Stickleback Behavior: A Brief Overview

Daniel Bagur
25 Penrheidol, Penparcau, Aberystwyth, Ceredigion, Wales, U.K., SY23 1QW
drbagur@postmaster.co.uk

They're unafraid to take on a fish 30 times their size. They're hardy enough to live in both the smallest freshwater streams and in the middle of the Atlantic Ocean. And behaviorally they're among the most fascinating and most-studied fishes in the world. As a marine and freshwater biologist, I've spent a great deal of time observing and admiring sticklebacks, and keeping up with current research that's constantly shedding new light on the richness of their behavior. How do sticklebacks live their lives? What are the most interesting aspects of their behavior? And how do such small fishes thrive in a world of comparative giants? These are some of the questions I explore in this all-too-brief introduction to stickleback behavior.

Morphology, Diversity and Distribution

Sticklebacks are dressed for battle, possessing large, overlapping, bony plates along their flanks and strong, erect spines. When their spines are locked into the upright position they resemble the spears and shields of Roman soldiers. Aside from these plates their skin is bare and scaleless. Shining silver with flecks of brown and green, sticklebacks can appear bluish in seawater.

Sticklebacks (family Gasterosteidae) are widely distributed between 35° and 74° in the northern hemisphere. The seven (or more) species are found in the sea, in estuaries, and in fresh water. In North America several species may occur together. Some species are anadromous, migrating from the sea into freshwater to breed. Other species spend the whole of their lives living in either salt water or fresh water. Sticklebacks are infrequently found in fast-flowing water as they are not very strong swimmers and are simply washed away from such places. Threespine sticklebacks (*Gasterosteus aculeatus*, Fig. 1) have even been found in the middle of the Atlantic Ocean, living just below the surface. This population was discovered by weather ships that just happened to be stationed in the area (Holmes, 1985).

Although sticklebacks are extremely sensitive—for example, they can detect temperature changes as small as 0.05°C (Bull, 1957)—they are very resilient fish, often surviving in water too polluted for other fish species to live. The ninespine stickleback (*Pungitius pungitius*, Fig. 2) is the hardiest in terms of dwindling oxygen and adverse temperatures and often exploits such waters, avoiding other fishes with which it would compete for food and territory (FitzGerald and Wootton, 1993).

Diet and Feeding

Sticklebacks are predominantly visual predators. Young fry feed on invertebrates, eventually including small fish as they grow (FitzGerald and Wootton, 1993). In the first few months of life threespine sticklebacks can increase their body weight by as much as 10% a day; as the fish grow this rate drops to about 2% a day in adults (Allen and Wootton, 1982).

Adult sticklebacks eat between 2.3 and 4.2 g of food a year (Wootton, 1999). They have very small teeth, which are essential for breaking up their prey. Being carnivorous, sticklebacks absorb around 90% of the food they consume, unlike herbivorous fishes, which have much lower absorption rates (Allen and Wootton, 1983). Interestingly, what makes threespine sticklebacks grow faster is not their ability to grab the most food fragments, but their ability to be selective and get the bigger fragments (Milinski, 1982).

Far from being stupid, sticklebacks make accurate risk assessments of their surroundings, and modify their feeding

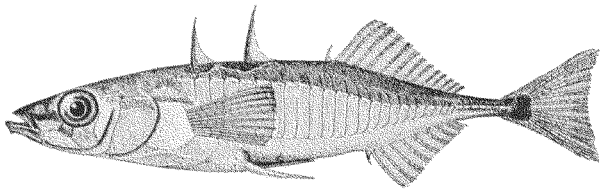

Fig. 1.
Threespine stickleback (*Gasterosteus aculeatus*).
Courtesy: NOAA Photo Library.

rates according to the numbers of predators in the area. Threespine sticklebacks make additional considerations. When offered a choice between a large shoal and a small shoal, a threespine stickleback will join the small shoal if it's hungry as this reduces competition for accessible food. If the fish is satiated it chooses the larger shoal as this group offers the best security against predators (Havre and FitzGerald, 1988). In fact, one researcher found that the hungrier the fish the looser the shoals became (Keenleyside, 1955).

Hungry sticklebacks also take more risks than do their satiated shoal mates. When feeding on daphnia, hungry sticklebacks lunge into the densest part of the swarm. More satiated sticklebacks attack the sparser regions. As noted by Milinski (1977), sticklebacks that feed in the denser part of the swarm are less aware of predators. In fact, only very hungry fish are prepared to take such a risk. Further research has shown that sticklebacks feed more slowly in the presence of predatory fish. Once food is found the sticklebacks feed in tight shoals gaining safety in numbers (FitzGerald and Wootton, 1993).

Courtship and Reproduction

The courtship behavior of sticklebacks is one of the best-known displays of color and behavior in the aquatic world. Sticklebacks become sexually mature between one and two years old and rarely live longer than four years (FitzGerald and Wootton, 1993). In the breeding season mature male threespine sticklebacks become aggressive and develop a bright red throat and belly which is beautifully contrasted by deep blue eyes. (Ninespine stickleback males have black breeding colors tinged with red.) Mature females become abdominally distended and their bellies turn slightly pink. Interestingly, in the Chehalis River in Washington, male threespine sticklebacks compete for territory with male Olympic mudminnows (*Novumbra hubbsi*), whose spawning color is black. This competition causes the male sticklebacks to turn black as well. By adopting the same color it seems that the sticklebacks are subjected to fewer attacks from territorial mudminnows (FitzGerald and Wootton, 1993).

In March, male sticklebacks claim a territory in shallow water. Threespine sticklebacks that spend their lives living in the same place are more ferociously territorial than their anadromous brethren (FitzGerald and Wootton, 1993). Fourspine sticklebacks (*Apeltes quadracus*, Fig. 3) in fresh water prefer to spawn over *Elodea* (Baker, 1971), whereas marine populations avoid fucus that is covered in filamentous algae (Courtenay and Keenleyside, 1983).

In North America, nest sites may be in short supply as up to four species of sticklebacks may be building their nests simultaneously. Once he claims a site a male defends it until June. Should an intruder present itself, the male adopts a vertical threat posture and swiftly and aggressively bites the intruder's fins. In the book *The New Compleat Angler*, the authors describe an incident in which a threespine stickleback was kept in an aquarium with a roach (a European cyprinid, *Rutilus rutilus*) that weighed over two pounds. The comparatively tiny stickleback attacked the roach repeatedly, biting at its fins until the pair had to be separated for the safety of the larger fish (Downes and Knowelden, 1983). Researchers have even observed ninespine sticklebacks fighting brook trout (*Salvelinus fontinalis*) (Gaudreault et al., 1986).

In the absence of such invasions the males set to work unearthing a pit in the ground by taking mouthfuls of earth and spitting them out away from the nest site. The fish then searches out fragments of vegetation from his territory and lugs them over to the pit. Rubbing himself against the fibrous plant matter he secretes some mucous from his kidneys (Wootton, 1999). This glues the loosely woven threads together. Once he is happy with the general size of the nest—which is approximately 5 cm wide and 8 cm long (Holmes, 1985)—he begins jostling the mass into shape with his body. When the nest has been crafted into the desired shape the male drives himself through the center to create a "spawning tunnel." After a few minor alterations and a final inspection the nest is ready. Ninespine sticklebacks make their nests amongst weeds about 10 cm above the ground. The fifteen-spine, or sea, stickleback (*Spinachia spinachia*) is entirely coastal and builds its apple-sized nest in algae below the low tide mark (FitzGerald and Wootton, 1993).

Once the nest is built the male turns his attention to the females. He opens his mouth, locks his spines into their defensive position, and performs a zigzag courtship dance. Rowland (1989) carried out some fascinating research into the mate choice of threespine sticklebacks. Using dummies of

Fig. 2.
Ninespine stickleback (*Pungitius pungitius*).
Photograph by John Lyons © Wisconsin DNR.

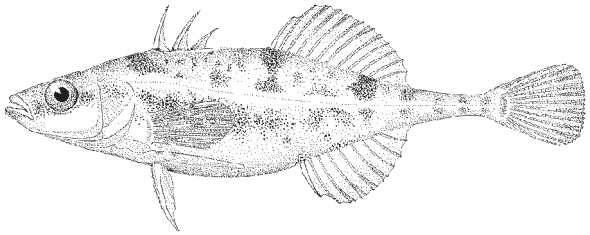

Fig. 3.
Fourspine stickleback (*Apeltes quadracus*).
Courtesy: Smithsonian Institution, National Museum of Natural History, Division of Fishes.

females, he watched as the males performed their courtship dances with greater vigor in front of the females with the most distended bellies. (Better-fed females produce slightly larger eggs [Fletcher and Wootton, 1995].) Interestingly, Rowland found that males preferred females with impossibly outsized bellies to those females that had the largest naturally occurring bellies. This is an example of what fish biologists call "super-normal stimulus"—something that has increased the earnings of many a Hollywood actress! Rowland also found that females preferred the largest males. This behavior makes sense because larger males expand their territories at the expense of smaller males and are better at defending their eggs (Stanley and Wootton, 1986). Highly aggressive males, however, mate less as they are always darting off to fight even if it means missing out on an eager female (Ward and FitzGerald, 1987). Male threespine sticklebacks that are very aggressive during the breeding season are also very daring around predators throughout the year (Huntingford, 1976, 1977). This research highlights stickleback individuality. Some are braver than others!

When the female accepts the male, he escorts her down to the nest, entices her into the tunnel, and quivers whilst touching her body until she lays her eggs. As soon as she has laid her eggs he fertilizes them and then chases her away. Males often breed with several females until they have between 300 and 1,000 eggs in the nest (Holmes, 1985). Some males have several nests at one time strewn throughout their territories. Females are less likely to refuse a male if his nest already contains eggs (Ridley and Rechten, 1981). Territorial male threespine sticklebacks have been observed darting over to a rival's nest and stealing a mouthful of eggs. They are often chased back into their own territory by an angry parent where they drop their haul into their own nest (Li and Owings, 1978). The female preference for nests containing eggs could simply be due to the increased boldness of the occupying male. If, however, the nest contained too many eggs then the female would choose to lay her eggs somewhere else. One explanation for this behavior is that the female is looking for a nest in which there's enough oxygen to keep the eggs alive (FitzGerald and Wootton, 1993).

Parental Care

In addition to being one of the few groups of fishes that build nests for their offspring, sticklebacks are excellent parents willing to risk everything in defense of their young. Males—except for fourspine stickleback and a form of threespine stickleback called the "white" stickleback—guard their nests and oxygenate the eggs by fanning them with their fins until they hatch. Their intense breeding colors steadily fade as they fan (Holmes, 1985). The more time males spend fanning their eggs, the more that hatch (FitzGerald and Wootton, 1993). Hatching time is temperature dependent. In one experiment the eggs hatched in six days at 25°C but took 40 days at 8°C (Wootton, 1976).

As the eggs develop the male tears extra holes in the nest to increase circulation and oxygen supply. Females and non-reproductive males form shoals during the breeding season. Although the breeding males are well equipped to deal with one or two intruders, these raiding parties often overpower the fathers and decimate the nests (FitzGerald and Wootton, 1993). Surprisingly, the fathers have a strategy to prevent this. When they see such a shoal approaching, they dash over to an area well away from the nest and adopt a frenzied feeding behavior. After seeing this, the shoal races past his nest and begins searching the "feeding grounds" for a meal (FitzGerald and Wootton, 1993). Not all sticklebacks are devoted fathers, however. The male white stickleback simply distributes the fertilized eggs amongst the algae and departs (MacDonald et al., 1995).

Some time between March and June the sticklebacks are born into a shallow, stillwater environment—early spring in extreme southern ranges and mid-summer in extreme northern ranges (Wootton, 1999). A newly hatched stickleback's first

sight is its highly protective father and numerous siblings. The father collects any wandering young into his mouth and spits them back into the nest in which they hatched. Just as he did before they emerged, the father continues to chase off intruders. Threespine stickleback males are less likely to flee from large predators such as rainbow trout if they are caring for eggs or young (Kynard, 1979). Intriguingly, the likelihood of threespine stickleback males staying with their young increases with both the number of offspring and their age (Pressley, 1981). Such parental care is vital as sticklebacks have poor adult survival (Wootton, 1999). The protective behavior of fathers ensures that a high proportion of the eggs survive to leave the nest. Proof of the stickleback fathers' competence comes from the fact that one recorded population of 4,000 increased to a vast 120,000 fish within one year (FitzGerald and Wootton, 1993). Another interesting aspect of paternal care is that sticklebacks reared by hand, in the absence of a father, show reduced predator response behavior in later life. It seems that the fish learn how to respond to predators from the father during their first few days (Huntingford et al., 1994).

Between 10 and 14 days after hatching the father leaves the fry to fend for themselves. With a huge number of natural predators, including invertebrates like dragonfly nymphs, this is a dangerous time (Wootton, 1999). The young fish gather together in large shoals, thereby gaining safety in numbers within the shallows. But how do such small fish deal with the threats presented by much larger predators?

Response to Predators

Sticklebacks deal with predators in different ways. Experiments show that some individuals dart off in an unpredictable direction and then dart for the closest cover. Others stand their ground remaining as still as possible (Huntingford and Giles, 1987). Their ability to lock their spines into position also provides some protection. Once they're locked the spines cannot be pushed back down by the jaws of a predator (FitzGerald and Wootton, 1993). Upon realizing this, predators often spit the fish out in disgust. Pike given an equal number of minnows and sticklebacks have been observed eating the minnows first (Hoogland et al., 1957).

The length of a stickleback's spines also influences its ability to protect itself. For example, ninespine sticklebacks are more vulnerable to predation than the longer-spined threespine species. As a result, the ninespine fish spends more time in the cover of weeds (Hoogland et al., 1957).

A stickleback's body armor seems to work, too. During an experiment in which a sample of sticklebacks was taken from one population, Reimchen (1988) found that over 13% of the fish showed evidence of having survived an attack (e.g., scars and broken spines).

Sticklebacks also appear to learn about the dangers that surround them. For example, a stickleback that survived an attack from a pike in the past reacts to the pike at a greater distance than does a stickleback that has never had a run-in with a pike (Huntingford et al., 1994).

Interestingly, sticklebacks that live in the presence of few predators—such as one population in Scotland—have all but lost their spines (Holmes, 1985).

Parasites

Predators aside, any body of water is teeming with potential parasites waiting to get a grip on their next victim. Sticklebacks are host to around 80 species of protozoan and macroparasites (Wootton, 1999). Males infested with such parasites are less vibrantly colored and in poorer condition than uninfested fish. One such parasite is the cestode *Schitstocephalus solidus*. This parasite enters a stickleback when it eats copepods that are already infested. Once consumed, the parasite enters the fish's abdomen, which often becomes bloated. In order for the parasite to complete its life cycle, the stickleback must be eaten by a bird (FitzGerald and Wootton, 1993). Infested fish have higher respiration rates and are more inclined to take advantage of the highly oxygenated surface layer of water. This makes them more at risk from birds. Once inside the bird the parasite matures sexually and releases its eggs, which are deposited back into the water with the birds' feces. Once in the water they are consumed by copepods and the cycle begins again (Wootton, 1999).

Sticklebacks as Research Tool

In the past, sticklebacks have been exploited for the production of fishmeal. Now, however, they are of little commercial or sporting importance. They are often kept in aquaria as they are small, survive well in captivity, and many populations are at low risk in terms of conservation status. For these reasons, along with their relatively short lifespan, they are widely used for scientific research and provide a valuable tool improving our understanding of fish ecology, behavior and biology. Despite the accessibility of sticklebacks, there is still much to learn about the lives of these intriguing fishes.

Literature Cited

Allen, J. R. M., and R. J. Wootton. 1982. Age, growth and rate of food consumption in an upland population of the three-spined stickleback, *Gasterosteus aculeatus* L. *Journal of Fish Biology* 21: 95-105.

———, and ———. 1983. Rate of food consumption in a population of three-spined sticklebacks, *Gasterosteus aculeatus*, estimated from the faecal production. *Environmental Biology of Fishes* 8: 157-162.

Baker, M. C. 1971. Habitat selection in fourspine sticklebacks (*Apeltes quadracus*). *American Midland Naturalist* 85: 239-242.

Bull, H. O. 1957. Behaviour: conditioned responses. *In*: Brown, M. E. (Ed.). *The physiology of fishes*. London: Academic Press.

Courtenay, S., and M. H. A. Keenleyside. 1983. Nest site selection by the fourspine stickleback, *Apeltes quadracus*. *Canadian Journal of Zoology* 61: 1443-1447.

Downes, S., and M. Knowelden. 1983. *The new compleat angler*. London: Orbis Publishing.

FitzGerald, G. J., and R. J. Wootton. 1993. The behavioural ecology of sticklebacks. *In*: Pitcher, T. J. (Ed.). *Behaviour of teleost fishes*. 2nd ed. London: Chapman & Hall.

Fletcher, D. A., and R. J. Wootton. 1995. A hierarchical response to differences in ration size in the reproductive performance of female three-spined sticklebacks. *Journal of Fish Biology* 46: 657-668.

Gaudreault, A., T. Miller, W. L. Montgomery, and G. J. FitzGerald. 1986. Interspecific interactions and diet of sympatric juvenile brook charr, *Salvelinus fontinalis*, and adult ninespine sticklebacks, *Pungitius pungitius*. *Journal of Fish Biology* 28: 133-140.

Havre, N. V., and G. J. FitzGerald. 1988. Shoaling and kin recognition in the threespine stickleback (*Gasterosteus aculeatus* L.). *Biology of Behaviour* 13: 190-201.

Holmes, N. 1985. *Along the riverbank—the living countryside*. London: Reader's Digest Association Ltd.

Hoogland, R. D., D. Morris, and N. Tinbergen. 1957. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as a means of defence against predators (*Perca* and *Esox*). *Behaviour* 10: 205-237.

Huntingford, F. A. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour* 24: 245-260.

———. 1977. Inter- and intra-specific aggression in male sticklebacks. *Copeia* 1977: 245-260.

———, and N. Giles, N. 1987. Individual variation in anti-predator responses in the three-spined stickleback (*Gasterosteus aculeatus* L.). *Ethology* 74: 205-210.

———, P. J. Wright, and J. F. Tierney. 1994. Adaptive variation in antipredator behaviour in threespine stickleback. *In*: Bell, M. A., and S. A. Foster (Eds.). *The evolutionary biology of the threespine stickleback*. London: Oxford University Press.

Keenleyside, M. H. A. 1955. Some aspects of schooling behaviour of fish. *Behaviour* 8: 183-248.

Kynard, B. E. 1979. Breeding behaviour of a lacustrine population of threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour* 67: 178-207.

Li, S. K., and D. H. Owings. 1978. Sexual selection in the three-spined stickleback. II. Nest raiding during the courtship phase. *Behaviour* 64: 298-304.

MacDonald, J. F., J. Bekkers, S. M. MacIsaac, and D. M. Blouw. 1995. Intertidal breeding and aerial development of embryos of a stickleback fish (*Gasterosteus*). *Behaviour* 132: 1183-1206.

Milinski, M. 1977. Do all members of a swarm suffer the same predation? *Zeitschrift für Tierpsychologie* 45: 373-388.

———. 1982. Optimal foraging: the influence of intraspecific competition on diet selection. *Behavioural Ecology and Sociobiology* 11: 109-115.

Pressley, P. H. 1981. Parental effort and the evolution of nest guarding tactics in the threespine stickleback, *Gasterosteus aculeatus*. *Evolution* 35: 282-295.

Reimchen, T. E. 1988. Inefficient predators and prey injuries in a population of giant stickleback. *Canadian Journal of Zoology* 66: 2036-2044.

Ridley, M., and C. Rechten. 1981. Female sticklebacks prefer to spawn with males whose nest contains eggs. *Behaviour* 76: 152-161.

Rowland, W. J. 1989. Mate choice and the supernormality effect in female sticklebacks (*Gasterosteus aculeatus*). *Behavioural Ecology and Sociobiology* 24: 433-438.

Stanley, B. V., and R. J. Wootton. 1986. Effects of ration and male density on the territoriality and nest-building of male three-spined sticklebacks (*Gasterosteus aculeatus* L.). *Animal Behaviour* 34: 527-535.

Ward, G., and G. J. FitzGerald. 1987. Male aggression and female mate choice in the threespine stickleback, *Gasterosteus aculeatus*. *Journal of Fish Biology* 30: 679-690.

Wootton, R. J. 1976. *The biology of the sticklebacks*. London: Academic Press.

———. 1999. *Ecology of teleost fishes*. 2nd ed. Dordrecht: Kluwer Academic Publishers.