

Evidence of positive fitness for asymmetric armor phenotypes in stickleback

T.E. Reimchen^a and P. Nosil^b

^aDepartment of Biology, University of Victoria, P.O. Box 1700, BC V8W 2Y2, Canada; ^bStation d'Écologie Théorique et Expérimentale (SETE), CNRS, Moulis 09200, France

Corresponding author: T.E. Reimchen (email: reimchen@uvic.ca)

Abstract

Subtle morphological asymmetries, common in most species, typically originate from developmental noise rather than being adaptive responses. However, diverse taxa exhibit left versus right biases in behavioural traits due to hemispheric specialization, raising the possibility that subtle morphological asymmetries have functionality. Here we provide a rare test of this hypothesis by investigating the extent to which subtle left and right departures from bilateral symmetry in the defensive apparatus of threespine stickleback (*Gasterosteus aculeatus* Linnaeus, 1758) influence: (1) susceptibility to predator capture and (2) fitness of asymmetric relative to symmetric fish. Using large samples ($N = 10\,126$), we found that left-biased asymmetries had lower frequencies of predator-induced injuries than did symmetrics, while the latter had lower frequencies than did right-biased asymmetries. This pattern occurred in four of five years and in each sex. Relative fitness based on ontogenetic shifts in frequencies within six cohorts showed both left and right-biased asymmetries often had a fitness advantage over symmetrics, but this varied among years in conjunction with shifts in bird versus trout predation. The results suggest that subtle departures from symmetry can comprise an axis of functional phenotypic space maintained by fluctuating ecological and selective processes.

Key words: fluctuating asymmetry, adaptation, laterality, predator-induced injuries, sexual dimorphism, diversifying selection

Introduction

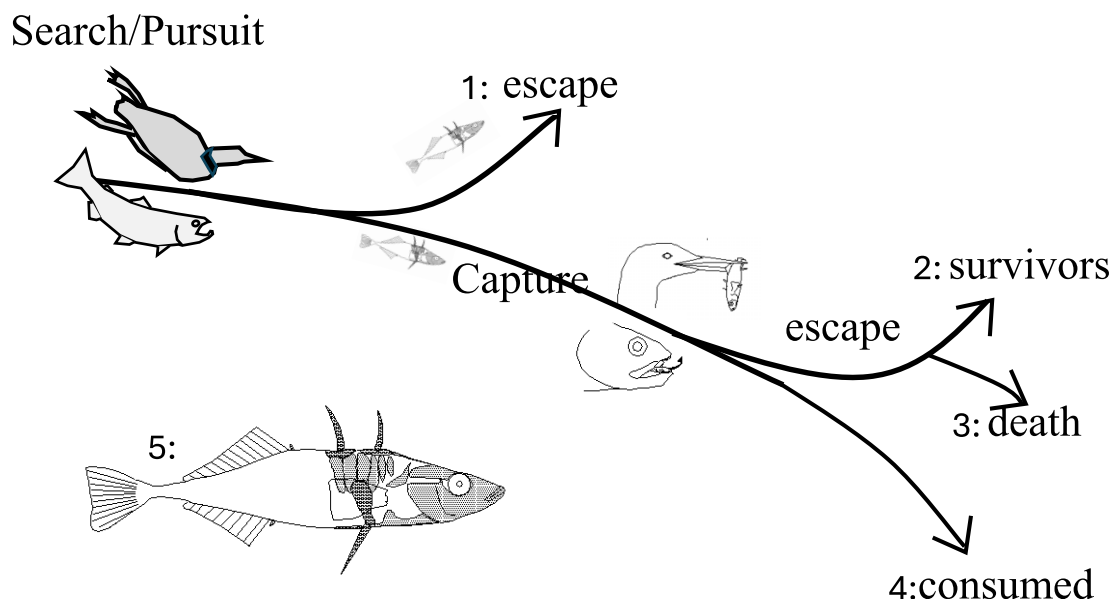
Despite the growing appreciation for complex and fluctuating selective regimes on quantitative variation in natural populations (Bell 2015), there has been much less attention directed to the ecological and selective influences on slight bilateral asymmetries. This is likely because subtle left-right departures from symmetry are often thought to arise from developmental noise (i.e., errors) and poor canalization (Van Valen 1962; Møller and Swaddle 1997; Allenbach 2011), leading to random “fluctuating asymmetry” (FA hereafter). Differentiating FA from directional asymmetries (DA hereafter) is traditionally statistically determined based on whether the population mean of the trait value on left and right sides differs (Palmer and Strobeck 1986). The majority of studies conclude that these subtle asymmetries, most with measurable heritability (Møller and Thornhill 1997), tend to be either neutral or maladaptive (Francis et al. 1985; Balmford et al. 1993; Thomas 1993; Martin and Lopez 2001; Nosil and Reimchen 2001; Gagliano et al. 2008; review in Leung and Forbes 1996). That said, it is important to acknowledge that DA is usually considered functional, but this designation is generally reserved for pronounced and consistently directional asymmetries.

We evaluate these assumptions concerning studies of asymmetry by taking advantage of long-term studies of predator-prey interactions with threespine stickleback (*Gas-*

terosteus aculeatus Linnaeus, 1758) at a remote lake on Haida Gwaii, western Canada. The ongoing study at this locality, begun in 1977, examined ecological factors influencing phenotypic variation in defense structures of the stickleback (review in Reimchen 1994). Monthly quantification of predation landscape showed that mean lateral plate numbers in the population increased in seasons and years with greater prevalence of predatory fish and decreased with increased avian piscivory (Reimchen 1995). Predator-induced injuries classified on several thousand stickleback from this population indicated that injury frequencies were highest on peripheral and non-modal plate phenotypes, suggesting increased predation risk on such phenotypes. Yet cohort analyses indicated that these peripheral phenotypes exhibited similar or higher fitness compared to modal phenotypes, consistent with the action of diversifying selection (Reimchen and Bergstrom 2023). This pattern aligns with Vermeij's (1982) argument that the presence of repaired predator-induced injuries in natural populations reflects positive fitness, as such individuals have effectively been “tested” by natural selection.

In the current paper, we extend these previous studies and compare incidence of predator-induced injuries among symmetric and asymmetric lateral plate phenotypes. Both FA and DA of lateral plates in stickleback have heritable signatures (Hagen 1973; Loehr et al. 2012). As well as quantifying absolute asymmetry, which is the major proxy in studies of FA

Fig. 1. Predator-prey schematic for threespine stickleback (*Gasterosteus aculeatus*) at Drizzle Lake, Haida Gwaii. #1: fish that have evaded detection or escaped during pursuit #2: fish that were captured but escaped with non-lethal injuries (see Reimchen 1988). #3: fish that were captured but escaped with lethal injuries (see Reimchen 2021). #4: fish that were pursued, captured and consumed (see Reimchen (1990, 1994) for each predator species). #5: representative adult stickleback (SL = 75 mm) with six lateral plates (positions 3 thru 8) from Drizzle Lake.



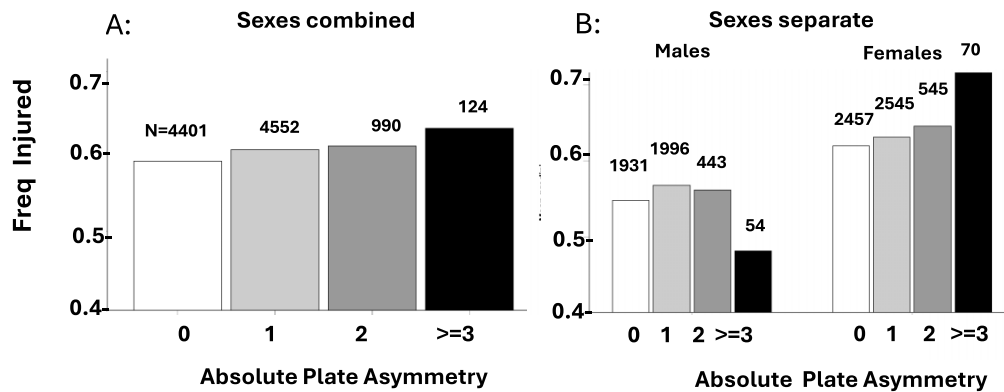
(Møller and Swaddle 1997), we focus on the sign of asymmetry, i.e., left versus right plate asymmetries. This is warranted because expanding evidence demonstrates that left or right behavioural asymmetries (laterality) occur among diverse vertebrate and invertebrate taxa (Bisazza et al. 1998; Frasnelli et al. 2012; Hori et al. 2017; Fuss et al. 2019), raising the prospect that subtle plate asymmetries could have ecological context, particularly in predator-prey interactions. We make and test several predictions. (1) Initially we test the data against the null model that there will no consistent associations between the occurrence of injuries on the stickleback in relation to the presence or absence of plate asymmetries (2) if differential injuries are found, we predict asymmetries (presumably unfit) will be captured at a higher rate (i.e., higher incidence of injuries). This allows several refined predictions to emerge: (a) frequencies of these asymmetric phenotypes will decline over ontogeny (lower fitness) versus (b) frequencies of these asymmetries will increase over ontogeny (higher fitness) since such individuals have been “tested” by natural selection. The data emerging from this within-lake investigation offer broader insight into the relatively weakly investigated ecological aspects of directionality in fluctuating asymmetry and urges the integration of subtle bilateral symmetry with that of other traits in the study of phenotypic variation. The focal themes examined in the current study are shown in the simplified infographic (Fig. 1).

Materials and methods

The study area is a 110-ha dystrophic lake (53°56'3.11"N; 132°4'29.64"W) located on the north-eastern region of the Haida Gwaii archipelago, western Canada. The lake contains

a population of large-bodied melanic threespine stickleback as well as an assemblage of predators of which the two most common are Cutthroat Trout (*Oncorhynchus clarki* Richardson, 1836) and Common Loon (*Gavia immer* Brünnich, 1764), widespread predators in coastal British Columbia. Collections of sticklebacks were made predominantly with standard minnow traps set in spring and summer between 1980 and 1988 and then intermittently (1989, 1990, 2006, 2010 through 2016) (permits—SM09-51584 and SM10-62059, MOE, Govt. of British Columbia; University of Victoria Aquatic Unit facility Standard Operating Procedure OA2003). For each collection, the fish were anaesthetized (Clove oil or MS222), then euthanized, and preserved in 10% formalin and later transferred to 95% ethanol. Lake biophysical data are described elsewhere (Reimchen 1994, 1995, 2021; Reimchen and Douglas 1980, 1984). For the present study, we include data on stickleback standard length (SL), sex, number and position of left and right lateral plates (Reimchen 1983), and predator-induced injuries. Capture by either predator group (salmonid or avian piscivores) resulted in fractured spines and/or integumentary lacerations. Many of these could not be reliably identified to specific predator group (trout or bird) while about one quarter of the fish had distinctive vertical parallel scars that unambiguously identified capture and escape from an avian piscivore (Reimchen 1988) while about 10% had major lacerations or punctures and were likely from trout injury (Reimchen 1992a). The remainder were classified as “indeterminate” (trout or bird). We suspect that substantial proportion of these “indeterminate” injuries are also from birds because stickleback escaping from trout have low survivorship (Reimchen 1992a). Incidence of injuries on each fish were examined for absolute and signed lateral plate number asymmetry (right-side minus left-side) and plate position asymme-

Fig. 2. (A) Frequency of injured fish (sexes combined) for threespine stickleback (*Gasterosteus aculeatus*) at Drizzle Lake, Haida Gwaii in relation to absolute plate asymmetry (right side minus left side). Sample sizes (N) shown above each bar. (B) Frequency of injured fish (sexes separate) in relation to absolute plate asymmetry (right side minus left side). Sample sizes (N) shown above each bar.



try (right-side minus left-side for each plate position). On a subsample of fish, age in years was determined from annular rings on pelvic spine cross-sections (Reimchen 1992b). From these ages, seven cohorts were identified based on hatching year (1977–1983). Frequencies of symmetric (SYM) and asymmetric (ASYM) phenotypes over ontogeny were then quantified in the yearly cohorts.

Statistical analyses

Because of departures from normality in samples, we primarily used non-parametric tests (Log-linear models with partial chi-squares and Pearson's chi-square). We also used z scores which are the individual parameter estimates from the LogLinear models. Initially, the entire dataset was pooled to look for broad trends in absolute asymmetry. Subsequently, we partitioned the data between the sexes and then for signed asymmetry. We partitioned among years and pooled adjacent years when sample sizes were small. We used t -tests to compare signed asymmetries against a value of zero to characterize fluctuating versus directional asymmetries. Position asymmetry was determined for each plate position (P1 through P10) to assess any directionality in asymmetry. Because some fish were symmetrical for number of plates but asymmetrical for position, we compared incidence of injuries in these "offset" phenotypes with symmetrical phenotypes.

Relative fitness (w) of symmetrical and asymmetrical plate phenotypes was calculated within each of six cohorts (identified by hatching year) based on Manly (1985, eqs 2.18):

$$\hat{w}_{ij} = \frac{[(2a_{ij} + 1) (2a_{cj-1} + 1)]}{[(2a_{ij} + 1) (2a_{cj-1} + 1)]}$$

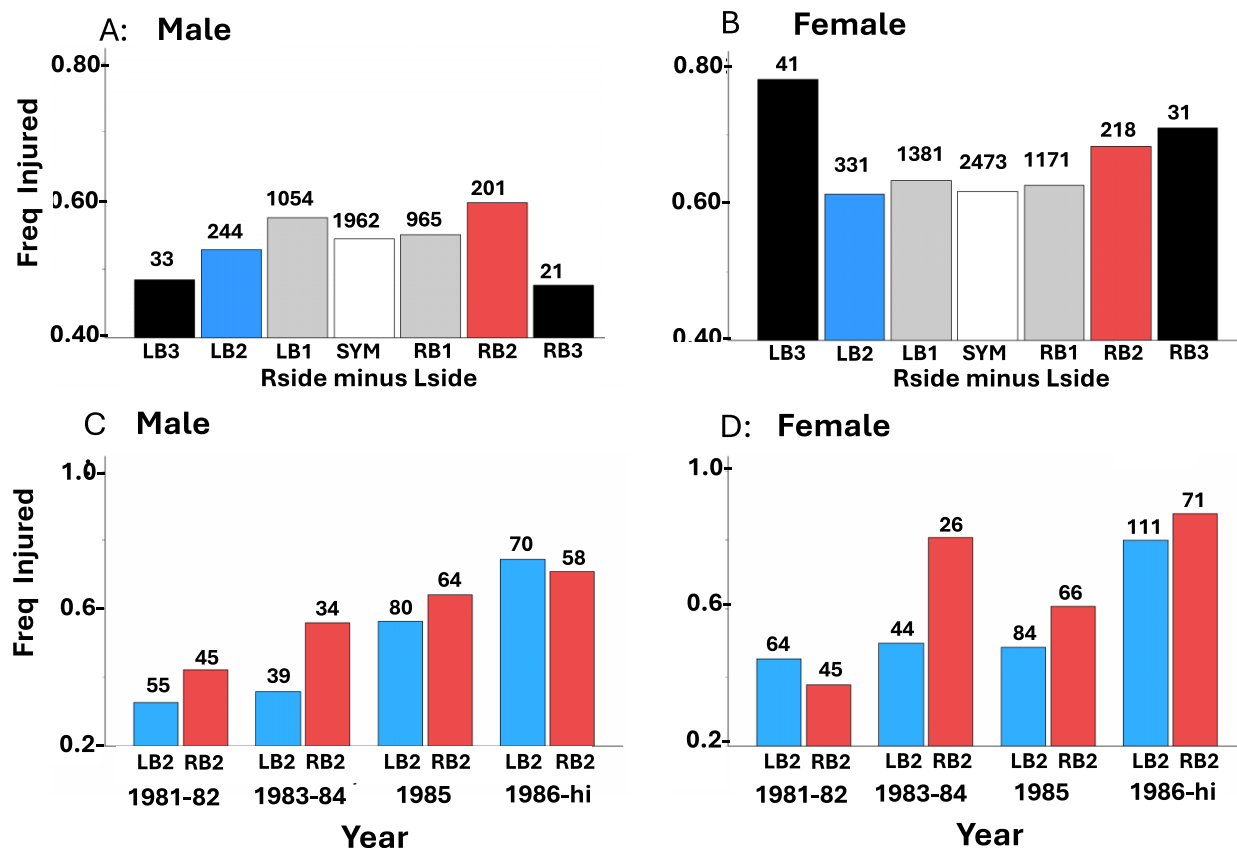
where "c" is the symmetric phenotype and "i" is the asymmetric phenotype, "j" is the number of fish after selection (age year ≥ 4) and "j - 1" the number of fish before selection (age year 2,3). Spearman's rho was used to compare relative fitness of left and right-biased asymmetries as well as the correlation between the sexes. All statistical analyses were performed with SPSS version 30.0.0.0.

Results

To provide context for the major results in this paper, we initially summarize here the lateral plate results from previous studies for this locality (Reimchen 1983; Reimchen and Bergstrom 2009) and combine these with additional fish measured for the current study (Supp. data Fig. 1). Among the 10 126 sticklebacks collected between 1980 and 2016, modal lateral plate number was 5 (range 0–10) with the highest number of asymmetries occurring on fish with either the fewest and the greatest number of plates (Supp. Fig. 1A). In total, 60% of the fish were asymmetric in number of plates of which the majority had a difference of one plate between sides (range 1–4) (Supp. Fig. 1B). In both sexes, these asymmetries occurred primarily at myomere positions 1 thru 3 and 8 thru 10, with the fewest asymmetries on the buttressing positions (4 through 7) (Supp. Figs. 1C and 1D). Considering signed asymmetries, for males (Supp Fig. 1E), there was an overall left-side bias ($t = 3.2$, $P < 0.001$, $N = 4481$) although the asymmetry did not differ significantly from zero in nine of the ten years. For females (Supp. Fig. 1F), there was also an overall left-bias ($t = 6.4$, $P < 0.001$, $N = 5645$) while four of the 10-year groups were not significantly different from zero (FA). Signed asymmetries also varied with respect to myomere position on the fish. For males (Supp. Fig. 1G), Pos#1 was marginally right-biased ($P < 0.07$) while Pos#2, #3, and #4 were significantly left-biased and with more posterior positions shifting from no bias to right-bias but none of these differed significantly from zero. Females (Supp. Fig. 1H) showed a very similar trend to males ($\rho = 0.72$, $P = 0.02$) with three positions (Pos#3, #4, and #6) significantly left-biased but the remaining positions not significantly different from zero, indicating FA.

For absolute plate asymmetry (Fig. 2), using pooled data with sexes combined, there was a very weak and non-significant increase in injuries with increased asymmetries (chi-square = 3.3, $P = 0.34$, $DF = 3$; Fig. 2A). Restricting comparison to the most asymmetric phenotype (≥ 3 plate difference) showed a 4.4% greater injury rate than symmetrics but without statistical support (chi-square = 1.0, $P = 0.34$,

Fig. 3. Frequency of injured fish for threespine stickleback (*Gasterosteus aculeatus*) at Drizzle Lake, Haida Gwaii, in relation to signed asymmetry (right side minus left side: LB2-left-biased by ≥ 2 plates, LB1-left-biased by one plate; Sym-symmetric; RB1-right-biased by one plate; RB2: right-biased by ≥ 2 plates). (A) Males. (B) Females. (C) Males LB2 versus RB2. (D) Females: LB2 versus RB2.



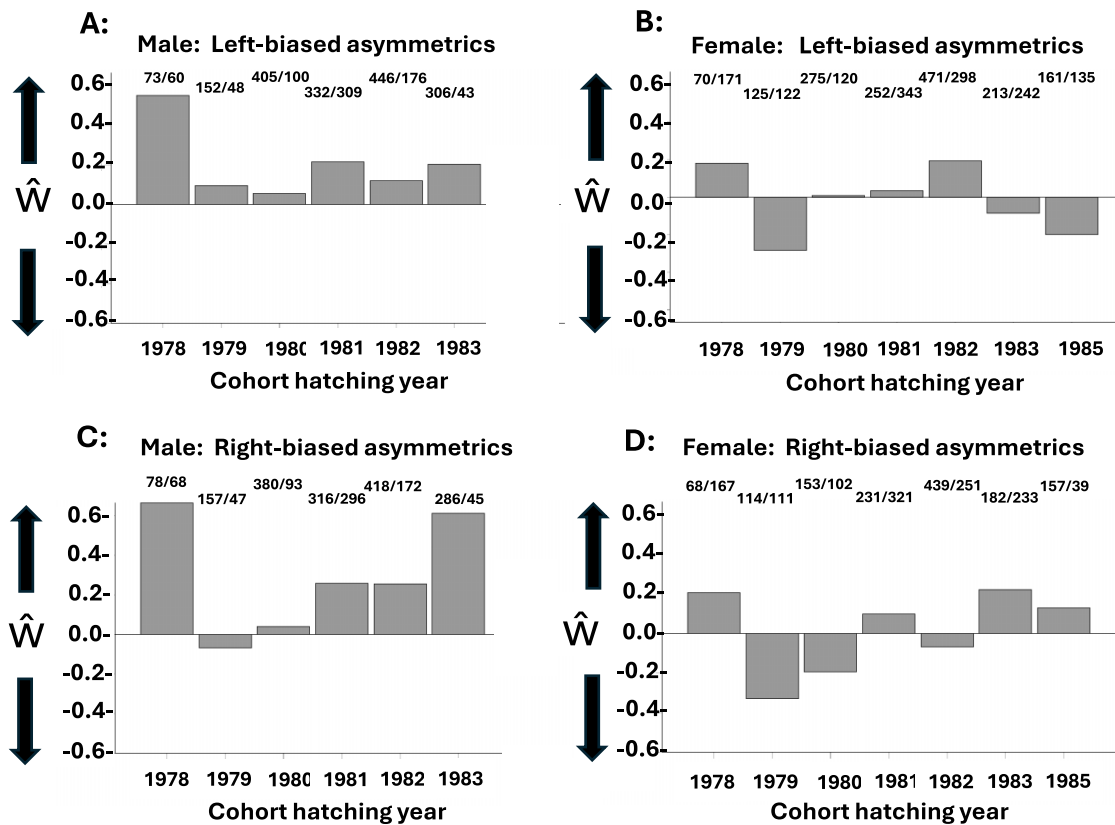
df = 1). Partitioning the sexes (Fig. 2B) showed elevated injuries in females relative to males (partial chi-square = 55.9, $P < 0.001$, df = 1). As well, the most asymmetric phenotypes (≥ 3 plate difference) had higher incidence of injuries in females than in males relative to symmetrics ($Z = 2.1$, $P < 0.04$).

For signed asymmetry (Fig. 3), the relative extent of injuries varied among phenotypes. For males (Fig. 3A) and females (Fig. 3B), phenotypes asymmetric by a single on either side had slightly but not significantly higher incidence of injuries than symmetrics (partial chi-square = 3.3, $P = 0.19$, df = 2). Right-biased asymmetrics with ≥ 2 plate difference (RB2) were more frequently injured than symmetrics (SYM) (partial chi-square = 5.7, $P < 0.02$) with no differences between the sexes ($Z = 0.68$, $P = 0.5$) and were more frequently injured than LB2 in both sexes (partial chi-square = 3.9, $P < 0.05$, DF = 1). In contrast, left-biased asymmetrics (LB2) did not differ from SYM in either sex (partial chi-square = 0.0, $P = 0.97$). Asymmetrics with ≥ 3 plate difference per side had marginally higher injuries than symmetrics in females (chi-square = 6.0, $P < 0.07$) and although injuries in males appear to be marginally lower than symmetrics, this is not supported (chi square = 0.87, $P = 0.36$). We also examined whether there was any temporal consistency to the elevated

injuries in RB2 relative to LB2. In males (Fig. 4C), two of the six-year groups showed a weak excess of injuries but only 1981 approached significance (chi-square = 3.4, $P < 0.07$). Females exhibited a marginal deficiency of injuries on RB2 in 1981 (chi-square = 3.3, $P < 0.07$, df = 1) while 1983 had a significant excess (chi-square = 9.8, $P < 0.003$, df = 1). A saturated model (predinjury*asymmetry*sex*year, Supp. data Table 1) retains the significant predinjury*asymmetry interaction (partial chi-square = 4.2, $P < 0.05$, df = 1). We repeated the Loglinear analysis using only younger fish (< 75 mm SL) and the predinjury*asymmetry interaction was accentuated (Supp. data Table 2).

Stickleback that were symmetric for total number of plates were occasionally asymmetric for position of plates (19% of 1962 males, 20% of 2473 females), the two sides usually offset by a single position (example, positions #4-#6 on one side versus #5-7 on the opposite side). Males for these position asymmetrics had non-significantly lower incidence of injuries than did symmetrics (52% vs. 55%, chi-square = 1.5, $P = 0.23$, df = 1) while females showed marginally higher injuries in position asymmetrics (64% vs. 61%, chi-square = 1.8, $P = 0.19$, df = 1). A saturated loglinear model indicates no overall association between position asymmetry and injury (partial chi-square = 0.14, $P = 0.7$) but a marginally ele-

Fig. 4. Relative fitness ($\hat{w}$) of left-biased and right-biased asymmetries relative to symmetrics for threespine stickleback (*Gasterosteus aculeatus*) at Drizzle Lake, Haida Gwaii. Bars above or below the horizontal indicate positive fitness relative to symmetrics for each yearly hatching cohort. (A) Males: left-biased asymmetries, (B) males: right-biased asymmetries, (C) females: left-biased asymmetries, and (D) females: right-biased asymmetries.



vated injuries in position asymmetries for females (partial chi-square = 2.8, $P < 0.01$).

Relative fitness ($\hat{w}$) of signed plate asymmetries varied among cohorts and between the sexes. For males, fitness of left-biased asymmetries (Fig. 4A) and right-biased asymmetries (Fig. 4B) were predominantly equal or greater relative to symmetrics, representing a 20% average advantage for left-biased and a 25% advantage for right-biased asymmetries. The largest differences occurred between the 1978 and 1979 hatching year cohorts where there was a sharp fitness reduction from the highest in 1978 to approximately equal fitness with symmetrics in 1979. This was followed by subsequent fitness increase in later cohorts. These cohorts largely comprise sub-adult and adult fish collected from 1981 to 1983. Fitness for left- and right-biased asymmetries were correlated with each other (Spearman's $\rho = 0.89$, $P < 0.02$). In contrast, females showed no consistent trends as mean relative fitness was similar for left-biased asymmetries ($\bar{x} = 0.98$) and right-biased ($\bar{x} = 1.0$) asymmetries (Figs. 4C and 4D) and the two sides were not correlated with each other ($P > 0.5$). Yet there were substantial differences among cohorts, the largest of which were the sequential reductions, from positive to negative fitness for both left and right-biased asymmetries, occurring between 1978 and 1979 when males also showed the large reduction. Temporal trends of higher or lower fitness estimates were correlated between females and males

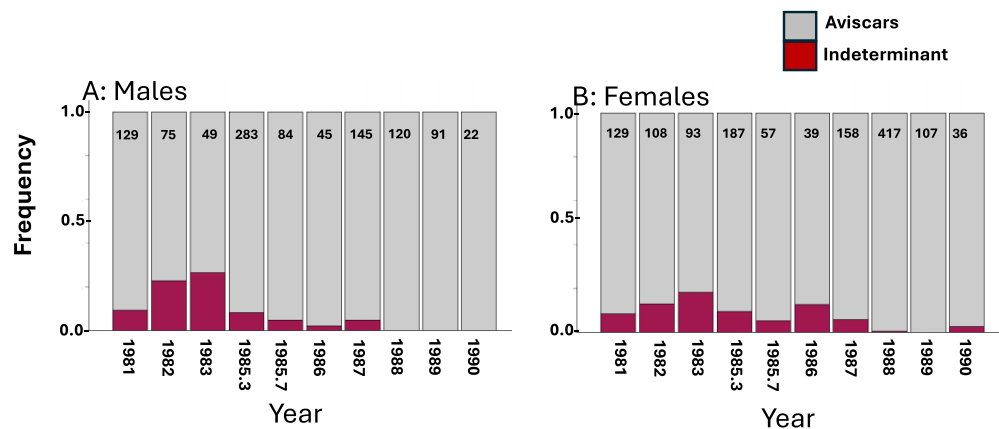
($\rho = 0.80$, $P < 0.03$; $N = 12$). Further comparisons of relative fitness for plate phenotypes that were asymmetric for position but symmetric for number of plates showed no differences in relative fitness relative to symmetrics (males: $\bar{x} = 0.98$, females $\bar{x} = 0.99$).

We examined the incidence of major lacerations (probable trout) relative to bird-induced scars on fish collected from 1981 and 1990. For males (Fig. 5A), there was a doubling of lacerations between 1981 and 1982, high levels in 1983 followed by a reduction to minimal number of lacerations in the late 1980s. Females (Fig. 5B) showed similar trends to those of the males ($\rho = 0.82$, $P < 0.005$). We also extracted demographic information from published data on total predation levels for trout and bird over this time period (Reimchen 1995; Figs. 5C and 5D). Consistent with the laceration data, there was a major reduction in bird predation and corresponding increase in lacerations from late 1981 to spring 1982 (Supp. Fig. 2).

Discussion

Natural variation in phenotypic traits is often analyzed in the context of its potential adaptive and functional significance. This has led to recognition that spatial and temporal variation in traits can be tied to variability in the selective landscape (Bell 2015; Stroud et al. 2023). The study of bilateral asymmetry has proceeded in a somewhat dif-

Fig. 5. Proportion of total injuries for threespine stickleback (*Gasterosteus aculeatus*) at Drizzle Lake, Haida Gwaii showing “indeterminant” lacerations (dark shading) versus bird scars (grey shading). “Indeterminant” category is restricted to major lacerations (probable trout injuries). (A) Males and (B) females.



ferent manner, due to the assumption that slight and non-directional departures from symmetry represent developmental errors rather than functional trait variation. Based on now widely recognized criteria (Van Valen 1962; Palmer and Strobeck 1986), different types of asymmetries are generally differentiated from each other statistically, depending on whether the mean population differences between the left and right and right sides differ significantly from zero (DA and FA, respectively). These population-level criteria generally implicate different origins of asymmetry, with FA interpreted as emerging from random, potentially costly, errors during development and DA emerging from heritable biases and potentially adaptive developmental responses. This divergent classification has facilitated a rich literature, some of it consistent with the inverse relationship between FA and fitness (Møller and Swaddle 1997), including multiple studies on lateral plates of threespine stickleback (Moodie and Reimchen 1976; Francis et al. 1985; Bergstrom and Reimchen 2002, 2003; Reimchen and Nosil 2001; Trokovic et al. 2012; Loehr et al. 2013; Lajus et al. 2019), but with mixed results overall (Clarke 1995; Reimchen 1997; Chivers et al. 2017; Schroder et al. 2023).

These mixed results may in part be tied to the fact that the distinction between DA and FA is often based on statistical criteria only and thus highly influenced by sample size and power. Consequently, potential ecological influences on asymmetries differing in the extent of departures from symmetry remain poorly understood, particularly when detected in large samples. This raises the possibility that even very subtle departures from symmetry, statistically classified as FA, may have functional significance. Testing this conjecture requires evaluating the relationship between left and right asymmetries and fitness, a task we have undertaken here. The results reported here challenge some traditional aspects of the interpretation of departures from symmetry and may help unify the study of asymmetry with that of other types of phenotypic variation. We elaborate below on our main findings, their potential interpretation, and promising avenues for future research.

Building on a multiyear research program in an insular population of threespine stickleback from western Canada, we examined whether there was any relationship between the incidence of predator-induced injuries, common on adult fish, and subtle bilateral asymmetries in lateral plates. About one-half of the samples in the current study conform to the definition of FA, the remainder showing a weak DA to the left side, a trend seen in other populations from the region (Bergstrom and Reimchen 2002, 2003). Bony lateral plates of threespine stickleback influence trunk flexibility (Reimchen 1983; Bergstrom 2002) and it thus seems plausible that asymmetric expression of these traits could lead to atypical swimming motion and a predicted increased capture rate. Indeed, greater capture of asymmetrical individuals has been observed in other taxa including insects (Møller 1996; Swaddle 1997a, 1997b; Forsman and Herrström 2004), fish (Tofts et al. 2016) and rodents (Galeotti et al. 2005).

Our results for pooled data (sexes combined) showed that for absolute asymmetry (sign ignored), which is the major metric in studies of FA (Palmer and Strobeck 1986, 2003; Graham et al. 2010), there is only a very weak and non-statistical increase in incidence of injuries among progressively more asymmetric fish (Fig. 3A). However, this analysis obscured ecologically informative differences that emerged when the sexes were separated. While males and females each had slightly increased incidence of injuries on weak asymmetries, yet on the most asymmetric phenotypes (≥ 3 plate difference), females had substantially elevated injuries relative to symmetrics while males had depleted injuries relative to symmetrics.

Could divergent responses in asymmetries between the sexes develop as responses to the predation landscape? It could mean that females are captured at higher rates than males or that the sexes are captured at similar rates but males are less likely to survive the capture. There is no evidence for the former option while the latter (increased mortality) could be relevant. In the current study population, stickleback are subject to predation from both trout and birds (Reimchen 1994). Stickleback with bird scars (aviscars) com-

monly usually show repair of the spine fractures indicating extended post-capture survivorship (Reimchen 1988). In contrast, those that escape from trout in experimental tanks generally have epidermal punctures and low survival, particularly those with missing plates (Reimchen 1991, 1992a). This would account for the lower incidence of injuries in males relative to females and very low injuries on the most asymmetric phenotypes as these would be most susceptible to punctures. This might also explain geographical trends in the low levels of asymmetry in stickleback populations where toothed piscivores such as cutthroat trout are the dominant predator (Moodie 1972; Moodie and Reimchen 1976).

We speculate that these asymmetries may be associated with the geometry of predator-prey interactions. Asymmetric behavioural responses of prey to their predators occur in multiple taxa and are known to improve survival of the prey (Bisazza et al. 1998; Güntürkün et al. 2000; Frasnelli et al. 2012; Hori et al. 2017; Hori 2022; Petrazzini et al. 2020; Hulthen et al. 2021). In butterflies, males with moderately asymmetric wings have higher reproductive success relative to symmetric or very asymmetric individuals, possibly due to increased turning ability in evasive flight, (Windig and Nylin 1999). Wall lizards (*Podarcis muralis* Laurenti, 1768) tend to escape to the right when presented with a predator threat from behind (Bonati et al. 2010). Top minnow (*Girardinus falcatus* Eigenmann, 1903) escape to the right on first exposure to a predator but then shifts to left with subsequent interactions (Cantolupo et al. 1995). Shiner perch (*Cymatogaster aggregata* Gibbons, 1854) that are strongly lateralized showed more rapid escape responses than less-lateralized individuals (Dadda et al. 2010). Stickleback show a graded level of evasive laterality in response to strength of predator cues, effects that are transmitted between generations (Berlinghieri et al. 2025). As well, stickleback are usually bilaterally asymmetric for sensory receptors such as the number of canal neuromasts on the plates (Planidin and Reimchen 2019, 2021). When presented with experimental predator cues, stickleback tend to position themselves with shelter on their right side and this is accentuated on fish with few plates (Planidin and Reimchen 2022).

Yet these examples of behavioural laterality in the prey may emerge from laterality in the approach and capture by foragers, including predators (review in Vallortigara and Rogers 2005). For example, pigeons (*Columba livia* Gmelin, 1759) show strong eye lateralization during foraging and this improves success (Gunturkun et al. 2000). Sailfish (*Istiophorus platypterus* Shaw and Nodder, 1792) show extensive individual lateralization when attacking small fish prey and this lateralization increases capture success (Kurvers et al. 2017). Avian piscivores, including loons (*Gavia* sp.), vary in the directionality of different marine fish species held in their bill suggestive of asymmetric capture (Reimchen and Bergstrom 2009). In the current study population, the ratios of left versus right predator-induced pelvic spine fractures on the stickleback differed among regions of the lake (Reimchen, unpublished data), results consistent with non-random orientation of capture. Such laterality appears to be deeply rooted in evolutionary history as predator-induced injuries on Cambrian trilobites are significantly biased to one side (Babcock 1993).

If this speculation is accurate, it might indicate that subtle asymmetries in stickleback represent functional adaptations to variability in the lateralized predation landscape.

Whatever the correct explanation for the differential incidence of injuries between asymmetrics and symmetric, direct measurement of fitness from cohort analyses shows that both left-biased and right-biased asymmetrics have an advantage relative to symmetric. This varies between sexes and among cohorts. Male asymmetrics averaged 20% advantage, ranging from 0% to 60% among cohorts, while female asymmetrics ranged from a 30% disadvantage to 20% advantage among cohorts and between the left- versus right-biased asymmetrics. Sampling effects cannot be rejected yet the positive and negative trends in fitness among sequential cohorts were significantly correlated between the sexes indicating population-level responses. For example, the large reduction in fitness between the 1978 and 1979 hatching year cohorts occurs for both males and females and coincides with highest levels of lacerations on this year class in 1982 and 1983. In addition, there was a large shift in actual predation levels from bird-dominated to trout-dominated consumption between 1981 and 1983 (Reimchen 1995). A reasonable inference from these data are that both left- and right-biased asymmetrics are at a disadvantage when subject to predation from trout but asymmetrics, at least for males, have an advantage against bird predation. This could be further influenced by frequency-dependent effects shifting over time, as has been shown in the behavioural asymmetries of scale-eating cichlids (Hori 1993).

We cannot currently identify whether the greater variance among cohorts in relative fitness for females compared with males is ecologically informative. The complexity of the predation landscape in these populations (22 species using stickleback), each with separate but overlapping habitat preferences (Reimchen 1994) and temporal differences in abundance (Reimchen and Douglas 2021) suggests the potential for localized differences in laterality and fitness of male and female asymmetrics. In most insular populations of stickleback from Haida Gwaii, the sexes differ in multiple body size-corrected traits, including jaw length, eye diameter, number of lateral plates and size of the pelvic girdle as well as differences in isotopically-defined niche space, all of which reflect differences in habitat and predation regime (Reimchen et al. 2016). In addition to this general dimorphism, its extent varies with respect to locality differences in the aquatic spectra, specifically, the dark waters of dystrophic lakes versus the clear waters of oligotrophic lakes (Reimchen et al. 2016). The amount of light is known to influence laterality in poeciliid topminnow fishes, low light levels showing less laterality than high light levels (Dadda and Bisazza 2012). If this is broadly applicable among taxa, it could be that the differences in fitness between the sexes for the different asymmetrics and among cohorts in our study is associated with the vertical zonation in the water column. Within a dystrophic lake such as the current study site, there is steep attenuation of light within several meters of the surface (Reimchen, unpublished observations) and consequently, one might predict that the extent and direction of asymmetric evasion from predators could vary over these sharp vertical gradients in

light. **Moodie and Moodie (1996)** have previously shown that male stickleback with asymmetric plates had a higher probability of having fry in their nest relative to symmetric males while recent studies by **McLean and Morrell (2021)** indicate that nesting male stickleback are more lateralized in their behaviour than non-reproductive males and more lateralized than females further exemplifying the value of differentiating sex and asymmetries in studies of population variation.

In broader context, the core and more general conclusion to emerge from this work is that even subtle signed departures from symmetry may have fitness consequences rooted in form and function. This conjecture challenges some of the conventional interpretations of asymmetry and requires tests in other organisms. However, the detailed spatial and temporal studies of signed asymmetries in this population (**Reimchen and Bergstrom 2009**, current study) have not been undertaken on other species. Absolute asymmetry, with the sign ignored, is the major metric in FA studies (**Palmer and Strobeck 1986**), yet combining left and right asymmetries can obscure significant differences in ecology and fitness between signed asymmetries. In stickleback, there are shifts among years from FA to DA and back to FA (**Reimchen and Nosil 2001**; **Reimchen and Bergstrom 2009**; current study) and similar shifts among plate positions along the vertebral axis, which as noted above may reflect statistical issues, functional variation, or a combination of these. Left and right-biased asymmetries occur with similar frequencies in littoral zones (FA) but shift to increased left-biased asymmetries (DA) in limnetic zones, the trends occurring in different seasons, in both young and adult age classes and in both sexes (**Reimchen and Bergstrom 2009**). Left-biased asymmetries have a lower isotopic signature than right-biased asymmetries with the same total number of plates (**Reimchen et al. 2008**). These meristic asymmetries, which fluctuate between FA and DA, are not readily interpretable as random developmental errors. Recent meta-analyses of FA conclude that there is often no consistent associations with fitness (**Lens et al. 2002**; **Graham et al. 2010**). Expanding recognition of hemispheric dominance and lateralized behaviour in many vertebrate and invertebrate taxa opens the possibility that the geometry of a predator approach to a prey or a prey's response to a predator is often asymmetrical and that the subtle morphological asymmetries, rather than random errors in development, could reflect functional adaptations between predator and prey and comprise a largely ignored axis in functional phenotypic space.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

Author information

Author ORCIDs

T.E. Reimchen <https://orcid.org/0000-0002-5578-8531>

Author contributions

Conceptualization: TER

Data curation: TER

Formal analysis: TER

Funding acquisition: TER

Investigation: TER

Methodology: TER

Project administration: TER

Resources: TER

Software: TER

Supervision: TER

Validation: TER

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Writing – original draft: TER

Writing – review & editing: TER, PN

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The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjz-2026-0017>.

References

- Allenbach, D.M. 2011. Fluctuating asymmetry and exogenous stress in fishes: a review. *Rev. Fish Biol. Fish.* **21**: 355–376. doi:[10.1007/s11160-010-9178-2](https://doi.org/10.1007/s11160-010-9178-2).
- Babcock, L.E. 1993. Trilobite malformations and the fossil record of behavioral asymmetry. *J. Paleontol.* **67**: 217–229. doi:[10.1017/S0022366000032145](https://doi.org/10.1017/S0022366000032145).
- Balmford, A., Jones, I.L., and Thomas, A.L. 1993. On avian asymmetry: evidence of natural selection for symmetrical tails and wings in birds. *Proc. R. Soc. Lond. B*, **252**: 245–251.
- Bell, G. 2015. *The evolution of life*. Oxford University Press.
- Bergstrom, C.A. 2002. Fast-start swimming performance and reduction in lateral plate number in threespine stickleback. *Can. J. Zool.* **80**: 207–213. doi:[10.1139/z01-226](https://doi.org/10.1139/z01-226).
- Bergstrom, C.A., and Reimchen, T.E. 2002. Geographical variation in asymmetry in *Gasterosteus aculeatus*. *Biol. J. Linn. Soc.* **77**: 9–22.
- Bergstrom, C.A., and Reimchen, T.E. 2003. Asymmetry in structural defenses: insights into selective predation in the wild. *Evolution*, **57**: 2128–2138. doi:[10.1111/j.0014-3820.2003.tb00390.x](https://doi.org/10.1111/j.0014-3820.2003.tb00390.x). PMID: 14575332.
- Berlinghieri, F., Vittorietti, M., Savoca, D., Pace, A., Nicolaus, M., Riedstra, B., et al. 2025. Parental predator exposure affects offspring boldness and laterality in the stickleback. *Anim. Behav.* **223**: 123–154. doi:[10.1016/j.anbehav.2025.123154](https://doi.org/10.1016/j.anbehav.2025.123154).
- Bisazza, A., Rogers, L.J., and Vallortigara, G. 1998. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neurosci. Biobehav. Rev.* **22**: 411–426. doi:[10.1016/S0149-7634\(97\)00050-X](https://doi.org/10.1016/S0149-7634(97)00050-X). PMID: 9579329.
- Bonati, B., Csermely, D., López, P., and Martín, J. 2010. Lateralization in the escape behaviour of the common wall lizard (*Podarcis muralis*). *Behav. Brain Res.* **207**: 1–6. doi:[10.1016/j.bbr.2009.09.002](https://doi.org/10.1016/j.bbr.2009.09.002). PMID: 19737579.
- Cantalupo, C., Bisazza, A., and Vallortigara, G. 1995. Lateralization of predator-evasion response in a teleost fish (*Girardinus falcatus*). *Neuropsychologia*, **33**: 1637–1646. doi:[10.1016/0028-3932\(95\)00043-7](https://doi.org/10.1016/0028-3932(95)00043-7). PMID: 8745121.
- Chivers, D.P., McCormick, M.I., Warren, D.T., Allan, B.J., Ramasamy, R.A., Arvizu, B.K., et al. 2017. Competitive superiority versus predation savvy: the two sides of behavioural lateralization. *Anim. Behav.* **130**: 9–15. doi:[10.1016/j.anbehav.2017.05.006](https://doi.org/10.1016/j.anbehav.2017.05.006).
- Clarke, G.M. 1995. Relationships between fluctuating asymmetry and fitness: how good is the evidence? *Pacific Conserv. Biol.* **2**: 146–149. doi:[10.1071/PC960146](https://doi.org/10.1071/PC960146).
- Dadda, M., and Bisazza, A. 2012. Prenatal light exposure affects development of behavioural lateralization in a livebearing fish. *Behav. Processes*, **91**: 115–118. doi:[10.1016/j.beproc.2012.06.008](https://doi.org/10.1016/j.beproc.2012.06.008). PMID: 22750279.
- Dadda, M., Koolhaas, W.H., and Domenici, P. 2010. Behavioural asymmetry affects escape performance in a teleost fish. *Biol. Lett.* **6**: 414–417. doi:[10.1098/rsbl.2009.0904](https://doi.org/10.1098/rsbl.2009.0904). PMID: 20089537.
- Forsman, A., and Herrström, J. 2004. Asymmetry in size, shape, and color impairs the protective value of conspicuous color patterns. *Behav. Ecol.* **15**: 141–147. doi:[10.1093/beheco/arg092](https://doi.org/10.1093/beheco/arg092).
- Francis, R.C., Havens, A.C., and Bell, M.A. 1985. Unusual lateral plate variation of threespine sticklebacks (*Gasterosteus aculeatus*) from Knik Lake, Alaska. *Copeia*, **1985**: 619–624. doi:[10.2307/1444752](https://doi.org/10.2307/1444752).
- Frasnelli, E., Vallortigara, G., and Rogers, L.J. 2012. Left–right asymmetries of behaviour and nervous system in invertebrates. *Neurosci. Biobehav. Rev.* **36**: 1273–1291. doi:[10.1016/j.neubiorev.2012.02.006](https://doi.org/10.1016/j.neubiorev.2012.02.006). PMID: 22353424.
- Fuss, T., Nöbel, S., and Witte, K. 2019. It's in the eye of the beholder: visual lateralisation in response to the social environment in poeciliids. *J. Fish Biol.* **94**: 759–771. doi:[10.1111/jfb.13953](https://doi.org/10.1111/jfb.13953). PMID: 30854659.
- Gagliano, M., Depczynski, M., Simpson, S.D., and Moore, J.A. 2008. Dispersal without errors: symmetrical ears tune into the right frequency for survival. *Proc. R. Soc. B Biol. Sci.* **275**: 527–534. doi:[10.1098/rspb.2007.1388](https://doi.org/10.1098/rspb.2007.1388).
- Galeotti, P., Sacchi, R., and Vicario, V. (2005). Fluctuating asymmetry in body traits increases predation risks: tawny owl selection against asymmetric woodmice. *Evol. Ecol.* **19**: 405–418. doi:[10.1007/s10682-005-8309-z](https://doi.org/10.1007/s10682-005-8309-z).
- Graham, J.H., Raz, S., Hel-Or, H., and Nevo, E. 2010. Fluctuating asymmetry: methods, theory, and applications. *Symmetry*, **2**: 466–540. doi:[10.3390/sym2020466](https://doi.org/10.3390/sym2020466).
- Güntürkün, O., Diekamp, B., Manns, M., Nottelmann, F., Prior, H., Schwarz, A., and Skiba, M. 2000. Asymmetry pays: visual lateralization improves discrimination success in pigeons. *Curr. Biol.* **10**: 1079–1081. PMID: 10996079.
- Hagen, D.W. 1973. Inheritance of numbers of lateral plates and gill rakers in *Gasterosteus aculeatus*. *Heredity*, **30**: 303–312. doi:[10.1038/hdy.1973.40](https://doi.org/10.1038/hdy.1973.40).
- Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science*, **260**: 216–219. doi:[10.1126/science.260.5105.216](https://doi.org/10.1126/science.260.5105.216). PMID: 17807183.
- Hori, M. 2022. Laterality of fish: antisymmetry in fish populations maintained by the interspecific interaction. In *Lateral asymmetry in animals: predator-prey interactions, dynamics, and evolution*. Springer Nature Singapore, Singapore. pp. 1–42. doi:[10.1007/978-981-19-1342-6_1](https://doi.org/10.1007/978-981-19-1342-6_1).
- Hori, M., Nakajima, M., Hata, H., Yasugi, M., Takahashi, S., Nakae, M., et al. 2017. Laterality is universal among fishes but increasingly cryptic among derived groups. *Zool. Sci.* **34**: 267–274. doi:[10.2108/zs160196](https://doi.org/10.2108/zs160196). PMID: 28770681.
- Hulthén, K., Heinen-Kay, J.L., Schmidt, D.A., and Langerhans, R.B. 2021. Predation shapes behavioral lateralization: insights from an adaptive radiation of livebearing fish. *Behav. Ecol.* **32**: 1321–1329.
- Kurvers, R.H., Krause, S., Viblanc, P.E., Herbert-Read, J.E., Zaslansky, P., Domenici, P., et al. 2017. The evolution of lateralization in group hunting sailfin. *Curr. Biol.* **27**: 521–526. doi:[10.1016/j.cub.2016.12.044](https://doi.org/10.1016/j.cub.2016.12.044). PMID: 28190733.
- Lajus, D.L., Golovin, P.V., Yurtseva, A.O., Ivanova, T.S., Dorgham, A.S., and Ivanov, M.V. 2019. Fluctuating asymmetry as an indicator of stress and fitness in stickleback: a review of the literature and examination of cranial structures. *Evol. Ecol. Res.* **20**: 83–106.
- Lens, L.U.C., Van Dongen, S., Kark, S., and Matthysen, E. 2002. Fluctuating asymmetry as an indicator of fitness: can we bridge the gap between studies? *Biol. Rev.* **77**: 27–38. doi:[10.1017/S1464793101005796](https://doi.org/10.1017/S1464793101005796). PMID: 11911372.
- Leung, B., and Forbes, M.R. 1996. Fluctuating asymmetry in relation to stress and fitness: effects of trait type as revealed by meta-analysis. *Écoscience*, **3**: 400–413. doi:[10.1080/11956860.1996.11682357](https://doi.org/10.1080/11956860.1996.11682357).
- Loehr, J., Herczeg, G., Leinonen, T., Gonda, A., Van Dongen, S., and Merilä, J. 2013. Asymmetry in threespine stickleback lateral plates. *J. Zool.* **289**: 279–284. doi:[10.1111/jzo.12005](https://doi.org/10.1111/jzo.12005).
- Loehr, J., Leinonen, T., Herczeg, G., O'Hara, R.B., and Merilä, J. 2012. Heritability of asymmetry and lateral plate number in the threespine stickleback. *PLoS One*, **7**: e39843. doi:[10.1371/journal.pone.0039843](https://doi.org/10.1371/journal.pone.0039843). PMID: 22792190.
- Manly, B.F. 1985. *The statistics of natural selection on animal populations*. Springer Science and Business Media.
- Martín, J., and López, P. 2001. Hindlimb asymmetry reduces escape performance in the lizard *Psammotromus algirus*. *Physiol. Biochem. Zool.* **74**: 619–624. PMID: 11517447.
- McLean, S., and Morrell, L.J. 2021. Sex differences in laterality are associated with reproduction in threespine stickleback. *Am. Nat.* **197**: 708–718. doi:[10.1086/714138](https://doi.org/10.1086/714138). PMID: 33989139.
- Møller, A.P. 1996. Sexual selection, viability selection, and developmental stability in the domestic fly *Musca domestica*. *Evolution*, **50**: 746–752. PMID: 28568932.
- Møller, A.P., and Swaddle, J.P. 1997. *Asymmetry, developmental stability and evolution*. Oxford University Press, UK.
- Møller, A.P., and Thornhill, R. 1997. A meta-analysis of the heritability of developmental stability. *J. Evol. Biol.* **10**: 1–16.
- Moodie, G.E.E. 1972. Predation, natural selection and adaptation in an unusual threespine stickleback. *Heredity*, **28**: 155–167. doi:[10.1038/hdy.1972.21](https://doi.org/10.1038/hdy.1972.21).
- Moodie, G.E.E., and Moodie, P.F. 1996. Do asymmetric sticklebacks make better fathers? *Proc. Roy. Soc. Lond. B*, **263**: 535–539.
- Moodie, G.E.E., and Reimchen, T.E. 1976. Phenetic variation and habitat differences in *Gasterosteus* populations of the Queen Charlotte Islands. *Syst. Zool.* **25**: 49–61. doi:[10.2307/2412778](https://doi.org/10.2307/2412778).
- Nosil, P., and Reimchen, T.E. 2001. Tarsal asymmetry, nutritional condition, and survival in water boatmen (*Callicorixa vulnerata*). *Evolu-*

- tion, 55: 712–720. doi:10.1554/0014-3820(2001)055[0712:TANCAS]2.0.CO;2. PMID: 11392389.
- Palmer, A.R., and Strobeck, C. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Annu. Rev. Ecol. Syst.* 17: 391–421. doi:10.1146/annurev.es.17.110186.002135.
- Palmer, A.R., and Strobeck, C. 2003. Fluctuating asymmetry analyses revisited. In *Developmental instability: causes and consequences*. Vol. 2003. pp. 279–319. doi:10.1093/oso/9780195143454.003.0017.
- Petrazzini, M.E., Sovrano, V.A., Vallortigara, G., and Messina, A. 2020. Brain and behavioral asymmetry: a lesson from fish. *Front. Neuroanat.* 14: 11. doi:10.3389/fnana.2020.00011.
- Planidin, N.P., and Reimchen, T.E. 2019. Spatial, sexual, and rapid temporal differentiation in neuromast expression on lateral plates of Haida Gwaii threespine stickleback (*Gasterosteus aculeatus*). *Can. J. Zool.* 97: 988–996. doi:10.1139/cjz-2019-0005.
- Planidin, N.P., and Reimchen, T.E. 2021. Ecological predictors of lateral line asymmetry in stickleback (*Gasterosteus aculeatus*). *Evol. Ecol.* 35: 609–629. doi:10.1007/s10682-021-10117-w.
- Planidin, N.P., and Reimchen, T.E. 2022. Behavioural responses of threespine stickleback with lateral line asymmetries to experimental mechanosensory stimuli. *J. Exp. Biol.* 225: jeb243661. doi:10.1242/jeb.243661.
- Reimchen, T.E. 2021. Evaluating compositional fidelity and sources of mortality of shoreline fish carcasses in a freshwater lake community in western Canada. *Palaios* 36: 260–268.
- Reimchen, T.E. 1983. Structural relationships between spines and lateral plates in threespine stickleback (*Gasterosteus aculeatus*). *Evolution*, 1983: 931–946.
- Reimchen, T.E. 1988. Inefficient predators and prey injuries in a population of giant stickleback. *Can. J. Zool.* 66: 2036–2044. doi:10.1139/z88-299.
- Reimchen, T.E. 1990. Size-structured mortality in a threespine stickleback (*Gasterosteus aculeatus*)–Cutthroat Trout (*Oncorhynchus clarki*) community. *Can. J. Fish. Aquat. Sci.* 47: 1194–1205. doi:10.1139/f90-139.
- Reimchen, T.E. 1991. Trout foraging failures and the evolution of body size in stickleback. *Copeia*, 1991: 1098–1104. doi:10.2307/1446106.
- Reimchen, T.E. 1992a. Injuries on stickleback from attacks by a toothed predator (*Oncorhynchus*) and implications for the evolution of lateral plates. *Evolution*, 46: 1224–1230. doi:10.1111/j.1558-5646.1992.tb00631.x.
- Reimchen, T.E. 1992b. Extended longevity in a large-bodied stickleback, *Gasterosteus*, population. *Can. Field Nat.* 106: 122–125. doi:10.5962/p.356892.
- Reimchen, T.E. 1994. Predators and morphological evolution in threespine stickleback. In *The evolutionary biology of the threespine stickleback*. Vol. 1994. pp. 240–276. doi:10.1093/oso/9780198577287.003.0009.
- Reimchen, T.E. 1995. Predator-induced cyclical changes in lateral plate frequencies of *Gasterosteus*. *Behaviour*, 132: 1079–1094. doi:10.1163/156853995X00469.
- Reimchen, T.E. 1997. Parasitism of asymmetrical pelvic phenotypes in stickleback. *Can. J. Zool.* 75: 2084–2094. doi:10.1139/z97-843.
- Reimchen, T.E., and Bergstrom, C.A. 2009. The ecology of asymmetry in stickleback defense structures. *Evolution*, 63: 115–126. doi:10.1111/j.1558-5646.2008.00520.x.
- Reimchen, T.E., and Bergstrom, C.A. 2023. Multi-generation selective landscapes and sub-lethal injuries in stickleback. *Evolution*, 77: 1101–1116. doi:10.1093/evolut/qpado32.
- Reimchen, T.E., and Douglas, S. 1980. Observations of loons (*Gavia immer* and *G. stellata*) at a bog lake on the Queen Charlotte Islands. *Can. Field Nat.* 94: 398–404. doi:10.5962/p.347128.
- Reimchen, T.E., and Douglas, S.D. 1984. Seasonal and diurnal abundance of aquatic birds on the Drizzle Lake Reserve, Queen Charlotte Islands, British Columbia. *Can. Field Nat.* 98: 22–28. doi:10.5962/p.355079.
- Reimchen, T.E., and Nosil, P. 2001. Lateral plate asymmetry, diet and parasitism in threespine stickleback. *J. Evol. Biol.* 14: 632–645. doi:10.1046/j.1420-9101.2001.00305.x.
- Reimchen, T.E., Ingram, T., and Hansen, S.C. 2008. Assessing niche differences of sex, armor and asymmetry phenotypes using stable isotope analyses in Haida Gwaii sticklebacks. *Behaviour*, 145: 561–577. doi:10.1163/156853908792451449.
- Reimchen, T.E., Steeves, D., and Bergstrom, C.A. 2016. Sex matters for defence and trophic traits of threespine stickleback. *Evolutionary Ecology Research*, 17: 459–485.
- Reimchen, T.E., and Douglas, S. 2021. Loon abundance and behaviour over four decades at a remote ecological reserve on Haida Gwaii, British Columbia, Canada. *Can. Field Nat.* 135: 28–38. doi:10.22621/cfn.v135i1.2617.
- Schröder, M., Windhager, S., Schaefer, K., and Ahnelt, H. 2023. Adaptability of bony armor elements of the threespine stickleback *Gasterosteus aculeatus* (Teleostei: Gasterosteidae): ecological and evolutionary insights from symmetry analyses. *Symmetry*, 15: 811. doi:10.3390/sym15040811.
- Stroud, J.T., Moore, M.P., Langerhans, R.B., and Losos, J.B. 2023. Fluctuating selection maintains distinct species phenotypes in an ecological community in the wild. *Proc. Natl. Acad. Sci.* 120: e2222071120. doi:10.1073/pnas.2222071120.
- Swaddle, J.P. 1997a. Developmental stability and predation success in an insect predator-prey system. *Behav. Ecol.* 8: 433–436. doi:10.1093/beheco/8.4.433.
- Swaddle, J.P. 1997b. Within-individual changes in developmental stability affect flight performance. *Behav. Ecol.* 8: 601–604. doi:10.1093/beheco/8.6.601.
- Thomas, A.L. 1993. The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners. *Proc. Roy. Soc. Lond. B.* 254: 181–189.
- Tofts, A.M., Johnson, D.W., and Carter, A.J. 2016. Strong nonlinear selection against fluctuating asymmetry in wild populations of a marine fish. *Evolution*, 70: 2899–2908. doi:10.1111/evo.13092.
- Trokovic, N., Herczeg, G., Ghani, N.I.A., Shikano, T., and Merilä, J. 2012. High levels of fluctuating asymmetry in isolated stickleback populations. *BMC Evol. Biol.* 12: 115. doi:10.1186/1471-2148-12-115.
- Vallortigara, G., and Rogers, L.J. 2005. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav. Brain Sci.* 28: 575–589. doi:10.1017/S0140525X05000105.
- Van Valen, L. 1962. A study of fluctuating asymmetry. *Evolution*, 2005: 125–142.
- Vermeij, G.J. 1982. Unsuccessful predation and evolution. *Am. Nat.* 120: 701–720. doi:10.1086/284025.
- Windig, J.J., and Nylin, S. 1999. Adaptive wing asymmetry in males of the speckled wood butterfly (*Pararge aegeria*). *Proc. R. Soc. Lond. Ser. B: Biol. Sci.* 266: 1413–1418. doi:10.1098/rspb.1999.0795.