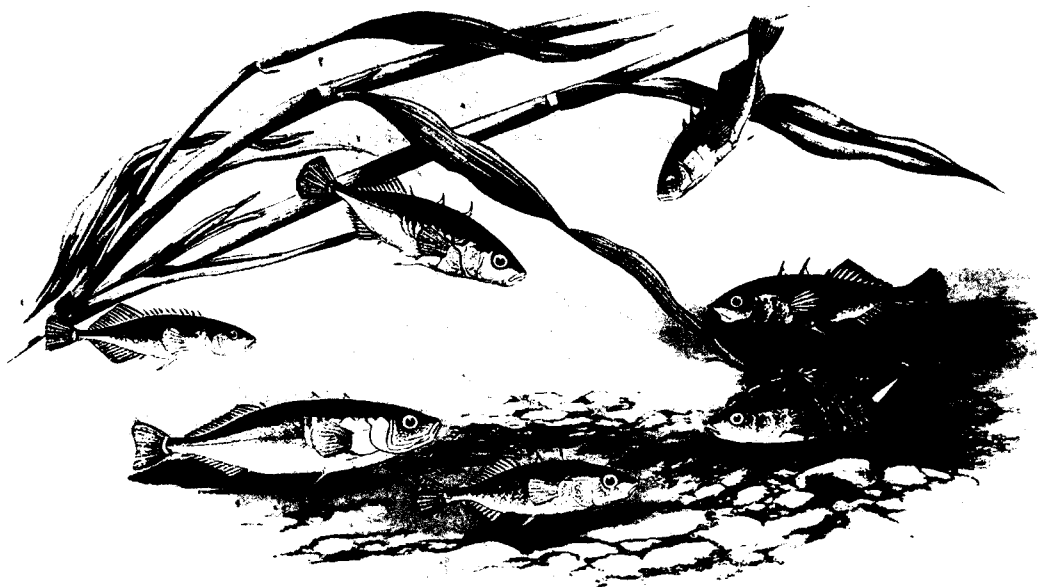


# Tinbergen's Legacy in *Behaviour*

SIXTY YEARS OF LANDMARK  
STICKLEBACK PAPERS



*Edited by* FRANK A. VON HIPPEL

*Including retrospectives by*

DESMOND MORRIS, THEO BAKKER, R.J. WOOTTON & Others

BRILL

# ***Retrospective: Living in the ecological theatre***

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The major processes underlying evolutionary change seemed quite well-established to this Canadian undergraduate in 1967. Although few questioned the primacy of form and function for character differences among species, the significance of variation within a species was in dispute, and one of the most prolific researchers of the 1970's and 1980's noted that '... some geographical variation within a species is clearly adaptive, but much is a non-adaptive product of history' (Gould, 1984). Variation within populations was generally considered developmental noise around an optimal phenotype preserved by normalizing and canalizing selection (Mayr, 1963; Futuyma, 1979), or in the case of discontinuous phenotypes, such as balanced polymorphisms, an adaptive response to ecological or physiological pressures (Ford, 1964).

My first exposure to intra-population variability was as a summer assistant to Ric Moodie, who was doing his PhD on a giant black stickleback from Haida Gwaii, an archipelago off the west coast of British Columbia. Ric identified differences in timidity and microhabitat of phenotypes which correlated with their number of bony lateral plates along their trunk (Moodie, 1972). The experience of studying these individual behavioural differences with Ric impacted my professional trajectory, including my choice of graduate school. I attended the University of Liverpool and worked under Arthur Cain and Philip Sheppard, both former students of E.B. Ford, who had carried out some of the seminal studies on the ecological genetics of natural populations of lepidopterans and molluscs (Ford, 1964).

My thesis research focused on shell colour variation in intertidal snails. I found a distinctive spatial geometry between the substrate, juvenile snails

and predatory fish that provided evidence for fine-tuned adaptation at several levels including ontogenetic, intrapopulation and macrogeographical variation (Reimchen, 1979, 1989). These data in combination with the apparent limited role of any obvious founder effects, pleiotropy or constraints that are often employed to account for large and small scale geographical variation led me towards pan-selectionism. My post-doctoral plans were to use similar approaches to examine the extent of ecological influence on continuous/quantitative traits. Van Valen (1965) had already written an important paper on morphological variability and niche breadth in bird populations proposing that intraspecific competition could favour the evolution of specialists when broad niche space was available (see also Levene, 1953). Although Van Valen focused on trophic structures, I was interested in variability in stickleback predator defences. Evidence already existed that among stickleback populations, mean number of bony lateral plates was associated with the presence of predatory fish and that in the absence of these predators, stickleback tended to have fewer plates (Hagen & McPhail, 1970; Hagen & Gilbertson, 1972; Moodie & Reimchen, 1976; Gross, 1978).

With this background and funds from Joseph Nelson, I made my way in 1976 to a cabin on Drizzle Lake in a remote bog on Haida Gwaii. There, my partner and I resided for the next decade, investigating variability in the endemic populations of stickleback. This was probably not the best period to do a detailed study of selection and variability within a population, given some of the shrill critiques at the time on pan-selectionism and adaptationism (e.g., Gould & Lewontin, 1979). Although the lake was off the electric grid, I installed photovoltaic panels on nearby treetops and a small wind generator on the lake shore, and was able to produce sufficient power for lights as well as various electronics such as a 'portable' computer, printer and photographic darkroom.

Residency at the lake throughout the year substantially modified my conceptual interpretation of selection in the wild. Each week would often reveal a shift in the abiotic and biotic conditions that I would not see again until the next year at the same time (e.g., Reimchen & Douglas, 1980). The predation regime in July was very different from that of October which was distinctive from that of April. It seemed to me that it would be impossible to meaningfully interpret variation without this temporal detail of life history interactions, and that the apparent widespread evidence for non-functional

variability in populations (Gould, 1984) was more likely a simple consequence of a limited understanding of the actual selective landscapes.

While stickleback researchers had focused on predatory fish as agents of selection (reviewed by Wootton, 1984), some of the first useful observations at our field site occurred when I saw avian piscivores capturing stickleback. Initially, these infrequent bouts of predation seemed of marginal demographic relevance compared with the impact of resident trout, but with daily surveys throughout the year, 16 species of avian piscivores, including grebes and loons, were observed each over a relatively narrow but different time window (Reimchen & Douglas, 1984). I established a three dimensional sampling grid for stickleback throughout the lake and made replicated transects every two months for three years and maintained records on the diel and seasonal foraging behaviour of trout and avian piscivores. The 19 transects allowed 11,000 stickleback to be scored for a diversity of traits. I found that variation in the frequency distribution of lateral plates among subadults, but not adults, was strongly concordant with seasonal and yearly shifts in the relative proportion of stickleback consumed by avian versus salmonid predators. As with concurrent studies of quantitative trophic characters on Galapagos finches (Grant et al., 1976) and more recent studies on trends in stickleback spine phenotypes from an adjacent lake (Reimchen & Nosil, 2002), the data suggested fine-tuned adaptations, with rapid population responses of subadults to seasonal periodicity in the selective landscape, described in one of the two papers reproduced here (Reimchen, 1995). Yet, the adult size classes, which are subject to only minor predation, showed no changes among seasons or years, indicating pseudostasis in morphology. Without having seen the cyclical trends in the subadults, this could have been interpreted as a developmental constraint to morphological change and limitation to the precision of adaptation (e.g., Gould & Eldredge, 1977).

Part of the morphological assessment of stickleback that I included in my field study was the extent of bilateral asymmetry of defence structures. An expanding literature at the time suggested that slight asymmetries reflected developmental instability from various combinations of inbreeding, physiological stress, parasitism and disruption of co-adapted gene complexes (Soulé, 1972; Parsons, 1990; Møller & Swaddle, 1997; Lemberget & McCormick, 2009; however, see Wiener & Rago, 1987). Consistent with fitness reduction, Ric Moodie and I had previously shown from a survey of some 20 Haida Gwaii lakes that plate asymmetries in stickleback were uncommon

in populations with abundant predatory fish (Moodie & Reimchen, 1976). However, during my seasonal transects at Drizzle Lake, I thought something was amiss, as about one-half of the stickleback were asymmetric for plates even though they experienced extensive predation. I had expanded stickleback collections from all of the unsampled lakes throughout the archipelago and this provided an ideal opportunity to evaluate baseline levels of asymmetry in over 100 of the undisturbed populations. My PhD student Carolyn Bergstrom undertook these analyses in the late 1990's. Results to emerge from some of this research showed that in most populations, 30% to 60% of all individuals were asymmetric (Bergstrom & Reimchen, 2000). As a proxy for developmental stress and instability, these frequencies seemed unexpectedly high for pristine populations that appeared to lack any obvious source of physiological stress. We expected that at least there would be widespread examples for reduction in frequency of asymmetries across age classes, particularly as these populations were subject to a diverse predation regime (Reimchen, 1994). Yet we did not observe any such evidence, implying that fitness between symmetrics and asymmetrics was similar.

This paper, as well as more recent data, indicate opposing processes on plate asymmetries, including their increased susceptibility to parasitism (Reimchen & Nosil, 2001), increased reproductive benefits relative to symmetric fish (Moodie & Moodie, 1996) as well as isotopic differences between left and right biased lateral plate asymmetries, possibly due to microhabitat differences in trophic niche (Reimchen et al., 2008; Reimchen & Bergstrom, 2009). The latter may be mediated through the lateralized capture behaviour of vertebrate predators (Bisazza et al., 1998; Vallortigara & Rogers, 2005). If these data are more broadly applicable, they suggest that fluctuating asymmetries are far more ecologically interesting than the mere by-product of developmental instability and may yield as yet hidden insights into individual niche space and fitness in the ecological landscape.

The second paper (Reimchen, 2000) reproduced here analyzes predator-handling failures of *Gasterosteus* differing in lateral plate and spine expression and offers a functional interpretation for the geological persistence and geographical distribution of the completely-plated morph, the ancestral phenotype in this taxon (Bell, 1981). Although the bony lateral plates covering the trunk of the threespine stickleback would seem to be an obvious predator defence, the widespread loss of posterior trunk plates in numerous freshwater populations subject to extensive predation weaken such an assumption

(reviewed by Bell, 1976; Wootton, 1976, 1984). Their persistence in marine waters from the Miocene (Bell, 1977) had been correlated with physiological adaptations to salinity and cold temperatures (Heuts, 1947) while their occurrence in some northern fresh waters could be a historical signature of post-glacial migration routes (Münzing, 1963), introgression from marine stickleback (Miller & Hubbs, 1969; but see Bell retrospective in this volume) as well as epistatic linkages to low water temperatures or extreme winter conditions (Hagen & Moodie, 1982). The reluctance of researchers to consider direct functionality to the complete row of lateral plates was probably due to the earlier and influential work of R. Hoogland, Desmond Morris and Niko Tinbergen, who in 1957 provided evidence that the long spines on stickleback reduced feeding success of predatory fish relative to that for short-spined and unspined species. The reluctance may also have been accentuated by the prevalence of morphological stasis in marine habitats and inferred developmental constraints (Cronin, 1985).

These constraints or the physiological correlations seemed improbable to me given the large taxonomic diversity of predators taking stickleback (Reimchen, 1994), but it was the occurrence of pursuit and manipulation failures by these predators that gave me insights to the functionality of the fully-plated condition. In a review of predator-prey literature, Vermeij (1982) argued that while successful predation produced demographic consequences to the prey, unsuccessful or inefficient predators were the engine of defensive adaptations. Emerging from my geographical surveys of stickleback on the islands, I started to suspect a relationship between water clarity, predator inefficiencies and stickleback defences. Low-plated stickleback prevailed throughout the archipelago and the only three populations with completely-plated stickleback occurred in mountain lakes which were distinctive because of their exceptional water clarity combined with a steep shore profile and lack of any littoral zone. These conditions were spectrally and structurally similar to the open clear water habitats of marine stickleback and I inferred that this would potentially facilitate increased probability of capture by predatory fish with the subsequent advantage to post-capture defensive armour. This led to a series of experiments on trout-handling behaviour (Reimchen, 1992), similar to those of Hoogland et al. (1957), but where both spines and plates were evaluated. I showed that the completely plated morph had higher escape probabilities than low-plated stickleback, even when the latter had much larger and more robust spines than the former. The higher

escape was probably due to abrasive interference between the plates and the pharyngeal jaws of predatory fish. This hypothesis received recent support in a natural experiment in Lake Washington where the completely-plated morph increased relative to the low-plated morph following recent improvements in clarity of the lake (Kitano et al., 2008) and provides a functional context to broader evolutionary trends (i.e. Bell, 2001; Peichel, 2005).

At the present, sitting at my laptop in Victoria, 1000 km from Drizzle Lake, and even further from the ecological theatre that structured natural selection within this remote population, I think that the substantive issues that emerged during our many years of observation on the lake were the predictable spatial and temporal variability in sources of mortality, variability in the efficiencies of predators, and the differences in these processes even among adjacent populations. These mortality factors are fundamental for interpreting intra- and inter-population phenotypic variability, yet are rarely characterized for most species. Determining the extent of fine-tuned adaptive variation and efficacy of selection in natural populations still has tremendous research potential one and a half centuries after the general framework of natural selection was established.

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