

Conservation and variation in the agonistic repertoire of the brook stickleback, *Culaea inconstans* (Kirtland)

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Abstract Interpopulation variability in behaviour is thought to play a role in the production of biological diversity on this planet. The brook stickleback, *Culaea inconstans*, is a prime candidate for investigations of such variability because mtDNA sequences indicate that it diverged into two distinct lineages 3.6–4.8 mya; more than enough time for differences to evolve. In this paper we show that, despite long periods of allopatry, the brook stickleback's agonistic repertoire has remained quite conservative. Existing variability represents shifts in the mean population frequencies (performance parameter) of some displays, rather than changes in the composition of the agonistic repertoire itself (presence or absence of behavioural elements).

Keywords Aggression · Performance · Interpopulation · Nebraska · Ontario

Introduction

Interpopulation variability in the structure (character description) and/or frequency of behavioural displays

has been documented for a wide variety of taxa, including insects, teleost fish, reptiles, birds and mammals (Martins et al. 1998 and references therein; see also Foster 1999). Although it is often implicated in speciation and the production of biological diversity (Foster and Endler 1999; Lahti et al. 2002 and references therein), we know little about the relationship between such behavioural variability and speciation. For example, how is the amount of interpopulation variability within a species related to the probability that at least one population, or group of populations, will undergo irreversible change? Is speciation more likely to be completed if variability is spread randomly throughout populations or concentrated in a few populations? What percentage of the variability in a species is carried by small, isolated (peripheral) populations that are easily extirpated?

To answer these questions, we need to delineate the distribution of behavioural variability in as many populations of a species as possible. The brook stickleback, *Culaea inconstans*, is an intriguing species with which to begin such an investigation because the specific designation “*inconstans*” means “changeable” in Latin and reflects the morphological variability of the group. Recently, molecular phylogeographic evidence has suggested that *Culaea inconstans* was subdivided into two genetically distinct lineages (9.2% sequence divergence: Mattern 2006) during the Pliocene (3.6–4.8 mya: Gach 1996; Mattern 2006), more than enough time for behavioural

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divergence to occur. The two lineages survived the Pleistocene glaciations in Mississippian (lineage M) and Atlantic (lineage A) refugia and are almost completely allopatric today.

This study represents the first attempt to describe, systematically, behavioural variability in the brook stickleback and to begin building a database comparable to that collected for its threespine relatives (Wootton 1976 and references therein). We examined interpopulation variability in the agonistic behaviours of courting males from three different populations (Sutherland, Nebraska [lineage M]; Algonquin Park and Tooley Creek, central and southern Ontario [lineage A]). All male gasterosteids in the [*Gasterosteus (Culaea, Pungitius)*] clade (Mattern and McLennan 2004) compete for access to territories, build nests, court females, then defend and care for the eggs and young fish (Wootton 1976 and references therein). The male agonistic repertoire is extensive in this group, encompassing chasing, biting, circle fighting and a rich assortment of threat behaviours, the structure of which appears to be conservative within the clade (see e.g., Pelkewijk and Tinbergen 1937; McKenzie 1969). Given such a large number of behavioural elements, the potential exists for selection to fine tune male agonistic repertoires in response to changes in environmental variables such as density, availability of nest sites and/or mates, and predation pressure (Huntingford 1982). Change may be expressed either overtly as differences in the composition of the repertoire itself (the expression of novel traits or loss of behavioural elements), or more subtly in shifts of the mean population performance factors (such as the duration or frequency of displays). This latter component has been documented for the threespine stickleback, in which different levels of aggressiveness, measured by recording the number of bites or bites plus charges and lunges a focal male directs towards an intruder enclosed within a glass tube, have been reported for numerous populations (e.g., Huntingford 1982; Gaudreault and FitzGerald 1985; Giles and Huntingford 1985; Scotti and Foster 2007).

Given that the brook stickleback populations are closely related, we expect to document some degree of behavioural conservatism (plesiomorphic traits) in addition to interpopulational differences. Overall, we are interested in answering two particular questions in this study: First, how much of the

agonistic behavioural repertoire is shared among the three populations and how much of it is unique to a particular population? And second, is behavioural variability more likely to come packaged as changes in performance parameters, in the presence/absence of traits, or both? This study thus represents the starting point in the search for answers to the general questions raised in the first paragraph, with the patterns presented herein acting as hypotheses for the distribution of behavioural variability and stasis within *Culaea inconstans* that can be tested with the addition of new populations.

Materials and methods

Adult brook sticklebacks were collected in early May of 2004 from Sutherland Creek, Nebraska (41°08'13N, 101°07'28W), Ring-Neck Pond, Algonquin Park, Ontario (45°34'52N, 78°23'19W) in 1993 and Tooley Creek, Ontario (43°52'11N, 78°46'53W) in 1992. Sutherland Creek runs between farmland and is characterized by clear water flowing gently over a soft silt and pebble substrate, while Tooley Creek is more marsh-like, with slow-moving turbid water frequently interrupted by patches of grass. Ring-Neck Pond is large, shallow, and heavily vegetated with clear water and a muddy substrate. In the initial investigations, changes in male color and/or behaviour across a complete breeding cycle were charted for a single population (Tooley Creek: McLennan 1993; Nebraska: Ward and McLennan 2006a,b). In this study, the extent of variability amongst populations was investigated by an interpopulation comparison of male-male aggression during the courtship phase.

Experiments were performed between May and August in 1992 (Tooley Creek), 1993 (Algonquin Park) and 2004 (Nebraska). The experimental protocol was identical across all experimental years: The fish were held in the lab under winter conditions (10–12°C; 12 h:12 h light–dark cycle) and high population density (Reisman 1961; Reisman and Cade 1967) in a 200-l opaque tank supplied with the continual flow-through of dechlorinated water to slow the reproductive cycle. Several sticks and stones were provided for shelter. Individuals were removed as needed and placed in a series of large community tanks that were maintained at optimal summer breeding conditions (16 h light:8 h dark,

16°C, low population density). Under these environmental conditions, fish usually became reproductively active within three days. Males that showed evidence of reproductive motivation (nest-building activity and/or the presence of nuptial colouration) were moved to individual 58-l test aquaria supplied with *Hygrophila* rooted in a peat-filled 10 cm diameter plastic dish, and an abundance of nesting material consisting of soft algae, grasses, and twigs collected from a nearby marsh. Males were permitted to build a nest and all of the males used in this study began building a nest within 72 h of introduction. Males that failed to build a nest within 5 days were replaced.

Once a male had completed his nest, he was presented with a territorial male from his population enclosed within a 12×5.5 cm glass jar, capped with fine mesh, and the interactions videotaped for a 5 min period. The frequencies of nine behaviours (Table 1) were scored from video playback using a

Sony Hi-8 digital recorder. The agonistic repertoire of the brook stickleback has been described in detail (Hall 1956; McKenzie 1969; Burks et al. 1985) and all of the behaviours examined in this study are easily identifiable, and comparable, across populations and studies. The nine behaviours investigated here represent the entirety of the male brook stickleback’s agonistic repertoire, although the nomenclature used in previous descriptions occasionally deviates to a small extent (e.g. ‘charge’ vs ‘lunge’). Experimental males were used only once, and all spawned successfully following the captive presentation.

Interpopulation variability in the frequency of displays was analyzed statistically with a MANOVA, followed by post-hoc tests to determine the source(s) of variation for each behavioural element. A set of canonical axes were constructed and the difference between populations in aggressive behaviour was visualized in multivariate space. The interaction

Table 1 Nine agonistic behaviours observed in male brook sticklebacks

Display	Description
Approach	Male approaches the intruder, usually in a direct line, with slow to normal swimming motions
Lunge	Male pauses, oriented towards the intruder, then moves rapidly forward, stopping short of striking the jar. Corresponds to “charge” of McKenzie (1969)
Head-down	Male assumes a position 45–90° head-down to the substrate, all fins and spines flared
Broadside	Male assumes a horizontal, slightly concave posture, close to the intruder, with dorsal and pelvic spines flared and pectoral fins erect. This display has generally been subdivided depending upon orientation of the focal male relative to the intruder into broadside (perpendicular) and lateral displays. Both orientations were combined in this study because movement of the captive fish often changed the relative orientation of the focal male, without the focal male himself moving. Broadside is generally thought to function as an assessment display during which males can measure themselves against their opponent (at least in terms of body size)
Dorsal roll	Male modifies a broadside threat display by tilting his body on a sagittal 45° angle towards the intruder, dorsal spines erect; thought to be a submissive display (McKenzie 1969)
Circle	Male circles the stimulus fish while engaged in the lateral broadside posture described above. In free fish circling is often a prelude to fighting, in which males align head to tail and chase one another in a tight circle, attempting to bite each other’s caudal peduncle or caudal fin
S-display	Male curves his body into a horizontal, sigmoid posture, usually while directly facing the stimulus fish. Spines may or may not be flared
Tailbeating	Male beats his tail laterally in a slow (approximately 4–10 beats per second), exaggerated manner. Pectoral fins are sculled rapidly forward opposing the forward thrust of the tail beat so the fish remains in one place
Bite	Male approaches the intruder and snaps at the jar

Definitions follow Hall (1956), McKenzie (1969), and Burks et al. (1985)

between traits in each population was investigated with Pearson correlations. All statistical analyses were performed using the statistics package SPSS.

Results

In total, 2,085 agonistic displays were recorded from Nebraskan males ($n=16$), 1,750 from Tooley Creek males ($n=33$) and 1,051 from Algonquin Park males ($n=17$; Table 2). The entire repertoire of nine aggressive displays was observed in all populations and none of the 66 males performed any novel behaviour. The MANOVA examining the effect of population on aggressive behaviour indicated highly significant differences between the groups (Wilks' $\lambda=0.14$, $F_{9,55}=37.54$, $P<0.001$). Subsequent univariate tests revealed that Nebraskan males performed significantly more lunging, tailbeating, biting, head-down threat and dorsal roll displays than either the Algonquin Park or Tooley Creek fish (Fig. 1), as well as a higher number of total aggressive displays per individual (One-way ANOVA: $F=11.39$, $P=0.002$: vs Algonquin, $P<0.001$; vs Tooley, $P<0.001$; Fig. 2). Tooley Creek males used S-threats significantly more often than Algonquin Park males ($F=3.94$, $P=0.04$). There was no difference among the three populations in the number of broadside displays ($F=1.17$, $P=0.32$), circle displays ($F=1.57$, $P=0.22$) or frontal approaches ($F=2.01$, $P=0.14$) performed. Except that

the frequency of S-threat displays performed by Algonquin males was more similar to that performed by Nebraskan males, the frequencies of all displays performed by Algonquin males and Tooley Creek males were statistically indistinguishable (Table 2 and Fig. 1).

Only the first canonical discriminant axis was significant ($\chi^2=108.02$, $df=18$, $P<0.001$) and accounted for 84% of the variation in behaviour. The first axis primarily separated the Nebraskan population from the Algonquin Park and Tooley Creek populations, the former being associated with greater frequencies of head-down threat, lunge, tailbeating and dorsal rolls (Fig. 3). The second axis failed to reliably separate Algonquin Park and Tooley Creek males. Individuals of both of these populations that were associated with the positive end of the axis performed greater frequencies of S-threats and frontal approaches but fewer circle threats, bites and broadside threats.

Lunge, broadside, tailbeat, bite and circle formed a positively correlated block of behaviours (agonistic suite) in all three populations, while S-threat was associated negatively with these behaviours in the Tooley Creek fish (Table 3).

Discussion

Most of the interpopulation variability in behavioural traits that has been reported in the literature involves changes to performance variables such as intensity or frequency rather than the addition or loss of behaviours (Ruzzante 1994; Martins et al. 1998; Price 1999), which is what the present study found. The composition of the male brook stickleback's agonistic repertoire was identical across three populations despite their separation in time and space. All males performed the full complement of nine aggressive displays. Comparing our results with previous descriptive studies of this species supports the suggestion that the components of the agonistic repertoire are stable across the species range. All of the displays described herein have been reported in two A-lineage populations from Ithaca, New York (Hall 1956) and London, Ontario (McKenzie 1969) as well as in three M-lineage populations from Saskatoon, Saskatchewan, Ft. Atkinson, Wisconsin and Oshkosh, Wisconsin (Burks et al. 1985).

Table 2 Mean frequencies of nine aggressive behaviours (se) and total aggressive displays performed by male brook sticklebacks towards conspecific male territorial intruders over a 5 min period

Behaviour	Nebraska ($n=16$)	Algonquin Park ($n=17$)	Tooley Creek ($n=33$)
Broadside threat	26.13 (5.55)	21.47 (2.21)	19.76 (1.70)
Tailbeat	32.25 (8.01)	9.70 (2.06)	6.63 (0.96)
S-threat	1.19 (0.41)	0.94 (2.40)	2.61 (0.50)
Circle threat	5.69 (2.17)	5.76 (2.58)	2.61 (0.51)
Bite	30.19 (5.13)	19.47 (4.27)	13.61 (1.96)
Head-down threat	14.06 (1.84)	0.12 (0.08)	2.0 (0.47)
Lunge	15.12 (3.80)	1.47 (0.27)	0.91 (0.26)
Approach	4.56 (0.77)	2.65 (0.64)	3.39 (0.46)
Dorsal roll	1.13 (0.43)	0.23 (0.14)	0.15 (0.06)
Total displays per male	130.31	61.82	53.03

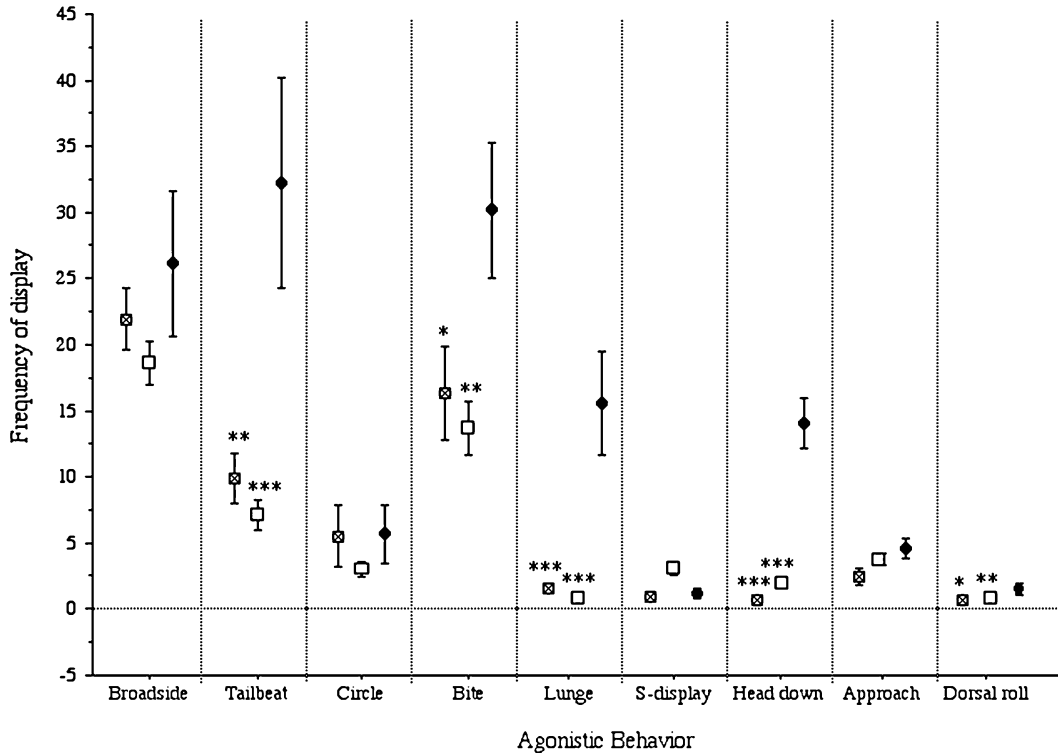


Fig. 1 Frequency (mean \pm standard error) of nine male agonistic behaviours in three populations of brook stickleback. *Closed circle* Nebraska ($n=16$); *open square* Tooley Creek, Ontario ($n=33$); *crossed square* Algonquin Park, Ontario ($n=17$).

Significance values are shown for comparisons between Nebraska and the other two populations. * $P<0.05$, ** $P<0.01$, *** $P<0.001$

While we did not observe any variability in repertoire composition amongst populations, we did uncover two differences in display frequencies. First, Tooley Creek males used the S-threat display more often than the

Algonquin Park fish. If the shape of the S-threat represents a compromise between the tendency to attack and the tendency to flee (Tinbergen 1951), then the “flight” tendency has been emphasized in the Tooley

Fig. 2 Total number of aggressive displays performed by male brook sticklebacks from Nebraska ($n=16$), Tooley Creek, Ontario ($n=33$), and Algonquin Park, Ontario ($n=17$). *Horizontal black bars* represent median values. *Upper and lower whiskers* represent maximum and minimum values, respectively. *Outliers* are shown as *open circles*. Significance values are shown for mean value comparisons between Nebraska and the other two populations. *** $P<0.001$

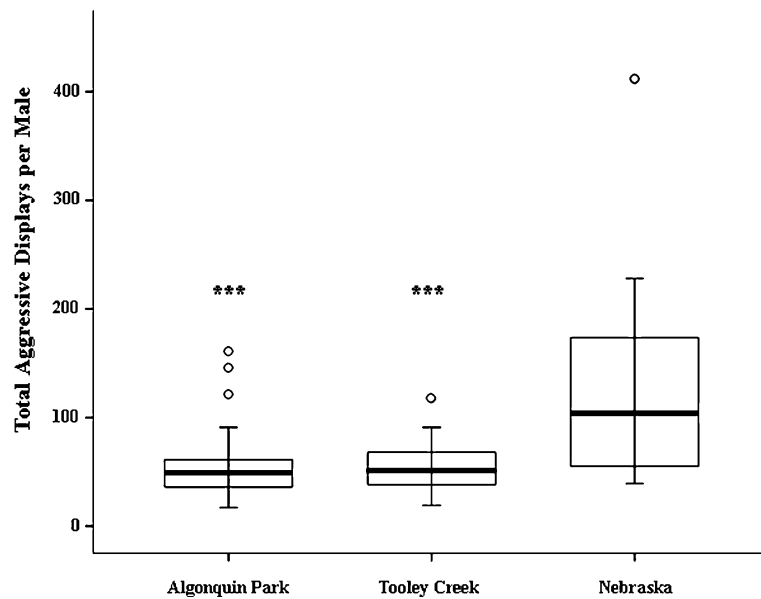
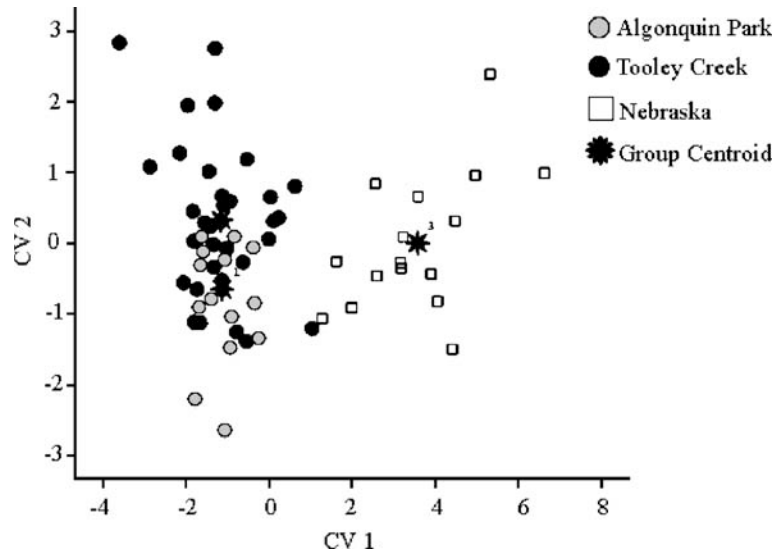


Fig. 3 Canonical variates analysis on the aggressive behaviour of three allopatric populations of brook stickleback. CV 1 accounts for 84% of the variation in behaviour



Creek fish. The number of S-threats was negatively correlated with all of the behaviours in the aggressive suite depicted in Table 3, which implies that these fish are either more fearful and/or more nervous than their counterparts from the other two populations. Although the relationship between S-threat and these behaviours was not significant in either Algonquin Park or Nebraskan males, it was in all cases positive, highlighting the subtle shift in the function of this

behaviour in the Tooley Creek population. Second, Nebraskan males showed higher frequencies of biting, lunging, tailbeating, dorsal threat displays and head-down threat displays, contributing to the general observation that males of this population are both more aggressive and more interactive than either the Tooley Creek or Algonquin males; the latter of whom did not differ in the total number of aggressive displays performed by individual males. This variability was only recorded over one year for each population, and as such may represent either ephemeral responses to local selective pressures (e.g., Huntingford 1982), or alternatively, may be fixed, heritable differences between populations. Resolution of this problem awaits further study.

Table 3 Pearson correlations (*r*) among agonistic behaviours in three brook stickleback populations

Behaviour	Nebraska (<i>n</i> =16)	Algonquin Park (<i>n</i> =17)	Tooley Creek (<i>n</i> =33)
Lunge–broadside	0.73 ^a	0.58 ^b	0.48 ^b
Lunge–tailbeat	0.87 ^a	0.54 ^c	0.39 ^c
Lunge–bite	0.93 ^a	0.54 ^c	0.65 ^a
Lunge–circle	0.80 ^a	0.55 ^c	0.45 ^b
Broadside–bite	0.87 ^a	0.62 ^b	0.53 ^a
Broadside–circle	0.84 ^a	0.70 ^b	0.68 ^a
Broadside–tailbeat	0.95 ^a	0.78 ^a	0.48 ^b
Tailbeat–bite	0.93 ^a	0.80 ^a	0.84 ^a
Tailbeat–circle	0.92 ^a	0.55 ^c	0.61 ^a
Circle–bite	0.83 ^a	0.65 ^b	0.62 ^a
S threat–broadside	NS	NS	−0.73 ^a
S threat–tailbeat	NS	NS	−0.53 ^a
S threat–circle	NS	NS	−0.43 ^b
S threat–bite	NS	NS	−0.61 ^a

^a Significant at the alpha=0.001 level
^b Significant at the alpha=0.01 level
^c Significant at the alpha=0.05 level

The aggressive traits comprising the agonistic repertoire of the brook stickleback were not independent from one another. Five of those traits, lunge, broadside threat, circle threat/fight, tailbeat and bite formed a correlated suite of behaviours in all three populations (see also the correlation between lunges and bites in three-spined sticklebacks; Huntingford 1976). McKenzie (1969) reported that the sequence ‘broadside–tailbeating–bite’ dominated the temporal pattern of aggressive encounters between adult male brook stickleback males from London, Ontario. The suite of correlated aggressive displays observed in this study mirrors that pattern of aggressive encounters, reconfirming the utility of such diagrams for studying sequences of behavioural performance. These behavioural correlations may have a genetic component.

Bakker (1986) showed that the intensities of juvenile, territorial and dominance aggression were genetically correlated to varying degrees in three-spined sticklebacks. Given the close phylogenetic relationship between the threespine and the brook stickleback (Mattern and McLennan 2004), we would expect similar mechanisms to eventually be uncovered for *C. inconstans*. Indeed, laboratory observations of Nebraskan males indicate that the intensity of aggression a male displays during male–male territorial contests is an accurate predictor of his likelihood of intruder attack during parental care (Ward and McLennan, unpublished data).

Although these data should be considered preliminary, our results, combined with those from previous studies, suggest that the patterns of similarities and differences in the agonistic repertoire may have been influenced by lineage affiliation. The two Atlantic lineage populations that we investigated (Algonquin Park and Tooley Creek) were more similar to one another in terms of aggressive intensity (less aggressive) than either was to the (more aggressive) representative from the Mississippian lineage (Nebraska). Burks et al. (1985) also reported that territorial males from lineage A (Urbana, Ohio) displayed fewer agonistic interactions, fewer displays, and briefer encounters than males from three M lineage populations (Saskatoon, Saskatchewan, Ft. Atkinson, Wisconsin and Oshkosh, Wisconsin). The addition of more populations from both clades is now needed to resolve whether the patterns of variability observed at the population level are maintained at the lineage scale of resolution (i.e. to clarify whether high levels of aggression are representative of the M-lineage as a whole or are particular to the Nebraskan population).

In summary, our results suggest that the composition of the brook stickleback's agonistic repertoire is relatively conservative over at least a moderate part of the species' range. Subtle differences in the frequency of behaviours are, however, apparent between populations (see Ishikawa and Mori 2000, for similar results with sexual behaviours in three populations of three-spined stickleback in Japan), and can contribute to population differences in the overall levels of male aggressive response towards a conspecific intruder. Given the extent of behavioural diversification documented for the North American Pacific coast *G. aculeatus* species group in as little as 12,000 years (Taylor and McPhail 2000), our results were initially

unexpected. The two brook stickleback lineages have been allopatric for between 3.6–4.8 mya (Gach 1996; Mattern 2005). One possible explanation for this difference is that the environment has been more influential in determining degrees of behavioural stasis and change in this group than has time on its own. *Culaea inconstans* populations tend to be found in similar habitats; namely small to medium sized vegetated streams and ponds with slow to moderate flow. *Gasterosteus aculeatus*, on the other hand, inhabits a wide range of environments, ranging from tidepools and estuaries, through large freshwater lakes to small acidic, tea stained creeks. If the diversification of the North American Pacific coast *G. aculeatus* complex has been largely driven by ecological speciation (Schluter 1996a, b), then the relative stability of *C. inconstans* may represent the opposite of this dynamic; rates of diversification constrained by stabilizing selection across populations living in similar habitats. Further research investigating the extent of interpopulation variability in courtship and spawning behaviour forms the next step in understanding the nature and extent of behavioural variability in this species and is currently being conducted.

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