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E. J. Brill — P.O.B. 9000 — 2300 PA Leiden
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STICKLEBACKS AS MODELS FOR ANIMAL BEHAVIOUR AND EVOLUTION

Preface

In 1984, an international symposium on stickleback behaviour took place to commemorate 50 years of ethological research on sticklebacks. The Second International Symposium on Stickleback Behaviour was held between 28 August and 1 September 1994 in Sassenheim near Leiden, 10 years after the first one. About 40 stickleback researchers from 9 countries came together to present and discuss the latest issues in research on stickleback behaviour. They represented 19 research groups, more than half of the research groups world wide that focus on sticklebacks. This time researchers from Russia and Eastern Europe were able to attend the symposium. Sadly, one of our most productive colleagues, Gerry FITZGERALD of the Université Laval, Quebec, Canada, died from a brain tumour in March 1994 at the age of 44 (see WHORISKEY, 1994).

Sympatric speciation.

A renewed interest in these small fish species is noticable partly because they have proven to be very suitable as models for animal behaviour and evolution (see BELL's, 1995, account of the symposium). Most research is done with the three-spined stickleback, *Gasterosteus aculeatus*, which actually appears to be a large species complex. The previously unexpected diversity among three-spined sticklebacks is impressively illustrated by the 'white stickleback' species that inhabits marine waters of Nova Scotia, Canada (papers of Max BLOUW's group by MACDONALD *et al.*). These sticklebacks are emancipated from paternal care, a behaviour that was thought to be a characteristic of all sticklebacks. Such unexpected divergence offers unique data which will facilitate understanding of 'normal' three-spined stickleback behaviour. For instance, emancipation from paternal care will cause changes in the operational sex ratio and male

parental expenditure, and thus will have a bearing on questions concerning factors that influence the selectivity of the sexes in mating (addressed in the papers by WOOTTON *et al.* and BAKKER & ROWLAND). Furthermore, female white sticklebacks do not get direct benefits from choosing mates, which is related to questions concerning the information content of male breeding coloration to 'choosy' females in sticklebacks (addressed in the paper by PERRIN).

Other cases of speciation and reproductive isolation were studied in Russia with respect to lateral plate morphs in three-spined sticklebacks and pelvic girdle phenotypes in the nine-spined stickleback (papers by ZIUGANOV and by ZIUGANOV & ZOTIN, respectively).

Comparison between species.

Similar benefits can be gained from comparisons between the stickleback genera. Examples are the papers by WILLMOTT & FOSTER on the four-spined stickleback, *Apeltes quadracus*, by ZIUGANOV & ZOTIN on the nine-spined stickleback, *Pungitius pungitius*, and by MACKNEY & HUGHES on the fifteen-spined stickleback, *Spinachia spinachia*. In contrast to most three-spined sticklebacks, the four-spined stickleback collects one clutch of eggs at a time in his nest and then builds a new nest layer on top of the old one. Rival males interfere during courtship by trying to steal fertilizations, but they do not try to steal eggs in order to bring them into their own nest, like three-spined sticklebacks do. In this species, the presence of eggs will probably not make the nest more attractive to females.

Male three-spined sticklebacks usually collect more than one clutch (sometimes up to 40, TCMB, unpublished data), and females prefer to spawn in nests that already contain eggs. Their problem is how to get the first clutch into their nest, and when to stop collecting more clutches and begin to care for the eggs (the latter issue was addressed by SARGENT *et al.*). They can promote spawning by making either themselves or their nests more attractive to females. A successful alternative reproductive tactic for less attractive males is to steal some eggs out of rival nests (whether or not preceded by fertilization attempts of the raider) and bring them into their own, empty nests (paper by MORI). Attractive males do not have these difficulties, but what makes a male attractive? A series of papers in this volume addressed this question: ROWLAND showed that

normal male courtship tempo is preferred by females, while BAUBE *et al.* and MCDONALD *et al.* showed that females pay more attention to colour intensity (or intensity contrast) than to brightness (or brightness contrast) or hue. The effectiveness of male signals depends therefore on physical properties of the habitat. Thus the photic environment can play an important role in determining optical signal design (MCDONALD *et al.*). The studies of ROWLAND and MCDONALD *et al.* are innovative in that they applied the new technique of video imaging in studying features of mate choice. BAUBE *et al.* and BAKKER & ROWLAND relied on the less flexible, classical technique of dummy presentations. In the former study, electrophysiologically-based mathematical models were used to relate female choice to perceived brightness and colour intensity of the applied colours. Responses to dummies depended not only on dummy traits but also on properties of the receivers: in BAUBE *et al.*'s study female courtship level influenced their selectivity, while in BAKKER & ROWLAND's study of male mate choice using dummies of ripe females, male attractiveness (blue eye colour) prevailed.

Comparison between populations.

FOSTER and BELL made a strong plea for the exploitation of highly diversified freshwater populations that have become isolated since the last deglaciation to study behavioural adaptation. FOSTER used this approach in studying conspicuousness of male courtship behaviour among populations from disparate geographic locations in North America in relation to the occurrence of cannibalism by raider packs. Inclusion of data on anadromous populations, from which freshwater populations have been derived, allows for statements about the direction of evolutionary change. BELL stressed the importance of independent evolution in the populations that are used in such an approach by constructing interpopulational phylogenies. He illustrated this with a molecular phylogenetic tree applied to morphological (pelvic reduction) data.

The adaptive significance of learning processes was addressed by MACKNEY & HUGHES and by PEEKE. A comparison of British populations of the three-spined stickleback with different life styles (anadromous *versus* freshwater) and the marine fifteen-spined stickleback made it clear that the rate at which acquired foraging skills are forgotten is related to the

stability of food composition in the natural habitat. PEEKE investigated the process of habituation of stickleback response to confined prey at the within-population level.

Sticklebacks are an important food source for a variety of predators. This aspect of sticklebacks was followed by KEMPER in an applied research project involving spoonbills. He showed that anadromous three-spined sticklebacks provide a higher food intake rate to spoonbills than the smaller freshwater sticklebacks. Migration of anadromous sticklebacks into the Dutch polder is, however, nowadays impossible. In order to improve the food availability for spoonbills, KEMPER designed and built a fish-ladder that enables anadromous sticklebacks to enter the polder again. This fish-ladder was visited on an excursion immediately after the symposium.

Intrapopulational comparisons.

Predators may exert strong selection pressures on stickleback behaviour and morphology. Impressive examples of this were given by REIMCHEN and by ZIUGANOV & ZOTIN. REIMCHEN showed that within the low plated morph of the three-spined stickleback, bird predators (diving birds) selected against high plate numbers while fish predators (trout) selected against low plate numbers, resulting in cyclical selection on plate number of sub-adults in a Canadian population. Predation experiments with nine-spined sticklebacks from Russian populations that had a complete pelvic girdle and those that lacked a pelvic girdle showed that the loss of the pelvic complex is advantageous under pressure from insect predators but disadvantageous under fish predation.

Sticklebacks harbour many parasite species. Three-spined sticklebacks are the intermediate host for the cestode parasite *Schistocephalus solidus* which grows enormously in their body cavity before it is transmitted to the final host (piscivorous birds). BARBER & HUNTINGFORD reviewed the effects this parasite has on foraging and shoaling behaviour of infected sticklebacks, thereby increasing its chances of transmission.

Temporal determinants of behaviour.

In the past, much work has been done on the temporal organization of stickleback behaviour, but only recently have SEVENSTER *et al.* taken up

the study of circadian rhythm in stickleback behaviour. However, no evidence of a circadian clock has been detected so far under the conditions used. The phenomenon of 'rest-periods' was discovered, but it remains questionable whether they can be considered as 'sleep-like' behaviour. In any case, they do not seem to occur on a circadian basis.

Outline and prospects.

The 23 papers in this stickleback-volume are grouped according to the following 6 themes: 'Mechanisms in sexual selection' (8 papers), 'Models of mate choice and parental care' (2 papers), 'Ecological influences on behaviour and morphology' (9 papers), 'Influences of experience on foraging' (2 papers), 'Circadian rhythm' (1 paper), and 'Applied stickleback research' (1 paper). Compared to the proceedings of the first symposium (VAN DEN ASSEM & SEVENSTER, 1985), there clearly is a renewed interest in problems of sexual selection in sticklebacks. Three further papers on this issue that were presented at the symposium (BAKKER & MUNDWILER, LINDÉN, and MCPHAIL) will be published elsewhere as will a paper on molecular phylogeny of species pairs (TAYLOR & MCPHAIL). The strength of sticklebacks as models for animal behaviour and evolution lies in their suitability for research at every possible level from the species to the intra-individual level. Particular fields were underrepresented at the symposium, notably physiology (apart from BORG & MAYER's review on the influences of androgens on behaviour) and genetics (apart from BAÑBURA & BAKKER's contribution on the genetics of lateral plate morphs, and TAYLOR & MCPHAIL's molecular phylogenetic study). Sticklebacks may not be the ideal organisms for doing physiological and genetical research but have been proven to be suitable. Research in these fields are needed in order to further strengthen the role of sticklebacks as models for animal behaviour and evolution. It is a challenge for future research to expand in these fields.

On average about 45 papers on sticklebacks are published yearly (Fig. 1). Since the First Stickleback Symposium, this adds up to about 500 papers including the proceedings of the first symposium in 'Behaviour' (VAN DEN ASSEM & SEVENSTER, 1985), and three books (WOOTTON, 1984; ZIUGANOV, 1991; BELL & FOSTER, 1994). The yearly fluctuations in publication rate suggests a 5-year cycle (Fig. 1). If one were to be ignorant of

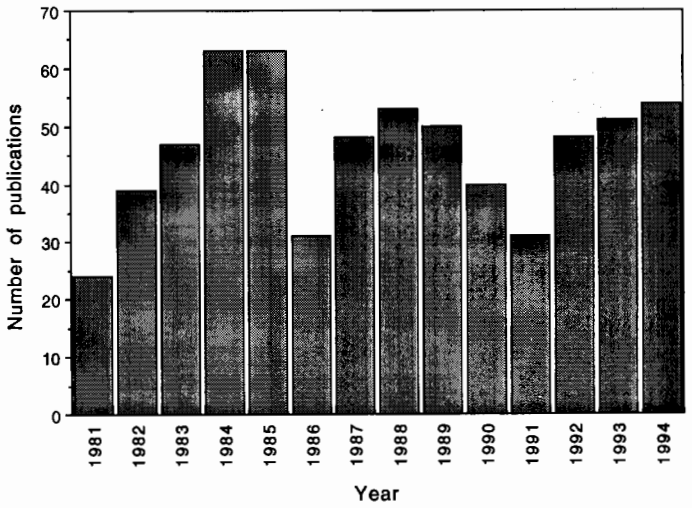

Fig. 1. Yearly number of publications dealing solely or mainly with sticklebacks in the period 1981-1994. Not included are unpublished theses and abstracts.

the activities of stickleback researchers, this cycle would be quite puzzling. The impact of the first symposium is clearly reflected in the low number of published papers in the year after the publication of its proceedings (VAN DEN ASSEM & SEVENSTER, 1985). We predict that the publication of the present 'Behaviour'-volume will result in a low 1996 publication output. The relatively low number of publications in 1991 precedes the multi-author book (15 chapters) edited by BELL & FOSTER (1994): the deadline for contributed chapters was set in 1991. It would be more beneficial and may further increase our knowledge of the behaviour and evolution of sticklebacks if symposia like the first two were to be organized more frequently. We suggest a rate of one every five year, so as not to disturb the 5-year cycle in published papers on sticklebacks.

Theo C. M. Bakker

Piet Sevenster

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