# Ecological causes of sex-biased parasitism in threespine stickleback

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Males and females can differ in levels of parasitism and such differences may be mediated by the costs of sexual selection or by ecological differences between the genders. In threespine stickleback, *Gasterosteus aculeatus*, males exhibit paternal care and territorial nest defence and the costs of reproduction may be particularly high for males relative to females. We monitored levels of parasitism for 15 years in a population of stickleback infected by four different parasite species. Consistent with general predictions, overall parasite prevalence (total parasitism) was greater in males than in females. However, this excess did not occur for each species of parasite. Males had higher prevalence of a cestode *Cyathocephalus truncatus* and a trematode *Bunodera* sp. relative to females, while females had higher prevalence of a cestode *Schistocephalus solidus* and nematodes. This suggested ecological sources to differences in parasitism rather than reproductive costs and therefore we examined diet of unparasitized stickleback, predicting that differences in dietary niche would influence relative parasitism. This was partially confirmed and showed that female stomach contents had increased frequency of pelagic items, the major habitat for the primary host of *S. solidus* whereas males exhibited increased frequency of benthic items, the dominant habitat of *C. truncatus* and *Bunodera*. Temporal shifts in the extent and direction of differential parasitism among years between the sexes were associated with temporal shifts in dietary differences. Our results, combined with those in the literature, suggest that ecological differences between genders could be a more important component to patterns of parasitic infection in natural populations than currently appreciated. © 2001 The Linnean Society of London

ADDITIONAL KEYWORDS: parasitism – sexual dimorphism – ecological selection – sexual selection – diet – resource partitioning – *Gasterosteus aculeatus* – Queen Charlotte Islands.

## INTRODUCTION

Parasites are major ecological players in communities and differential parasitism can occur between males and females (Bundy, 1988; Zuk, 1990; Poulin, 1996a for review). Such sex-biased parasitism may result from differences in immunocompetence resulting from unequal costs of reproduction or from natural selection favouring ecological divergence which results in differential exposure to infectious agents (Selander, 1966; Trivers, 1976; Reimchen, 1980; Hamilton & Zuk, 1982; Slatkin, 1984; Tinsley, 1989; Houston & Shine, 1993; Perry, 1996). There is theoretical, experimental and field evidence to suggest that males should be more heavily infected than females, possibly due to the costs of sexual selection (Batra, 1984; Folstad *et al.*, 1989; Folstad & Karter, 1992; Poulin, 1996a; Wedekind & Jacobson, 1998). For example, competition for mates extracts costs on reproductive males and, consequently, males may be operating closer to their physiological limits than females (Trivers, 1972; Zuk, 1990; Clutton-Brock & Parker, 1992). This can result in higher levels of stress and reduced immunocompetence in males relative to females (Herbert & Cohen, 1993 for review). Elevated testosterone levels can also lead to immuno-suppression which further increases susceptibility of infection or disease (Folstad *et al.*, 1989; Folstad & Karter, 1992; but see Wedekind & Jacobson, 1998). However, differences in parasitic infection between

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genders might arise from ecological rather than sexual selection. For example, niche partitioning involving habitat or diet (c.f. Selander, 1966; Grant, 1975; Reimchen, 1980; Grant, 1985; Shine, 1989; Raymond *et al.*, 1990; Houston & Shine, 1993) can result in differential exposure to parasites unrelated to the unequal costs of reproduction (e.g. Tinsley, 1989). Such an ecological origin to parasitism would predict that either males or females could exhibit excess parasitism dependent on their probability of encountering the parasite and that excess parasitism in males cannot be immediately ascribed to reduced immunocompetence. However, the relative importance of niche partitioning as a general explanation for gender differences in parasitism has not been established.

Costs of reproduction for males may be especially high in fishes such as stickleback (Gasterostidae) where males provide all the parental care and exhibit all the territorial defence (van den Assem, 1967; Fitzgerald, Guderley & Picard, 1989; De-Fraipont, Fitzgerald & Guderley, 1992; Bakker, 1994 for review). As a result of these costs, stickleback provide a model system well suited to testing hypotheses concerning differential parasitism between the sexes (Zuk, 1990). Evolutionary studies of undisturbed stickleback populations from the Haida Gwaii (formerly Queen Charlotte Islands) off the west coast of Canada over the last three decades (Moodie & Reimchen, 1976; Reimchen, 1994) have allowed sampling over extended time series and provide a unique opportunity to investigate temporal associations between sex and parasitism in individuals from natural populations.

Threespine stickleback (*Gasterosteus aculeatus*) from Boulton Lake in the Queen Charlotte Islands, B.C. are infected by four species of parasites, including two cestodes, a trematode and a nematode (Reimchen, 1982, 1997). Using stickleback from this population as a model, we monitored parasitism of males and females for 15 years and initially tested for differential parasitism between the sexes. Secondly, we examined ontogenetic trends in relative infection between the genders predicting that the differential should be most expressed during reproduction, and thirdly we examined whether there was heterogeneity in any trends over time. Based on the high costs of reproduction in male stickleback and on the literature concerning the costs of sexual selection and male-biased parasitism in general, we predict males will exhibit higher parasite prevalence than females for all four parasite species.

However, there are ecological factors that could facilitate differences in parasitism between males and females in the Boulton Lake population. While males and females are both found throughout the lake, males tend to be more prevalent in littoral habitats whereas females are more limnetic (Reimchen, 1980) and this could influence patterns of parasitism by mediating exposure to infected primary hosts. The largest parasite infecting Boulton Lake stickleback is the coelomic tapeworm *Schistocephalus solidus*. This parasite utilizes a pelagic copepod as a primary host, stickleback as a secondary host and birds as definitive hosts (Clarke, 1954). The second largest parasite is the intestinal tapeworm *C. truncatus*, which utilizes benthic amphipods as primary hosts and fish as the definitive hosts (Vik, 1958). Nematodes (*Eustrongylides* spp.), which encyst in the muscle, utilize aquatic oligochaetes as primary hosts, while stickleback and avian piscivores are intermediate and definitive hosts respectively (Hoffman, 1967). Trematodes (*Bunodera* sp.) occur in the lower intestine and use a variety of primary and secondary hosts, including molluscs and crustaceans, while definitive hosts are fish (Cannon, 1971; Skorping, 1981). Consequently, the composition of the diet of each gender was also monitored over the sample period to test for potential niche partitioning between genders that could result in differential exposure to infected primary hosts. If niche variation, rather than reproductive costs, are involved in levels of parasitism, we predict that differential parasitism between male and female stickleback will be species-specific and associated with differences in spatial and dietary components of the ecological niche. Specifically, as females are more limnetic than males, we expect higher consumption of zooplankton in females and as a result higher infections by *S. solidus*. Furthermore, our long-term data base provides an opportunity to test whether there are temporal shifts in differential parasitism between the sexes and whether this is associated with temporal shifts in any dietary differences between the genders.

## STUDY AREA AND METHODS

The investigation was carried out using samples from Boulton Lake, Graham Island, off the coast of central British Columbia, western Canada (habitat data and sampling protocols in Reimchen, 1980, 1982). The stickleback occupy all major habitats (littoral, limnetic, benthic, pelagic) of the 15 ha lake and are preyed upon by macro-invertebrates and diving birds. Samples of stickleback were obtained in 1970, 1971, and 1975–1987. In addition to the measurements of body length (SL), spine morphology, gender and stomach contents, specimens were also scored for the number of *S. solidus* ($N = 20\,346$), *C. truncatus* ($N = 19\,695$) and nematodes ($N = 19\,873$). The contracted length of the largest plerocercoid was also recorded for *S. solidus*. The trematode *Bunodera* sp. was only scored systematically during the latter part of the study ($N = 5272$). Detailed descriptions of scoring for morphology, parasite infection, sex and SL are described in Reimchen (1980, 1982, 1997). In some individuals (<100), the gonads were

extensively atrophied and sex could not be determined.

We compared (pooled G-tests, $G_P$) the prevalence (presence/absence) and intensity (number) of parasites for male and female stickleback. We report results for prevalence only as trends were congruent for the two indices of parasitism. For each of the large-bodied parasites (*S. solidus, C. truncatus* and nematodes), we examined single species infection rates between the sexes and excluded fish that were infected with either of the two alternate large parasites. For *Bunodera*, we excluded all multiple species infections. We partitioned data among size-classes of fish and tested (heterogeneity G-tests, $G_H$) for continuity of trends across size classes and among years over the study period (1970–1987). Yearly comparisons for *C. truncatus* and nematodes were restricted to adult ($\geqslant 45$ mm) fish, as juveniles and yearlings are not generally infected.

We tested for differences in diet between the sexes (G-tests). Only non-parasitized fish were compared as parasites are known to modify stickleback behaviour (Lobue & Bell, 1993; Reimchen, 1982; Ness & Foster, 1999). Unparasitized stickleback ($N = 9089$) were examined and for each specimen the presence or absence of various food items was recorded. The major taxonomic groups identified were (listed in decreasing frequency) cladocerans (*Bosmina* spp., Chydoridae, *Leptodora kindtii, Polyphemus* spp.), chironomids, other dipteran larvae (Culicidae, Heleinae), amphipods (*Gammarus* spp.), surface insects, zygopterans, copepods (*Diaptomus* spp.) and trichopterans. Fish stomachs in which food items were digested and unidentifiable were scored as (1) benthic, if they contained more than 80% dark organic matter indicative of benthic prey items, (2) pelagic, if they contained more than 80% zooplankton remnants and (3) mixed, for combinations of benthic and pelagic. We excluded these fish from taxon-specific comparisons and tested separately whether the proportion of fish scored as 'benthic' differed between the sexes. We grouped the common, distinguishable dietary items into four broad categories; cladocerans (all spp.), chironomids (all spp.), Culicid larvae (90% Culicidae spp. + 10% Heleinae spp.) and macrobenthos (amphipods, zygopterans, trichopterans) and compared overall consumption of each between genders. We also partitioned the samples into two major size classes (yearlings <45 mm, adults $\geqslant 45$ mm) and tested for heterogeneity between size classes (heterogeneity G-tests). We examined yearly trends in dietary differences between the genders and compared these differences to differences in parasitism. Consumption of macrobenthos was too low in subadults to allow meaningful yearly comparisons.

There was evidence for slight dietary shifts among fish collected from different regions of the lake (unpublished data) and to minimize any potential bias to gender comparisons, we initially compared diet among seined fish collected from the same region of the lake (beach captures). We then examined associations between diet and gender using data from fish captured by minnow traps from all seven localities in the lake. These pooled results include only the localities a food item was detected in and were tested for heterogeneity (heterogeneity G-tests) in trends among localities.

We also specifically compared consumption of copepods and amphipods between the genders as these prey items act as primary host for *S. solidus* and *C. truncatus* respectively. When testing for gender differences in these items we report results seasonally (Winter: Nov.–Apr.; Summer: May–Oct.) and include fish captured by seining and traps. As comparison between males and females for each parasite species and food item tests a different hypothesis, we did not adjust overall significance levels for the number of parasite species and food items examined (Rice, 1989). However, within each parasite species and food item we corrected significance levels from G-tests for multiple comparisons (sequential Bonferroni method).

We examined whether temporal shifts in temperature were associated with temporal shifts in stickleback diet and tested whether shifts in the diet were associated with temporal shifts in overall parasite prevalence. To partially control for seasonal variability in temperature, diet and levels of parasitism we examined such associations in two seasons; winter and summer. To examine associations between temperature and diet we calculated the consumption frequency of zooplankton (cladocerans + copepods) and macrobenthos (macrobenthos + chironomids) for each gender for subadults and adults for each month of sampling (1970–1987) and used Spearman rank correlation (SR) to test whether these monthly dietary frequencies were correlated with monthly temperature means. We used Spearman rank correlation to test whether the diet (monthly frequency of a food item) of unparasitized fish within a monthly sample was correlated with prevalence of infection by each parasite species in a sample. Significance levels were adjusted for multiple comparisons using the sequential Bonferroni method. Lagging food consumption a few months before or after infection prevalence did not reveal any significant relationships. All statistical analyses were done using SPSS (v. 9.0).

## RESULTS

### RELATIVE PARASITISM

Among the 19 760 fish scored for sex and for the prevalence of the three large-bodied parasite species, the overall frequency of parasitic infection (all parasites grouped) was significantly higher in males than in females (26.4%, 22.5% respectively, $G_{P1} = 39.35$,

**Table 1.** Log-likelihood G-tests comparing the relative number of individuals infected by four parasite species (*S. solidus, C. truncatus, Bunodera* sp., Nematodes) between male and female *G. aculeatus* from Boulton Lake. Results exclude multiple species infections

| Parasite | % Males infected | % Females infected | N | G |
|---|---|---|---|---|
| *S. solidus* | 13.5 | 15.3 | 17314 | 11.49*** |
| *C. truncatus* | 21.2 | 10.1 | 9902 | 223.54*** |
| *Bunodera* sp. | 47.5 | 42.7 | 3761 | 8.64** |
| Nematodes | 1.9 | 2.4 | 15147 | 3.55 |

** *P*<0.01, *** *P*<0.001.

$P$<0.001, $N$ = 19 760). For infected fish, number of parasite species was also associated with gender, with males exhibiting increased likelihood of having multiple vs. single species infections compared with females (21.1% and 17.9% multiple infections for males and females respectively, G = 8.71, *P*<0.01).

This marginal excess parasitism of male stickleback did not persist when samples were partitioned by single species infections (multiple species infection excluded). Female stickleback had increased prevalence of *S. solidus* relative to males ($G_{P1}$, *P*<0.001) and a non-significant excess of nematodes (GP1, *P* = 0.06) whereas males had higher prevalence of *C. truncatus* ($G_{P1}$, *P*<0.001) and *Bunodera* ($G_{P1}$, *P*<0.01, Table 1). Size of *S. solidus* differed between the genders as females were more likely to have mature plerocercoids and this effect was accentuated during winter months (Table 2).

Ontogenetic comparisons were generally consistent with pooled effects, although heterogeneity among size classes in relative infection rates was detected (Fig. 1). For *S. solidus*, female sticklebacks had greater infection than did males in yearlings (30–39 mm) and adults (>50 mm) size classes whereas infection rates were similar in the other size classes ($G_{H4}$ = 28.94, *P*<0.001). For *C. truncatus*, which occurred only in subadult and adult stickleback, males had higher prevalence of infection than females in each size class and differences were accentuated in the largest fish ($G_{H2}$ = 110.34, *P*<0.001). For nematodes, female stickleback had higher infection than did males in each size class and this effect was most accentuated in the largest fish ($G_{H4}$ = 14.72, *P*<0.01). For *Bunodera*, male sticklebacks exhibited increased prevalence of infection relative to females in the two smallest size classes and similar infection rates in larger fish ($G_{H4}$ = 4.37, *P*>0.25).

There was variability among years in the direction and extent of differential parasitism of the sexes. *S. solidus* infections were female-biased in 1970, 1975 and 1976 (*P*<0.05, G-tests) whereas males had greater infection rates in 1981 (*P*<0.01, G-test; $G_{H14}$ = 30.19,

**Table 2.** Log-likelihood G-tests comparing the relative number of individuals with small (<15 mm) vs. large (⩾15 mm) *S. solidus* plerocercoids between male and female *G. aculeatus* from Boulton Lake. Results are shown for winter (Nov.–Apr.) and for summer (May–Oct.)

| Size class (mm) | % of males with large plerocercoids | % of females with large plerocercoids | N | G |
|---|---|---|---|---|
| Winter | | | | |
| 11–29 | 41.2 | 50.0 | 19 | 0.57 |
| 30–39 | 61.1 | 72.7 | 62 | 0.79 |
| 40–49 | 62.5 | 69.6 | 146 | 0.17 |
| 50–56 | 38.5 | 50.0 | 85 | 0.59 |
| 57–70 | 0.00 | 42.1 | 22 | 2.98 |
| Total (df 5) | | | | 4.59 |
| Pooled | 47.5 | 62.9 | 334 | 4.75* |
| Heterogeneity (df 4) | | | | 0.16 |
| Summer | | | | |
| 11–29 | 50.3 | 16.7 | 332 | 5.73 |
| 30–39 | 44.3 | 59.6 | 470 | 9.91** |
| 40–49 | 49.1 | 45.2 | 608 | 0.29 |
| 50–56 | 40.9 | 42.3 | 437 | 0.07 |
| 57–70 | 42.2 | 37.2 | 263 | 0.58 |
| Total (df 5) | | | | 16.57** |
| Pooled | | | | 0.01 |
| Heterogeneity (df 4) | | | | 16.57** |

* *P*<0.05, ** *P*<0.01.

*P*<0.01; Fig. 2). *C. truncatus* infections were male-biased in 14 of 15 years ($G_{H14}$ = 11.34, *P*>0.50; Fig. 3). Nematode infections were similar in most years but included two years (1980, 1981) with a marked female bias followed by a male bias in 1982 ($G_{H13}$ = 28.19, *P*<0.01; Fig. 4). Relative *Bunodera* infections of the sexes did not vary significantly among years ($G_{H6}$ = 6.36, *P*>0.25).
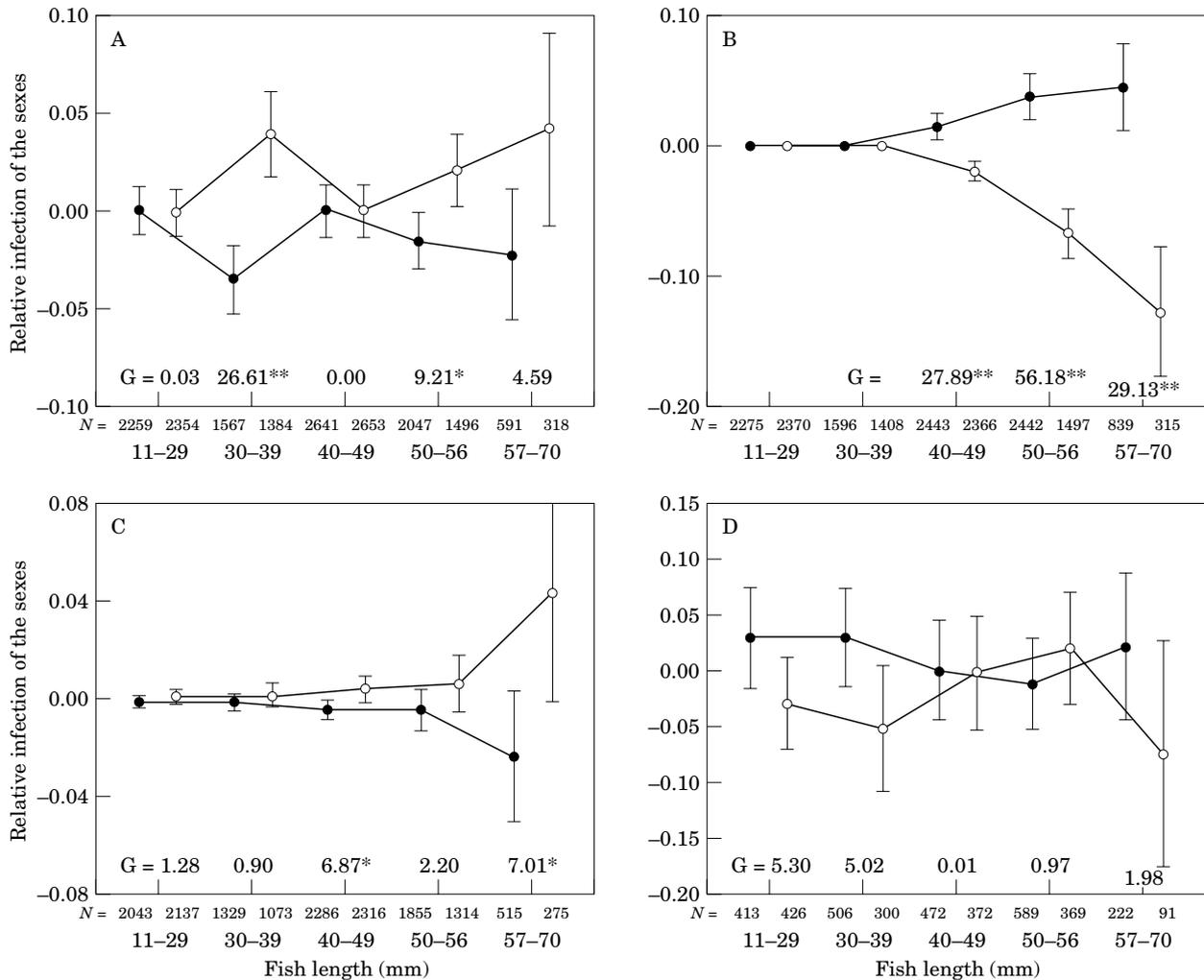
**Figure 1.** Relative parasite prevalence for (●) male and (○) female *G. aculeatus* for five size classes of stickleback. Each pair of error bars shows the mean (±95% CI) parasite prevalence for males and females within a size class, where the overall mean for each size class has been subtracted from each gender for graphical clarity. G-test statistics and Bonferroni corrected probabilities (* $P<0.05$, ** $P<0.01$) are shown below each male/female pair. Probabilities are adjusted for multiple comparisons (sequential Bonferroni method; Rice, 1989). There was significant heterogeneity among size classes in relative infection rates for all four species. (A) *S. solidus*. (B) *C. truncatus*. (C) *Bunodera* sp. (D) Nematode.

### DIET

Among the four food groups (cladocerans, chironomids, culicids and macrobenthos), cladocerans were more prevalent in females than in males ($G_{P1}$, $P<0.001$; Table 3) while macrobenthos were much more common in males than in females ($G_{P1}$, $P<0.001$). The grouped data showed no significant differences in relative consumption of chironomids or culicids. For fish with partially digested stomach contents, which were excluded from previous analyses, a significantly greater proportion of males than females were scored as benthic (8.6%, 4.7% respectively, $G_{P1}=15.23$, $P<0.001$, $N=2487$).

We then compared the consumption of each of the food categories between males and females in two size classes (<45 mm, ≥45 mm) and tested for heterogeneity between size classes (Fig. 5). Cladocerans were more common in females than in males in adults but not in yearlings. However, no statistical heterogeneity between size classes was detected ($G_{H1}=1.51$, $P<0.25$). For chironomids, we detected elevated consumption of chironomids in male yearlings ($P=0.06$ after Bonferroni correction), but slightly female-biased consumption in adults ($G_{H1}=3.86$, $P<0.05$). Differences between the genders in the consumption of culicids varied between size classes ($G_{H1}=5.11$, $P<0.05$). In
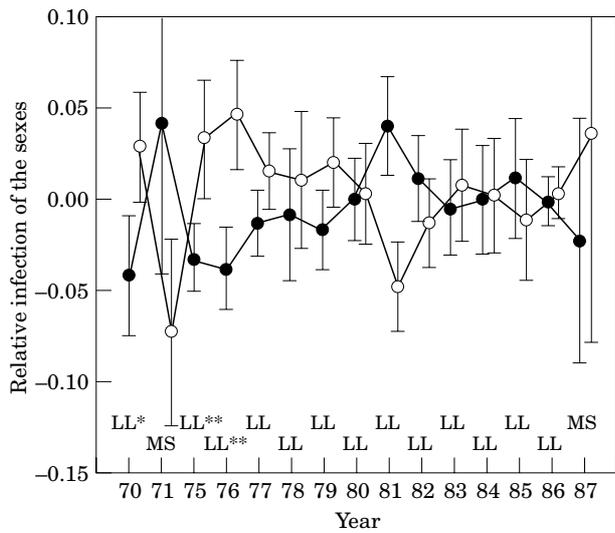
**Figure 2.** Yearly trends in relative prevalence (mean ±95% CI) of *S. solidus* infection for (●) male and (○) female stickleback. Each pair of error bars shows mean parasite prevalence for males and females within a year, where the overall mean for each year has been subtracted from each gender for graphical clarity. Bonferroni corrected probabilities from G-tests (* *P*<0.05, ** *P*<0.01) are shown below each male/female pair. Sample sizes are shown above the horizontal axis (S – small, *N*<50; M – medium, *N*=50–100; L – large, *N*>100).
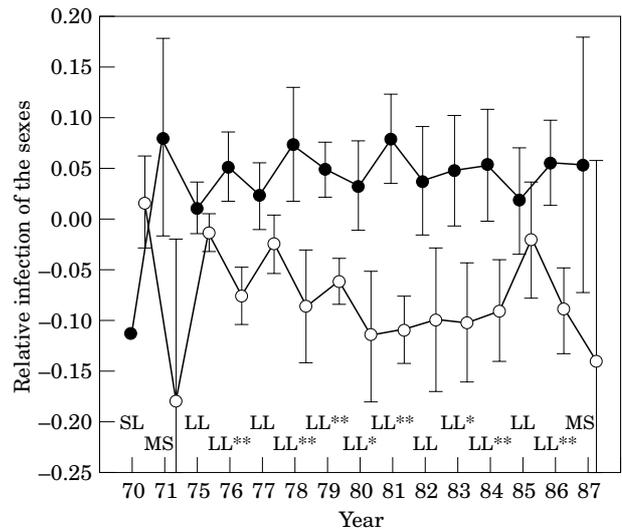


**Figure 3.** Yearly trends in relative prevalence (mean ±95% CI) of *C. truncatus* infection for male and female stickleback. Includes all fish ⩾45 mm SL. Bonferroni corrected probabilities from G-tests (* *P*<0.05, ** *P*<0.01) are shown below each male/female pair. Sample sizes are shown above the horizontal axis (S – small, *N*<50; M – medium, *N*=50–100; L – large, *N*>100). For details see Fig. 1.

subadults, culicid consumption was slightly female-biased, but was male-biased in adults. Size-related analyses revealed macrobenthos was more common in males vs. females in both subadults and adults but also showed differences were accentuated in adults ($G_{H1}=10.43$, *P*<0.01). For fish with digested stomach contents, a higher proportion of males than females were scored as benthic in both subadults and adults ($G_{H1}=2.57$, *P*>0.10).

We also compared the prevalence of the four main food types between adult males and females captured using minnow traps from all localities in Boulton Lake. These comparisons included fish from seven localities and yielded a non-significant female bias for cladoceran prevalence (34.9%, 33.8% females and males respectively, $G_{P1}=0.17$, *P*=0.68, *N*=1275; $G_{H6}=10.65$, *P*=0.10) and a significant, but heterogeneous, female bias in chironomid prevalence (46.4%, 38.6% females and males respectively, $G_{P1}=7.942$, *P*<0.01, *N*=1321; $G_{H6}=13.47$, *P*<0.05). Culicid consumption occurred only in one of the other seven localities and was similar between the gender classes (0.6%, 1.0% females and males respectively, $G=0.36$, *P*=0.55, *N*=862). The prevalence of macrobenthos was significantly higher in males than in females, but we detected heterogeneity



**Figure 4.** Yearly trends in relative prevalence (mean ±95% CI) of nematode infection for male and female stickleback. Includes all fish ⩾45 mm SL. Bonferroni corrected probabilities from G-tests (* *P*<0.05, ** *P*<0.01) are shown below each male/female pair. Sample sizes are shown above the horizontal axis (S – small, *N*<50; M – medium, *N*=50–100; L – large, *N*>100). For details see Fig. 1.
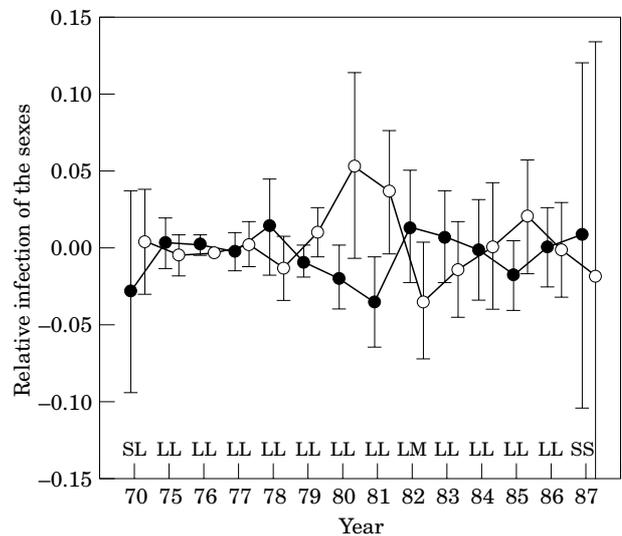
**Table 3.** Log-likelihood G-tests comparing the relative number of stickleback stomachs with each of four main food types present between male and female *G. aculeatus* from Boulton Lake. Results are given for stickleback captured by seining between 1970 and 1986

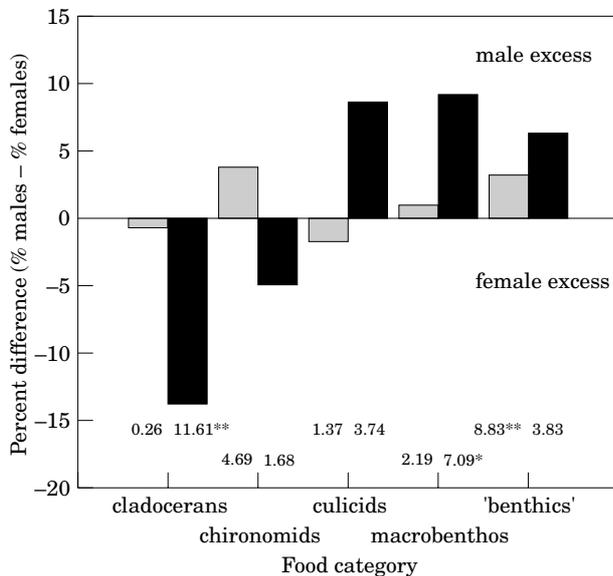| Prey item | % prevalence in males | % prevalence in females | $N$ | G |
|---|---|---|---|---|
| Cladocerans | 75.4 | 80.7 | 3222 | 13.38*** |
| Chironomids | 39.6 | 37.2 | 3971 | 2.51 |
| Culicids | 17.6 | 17.6 | 2826 | 0.00 |
| Macrobenthos | 8.2 | 4.7 | 3964 | 19.71*** |

*** $P<0.001$.



**Figure 5.** Relative consumption (% male–% female) of food items between sexes of *G. aculeatus* for subadult (▦; 15–45 mm) and adult (■; 45–75 mm) fish. Results are shown for differences in consumption of cladocerans, chironomids, culicids, macrobenthos. Also shown is the difference in the proportion of males vs. females scored as 'benthic' for fish with digested stomach contents (see methods). G-test statistics and Bonferroni corrected probabilities (* $P<0.05$, ** $P<0.01$) are shown above the horizontal axis.

for *S. solidus* and *C. truncatus* respectively (Table 4). In subadults, copepod consumption was significantly greater in females than in males during winter (Nov.–Apr.) ($P<0.01$, G-test) and similar between genders in summer (May–Oct.) ($P=0.31$, G-test). In adults, copepod consumption was significantly female-biased in both summer and in winter ($P<0.05$, G-tests). Amphipod consumption was significantly greater in adult males than in adult females during winter ($P<0.01$, G-test) and similar between genders during summer ($P=0.87$, G-test).

Relative *S. solidus* infection between the genders tended to be female-biased but this pattern was reversed in 1981 (Fig. 2). The most pronounced differences between the sexes in nematode infection also occurred in this year. We examined whether a switch in dietary differences between the sexes coincided with these differences in relative parasite prevalence. This was observed as cladoceran consumption was female-biased from years 1976–1980 but switched to male-bias in 1981 (Fig. 6). This trend occurred in both subadults and adults. Relative chironomid consumption also exhibited a reversal. Chironomids were more common in males than females from 1976 to 1980, but this pattern was reversed in 1981. For culicid and macrobenthos consumption and for fish scored as benthic (digested food items), we detected no marked reversals among years in relative frequency between the genders.

Such temporal variability in diet and relative parasitism could be tied to temporal variability in biophysical parameters. Examination of weather data for Haida Gwaii revealed 1981 was an unusually warm and wet year. Mean yearly temperature gradually increased through the 1970s and reached a study period high in 1981 (Fig. 7). The spring (Jan.–Apr.) of 1981 was the second warmest spring of the study period while the summer (May–Sept.) of 1981 was the second warmest summer. The spring of 1981 had the highest rainfall of all the springs in the study period.

in this trend among localities (29.3%, 16.9% respectively, $G_{P1}=33.10$, $P<0.001$, $N=1598$; $G_{H6}=30.87$, $P<0.001$).

Males and females also differed in the consumption of copepods and amphipods, which act as primary hosts

**Table 4.** Log-likelihood G-tests comparing the presence of amphipods and copepods between male and female *G. aculeatus* stomach contents. Results are given for subadults (<45 mm) and adults (⩾45 mm) in winter (Nov.–Apr.) and summer (May–Oct.) seasons

| Prey item | Winter | | | | Summer | | | |
|---|---|---|---|---|---|---|---|---|
| | % in males | % in females | N | G | % in males | % in females | N | G |
| Subadults | | | | | | | | |
| Copepods | 2.3 | 7.2 | 483 | 6.89** | 2.4 | 1.9 | 3884 | 1.03 |
| Adults | | | | | | | | |
| Amphipods | 19.6 | 10.7 | 638 | 9.94** | 10.9 | 11.2 | 1706 | 0.03 |
| Copepods | 2.8 | 6.0 | 638 | 3.95* | 2.5 | 4.4 | 1706 | 4.63* |

\* $P<0.05$, \*\* $P<0.01$, \*\*\* $P<0.001$.

## ASSOCIATIONS BETWEEN DIET, TEMPERATURE AND PARASITISM

We tested whether the temperature within a sample month (each month of sampling 1970–1987) was associated with stickleback diet within that sample month. This was done for two separate seasons (Winter: Nov.–Apr.; Summer: May–Oct.). For winter, we detected a positive correlation between mean monthly temperature and the monthly consumption frequency of macrobenthos (rho = 0.47, $P<0.001$, $N=82$, SR), indicating stickleback consumed more macrobenthos overall during relatively warm sample months in winter. Conversely, we detected a negative correlation between mean monthly temperature in summer and the monthly consumption of macrobenthos (rho = $-0.18$, $P<0.05$, $N=156$, SR), indicating stickleback tended to consume less benthos during warm sample months in summer. All other correlations between diet and temperature were non-significant (rho<0.15, $P>0.10$, SR).

We also tested whether the diet of unparasitized stickleback (frequency of a food item) within a monthly sample was associated with the prevalence of a parasite species in a sample. This was confirmed in two cases. In winter, the prevalence of cladocerans within a sample was negatively correlated with the prevalence of *C. truncatus* infection within a sample (Fig. 8) and this correlation was significant after correction for multiple comparisons (cladocerans, rho = $-0.67$, $P<0.01$, $N=27$, SR). The sample consumption frequency of chironomids was positively correlated with the sample prevalence of *Bunodera* sp. infection in winter (rho = 0.81, $P<0.05$, $N=11$, SR). All other correlations between sample prevalence of a food item and the sample prevalence of parasitism were non-significant after correction for multiple comparisons (rho<0.36, $P>0.10$, SR).

## DISCUSSION

We tested two hypotheses concerning differential parasitism between the sexes. Firstly, we tested whether male stickleback exhibit elevated levels of overall parasitism relative to females, as predicted from the costs of sexual selection. Secondly, we tested whether any potential dietary niche variation between the genders influenced gender differences in parasitic infection. Differential parasitism between the sexes has been reported in a wide range of taxa, including amphibians (Hollis, 1972; Tinsley, 1989), mammals (Beital, Knapp & Vohs, 1974; Langley & Fairly, 1982; Folstad *et al.*, 1989), fish (Batra, 1984; Tierney, Huntingford & Crompton, 1996) and birds (Poulin, 1996a for review in vertebrates). Such sex-biased parasitism can result from differences in immunocompetence with males predicted to bear a greater cost of sexual selection and the immunosuppressive effects of testosterone production (Folstad *et al.*, 1989; Zuk, 1990; Clutton-Brock & Parker, 1992; Folstad & Karter, 1992), and thus to be more susceptible to parasitic infection than females. This may be especially true for stickleback, where paternal care and territorial nest defence can render reproduction particularly costly for males (van den Assem, 1967; Wootton, 1976; Fitzgerald *et al.*, 1989; Bakker, 1994 for review). Despite these costs, we failed to find a consistent male bias in parasite prevalence when comparisons between male and female stickleback were partitioned to single species infections. Instead, our results suggest ecological differences between genders or phenotypes may be important predictors of parasitism in individuals from natural populations (see also Reimchen & Nosil, 2001). Presumably, choice of hosts by parasites also represents an adaptive strategy aimed at maximizing fitness (Holmes, 1976).

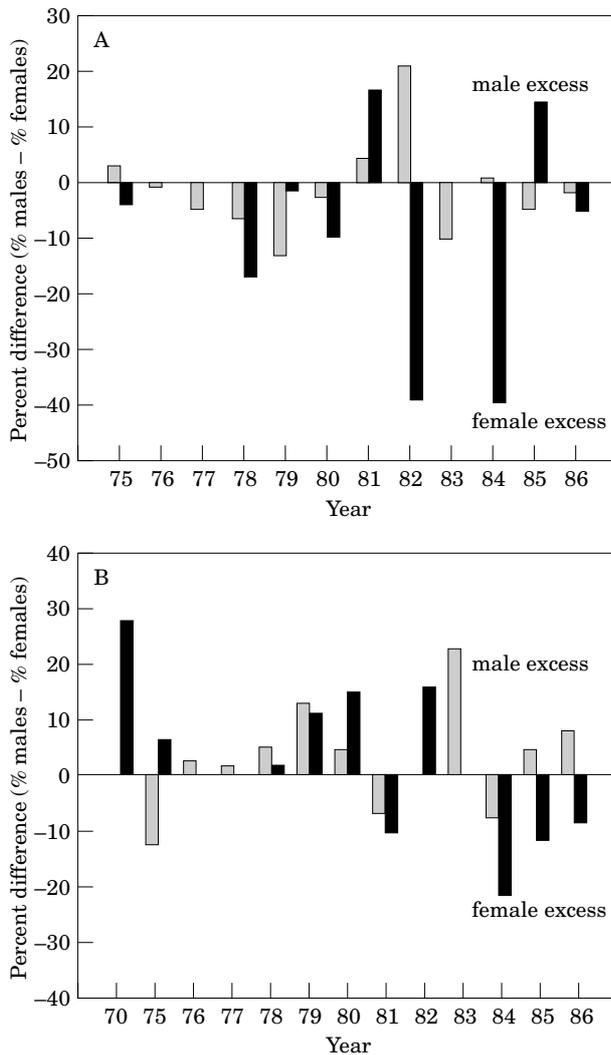Male and female stickleback from Boulton Lake exhibit differences in habitat use (Reimchen, 1980) and,

**Figure 6.** Yearly differences in relative consumption (% male–% female) of (A) cladocerans and (B) chironomids between the sexes of *G. aculeatus*. Results are shown for subadults (▦; 15–45 mm) and adults (■; 45–75 mm) for all yearly samples including the diet of at least 20 individuals.



**Figure 7.** Mean yearly temperatures (°C) for the Haida Gwaii (solid line) and mean spring (Jan.–Apr.) rainfall (dashed line). Yearly means are the average of monthly means.



**Figure 8.** Relationship between the mean prevalence of cladocerans in a sample (each month of sampling, 1970–1987) and the mean prevalence of *C. truncatus* infection during winter (Nov.–Apr.). The inverse relationship is significant ($P < 0.01$, SR). Numbers above each point on the scatter plot refer to the year of sample.

consequently, we predicted that inter-gender differences in parasitic infection would be species-specific and associated with differences in spatial or dietary components of the ecological niche. Consistent with this prediction, patterns of differential parasitism between the genders were species-specific and these patterns are potentially interpretable in terms of dietary variation between the genders.

Males were more likely to be parasitized by *C. truncatus* and *Bunodera* sp., whereas females were more likely to be parasitized by *S. solidus* or nematodes. These patterns could arise from dietary niche variation
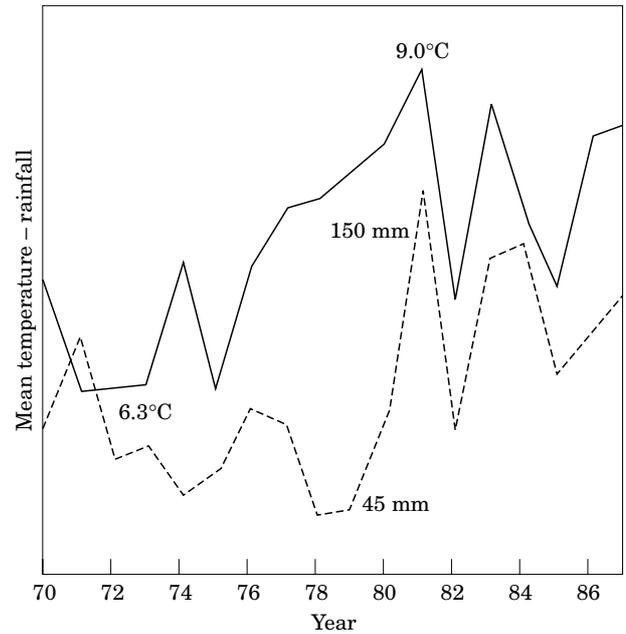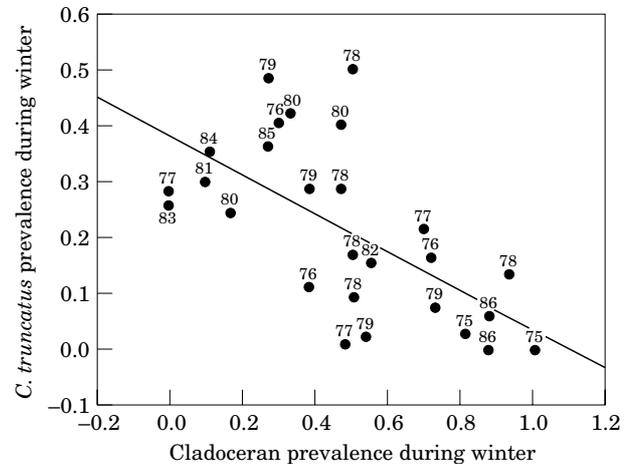
which results in differential exposure to infected primary hosts. Males and females differed statistically in the relative consumption of two of the four main food categories, with males consuming more benthic items

and females consuming more cladocerans. Increased cladoceran consumption by females is indicative of a more pelagic diet as few cladocerans are mud-dwelling (Ward & Whipple, 1959). Macrobenthos, such as trichopterans and zygopterans, were more common in males than in females and this suggests males utilize more littoral and benthic dietary niche than females. Also, zooplankton-free, digested benthos was more prevalent in males than in females. Chironomids are benthic and were more prevalent in juvenile and subadult males than in similar size females.

A pelagic/benthic dietary separation between the genders in Boulton Lake is consistent with spatial and morphological gender differences in the population. For example, males tend to be associated with littoral habitat and exhibit reduction in the pelvic and dorsal spines that are part of the stickleback defence apparatus, whereas females exhibit the opposite trend. Potentially, this results from spines being an advantage against pelagic predators such as avian piscivores, but a disadvantage against benthic grappling predators such as dragonfly larvae (Reimchen, 1980). Similar spatial or dietary differences among stickleback phenotypes differing in morphological characters such as lateral plates and pelvic spines and trophic structures such as gill rakers have been documented both in other natural populations (McPhail, 1983; Schluter & McPhail, 1992; Larson & McIntire, 1993) and experimentally (Bentzen & McPhail, 1984; Schluter, 1993, 1994, 1995). Such niche variation may result in differential exposure to infected prey between genders. The benthic habit of males may result in increased exposure to amphipods, the primary host of *C. truncatus*. Alternatively, the pelagic diet of females may result in increased exposure to pelagic copepods, which act as primary hosts of *S. solidus*. For example, we detected an inverse association between monthly cladoceran consumption in winter and monthly prevalence of *C. truncatus*, suggesting that increased cladoceran consumption reduces exposure to benthic food items such as amphipods. However, the oligochaete primary host of nematodes, which are slightly more prevalent in females, tend to also be benthic (Clifford, 1991).

These associations between sex, diet and parasitism are supported by inter-gender differences in the consumption of potentially infected prey items. Species which act as primary hosts for the parasite species observed in this study were rarely observed in stickleback stomachs. However, when they did occur, trends were highly consistent with the observed differences between the genders. Males were more likely to consume amphipods, the primary host of *C. truncatus*. Females were more likely to consume copepods, the primary host of *S. solidus*. This provides strong evidence for differential exposure to infected prey between the genders.

A relationship between diet and parasitism is further supported by associations between shifts in dietary differences between genders and shifts in sex-biased parasitism. From 1976 to 1980 *S. solidus* infections tended to be female-biased while nematode infections were similar between the sexes until 1980. Congruent with the differential for *S. solidus*, female diet during these years exhibited an excess of cladocerans while male diet tended to show increased consumption of chironomids relative to females. In 1981, a marked shift to a male bias for *S. solidus* infection occurred and this was accompanied by divergence in relative nematode infections (female-biased). Coinciding with these shifts in relative parasitism, we detected shifts in the dietary differences between the genders. In 1981, cladoceran consumption switched to a male bias while chironomid consumption switched to a female bias (trends opposite to preceding years). The excess cladoceran consumption by males could have increased relative exposure to pelagic copepods infected by *S. solidus*. Conversely, female-biased chironomid consumption in 1981 could have increased exposure to benthic oligochaetes infected by nematodes. This suggests the temporal shifts in relative parasitism were caused by shifts in the diet that resulted in changes in exposure to infected prey items. Shifts in temperature or other biophysical parameters provides one plausible mechanism that could account for the temporal shifts in gender biases in diet and parasitism.

Our results are consistent with a number of studies that have examined associations among sex, ecology, diet, and parasitism. In another study of stickleback, females also had heavier *S. solidus* infection than males but this study did not examine dietary differences (Tierney *et al.*, 1996). In the central mudminnow (*Umbra limi*), seasonal differences in *Neoechinorhynchus limi* infection were correlated with dietary shifts (Muzzal, 1984). Batra (1984) suggests helminth infection in three species of cichlids is greater in males than in females due greater food consumption, and thus increased probability of consuming an infected prey item, in males. Similar associations have been reported in non-fish species. In wood mice (*Apodemus sylvaticus*), the ectoparasitic tick *Ixodes ricinus* was more common in males, who cover much more ground than females, and flukes were most common during a period of intensive feeding on invertebrate primary hosts (Langley & Fairly, 1982). In spadefoot toads, male reproductive behaviour requires spending long periods of time in the water which increases contact with the parasite *Pseudodiplorchis americanus* (Tinsley, 1989). Consequently, males toads are more heavily infected by *P. americanus* than females, who spend less time in the water. However, some studies on stickleback (Font, 1983; Bakker & Mundwiler, 1999) and other fish species (Lawrence, 1970; Muzzal, 1980) have found no significant differences in parasitism between genders. Conceivably,

host-sex/parasite interactions are mediated by the ecology of the interaction. Also, our results indicate slight differences in parasitism between the genders may not be detected unless populations are sampled over multiple years.

In a recent comparative analysis (Poulin, 1996b) helminth growth was found to be greater in male than in female hosts. However, our result demonstrate females have an increased probability of harbouring large plerocercoids during winter and this suggests parasite growth may be increased in the more common host. Alternatively, differences in *S. solidus* size simply reflect differences in the time since infection, with increased time for growth resulting in increased size.

It is important to note that not all of the variability in parasitic infection between genders can be attributed to dietary differences. For example, there was heterogeneity in some parasitic or dietary trends among years and size classes and this heterogeneity was not always congruent with differences between the genders in relative parasitism or diet. Potentially, selective mortality also influences observed rates of infection. Fish infected with *S. solidus* exhibit a number of behavioural modifications, including increased buoyancy, reduced swimming speed and reduced responsiveness, which may make them more vulnerable to avian predators (Giles, 1983; Milinski, 1985; Lobue & Bell, 1993; Tierney, Huntingford & Crompton, 1993; Ness & Foster, 1999). Females are more likely to be infected by *S. solidus* than males and thus may be more likely to suffer behavioural modifications and thus predation. Also, five species of avian piscivores forage on stickleback from Boulton Lake and these species exhibit differential foraging effort between limnetic and littoral regions of the lake (Reimchen, 1980). Temporal changes in the relative amount of littoral vs. limnetic foraging could influence the relative numbers of males (primarily littoral or benthic) or females (primarily pelagic) predated, and thus influence observed levels of male vs. female infected fish.

It is also possible that the female-biased *S. solidus* parasitism detected in this study results from higher mortality of parasitized males. This could occur if males are generally more stressed than females, due to the rigours of parental care during the reproductive season. However, this is inadequate to account for our results. Firstly, pronounced female-biased *S. solidus* parasitism occurred in pre-reproductive fish (30–39 mm), where males would not be subjected to greater stress than females. Secondly, patterns of differential parasitism for *C. truncatus* were opposite to those for *S. solidus* (i.e. male-biased), suggesting sex-biased parasitism is unlikely to reflect increased mortality of infected adult males relative to females.

The results of this study expand on previous work on sexual dimorphism (Reimchen, 1980; Shine, 1989 for review) and intra-population variability in general (Schluter & McPhail, 1992; Reimchen, 1995). Sexual dimorphism has been investigated in a wide range of species, but is often attributed to the action of sexual selection (e.g. Trivers, 1976; Perry, 1996) rather than to ecological causes. However, researchers have shown intra-specific resource partitioning in response to competition or other ecological factors (Selander, 1966; Grant, 1975; Raymond *et al.*, 1990; Houston & Shine, 1993; Schluter, 1994) and the opportunity for ecological release (Traniello & Beshers, 1991) can partially account for differences between genders or phenotypes. Morphological differences may arise as adaptations to divergent selection regimes between ecological niches (Reimchen, 1980, 1995) and to facilitate the utilization of different food resources (Shine, 1991; Houston & Shine, 1993). Stickleback are the only species of fish in Boulton Lake. Spatial and dietary niche differences between the genders may be driven by intraspecific competition for resources in the benthic habitat and may be facilitated by the opportunity for females to exploit a pelagic niche in the absence of other competitive species of fish in open-water regions. However, dietary differences between the genders were also detected when males and females occupied similar habitat, suggesting micro-spatial niche variation.

In summary, our results show infection rates in Boulton Lake stickleback were species-specific and broadly associated with dietary differences, suggesting ecological selection plays a major role in moulding parasite–host interactions. Examination of this long-term data base also revealed that temporal shifts in differential parasitism can be associated with temporal shifts in the diet. Although numerous studies have reported sex-biased parasitism (Poulin, 1996a for review), very few have looked for ecological differences between the genders that could provide a mechanism to account for such biases (but see Tinsley, 1989). As this is one of the first studies to examine sex differences in parasitism in relation to dietary niche variation over multiple years, our results suggest associations between host-sex and parasitism are best interpreted in terms of both reproductive strategies and ecological differences between the genders. Niche partitioning between the sexes may be a cause of sexual dimorphism (Selander, 1966; Reimchen, 1980; Slatkin, 1984; Shine, 1989, 1991; Anholt, 1992) and could contribute to sex-biased parasitism.

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