

NOTES

Dietary differences between phenotypes with symmetrical and asymmetrical pelvis in the stickleback *Gasterosteus aculeatus*

T.E. Reimchen and P. Nosil

Abstract: Differential parasitism among phenotypes within populations can result from intrinsic factors such as immunocompetence or extrinsic factors such as ecological overlap with pathogens. In a recent study of a population of sticklebacks (*Gasterosteus aculeatus*) from Boulton Lake, British Columbia, relative cestode infections were related to pelvic-girdle symmetry. Adult sticklebacks with an asymmetrical pelvis had a higher incidence of infections than fish with a symmetrical pelvis, yet the pattern was reversed among yearlings. In the current study we test whether this unexpected result for yearlings, which is inconsistent with general theory coupling asymmetry with reduced immunocompetence, might be due to ecological factors rather than to differences in immunocompetence. We analyze the diet of 9089 uninfected sticklebacks collected during a 15-year study and show that male and female yearling sticklebacks with an asymmetrical pelvis are more benthic than symmetrical phenotypes. This could reduce the probability of exposure to pelagic copepods, the primary hosts of the cestode *Schistocephalus solidus*, and thereby lead to lower infection rates relative to pelagic fish. This finding would account for the unusual reversal in relative parasitism in this population and raises the possibility of finding further diet-induced causes of differential parasitism in studies of asymmetry.

Résumé : Le parasitisme qui affecte différemment les divers phénotypes au sein des populations peut être attribuable à des facteurs intrinsèques tels l'immunocompétence ou à des facteurs extrinsèques comme le chevauchement écologique avec des pathogènes. Au cours de l'étude récente d'une population d'épinoches (*Gasterosteus aculeatus*) au lac Boulton, Colombie-Britannique, les infections dues aux cestodes étaient reliées à la symétrie de la ceinture pelvienne. Les infections étaient plus fréquentes chez les poissons adultes asymétriques, mais cette tendance était inversée chez les poissons de l'année. Dans cette étude, nous avons vérifié si ce résultat inattendu chez les poissons de l'année, qui ne cadre pas avec la théorie générale qui relie l'asymétrie à une réduction de l'immunocompétence, peut s'expliquer par des facteurs écologiques plutôt que par des différences d'immunocompétence. Nous avons analysé le régime alimentaire de 9089 épinoches saines récoltées sur une période de 15 ans et nous démontrons que les femelles asymétriques de l'année ont un mode de vie plus benthique que les femelles à phénotype symétrique. Cela pourrait avoir pour effet de réduire la probabilité de contact avec des copépodes pélagiques, hôtes primaires du cestode *Schistocephalus solidus*, et, de ce fait, donner lieu à des taux d'infection plus faibles que ceux des poissons pélagiques. Ces résultats expliquent le renversement du parasitisme relatif observé chez cette population et laissent croire que des différences dans les régimes alimentaires peuvent être à l'origine du parasitisme différentiel rencontré au cours d'études de l'asymétrie.

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Introduction

Departures from bilateral symmetry in morphological characters occur at low frequency in many species and may be caused by developmental stress or genetic factors (Palmer and Strobeck 1986; Palmer 1994). Inverse associations between asymmetry and fitness have been reported (Møller

1991; Kodric-Brown 1997; for review see Møller 1997; but see Clarke 1998), owing to competitive inferiority of asymmetrical phenotypes (Thornhill 1992; Allen and Simmons 1996; Møller and Zamora-Munoz 1997; Hunt et al. 1998; Nosil and Reimchen 2001) or elevated levels of parasitic infection (Bonn et al. 1996; Møller 1996a; for review see Møller 1996b; Markusson and Folstad 1997; Reimchen 1997).

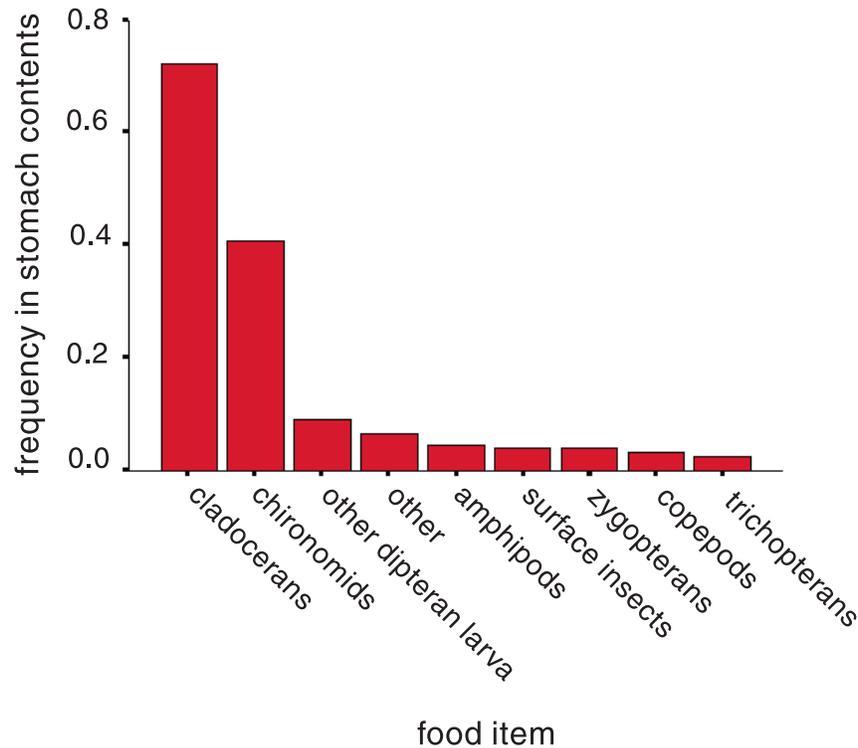
During investigations of insular lake populations of the threespine stickleback, *Gasterosteus aculeatus*, from the Queen Charlotte Islands in western Canada (see review in Reimchen 1994), a population was identified that exhibited variability in the pelvic girdle. There were three major pelvic phenotypes: a complete girdle, one half girdle, and no girdle (Reimchen 1980). Adult fish with an asymmetrical pelvic girdle had higher incidence of cestode (*Schistocephalus solidus*, *Cyathocephalus truncatus*) and nematode infections than

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Fig. 1. Overall frequencies of various food items present in stomachs of unparasitized sticklebacks (*Gasterosteus aculeatus*) in Boulton Lake ($n = 9089$).



did symmetrical fish of equivalent size (Reimchen 1997). Results for the adult fish were consistent with theoretical predictions coupling stress, asymmetry, and reduced immunocompetence and suggest that asymmetrical individuals have an increased susceptibility to infection (Wakelin 1978; Herbert and Cohen 1993; for review see Møller 1996b; Markusson and Folstad 1997). However, juvenile and yearling fish with an asymmetrical pelvis had lower incidence of *S. solidus* infections than did symmetrical fish, and this did not match any known process or prediction as it suggested that asymmetrical fish had increased immunocompetence relative to symmetrical fish. Reimchen (1997) proposed that, rather than indicating an ontogenetic switch in immunocompetence, this reversal of differential parasitism could simply occur if there were spatial or other ecological differences between symmetrical and asymmetrical phenotypes that influenced exposure to parasites.

In this paper we test two components of this proposal by investigating (1) whether there are dietary differences between symmetrical and asymmetrical sticklebacks that would contribute to the reduced parasitism of asymmetrical phenotypes in yearlings through reduced encounter rates with infected primary hosts of each parasite, and (2) whether observed differences in the diet are the result of competitive superiority of symmetrical fish.

Study area and methods

The investigation was carried out at Boulton Lake, Graham Island, off the coast of central British Columbia in western Canada. Sticklebacks were collected in 1970, 1971, and 1975–1986 and scored for standard length (SL), spine phenotype, sex, parasite in-

fections, and stomach contents (for details see Reimchen 1980, 1982, 1997). For the present study, data on the stomach contents of unparasitized sticklebacks ($n = 9089$) were analyzed, as previous studies have shown that diet and other aspects of the behavior of parasitized fish are modified (Reimchen 1982; Lobue and Bell 1993; Ness and Foster 1999). The major taxonomic groups were (in order of decreasing frequency) cladocerans (*Bosmina* spp., *Chydoridae* spp., *Leptodora kindtii*, *Polyphemus* spp.), chironomids, other dipterans (Culicidae spp., Ceratopogonidae spp.), amphipods (*Gammarus* spp.), surface insects, zygopterans, copepods (*Diaptomus* spp.), and trichopterans (Fig. 1). To increase the sample size and allow for comparisons within single years we grouped the more common dietary items into three broad categories: cladocerans (all species), chironomids (all species), and culicids (all species). We grouped the two symmetrical phenotypes into a single category and compared diets between symmetrical and asymmetrical phenotypes (see Reimchen 1997). We also partitioned each sample into two size classes, yearlings (<4.5 cm SL) and adults (≥ 4.5 cm SL), and compared overall consumption (log-likelihood G test, G_p) of the three major prey types between pelvic phenotypes. There was evidence that stickleback diets varied among localities, consequently we present results initially for fish captured from the single locality (beach) where sample sizes were largest, and we test for continuity in trends across time (heterogeneity G test, G_H ; Sokal and Rohlf 1981). We then examined associations between diet and pelvic asymmetry using data from all localities and tested for heterogeneity in trends among localities (G_H). Pooled results for each food type include only years or localities in which the food item was scored. Thus, sample sizes and degrees of freedom vary among groups. We also compared (G test) the consumption of specific rare items (amphipods, copepods, trichopterans, zygopterans, surface insects), which were excluded from grouped analyses, between the pelvic phenotypes.

Intraspecific food partitioning can be subtle, and differences between phenotypes may not be detectable if specific food items are

Table 1. Log-likelihood G tests on yearling (<4.5 cm) and adult (\geq 4.5 cm) male and female sticklebacks (*Gasterosteus aculeatus*) from a beach locality on Boulton Lake, comparing the consumption frequency (percentage of stomach contents with an item present) of three food categories between phenotypes with a symmetrical (S) and an asymmetrical (AS) pelvis.

	Percentage		n	G_P	P	G_H	df	P
	S	AS						
Cladocerans								
Yearling males	84.6	84.9	1325	0.14	0.91	13.17	12	>0.50
Adult males	34.2	34.5	581	0.02	0.96	5.74	9	>0.75
Yearling females	85.5	84.2	1274	0.20	0.66	15.95	12	>0.25
Adult females	33.8	45.2	279	2.00	0.15	10.54	9	>0.10
Chironomids								
Yearling males	37.3	42.3	1744	2.49	0.12	8.25	13	>0.90
Adult males	24.3	24.6	1093	0.01	0.94	15.03	11	>0.25
Yearling females	34.2	40.3	1670	3.64	0.06	11.11	13	>0.75
Adult females	28.4	26.8	640	0.92	0.33	6.42	11	>0.90
Other dipterans								
Yearling males	15.3	13.3	1319	0.57	0.45	13.09	11	>0.25
Adult males	1.4	1.8	406	0.03	0.86	1.97	4	>0.75
Yearling females	18.5	16.3	1142	0.49	0.48	11.50	10	>0.50
Adult females	4.1	0.0	57	0.62	0.43	1.39	2	>0.25

Note: G -test statistics and probabilities testing for heterogeneity among years (G_H) and for an overall pooled (G_P) effect are given. None of the G tests are statistically significant at $P < 0.05$.

grouped into broad categories. Between 1975 and 1981 (74% of the total sample size), more specific food items were consistently differentiated. Consequently, we examined these dietary effects and the prevalence of parasitism in these years. The mean proportion of fish with *S. solidus* or *C. truncatus* infection and the mean proportion of fish stomachs containing each of 15 food items were calculated for each month of sampling between 1975 and 1981. Calculations for *C. truncatus* were restricted to fish >40 mm SL, as smaller fish are not infected, and to winter months (November–April), as *C. truncatus* infections are rare in summer. We tested for correlations between the diet of unparasitized fish within a sample (each month of sampling) and the prevalence of parasitism (for each species separately) within a sample using Spearman's rank correlation (SR). Dietary items associated with the prevalence of parasitic infection will be referred to as predictor food items. We then used G tests of whether consumption of each of the predictor food items differed between pelvic phenotypes in yearling and adult sticklebacks for each year between 1975 and 1981, using beach-captured sticklebacks, and tested for heterogeneity among years. We also report pooled results from all localities and test for heterogeneity among localities. Wilcoxon's signed-rank (WSR) tests were used to test for trends. We also compared the size of symmetrical and asymmetrical fish within a cohort by means of one-sample t tests and WSR tests. All analyses were performed using SPSS (version 9.0). We used the sequential Bonferroni correction for multiple tests where appropriate (Rice 1989).

Results

General dietary comparison

There were marginal differences in the common taxa in the diet between symmetrical and asymmetrical phenotypes, depending on the size class of fish and the dietary group (Tables 1, 2). For both sexes, asymmetrical yearlings showed increased consumption of chironomids relative to symmetrical yearlings, both beach-captured fish ($P = 0.12$ for males and $P = 0.056$ for females) and those from all localities combined ($P = 0.09$ for males and $P < 0.05$ for females). For

yearlings we used pelvic condition (symmetrical/asymmetrical), sex (male/female), and chironomids (presence/absence) as factors in a hierarchical log-linear analysis and identified a unique partial association between pelvic asymmetry and chironomid presence that was independent of sex (33.9 and 40.1% of symmetrical and asymmetrical fish with chironomids present, respectively, $n = 5196$, pelvic asymmetry \times chironomid interaction, partial $\chi^2 = 5.42$, $df = 2$, $P < 0.05$). Adult sticklebacks showed no trends in chironomid consumption between pelvic phenotypes, using the beach-captured fish or those from all localities combined. The pelvic phenotypes did not differ statistically in the relative consumption of cladocerans and "other dipterans" for either yearling or adult sticklebacks of either sex from beach-captured fish or those from all localities combined.

We tested whether pelvic phenotypes differed in their consumption of the less common food items (copepods, amphipods, zygopterans, trichopterans, surface insects). In yearling males, symmetrical phenotypes showed increased consumption of surface insects relative to asymmetrical individuals (19 and 8%, respectively; G test, $G_1 = 3.88$, $P < 0.05$, $n = 687$), but no differences among the remaining items (G test, all $P > 0.25$). Among adult males, adult females, and subadult females, there were no differences in relative consumption of any group (G test, all $P > 0.25$).

Consumption of predictor food items

We examined associations between the diet of unparasitized fish (each month of sampling from 1975 to 1981) and the prevalence of *S. solidus* and *C. truncatus* infection in each sample. Of the 15 food categories in stickleback stomachs during this period, the relative consumption of four taxa, *Bosmina* sp. 2, Culicidae, Chydoridae, and Ceratopogonidae, was positively and significantly correlated with the prevalence of *S. solidus* infection (SR, $P < 0.05$, Bonferroni cor-

Table 2. Log-likelihood G tests on yearling (<4.5 cm) and adult (4.5 cm) male and female sticklebacks from all localities on Boulton Lake, comparing the consumption frequency (percentage of stomach contents with an item present) of the three food categories between phenotypes with a symmetrical (S) and an asymmetrical (AS) pelvis.

	Percentage		n	G_P	P	G_H	df	P
	S	AS						
Cladocerans								
Yearling males	85.1	83.1	2212	0.34	0.34	10.95	6	>0.05
Adult males	42.3	43.1	1312	0.05	0.83	8.94	7	>0.25
Yearling females	85.9	85.3	2088	0.09	0.76	4.84	5	>0.25
Adult females	48.5	53.3	974	1.17	0.28	7.61	8	>0.25
Chironomids								
Yearling males	39.7	44.4	2240	2.91	0.09	5.50	7	>0.50
Adult males	40.7	39.7	1317	0.07	0.79	5.30	7	>0.50
Yearling females	38.1	44.5	2104	4.88	<0.05	1.22	5	>0.90
Adult females	47.2	53.8	1006	2.35	0.13	13.92	8	>0.05
Other dipterans								
Yearling males	14.5	13.9	1674	0.08	0.79	3.47	3	>0.25
Adult males	7.8	5.2	1077	1.37	0.24	0.90	3	>0.75
Yearling females	16.1	15.9	1560	0.01	0.94	8.15	3	>0.025
Adult females	5.1	1.9	697	2.56	0.11	1.53	3	>0.50

Note: G -test statistics and probabilities testing for heterogeneity among localities (G_H) and for an overall pooled (G_P) effect are given.

Table 3. Spearman's rank correlations between the frequency of *Schistocephalus solidus* infections in a monthly sample and the frequency of 15 food items in stickleback stomachs in a monthly sample.

Food item	Spearman's ρ	P
<i>Bosmina</i> sp. 1	0.27	0.11
<i>Gammarus</i> spp.	0.14	0.39
Chironomids (all species)	0.11	0.50
Cladoceran species	0.30	0.06
<i>Bosmina</i> sp. 2	0.55	0.001*
Culicids (all species)	0.49	0.002*
<i>Leptodora kindtii</i>	0.27	0.09
<i>Diaptomus</i> spp.	0.21	0.20
Chydorids	0.54	0.001*
Ceratopogonids (all species)	0.64	0.001*
Surface insects	0.22	0.18
Fish fry	0.07	0.97
<i>Polyphemus</i> spp.	0.42	0.01
Trichopteran (all species)	0.21	0.21
Coleopterans (all species)	0.19	0.26

Note: Samples were taken between 1975 and 1981 ($n = 42$).

* $P < 0.05$ after sequential Bonferroni corrections.

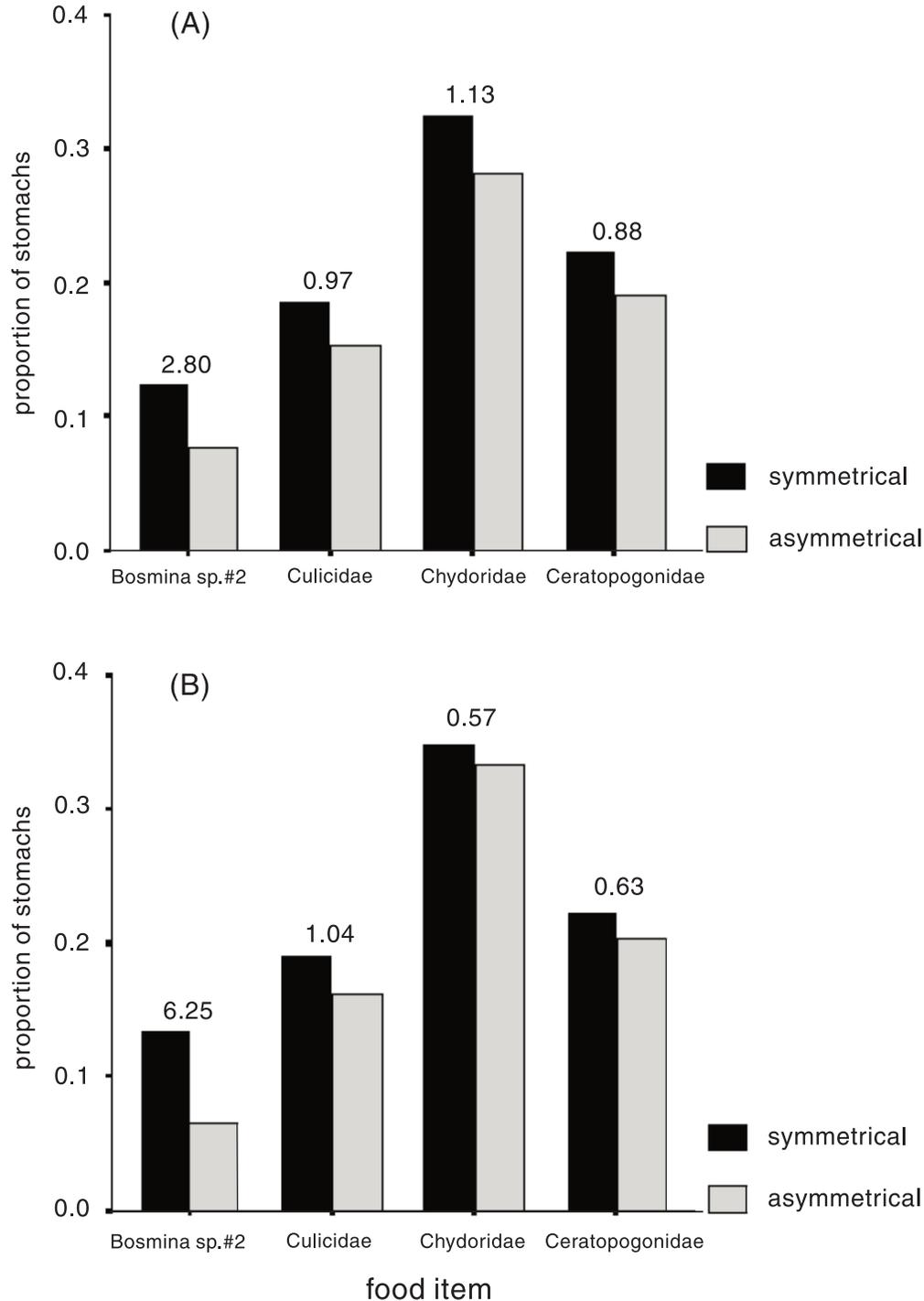
rection; Table 3) and accounted for a significant proportion of the variability in *S. solidus* infection among samples (multiple regression, $r^2 = 0.35$, $F_{[4,34]} = 4.54$, $P < 0.005$). There was no significant correlation between the prevalence of *S. solidus* and copepods, the primary host of this parasite, possibly because of their very low frequency in the diet (<4%). Therefore, we tested whether there were any associations between copepods and the predictor food items. Results demonstrate that the predictor food items accounted for 40% of the variability in sample differences in copepod prevalence (multiple regression, $r^2 = 0.40$, $F_{[4,34]} = 5.58$, $P <$

0.001). No significant correlations were detected between food items and monthly prevalence of *C. truncatus* (SR, all $P > 0.05$).

We then tested whether the consumption of each of the four predictor food items differed between the spine phenotypes, predicting that for yearling fish, symmetrical phenotypes would show greater consumption. For beach-captured fish (pooled across years), the differences were slight (G test, *Bosmina* sp. 2 in females, $P < 0.05$, all other $P > 0.05$), with symmetrical yearlings of both sexes exhibiting marginally greater consumption of each of the four predictor food items than asymmetrical individuals (Fig. 2; WSR test, $Z = -2.52$, $P < 0.05$, $n = 8$). Analyses of yearly trends (males and females combined) revealed that symmetrical beach-captured individuals showed greater consumption of *Bosmina* sp. 2 than did asymmetrical individuals in 9 of 12 years (WSR test, $Z = -1.96$, $P < 0.05$) and greater consumption of the other predictor food items in 8 of 12 years (WSR test, Ceratopogonidae, $Z = -1.49$, $P = 0.13$; Chydoridae, $Z = -1.57$, $P = 0.12$; Culicidae, $Z = -1.18$, $P = 0.24$). When the probabilities for each test were combined, overall differences were significant ($\chi^2 = 17.14$, $df = 8$, $P < 0.05$; Sokal and Rohlf 1981). There was no statistical heterogeneity in this trend among years for any of the predictor food items (heterogeneity G test, all $P > 0.10$). For all localities combined, differences were also slight (G test, all $P > 0.05$), with symmetrical phenotypes of both sexes exhibiting greater consumption of each of the four predictor food items than asymmetrical phenotypes (Table 4; WSR test, $Z = -2.52$, $P < 0.05$, $n = 8$). There was heterogeneity among localities only in consumption of *Bosmina* sp. 2 by females (heterogeneity G test, $G_{H2} = 7.23$, $P < 0.05$; all other $P > 0.10$).

We performed the same analyses of the relative consumption of each of the four predictor food items by adult sticklebacks, predicting that symmetrical phenotypes would show

Fig. 2. Proportions of stomachs of symmetrical and asymmetrical yearling (<45 mm SL) male ($n = 803$ and 131 for symmetrical and asymmetrical males, respectively) (A) and female ($n = 809$ and 123 for symmetrical and asymmetrical females, respectively) sticklebacks (B) containing four predictor food items between 1976 and 1981. Variability in the monthly prevalence of each of these food items was positively correlated with variability in the monthly prevalence of *Schistocephalus solidus* infection. Asymmetrical yearlings of both sexes exhibited increased consumption of each of the predictor food items relative to symmetrical yearlings (WSR test, $P < 0.05$). The value shown above each pair of bars is the test statistic from log-likelihood G tests.



lower consumption. We detected no consistent trends or associations for beach-captured fish (G test, all $P > 0.25$; WSR test, greater consumption by symmetrical fish in 3 of 8 comparisons, $Z = -0.28$, $P = 0.78$, $n = 8$; heterogeneity among

years, all $P > 0.10$) but a marginal and nonsignificant tendency towards increased consumption of predictor food items by symmetrical adults when localities were combined (Table 4; WSR test, $Z = -1.26$, $P = 0.21$, $n = 8$; heterogeneity among

Table 4. Log-likelihood G tests comparing the frequency of consumption (percentage of stomach contents with an item present) of predictor food items between phenotypes with a symmetrical (S) and an asymmetrical (AS) pelvis in yearling (<4.5 cm) and adult (4.5 cm) male and female sticklebacks from all localities in Boulton Lake.

Predictor food item	Percentage		n	Pooled G	P
	S	AS			
Yearling males					
Dipteran larvae	16.8	12.4	1399	2.76	0.10
Chydorids	24.9	19.8	1342	2.56	0.11
Culicids	16.5	15.3	1275	0.18	0.68
<i>Bosmina</i> sp. 2	12.6	11.2	1275	0.30	0.59
Yearling females					
Dipteran larvae	16.9	14.6	1357	0.68	0.41
Chydorids	25.4	23.4	1386	0.37	0.55
Culicids	17.1	16.5	1264	0.43	0.84
<i>Bosmina</i> sp. 2	13.2	10.3	1264	1.28	0.26
Adult males					
Dipteran larvae	6.8	5.5	1370	0.53	0.47
Chydorids	3.8	3.2	1169	0.13	0.72
Culicids	12.4	7.0	411	1.57	0.21
<i>Bosmina</i> sp. 2	2.2	1.7	1141	0.21	0.65
Adult females					
Dipteran larvae	6.3	6.7	1056	0.04	0.85
Chydorids	3.2	3.4	865	0.01	0.93
Culicids	5.1	1.2	414	3.04	0.08
<i>Bosmina</i> sp. 2	2.5	0.7	865	2.53	0.11

localities, all $P > 0.10$). Yearly trends showed no directionality (WSR test, all $P > 0.30$; combined probabilities, $P = 0.90$).

Body-size comparisons

If asymmetrical fish are competitively displaced into a suboptimal dietary niche by symmetrical fish, their body growth rate should be compromised. To test this, we compared SLs of symmetrical and asymmetrical sticklebacks within yearling and adult age cohorts using all the large ($n \geq 150$) monthly samples of males and females. Results demonstrate that both yearling and adult asymmetrical and symmetrical fish within a cohort are similar in size (one-sample t test, yearlings, mean paired difference = -2.11 , $t_{29} = -0.45$, $P = 0.66$; adults, mean paired difference = 3.21 , $t_{28} = 1.41$, $P = 0.17$). As well, there was no evidence of directionality in signed trends for yearlings (WSR test, $Z = -0.18$, $P = 0.86$) or adults (WSR test, $Z = 1.18$, $P = 0.24$). Therefore, we reject the hypothesis that asymmetrical fish are displaced into a suboptimal dietary niche.

Discussion

Associations between asymmetry and parasitism have been reported in diverse taxa, including insects, birds, mammals, and fish (Bonn et al. 1996; Møller 1996a; for review see Møller 1996b; Markusson and Folstad 1997; Reimchen 1997). Such associations may arise from differential immunocompetence and differential exposure to parasites. Symmetrical and asymmetrical pelvic phenotypes in sticklebacks from Boulton Lake exhibited unusual trends in *S. solidus* infection

rates: in the asymmetrical fish, juveniles exhibited decreased parasite prevalence but adults exhibited increased parasitism (Reimchen 1997). We predicted that this unexpected parasitism observed in juveniles would be more readily explained by postulating dietary differences between symmetrical- and asymmetrical-pelvis phenotypes among juveniles than by invoking shifts in relative susceptibility and immunocompetence. This is reasonable, given that the general seasonal and ontogenetic differences in parasite prevalence in Boulton Lake sticklebacks are correlated with seasonal and ontogenetic changes in dietary composition (Reimchen 1982).

Dietary-niche differences were detected among juvenile pelvic phenotypes in the direction predicted that would lead to reduced *S. solidus* infections in asymmetrical phenotypes. We initially tested for differential consumption of copepods and amphipods, the primary hosts of *S. solidus* and *C. truncatus*, respectively, but found no differences, possibly because both of these items were exceptionally rare in the diet. However, we found that the asymmetrical individuals showed marginally higher consumption of chironomids, a benthic food resource, than did the symmetrical individuals and showed lower consumption of surface insects and other food items usually found in association with *S. solidus* infection (predictor food items). These differences suggest that asymmetrical yearlings occupy a more benthic niche and this could result in a lower rate of contact with the pelagic copepod that is the primary host of *S. solidus*.

Dietary differences among phenotypes within a population can result from competitive interactions and it is possible that asymmetrical pelvic phenotypes in sticklebacks are displaced into a suboptimal benthic niche by competitively superior symmetrical individuals. A comparable process occurs in blackbirds (*Turdus turdula*), where individuals with greater fluctuating asymmetry are found in lower quality habitat patches (Møller 1995), and in water boatmen (*Callicorixa vulnerata*), where individuals with greater fluctuating asymmetry exhibit reduced nutritional condition in natural ponds and reduced survival rates under resource-limited conditions (Nosil and Reimchen 2001). A predicted result of reduced trophic competitive ability would be a reduced growth rate (Peckarsky and Cowan 1992; Siikavuopio et al. 1996). However, we detected no difference in relative body sizes of symmetrical and asymmetrical sticklebacks within cohorts, suggesting that asymmetrical individuals are not competitively compromised. This suggests that observed dietary differences are the result of niche partitioning. Examination of lake spatial data among phenotypes (Reimchen 1980) demonstrates that in 10 of 12 comparisons (binomial test, $P < 0.05$), the relative abundance of sticklebacks with an asymmetrical pelvis was greater offshore than inshore compared with other pelvic phenotypes. As pelvic asymmetry in Boulton Lake sticklebacks is highly directional, suggesting a genetic origin of the asymmetry (Palmer 1994), it is possible that each of the pelvic phenotypes, including asymmetrical, exhibits ecological specialization to occupy different niches.

Adult sticklebacks with an asymmetrical pelvis have more cestode and nematode infections than do symmetrical fish (Reimchen 1997) and we tested for dietary effects among phenotypes. We found no significant differences or trends in the diet that would have contributed to the differential parasitism and this suggests that the differential parasitism is due

to increased susceptibility to parasitic infection rather than to differential exposure to infected prey. This result is congruent with the results of other studies linking asymmetry to decreased immunocompetence and increased parasitism (e.g., Thornhill and Gangestad 1993; Bonn et al. 1996; Møller 1996a; for review see Møller 1996b; Markusson and Folstad 1997).

In summary, examination of a long-term database shows a small but significant difference in diet between symmetrical- and asymmetrical-pelvis phenotypes in yearling sticklebacks and this may account for the unusual patterns of parasitism in this population. Asymmetrical sticklebacks appear to occupy a slightly different dietary niche than do symmetrical phenotypes and as a result have reduced rates of encounter with pathogens. This suggests that the differential parasitism observed in studies of asymmetry (Møller 1996b) warrant both ecological and immunological consideration.

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