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GEOGRAPHIC VARIATION IN AGONISTIC RESPONSES OF TERRITORIAL MALE BROOK STICKLEBACKS, *CULAEA INCONSTANS* [1]

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ABSTRACT. Territorial aggressive behavior was studied in male brook sticklebacks collected in Saskatoon, Saskatchewan; Oshkosh, Wisconsin; Ft. Atkinson, Wisconsin, and Urbana, Ohio. In the 20 h of observation 1,167 individual encounters with 3,305 separate aggressive displays were observed. Aggressive behavior was observed to be complex with at least 12 distinct aggressive display postures observed.

Fish from Saskatoon, Oshkosh, and Ft. Atkinson demonstrated several similarities in their territorial behavior. Charging was the most frequently observed display in all three populations. Also, biting, sigmoid and broadside displays were within the top four most frequent displays in all three populations of fish. The relative frequency of all aggressive postures were similar. Analysis of following event display frequencies (the frequency that one display follows another) also showed striking similarity in the behavior of territorial males from Wisconsin and Saskatchewan.

The Urbana population varied significantly from the other populations. The Urbana fish showed fewer postures, had shorter encounters, and did not display any attack postures (agonistic displays which typically lead to an attack or bite).

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INTRODUCTION

The stickleback family, Gasterosteidae, has been the subject of rather extensive behavioral studies. Aggressive behavior has been studied in the threespine stickleback, *Gasterosteus aculeatus* (van den Assem 1967, Huntingford 1981), in and between the fourspine stickleback, *Apeltes quadracus,* and the threespine stickleback (Rowland 1983) in *Pungitius pungitius,* the ninespine stickleback (Hoogland et al. 1957, and Huntingford 1977), and in the brook stickleback, *Culaea inconstans* (McKenzie 1969a + b, Reisman and Cade 1967.)

The brook stickleback is the only completely freshwater North American stickleback. It has a rather broad range in North America. It is found in ponds, lakes and streams from British Columbia to New Brunswick and from Nebraska to New York (Nelson 1969). Fish are observed to vary in several important morphological characteristics within this range. Significant differences in dorsal and pelvic spine length and in body depth have been observed (Nelson 1969). Spin length is generally greatest in the Ohio/Wisconsin region and is observed to decrease as one moves northwest within the range. Also the pelvic skeleton is largest in proportion to the body size in fish observed in the Wisconsin to New York populations and least developed in the northwestern populations (Nelson 1969).

The observation of clinal variation in morphological characteristics of the brook stickleback led us to investigate the behavioral responses of sticklebacks in relation to geographic distribution. In this study we report results on the agonistic behavior of territorial male fish from populations in Ohio to the Northwest area of Saskatoon, Saskatchewan, Canada. Males showed a

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very complex pattern of territorial aggressive behavior. The Urbana, Ohio fish varied most morphologically and in their behavior from the other populations studied. The fish from Saskatoon, Saskatchewan; Oshkosh, Wisconsin, and Ft. Atkinson, Wisconsin, showed surprising similarities in behavior considering the complexity observed in aggressive behavior.

METHODS AND MATERIALS

Fish were collected or purchased from Saskatoon, Saskatchewan; Ft. Atkinson, Wisconsin; Oshkosh, Wisconsin, and Urbana, Ohio (fig. 1). Prior to and throughout the duration of the study, environmental conditions were maintained at the optimum level for eliciting territorial reproductive behavior (Winn 1960, Reisman 1961, and Smith 1970). Since the sexes are difficult to distinguish until the reproductive cycle begins, eight to 12 fish from one area were placed in a 115-×-40-cm, 120-l tank. Reproductive males were selected for the study and four reproductive males were left in the tank. The tanks had plants and rocks to serve as cover along with material for nesting. Males used in this study showed dark skin coloration, black bar eyes and nest-building behavior.

The fish were observed through 4-×-10-cm slits in a black plastic screen hung in front of each tank. Fish from each area were observed for a total of five h each. The frequency and order of occurrence of the different display patterns were recorded. Observations consisted of 30-min periods during which the observer watched two territorial fish in the same tank for 15 min each, while another observer recorded these data.

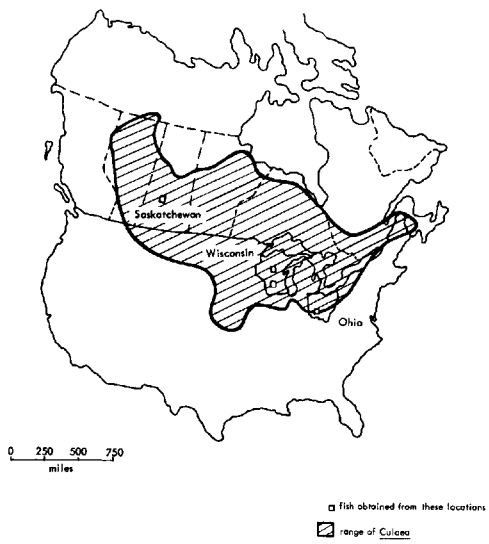

FIGURE 1. Range and collection sites of male sticklebacks (Trautman 1957).

DESCRIPTION OF AGONISTIC BEHAVIORAL DISPLAYS

FRONTAL APPROACH (fa) — The displaying fish moves towards the other territorial male with its head pointing towards the intruder.

BROADSIDE (bs) — The territorial fish orients itself at a right angle to the intruder.

LATERAL DISPLAY (la) — The territorial male orients itself in a side-by-side manner with the other fish typically with its head towards the other fish's tail.

SIGMOID (s) — The displaying fish contorts its body into the form of an "S" its head directed at the other fish.

SIGMOID ATKINSON (sa) — A low intensity "S" in which the territorial male's body is bent into only half an "S."

HEAD DOWN (hd) — As a reproductive male approaches another fish, its head is positioned down at approximately 45° angle.

TAILBEATING (tb) — A display in which the fish sways or beats its tail side-to-side at a rapid rate.

FOLLOW (fo) — A fish swims slowly in the direction of a fleeing fish. This appears to be a low intensity charge.

CHARGE (ch) — The displaying fish darts at another.

CIRCULAR FIGHTING (cf) — The two fish chase each other in a circle that has a diameter of five to 10 cm. The chasing is head to tail.

BITING (bi) — The displaying fish bites the other fish.

DRAGGING (dg) — After a bite the displaying fish holds onto the other and drags him for some distance.

TERMINATION (te) — The fish terminates the encounter by fleeing or by no longer participating in aggressive display.

RESULTS

TERRITORIAL BEHAVIOR. The total number of aggressive displays range from a low of 25 displays observed in males collected from Urbana, Ohio, to 1,724 displays

TABLE 1

Number and length of aggressive encounters between territorial male sticklebacks.

Location	Number of Displays	Number of Encounters
Urbana, Ohio	25	18
Ft. Atkinson, Wisconsin	837	297
Oshkosh, Wisconsin	618	168
Saskatoon, Canada	1729	593

TABLE 2

Average number of displays per encounter between two territorial males.

Area	Average Number of Displays Per Encounter
Urbana, Ohio	1.38
Ft. Atkinson, Wisconsin	2.82
Oshkosh, Wisconsin	3.68
Saskatoon, Canada	2.92

within the five-h observation period in the Saskatoon, Saskatchewan, males (table 1). The number of displays observed per unit time appears to increase as one moves from Ohio to the northwest part of the range of the brook stickleback (table 1). In some populations not all of the range of aggressive displays were observed.

The number of displays in an encounter ranged from one up to 15. The average length of an encounter ranged from 1.38 displays per encounter in the Urbana, Ohio, fish to 3.68 displays per encounter in the Oshkosh, Wisconsin, fish (table 2). There were no statistically significant differences in average encounter length between any of the populations.

In terms of the frequency of individual display occurrence within a group, it was observed that the Saskatoon, Oshkosh, and Ft. Atkinson fish showed several similarities. The charge was the highest frequency display in all three populations. The broadside, sigmoid, and bite were the next most commonly observed behaviors. Variation was observed in the relative frequencies of these behaviors among the three populations. However, the similarities between the three populations are striking. In the Urbana, Ohio, fish only three behaviors were observed. Two of the displays (broadside and sigmoid) were in the four most commonly observed behaviors in the three other populations (table 3). The third display (lateral display, la) was a high frequency display in the other three populations.

Each half-hour observation period consisted of observing two different male fish, each for 15 min. Table 4 shows the comparison of two fish and the frequency at

TABLE 3

Frequency of individual display postures within a geographic group.

Frequency	Urbana	Ft. Atkinson	Oshkosh	Saskatoon
1	bs* (40%)	ch (49%)	ch (25%)	ch (48%)
2	la (36%)	bi (18%)	s (20%)	bs (17%)
3	s (24%)	s (10%)	bs (17%)	bi (16%)
4	—	bs (6%)	bi (10%)	s (6%)
5		cf (5%)	la (7%)	fa (5%)
6		la (4%)	hd (6%)	fo (4%)
7		fa (4%)	fa (5%)	la (3%)
8		hd (2%)	tb (5%)	hd (1%)
9		sa (1%)	cf (4%)	tb (1%)
10		tb (1%)	fo (2%)	cf (1%)

*bs = broadside, ch = charging, la = lateral display, s = sigmoid display, bi = biting, cf = circular fighting, fa = frontal approach, hd = head down display, fo = follow, tb = tailbeating, sa = sigmoid atkinson, dg = dragging, te = termination.

TABLE 4

Frequency of individual display occurrence comparing two fish from the same collection point.

Saskatoon a		Saskatoon b		Ft. Atkin. a		Ft. Atkin. b	
ch*	38.0%	ch	42.0%	s	43.0%	s	41.0%
bs	26.6%	bi	22.0%	ch	27.0%	ch	19.0%
bi	12.4%	bs	19.0%	hd	15.0%	hd	17.0%
fo	10.4%	fo	3.0%	bs	6.0%	bs	17.0%
s	6.0%	la	3.0%	bi	4.0%	tb	6.0%
la	4.7%	s	3.0%	la	4.0%		
fa	1.9%	tb	3.0%				
		fa	2.9%				
		cf	2.0%				

*bs = broadside, ch = charging, la = lateral display, s = sigmoid display, bi = biting, cf = circular fighting, fa = frontal approach, hd = head down display, fo = follow, tb = tail-beating, sa = sigmoid atkinson, dg = dragging, te = termination.

which various displays were observed. These data indicate that the variance between two fish from the same collection point was as great or greater than the differences observed between fish collected from Oshkosh, Ft. Atkinson, and Saskatoon.

Another way to analyze stickleback aggressive behavior is to determine the frequency with which one aggressive behavioral posture follows another. When this was done, several interesting observations were made. The Wisconsin and Saskatoon fish showed many similarities, even though their behavioral displays were complex. The Urbana fish were strikingly different, again because of the low frequency of encounters (fig. 2 and table 5).

DISCUSSION

Clearly the territorial behavior of male brook sticklebacks is more complex than previously thought. We observed 12 distinctive aggressive displays. One display has not been described previously. We have named this display the "follow." In this display a territorial male slowly follows an intruding male out of his territory. It is

TABLE 5

Following event frequency; twenty most frequent display pairs.

Population: Urbana	Ft. Atkinson	Oshkosh	Saskatoon
la* → te 6(24%)	ch → ch 155(18%)	ch → ch 42(7%)	ch → bi 270(16%)
bs → te 6(24%)	ch → bi 119(14%)	ch → bi 39(6%)	ch → te 265(15%)
s → te 6(24%)	ch → te 109(13%)	ch → te 36(6%)	ch → ch 249(14%)
bs → s 4(16%)	bi → te 63(7%)	bi → te 32(5%)	bs → ch 206(12%)
la → bs 2(8%)	bi → ch 61(7%)	s → te 31(5%)	bi → te 162(9%)
la → s 1(4%)	s → te 42(5%)	ch → s 26(4%)	bi → ch 77(4%)
———	fo → te 24(3%)	la → s 23(4%)	s → te 50(3%)
———	bs → te 18(2%)	hd → te 19(3%)	fa → ch 42(2%)
———	cf → ch 16(2%)	bs → s 19(3%)	fo → te 42(2%)
———	cf → bi 16(2%)	bs → ch 19(3%)	bs → te 38(2%)
———	s → bs 13(1%)	bs → te 19(3%)	ch → bs 25(1%)
———	bi → cf 13(1%)	s → tb 18(3%)	bi → s 20(1%)
———	bi → bi 12(1%)	s → s 18(3%)	fa → te 17(1%)
———	la → te 11(1%)	s → cf 18(3%)	la → s 14(1%)
———	la → s 11(1%)	s → bs 15(2%)	bs → fo 14(1%)
———	bs → ch 10(1%)	bs → la 12(2%)	s → ch 13(1%)
———	ch → cf 10(1%)	bi → ch 11(2%)	la → bs 12(1%)
———	fa → te 9(1%)	bs → hd 10(2%)	bs → s 12(1%)
———	s → ch 9(1%)	bs → bs 10(2%)	la → te 11(1%)
———	fa → ch 8(1%)	bi → bi 9(1%)	s → bs 11(1%)

*bs = broadside, ch = charging, la = lateral display, s = sigmoid display, bi = biting, cf = circular fighting, fa = frontal approach, hd = head down display, fo = follow, tb = tailbeating, sa = sigmoid atkinson, dg = dragging, te = termination.

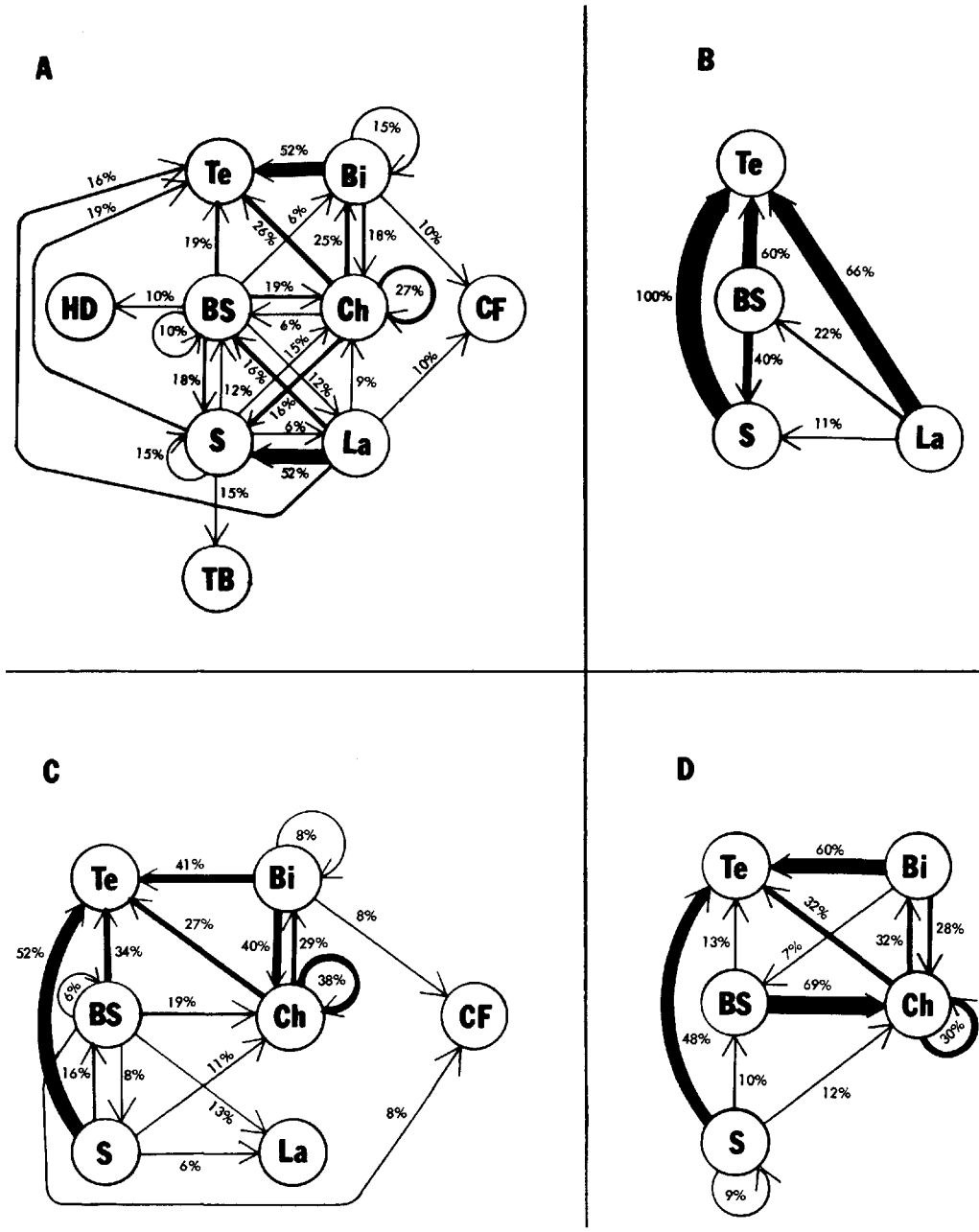

FIGURE 2. Following event frequency. This figure lists the frequency at which one display was followed by another. A. Oshkosh, B. Urbana, C. Ft. Atkinson, D. Saskatoon. bs = broadside, ch = charging, la = lateral display, s = sigmoid, bi = biting, cf = circular fighting, fa = frontal approach, hd = head down, fo = follow, tb = tailbeating, sa = sigmoid atkinson, dg = dragging, te = termination.

easily differentiated from a charge. Both the charge and follow display were observed in the same fish during a 15-min observation time period. The follow was observed in fish from all but the Urbana population. In the Ft. Atkinson fish we observed another unique behavior which seemed to be a variation of the sigmoid posture. This appears to be a low intensity sigmoid in which the fish bends its body in a partial "S." Individual Ft. Atkinson fish were observed to use both postures.

The Oshkosh, Ft. Atkinson, and Saskatoon fish showed many similarities in behavior. Frequency and frequency order in which displays were observed were similar in all three populations. The charge was the most frequently observed display in these three populations. The next most commonly observed behaviors were the sigmoid, broadside, and bite. With these three displays, the order was slightly different in each population. Even as one goes down the rest of the list ranking frequency of individual displays, one observes many similarities in the three populations. The variation in behavior in the three populations seems no greater than between various individuals within the same population (tables 3 and 4). Encounter length was similar in all three populations. The average encounter length varied from 2.82 to 3.68 (table 2). Following event frequencies were similar to the extent that our study permits analysis. The greatest variation between populations was the number of displays observed during the five-h period. A three-fold difference in the number of displays observed was found.

The behavior of the Urbana fish varied significantly from the other three populations studied. The Urbana fish showed the fewest displays, fewest number of different displays, shortest encounters and very few attack postures (charging, biting, and dragging). The Urbana fish showed the greatest difference in morphological characteristics when comparing the four populations. A distinct difference in spine length in the Urbana fish was observed. The spines were larger. Spine length was similar in fish from the other three populations studied. Also, territorial males from Urbana were significantly lighter in coloration than other territorial fish. We could not distinguish by color males from the other three populations. It is not clear if the difference in coloration of the Urbana territorial males accounts for the significant differences in aggressive behavior observed within this population. This possibility needs to be studied in the brook stickleback to see if it is similar to the threespine stickleback in this regard (Pelkwijk and Tinbergen 1937). Another possible explanation for the dramatic difference in the behavioral patterns found in the Urbana fish is their geographical isolation from other populations (Trautman 1957). Further work is needed to determine if the differences in behavior observed in the Urbana fish is a reflection of clinal variation in morphology (Nelson 1969) or if it is the result of their geographic isolation (Trautman 1957). More populations from Ohio, Michigan, and Wisconsin need to be studied.

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