evolution of stickleback characteristics when historical information on the direction of character change is lacking.

Despite the difficulties that arise from a lack of phylogenetic data, threespine sticklebacks possess outstanding features for ongoing studies in evolutionary biology. In addition to numerous practical features such as the amenability of breeding to observation in situ, the most outstanding feature of sticklebacks is the numerous repeated invasions of relatively isolated freshwater habitats. Comparative biology often suffers from the lack of replicated natural experiments, and sticklebacks offer a profusion of such cases. With a more complete phylogenetic framework, further analyses of the genetic bases of variation in ecology and behavior, and the application of more consistent methodologies for data collection across populations, research on threespine sticklebacks will contribute substantially to the exploration of many fundamental issues in evolutionary biology.

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