

Retro- and perspective: Determinants of dominance

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In the seventies of the last century, research on the function and causation of aggression was promoted in the Netherlands by a priority programme of the Netherlands Organization for the Advancement of Pure Research (ZWO, nowadays called NWO; see Wiepkema & van Hooff, 1977). Geert van Oortmerssen, a pupil of Gerard Baerends of the University of Groningen, was involved in this programme. In the mid-seventies, I was doing a Masters project in his research group concerning the genetics of aggressiveness in wild house mice, *Mus musculus domesticus*, by performing artificial selection experiments. These selections led to the so-called SAL (short attack latency) and LAL (long attack latency) mice (van Oortmerssen & Bakker, 1981), which would become a classical example of behavioural syndromes (“animal personalities”).

Geert van Oortmerssen evoked my interest in behaviour genetics and aggression. After my MSc examination in 1978, I inquired after a PhD position at the University of Leiden. I was encouraged by Geert van Oortmerssen, who informed me that a ZWO grant application of Maarten 't Hart, nowadays a famous Dutch literary writer, and Piet Sevenster on aggressiveness in sticklebacks had recently been awarded. I was very eager for a PhD study, and this project would be perfectly tailored to my interests. Moreover, in addition to the universities of Groningen and Utrecht, the University of Leiden was a Mecca of ethology in the Netherlands. I obtained the position and moved with my wife Petra, also a biologist, and my three-year-old son, Baldwin, to Leiden. The ethology research group at the University of Leiden was at that time led by Jan van Iersel and after his retirement in 1984 by

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Piet Sevenster, who had been Niko Tinbergen's assistant during his first year in Oxford. Piet Sevenster would be my supervisor. This made me a proud, second generation pupil of Tinbergen. It was fitting that I received the Niko Tinbergen prize of the "Ethologische Gesellschaft" (the society of ethologists of German speaking countries) in 1990 for my PhD dissertation!

I learned a great deal from Piet, not only about sticklebacks but also about observing animals, data interpretation, and ethology. He was also a great naturalist and art lover. The PhD project concerned the genetic basis of aggressiveness in three-spined sticklebacks, *Gasterosteus aculeatus* L. (Bakker, 1986). Mine was a very elaborate project involving six artificially selected lines and a control line. It was subsidized for three years but continued for some more years. Piet Sevenster had organized grant money for an extension of the project by another three years, but this was conditionally bound to the appointment of another PhD student than me, who would then take over the project. Piet Sevenster refused to do so because he was convinced that only I could handle the project. Thus we did not get the money for the extension, and some very tough years of unemployment followed. My family consisted in the meanwhile of four persons: our son Oliver was born one year after we moved to Leiden.

It is a great pity that we did not conserve the selection lines; molecular genetics was not common practice at that time. During the first three years of the project, I had the luxury of a full-time personal assistant, Els Dekker, who was a biologist, and helped with breeding, maintenance of the fish, and data collection. Without her help this ambitious research programme would have been impossible. Her tasks would later kindly and very competently be taken over by Enja Feuth-de Bruijn, a biologist with a permanent position as a technical assistant in the research group of Piet Sevenster.

The ethology research group of the University of Leiden had a long tradition in stickleback research and produced many seminal works (e.g., ter Pelkwijk & Tinbergen, 1937; van Iersel, 1953; Sevenster, 1961; van den Assem, 1967). It had great aquarium facilities, which were partly reorganized to house the many small 10 litre tanks that I used for the selection experiments. My start in stickleback research was also the start of a friendship with Tijs Goldschmidt, who did field studies on sticklebacks in close connection with Piet Sevenster. Later, Tijs completed a PhD study on haplochromine cichlids in Lake Victoria and wrote about his experiences in a successful book, *Darwin's Dreampond* (Goldschmidt, 1996, translation of the original 1994

Dutch book *Darwins Hofvijver*). This book marked the beginning of his career as a literary writer. Tijs helped me to catch the base population of stickleback for my PhD research. He knew all the places where stickleback could be found near Vaassen, in the middle of the Netherlands. He had many good connections with local people, so we easily obtained permission to sample fish on private areas. We sampled sticklebacks from many different places in an area of about 35 km² in order to collect a heterogeneous sample to begin the artificial selection. Tijs surprised me not only by his great knowledge of sticklebacks and behavioural ecology but also by not hesitating whatsoever to step into brooks with his normal daily clothes and shoes as if water was part of his daily life.

The 1983 *Behaviour* paper (Bakker & Sevenster, 1983) on the determinants of dominance was my first stickleback paper and my second paper in a refereed journal. Although I was the first author, the correspondence to the journal was handled by Piet Sevenster. There was no discussion about that and hardly about the choice of the journal. *Behaviour* was the preferred journal for Dutch ethologists. The managing editor at that time was Gerard Baerends from the University of Groningen. I remember that he wrote to Piet Sevenster that the writing was not the high quality he was used to from Piet. Piet did not like that at all and he further improved my not perfect English. I cannot remember other comments as I did not get the correspondence. After one round of revision, the manuscript was readily accepted. The publication was well received by the scientific community. It is well cited: between one and five times almost every year since the year of its publication. In the year 2000 it was cited ten times, probably reflecting the growing interest in intra-sexual selection after two decades of a focus on inter-sexual selection by female mate-choice.

What was new in our paper and why was it cited so well? The strength of our paper was, I think, the exploration of and evidence for the multifarious influences on dominance in male sticklebacks: genetics, experience, aggressiveness, and red nuptial colouration. The analyses were facilitated by the discovery that isolated, reproductively active males can be ranked into a linear order of dominance based on the outcomes of dyadic dominance tests among them. Dominance tests implied the introduction of two reproductively active males in a neutral tank that is only large enough for the establishment of one territory. The rank in the dominance "hierarchy" was called dominance ability.

Genetics

Genetic influences were only briefly described in the 1983 paper by referring to my forthcoming PhD dissertation (Bakker, 1986; see section Behavioural Genetics, Phylogenetics & Speciation). Based on three generations of artificial selection for high and low dominance ability, the realized heritability for dominance ability was estimated at 0.34 (Bakker, 1986). This estimation was of similar magnitude as the heritability of various forms of aggressiveness (juvenile, male territorial, female) in sticklebacks of this population (Bakker, 1986, 1994a, b), and of the mean heritability of behavioural traits in animals in general (e.g., Roff, 1997). The data pointed to an asymmetry of the response to selection as only the selection for lowered dominance ability was successful in comparison to an unselected control line.

After my PhD study, I extended the behaviour-genetics of aggressiveness in sticklebacks by a comparison of lab-bred progeny from two Dutch stickleback populations with a different life history and their reciprocal crosses (Bakker et al., 1988; Bakker, 1994a). I was assisted by Enja Feuth-de Bruijn. This study provided further evidence for genetic variation in dominance ability. Males from the same freshwater population as we had used for our selections won about three quarters of dyadic combats against lab-bred males from an anadromous population (Bakker, 1994a). This outcome again confirmed that fish from the freshwater population had been selected for high dominance abilities under natural conditions. I am not aware of other genetic studies on stickleback dominance.

Experience

In addition to genetic influences, experience also has a decisive effect on the probability of winning a dominance fight. We experimentally showed in our 1983 paper that previous dominance or inferiority experience is also a determinant of dominance. Thereafter we extended the study of experiential effects on dominance by prolonging the interval between experience and the following dominance test to three or six hours (Bakker et al., 1989). Now an asymmetrical effect of prior winning and losing on dominance became evident: the effect of prior losing was stronger and longer lasting than that of prior winning. This is not unique for sticklebacks, but quite a general

phenomenon and may be explained by different physiological mechanisms involved (e.g., Hsu et al., 2006; Oliveira et al., 2009).

Experiential effects on dominance are furthermore revealed by the almost linear ranking of a group of isolated males when tested in all pair-wise combinations for dominance ability (Bakker & Sevenster, 1983; Bakker, 1986). There are several recent theoretical papers that predict a linear dominance order by only winner and loser effects (reviewed in Hsu et al., 2006; Dugatkin & Dugatkin, 2007; Hock & Huber, 2009). Interestingly, the stability of the dominance hierarchy in a group of non-reproductive sticklebacks was affected by environmental disturbances such as increased turbulence, lowered water levels (simulated drought), or hypoxia (Sneddon & Yerbury, 2004; Sneddon et al., 2006).

Aggression

To our surprise, aggressiveness was not consistently associated with dominance ability (Bakker & Sevenster, 1983; see also FitzGerald & Kedney, 1987; Rowland, 1989). This was affirmed by the fact that the successful selection for dominance ability was not accompanied by significant changes in territorial aggressiveness (Bakker, 1986, 1994b). In agreement with this is the absence of a significant correlation between aggressiveness as determined in standard aggression tests (Bakker, 1986) and dominance ability in the population comparison (Bakker, 1994a; Bakker & Feuth-de Bruijn, unpubl. data: freshwater population: $r_s = 0.25$, $n = 10$, ns; anadromous population $r_s = 0.19$, $n = 10$, ns).

Colouration

The fourth determinant of dominance that we considered in our 1983 paper was the degree of red nuptial colouration. Because the lines selected for high and low dominance ability diverged significantly for redness (Bakker, 1986, 1994a), we became aware that the red breeding colouration of stickleback males might be an important determinant of dominance by its intimidating effect on rivals. Also within generations of the high and low dominance lines, dominance correlated significantly with redness (Bakker & Sevenster, 1983). We also found parallel changes in redness and dominance of lines selected

for high and low territorial aggressiveness (Bakker, 1986, 1994a, b). Remember that parallel changes between dominance and territorial aggressiveness were absent in the lines selected for dominance (Bakker, 1986, 1994a, b) suggesting two genetically distinct physiological pathways for colour changes in the dominance lines and the territorial aggression lines. There were no significant correlations between redness and territorial aggressiveness in the successive generations of the dominance lines (Bakker & Sevenster, 1983) or in the successive generations of the other selection lines (Bakker, unpubl. data). This contrasts to some other studies (Rowland, 1984; McLennan & McPhail, 1989, 1990). Regardless, the association between redness and dominance that we assessed was of a correlative nature.

We conducted some preliminary experimental tests inspired by methods used by Semler (1971), an early experimental study on sexual selection by female mate-choice. We coloured males artificially with nail-polish (Bakker & Sevenster, 1983). Although the effects of the manipulation on dominance pointed in the expected direction, we were not convinced by the data because "the colour was rather too flashing, the paint came off during the tests and the fish seemed to be ill affected" (Bakker & Sevenster, 1983). Only in 1997 was a convincing experimental test published that showed that red belly colouration of male sticklebacks functions as a threat signal (Baube, 1997).

Charles (Charlie) L. Baube was a PhD student of Bill Rowland. I met Charlie while I was a guest in Bill's lab in 1992, where he introduced me to and helped me with reflection spectrophotometry of stickleback throats. He applied and extended a method employing coloured light that Milinski and I had used in 1990 in a mate-choice context. Charlie performed similar dominance tests as we did in our 1983 paper but now under different illumination. Illumination was manipulated by theatrical gels such that it optimized the stimulation of desired photopigments (L: sensitive to long wavelengths; M: sensitive to medium wavelengths; S: sensitive to short wavelengths) while minimizing stimulation of the remaining photopigments. Ultraviolet-sensitive photoreceptors in sticklebacks were only described in 2004 (Rowe et al., 2004), so Charlie concentrated on the three photoreceptors that were sensitive in the wave range visible to humans. Dominance tests were conducted under illumination that maintained male red colouration (W: white light of the same intensity as the other treatments by using neutral density filters; SML: provided S, M and L wavelength light) or eliminated male red colouration (SM: provided S and M wavelength light; L: provided L wavelength light). Only under W and SML illumination was male

redness significantly positively correlated with the probability to initiate and win a dominance fight. This is a solid experimental demonstration that redder males have greater dominance abilities because of their redness.

The recognition that red colouration is important in male-male competition dates back to Tinbergen (e.g., ter Pelkwijk & Tinbergen, 1937; Tinbergen, 1948, 1951), who strongly promoted that red serves as a sign stimulus eliciting territorial aggression. Early experiments with dummies of male stickleback presented inside the territory of a male showed the aggression-releasing effect of a red belly (ter Pelkwijk & Tinbergen, 1937; Tinbergen, 1948, 1951). Crude red-bellied dummies elicited more attacks from the territory owner than did more realistic dummies that lacked a red belly. The results were so clear-cut (Tinbergen claimed that even red postal vans visible from the tank were attacked) that no need was felt for a quantitative analysis. Nevertheless, in 1949 such an analysis was made by Collias while he was a guest in Tinbergen's laboratory in Leiden, but the results were published much later (in Baerends, 1985, reproduced in this section, and Collias, 1990).

Collias's experiments affirm the statements of Tinbergen, although not as clearly as Collias (1990) suggested because his analysis suffers from pseudoreplication (Milinski, 1997). A red-bellied or grey-bellied dummy was presented for five minutes very close (7–13 cm) to a male's nest. After a pause of ten minutes the alternative dummy was presented. This was repeated several times per male using ten different males. However, two males had eggs in their nests. The repeated presentation of dummies may have caused sequence effects (Milinski, 1997). But the most serious problem is that all bites against the red or the grey dummy were summed up, causing pseudoreplication. If we do the most conservative analysis (only first tests with the red and grey dummy, only males without eggs), then males are not addressing significantly more bites to the red dummy than to the grey one (Wilcoxon matched-pairs signed-ranks test, $n = 8$, $P = 0.61$)! If we take the mean number of bites per male (but exclude males with eggs), then the red-bellied dummy received more bites than the grey one, indeed (Wilcoxon matched-pairs signed-ranks test, $n = 8$, $P = 0.012$). Yet this was not that self-evident, because several other studies failed to show an aggression-releasing effect of a red belly (for a review see Rowland, 1994). For example, Rowland (1982; Rowland & Sevenster, 1985) found that when he simultaneously presented a dummy with a red belly and another one without, the latter was significantly more often attacked by the territory owner.

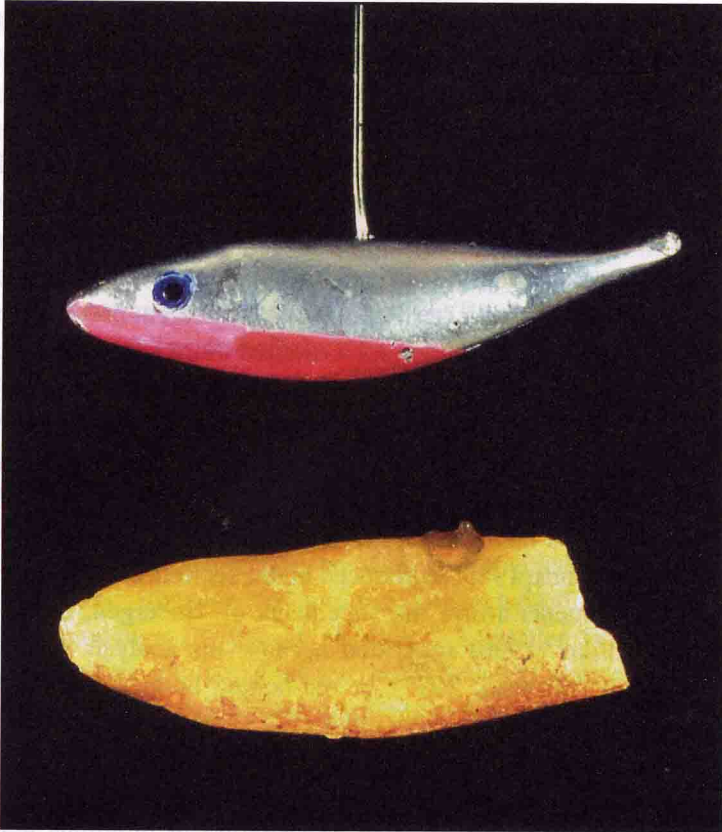


Figure 1. Dummies of male three-spined sticklebacks used in behavioural research by W.J. Rowland in the 1980's–1990's and by N. Tinbergen and co-workers in the 1930's–1940's.

One explanation for this discrepancy concerns differences in the red colouration used in the various studies to test its aggression-releasing effect. Tinbergen and co-workers made their dummies out of wax and the red belly was applied with a mix of red powder and shellac. I was very lucky and surprised to find the remainder (something more than half a fish measuring about 4.4 cm; Fig. 1) of such a dummy of a stickleback male during the preparations for a renovation of the aquarium rooms in Leiden. I was in charge of the renovations, and in about 1985 I found the jewel somewhere in a dusty corner of the big (70 m²) aquarium room on the fifth floor of the tower (“Torengbouw”) of the Zoology building (van der Klaauw Laboratory).

Piet Sevenster identified it as a wax dummy of a male used by Niko Tinbergen and his students. Piet must have foreseen this find when he wrote in our 1983 paper: "Some of Tinbergen's early paraffin dummies are still available in our laboratory." Traces of the red colour that was applied with shellac were still visible on the ventral side. Piet assured me that the intensity and hue of the red colour were still very well comparable to the colouration at the time of usage. I carefully dropped the dummy in an envelope, wrote "Tinbergen dummy" on it and put it in a cupboard in my room on the fourth floor. When I moved to Bern, Switzerland in 1988 to join the behavioural ecology research-group of Manfred Milinski, I left the dummy in the cupboard in Leiden. That was a big mistake. The dummy got lost, Enja Feuth-de Bruijn told me, likely after the retirement of Piet in 1989. Stickleback research disappeared in Leiden (and from the Netherlands until recently: Niels Dingemanse introduced it again at the University of Groningen, e.g., Dingemanse et al., 2009) and was replaced by research on birds. The aquarium rooms were made suitable for bird keeping. Unfortunately, during the transformation of research topics and researchers the dummy was lost.

There is a striking difference between the red of Tinbergen's wax dummy and the red of Rowland's plastic dummy (Fig. 1). "Rowland's red colour appears stronger, mainly due to a difference in contrast with the body colour, in hue (Rowland's red is less orange than Tinbergen's colour) and to some extent in colour intensity" (Bakker & Milinski, 1993). The strong red of Rowland's dummy had an intimidating effect on the territory owner rather than an aggression-releasing effect. Rowland admits that "It is thus possible that the colouration of these dummies was supernormal" (Rowland et al., 1995). The intimidating effect of red was also noted by Tinbergen (1948) when he replaced a territory owner by a dummy. A dummy with a red belly was more effective in inhibiting rival males from intruding into the territory than a non-red dummy was. Male red colouration thus has a dual effect: provocation and intimidation by activating both aggression and fear.

Whether aggression or fear dominates depends on many factors, like the relative redness of the rival (e.g., Sevenster, 1949; Fig. 1), how close the rival is to the nest as aggression increases closer to the nest (van Iersel, 1958; Rowland, 1994), and whether the male is inside his territory or on neutral ground (Rowland et al., 1995; Bolyard & Rowland, 1996). The context-dependent response to red was nicely demonstrated by Rowland and co-workers. They quantified male aggression against video playbacks that were presented on

monitors manipulated for the intensity of the red channel (Rowland et al., 1995; Bolyard & Rowland, 1996).

It is obvious that the aggression-releasing effect of a red belly cannot account for the evolution of the red belly by intra-sexual selection and must be a secondary effect; it may be rather disadvantageous to its bearer to provoke aggression of rivals. Yet male-male competition might have played a role in the evolution of the male's red breeding colouration through its intimidating effect on rivals. The advantage of a red belly in intra-sexual selection is evident from the increased probability of winning of males with high red scores in male-male competition when new territories are settled (Bakker & Sevenster, 1983; Bakker, 1994a; McKinnon, 1996; Baube, 1997; but see FitzGerald & Kedney, 1987; Rowland, 1989; and Bakker, 1994a). Red has an intimidating effect on rivals, so that redder males attack faster (Baube, 1997). The male that attacks first has a greater probability of winning a dominance fight (FitzGerald & Kedney, 1987; Bakker et al., 1989; Baube, 1997; Guderley & Couture, 2005). Thus being red has clear fitness advantages.

The advantages are further augmented by female mating preferences for redder males (Milinski & Bakker, 1990; for a recent review see McLennan, 2007). Interestingly, male-male competition amplifies the differences in redness between males (Candolin, 1999a) and increases the honesty of the red signal with respect to parental ability (Candolin, 2000a, b). Redness is associated with various male qualities (see McLennan, 2007 for a review), though not universally so. Especially its relationship with physical condition (e.g., Milinski & Bakker, 1990; Bakker & Mundwiler, 1994) and aggressiveness (e.g., Rowland, 1984; McLennan & McPhail, 1989; McKinnon, 1996) makes redness an honest intimidating factor signalling resource holding power. McLennan et al. (1988) suggested, however, that the evolution of colour patterns in the Gasterosteidae is more strongly correlated with inter- than with intra-sexual selection.

One issue regarding redness is still unclear and should be tackled in future research. Most studies measured one aspect of redness. It is therefore equivocal which aspect is important in intra- and inter-sexual selection. Some researchers measured red intensity, others red area (relative to lateral body area). Of course, the assessment of colour variables has become more accurate since our 1983 study. In the 1980's human-based colour scales were practised, followed in the 1990's by digital photography and measurement of the colour variables using a densitometer or image analysis software. In the

past decade, reflection spectrophotometry has been more often applied. The latter method is the most accurate because it is independent of human vision. Colour vision in sticklebacks, however, is roughly comparable to human vision (Rowe et al., 2006), so that, at least for the judgment of red colouration, different methods may give a comparable ranking of males (Bakker, 1993; Rowe et al., 2006). One should realize though that less accurate methods may be too conservative to find significant effects. In our 1983 paper and in Bakker (1986, 1994a) I used a four-point colour scale that predominantly ranked red area but also included red intensity. Rowland (1984, 1989) probably used a similar ranking system. Baube's (1997) nine-point colour scale was solely based on red area. In some studies, females preferred males with the most intense red colouration (e.g., Milinski & Bakker, 1990; Bakker, 1993; Bakker & Mundwiler, 1994), but males with the relatively largest red area in others (e.g., Candolin, 1999a). Candolin (e.g., 1999a, b) measured various aspect of redness but got the most consistent effects for red area. In inter-sexual selection, the exact hue of the orange-red belly seemed less important in one study (Baube et al., 1995) but explained choice behaviour in another (Bakker et al., 1999). Thus there is an obvious need for studies that compare the importance of various aspects of redness, when possible combined with ultraviolet signals, in intra- and inter-sexual selection. Most ideally these studies should cover inter-population variation as well.

Other determinants of dominance

There are probably more determinants of dominance in sticklebacks that we did not consider in our 1983 paper. The most obvious one is body size, which was excluded by matching the contestants as much as possible for body size in our and almost all other stickleback studies on dominance. Surprisingly only one experimental study considered body size difference (reviewed in Rowland, 1994), which is probably the most universal determinant of dominance in the animal kingdom. Body size was an important determinant of dominance when differences in body mass between stickleback males exceeded 15% (Rowland, 1989).

Another potential determinant of dominance may be ultraviolet (UV) reflections of male sticklebacks. UV signals have been excluded thus far as dominance tests were performed under artificial illumination that hardly contains UV wavelengths. Recent studies found that sticklebacks possess UV

photoreceptors (Rowe et al., 2004), and that male sticklebacks reflect in the UV (Rick et al., 2004). Territorial aggression tests revealed that males directed more aggression to opponents under full-spectrum light including UV than to males seen under illumination excluding UV (Rick & Bakker, 2008a). So UV signals may be another determinant of dominance that should be investigated, especially because UV signals are at least as important as red colouration in female mate-choice of sticklebacks (Rick & Bakker, 2008b).

There is no evidence that in sticklebacks other sensory systems are involved in establishing dominance relationships (see excellent review of McLennan, 2007). However, a potential candidate may be olfactory cues. It was generally believed for a long time that olfaction does not play a prominent role in stickleback life (reviewed in Rowland, 1994) but this view is changing (e.g., Reusch et al., 2001; see review by McLennan, 2007). For instance, in a mate-choice context kin recognition by females is triggered by olfactory cues (Mehlis et al., 2008). Whether olfactory cues also play a role in male-male competition was tested by quantifying aggression of territorial males against two identical computer animations (the modern equivalent of dummies: Künzler & Bakker, 1998) that differed in the scent in front of the animations. In front of one animation water conditioned by a familiar brother was introduced, and in front of the other animation water of an unfamiliar unrelated male was introduced (Mehlis et al., in press). Males were, however, equally aggressive against both animations. Yet familiarity may play a role in a competitive context (Utne-Palm & Hart, 2000).

In conclusion, proximate studies on dominance in sticklebacks are accumulating, so our 1983 paper marked rather the beginning of a revived interest in proximate factors. I expect in the future a further intensification of studies on dominance in sticklebacks, especially of genetic studies that will explore the molecular basis of complex traits using genome sequence data (Kingsley & Peichel, 2007). These will then form the basis to study genetic population differences in order to understand adaptive evolution of dominance in sticklebacks.

Acknowledgements

I want to dedicate this contribution to two persons who decisively influenced my scientific interests. First, I would like to dedicate it to the memory of William (Bill) J. Rowland, who suddenly died in 2004. He very much stimulated my interest in sexual selection in sticklebacks. Second, I would like to dedicate it to the 85th birthday of Piet Sevenster, who taught me everything about sticklebacks and science.

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