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VARIABLE PREDATION REGIMES PREDICT THE EVOLUTION OF SEXUAL DIMORPHISM IN A POPULATION OF THREESPINE STICKLEBACK

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Abstract.—Sexual dimorphism is widespread in nature and can be influenced by sex-specific natural selection resulting from ecological differences between the sexes. Here we show that contrasting life-history pressures and temporal shifts in ecology can exert a strong influence on the evolution of sexual dimorphism. The bony spines exhibited by stickleback are a defense against open-water avian predators but may be detrimental against benthic macroinvertebrate predators. Female stickleback from a coastal lake in western Canada occupy a more open-water ecological niche and exhibit greater dorsal and pelvic spine number than males, but the magnitude of these differences varies among life-history stages, seasons, and years. Ecological data on diet and parasite load and 62 seasonal estimates of selection over a 15-year period show that selection favors increased spine number in females and decreased spine number in males, but only when pronounced ecological differences between the sexes results in differential exposure to the two, divergent predation regimes. Thus occasional sex-reversals in ecological niche reversed the mode of selection. These processes caused a predictable response in the subsequent generation, indicating that divergent predation caused evolutionary change in dimorphism. However, temporal oscillations in sex-specific selection resulted in no net change in sexual dimorphism over the 15-year study period, indicating that fluctuations in directional selection can be responsible for long-term stasis. Replicated shifts in selective regime can demonstrate the primacy of ecological processes in driving evolution and our results illustrate how such shifts are detectable using long-term monitoring of natural populations.

Key words.—Antipredator traits, divergent selection, *Gasterosteus*, natural selection, predation.

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Long-term evolutionary studies in natural populations are extremely rare, despite the widespread acceptance of their utility in ecology (Likens 1989). The few existing studies have yielded new insight into the role of predictable and nonuniform events in evolutionary change (Ehrlich and Mason 1966; Grant and Grant 2002). One of these, a 30-year study of Darwin's finches (Grant and Grant 2002), revealed that multiple factors interact to determine the outcome of evolution, including competition, different forms of natural selection, rare and unpredictable climatic events, and introgressive hybridization. Previous long-term studies of evolution have typically focused on differences between species or ecotypes. Another form of variability, namely differences between the sexes, has received little attention, despite the fact that sexual dimorphism is widespread in nature and varies among life-history stages and time periods (Badyaev 2002; Schulte-Hostedde et al. 2002).

Sexual dimorphism itself has attracted the attention of evolutionary biologists since the time of Darwin (Darwin 1874), and can be influenced by multiple factors including niche differentiation and natural selection (Selander 1966; Slatkin 1984; Shine 1989; Butler et al. 2000), genetic correlations (Lande 1980), allometry (Fairbairn 1997), phylogenetic history (Cheverud et al. 1985; Fairbairn 1997) and the most commonly investigated mechanism, sexual selection (Price 1984; Cheverud et al. 1985; Fairbairn 1997; Preziosi and Fairbairn 2000; Ferguson and Fairbairn 2000; Badyaev and Martin 2000). Sexual dimorphism has been extensively studied theoretically (Lande 1980; Slatkin 1984) and comparatively (Cheverud et al. 1985; Shine 1991; Bulter et al. 2000). In contrast, existing field studies are useful but have typically considered only selection on adults during one or a few seasons (Price 1984; Ferguson and Fairbairn 2000; Preziosi and Fairbairn 2000; Badyaev and Martin 2000; Schulte-Hostedde et al. 2002). Long-term investigations of the evolution of this dimorphism in natural populations are lacking and have numerous potential and unique benefits, including the ability to elucidate the effects of spatial, temporal, and ontogenetic shifts in sex-specific selection on the evolution of sexual dimorphism. For example, reversals in sex-specific selection between different age classes, life-history stages (Schluter et al. 1991), or time periods (Schulte-Hostedde et al. 2002) can prevent the evolution of sexual dimorphism, despite the presence of strong, sex-specific selection. Such heterogeneity in selection can be detected through long-term monitoring of natural populations. Here we report the results of a 15-year ecological and evolutionary study of natural selection on male and female stickleback from multiple-age classes, thus providing a comprehensive test of the role of selection in evolution of sexual dimorphism.

More specifically, we examine sex-specific exposure to predation. Predation regimes can vary temporally, spatially, and across life-history stages. Thus antipredator defenses are useful for examining heterogeneity in selection (Reimchen 1979, 1995; Vermeij 1987; Reimchen and Nosil 2002), although these are rarely used to study differences in selection between the sexes (but see Jormalainen and Merilaita 1995). The dorsal and pelvic spines of threespine stickleback (*Gasterosteus aculeatus*) are a defensive adaptation against gape-limited predators (Hoogland et al. 1957; Gross 1978; Reimchen 1983). Thus, populations exposed to elevated levels of vertebrate predation have larger or more robust spines than populations with reduced vertebrate predation (Hagen and Gilbertson 1972; Moodie and Reimchen 1976). Conversely,

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consideration of functional design, geographic surveys and controlled experiments indicate that grappling benthic invertebrate predators, such as odonate naiads, produce selection favouring spine reduction (Reimchen 1980; Reist 1980; Ziuganov and Zotin 1995; Vamosi 2002). In several freshwater lakes from North America and Europe, sticklebacks exhibit variability in the number of dorsal and pelvic spines (Moodie and Reimchen 1976; Bell 1988), providing rare opportunities to test for associations between predation regime and mode and strength of selection acting on each sex.

One of these spine-variable stickleback populations occurs at Boulton Lake on the Queen Charlotte Islands, western Canada, where stickleback exhibit 0–6 spines (0–3 dorsal spines, 0–2 pelvic spines, 0–1 anal spine) and live up to three years (Reimchen 1980). At this locality, divergent predation regimes vary both spatially and temporally such that avian piscivores forage primarily in open-water regions of the lake and are most common during autumn and winter, whereas macroinvertebrate predators such as odonate naiads are prevalent in benthic regions and are most active during summer (Reimchen 1980). Estimates of selection on spine number over a 15-year period revealed that selection on juvenile stickleback favors decreased spine number in summer, when odonates are most prevalent, but increased spine number in winter, when avian predation is strongest (Reimchen and Nosil 2002). Moreover, the direction and magnitude of selection on spine number in older fish was correlated with temporal shifts in exposure to the divergent predation regimes. Strong selection for decreased spine number was associated with time periods in which the majority of fish were foraging in the benthic region, whereas strong selection for increased spine number was associated with time periods in which most fish were foraging in the open-water regions of the lake (Reimchen and Nosil 2002). Thus, previous studies indicate that intrapopulation variability in spine number is a functional adaptation to spatial and temporal variability in the two predator groups, but have not examined differences in selection acting on each of the sexes.

Stickleback from Boulton Lake are sexually dimorphic such that females exhibit greater mean spine number than males and are generally more prevalent in open-water regions of the lake (Reimchen 1980). Thus, relative to males, females exhibit a more pelagic diet, are more likely to be infected by parasites with pelagic hosts, and are less likely to be infected by parasites with benthic hosts (Reimchen and Nosil 2001). These ecological differences between the sexes increase throughout ontogeny. Thus habitat use, diet, and levels of parasitism are similar between the sexes in juvenile fish, begin to differentiate between the sexes in subadults, and are markedly different between the sexes in adults (Reimchen 1980; Reimchen and Nosil 2001). Ecological differences between the sexes also vary among time periods within the age classes, such that occasional sex reversals in ecological niche occur (Reimchen and Nosil 2001). These ontogenetic and temporal differences between the sexes in the magnitude of ecological divergence allowed us to extend previous work on selection on spine number in this population by explicitly testing for associations between sex-specific ecology, sex-specific selection, and sexual dimorphism. For example, any single episode of selection can act to increase, maintain, or decrease existing levels of dimorphism. Because females are more heavily spined than males, selection in Boulton Lake will increase levels of dimorphism when it favors spine expression in females but spine reduction in males. Conversely, if selection favors spine reduction in females but spine expression in males, it will decrease levels of dimorphism.

The hypothesis that shifts in sexual dimorphism in spine number are driven by shifts between the sexes in exposure to divergent predation regimes requires that the sexes exhibit ecological differentiation and predicts that (1) the direction and magnitude of selection on spine number varies between the sexes; (2) sex-specific selection results in a predictable evolutionary response in the subsequent generation; and (3) sex-specific selection is caused by ecological differences between the sexes that result in differential exposure to the divergent predation regimes. Here we combine ecological data on habitat use, diet, and parasite load with estimates of selection, and data on intergenerational shifts in spine number, to test whether these predictions are met. Collectively, our results provide insight into the role of ecology in the evolution of sexual dimorphism.

MATERIALS AND METHODS

Sampling

Collections of stickleback were made from 1970 to 1987 using minnow traps, trawls, and beach seines. A total of 20,368 stickleback were scored for the number of dorsal, pelvic, and anal spines (for details, see Reimchen 1980). Standard length (SL) was measured on each specimen and sexual dimorphism in spine number was calculated as mean spine number in females minus mean spine number in males (for various samples as appropriate, see below). Stickleback 20–35 mm SL represent juveniles, 35–45 mm SL represent subadults, and 45 mm+ represent adults (Reimchen 1980; Reimchen and Nosil 2002).

Estimates of Sex-Specific Selection

Sex-specific selection was estimated using previously published selection differentials (Reimchen and Nosil 2002). In brief, selection within each sex was estimated by comparing trait distributions before and after seasonal bouts of selection (winter, summer) for three different cohorts (juvenile, subadult, adult), yielding standardized directional selection differentials for each of these ‘‘episodes’’ of selection (Lande and Arnold 1983; Endler 1986). Estimates of selection were available for both sexes in a total of 31 paired samples (same episode of selection and same age class). Differences between the sexes in the direction and magnitude of selection for each episode of selection were calculated as the signed difference in female selection differential minus male selection differential. We note that spine number in stickleback has known functional significance and is fully expressed early in life (Reimchen 1980, 1983), thus our selection analyses minimize problems associated with selection on correlated characters (Lande and Arnold 1983) and variable growth trajectories (Badyaev 2002).

Estimating the Intergenerational Response to Selection

We estimated the intergenerational response to selection using two types of comparisons. First, for all seven episodes of selection on adults in which differentials for both sexes were available, we obtained the intergenerational shift in dimorphism between adults (generation 1) and the juveniles from the next generation (generation 2) by comparing sexual dimorphism in the adults before the episode of selection (generation 1) to sexual dimorphism in juveniles from generation 2. For adult winter survival, 20–35 mm fish from the current fall were considered the next generation. For adult summer survival, 20–35 mm fish from the following years fall were considered the next generation (for details, see Reimchen and Nosil 2002). These shifts in mean spine number were then compared to sex differences in selection on adults (female differentials minus male differential) using bivariate correlation.

Second, estimates of selection were available for both sexes at all three successive life-history stages within the same generation in three cases (juvenile, subadult, and adult survival for three different generations of stickleback). For these, we compared sexual dimorphism in juveniles from the generation where successive estimates of selection were available (generation 1) to sexual dimorphism in juveniles from the subsequent generation (generation 2; estimated as above). We then compared these shifts in sexual dimorphism between successive generations of juveniles to the additive effects of sex-specific selection at the three life-history stages, calculated as (female minus male differential in juveniles) + (female minus male differential in subadults for the episode following the episode for juvenile selection) + (female minus male differential in adults for the episode following the episode for subadult selection). For example: selection averaged over the lifetime of juveniles born in the fall of 1978 would be estimated as (juveniles Winter, 1978/1979) + (subadults Summer 1979) + (adults Winter 1979/1980) (for details, see Reimchen and Nosil 2002).

Ecological Differences between the Sexes

In previous studies, stickleback from Boulton Lake were scored for number of parasites, including those with *Schistocephalus solidus* (n = 20,346) and *Cyathocephalus truncatus* (n = 19,695), and for stomach contents (Reimchen 1980, 1997; Reimchen and Nosil 2001). *Schistocephalus solidus* utilizes a pelagic copepod as a primary host and thus infection rates by this parasite acts as a proxy for a pelagic niche. *Cyathocephalus truncatus* uses benthic amphipods as primary hosts and thus infection rates by this parasite act as a proxy for a benthic niche. As a measure of how benthic the diet of stickleback was within each episode of selection, we calculated for all unparasitized stickleback (n = 9089) the proportion of individuals within that episode who had benthic macroinvertebrates (amphipods, zygopterans, or trichopterans; these are unambiguous indicators of a benthic dietary niche, Reimchen and Nosil 2001, 2002) present in their stomachs.

For each episode of selection where data were available, differences between the sexes in diet and parasite load, respectively, were calculated as (diet, percent female consumption minus percent male consumption; parasites, percent females infected minus percent males infected). Associations between differences between the sexes in selection and differences in ecological variables were assessed using bivariate correlation. Due to the a priori prediction that differences in selection would be positively related to differences in ecology, all statistical tests are one tailed.

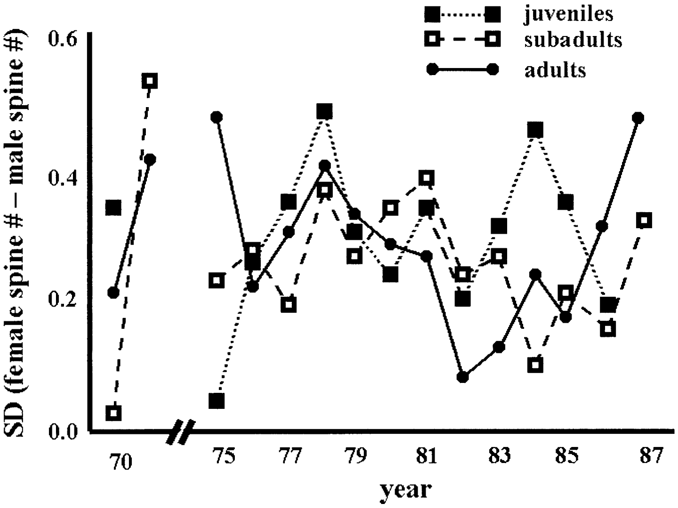

FIG. 1. Sexual dimorphism in spine number (SD, female spine number–male spine number) was consistently biased towards increased spine number in females versus males. However, the magnitude of sexual dimorphism varied drastically among life-history stages and among years. Such variability in dimorphism could result from highly variable, yet potentially predictable, shifts in natural selection.

RESULTS

Sex-Specific Selection on Spine Number

Our data on spine-morph frequencies over the 15-year study period revealed evidence of substantial between-season shifts in the relative frequency of the different spine phenotypes, with the magnitude of sexual dimorphism varying considerably among age classes and time periods (Fig. 1; Table 1). Thus, estimates of directional selection show that the direction and magnitude of selection on total spine number varied between the sexes such that a wide range of sex-specific selection was detected (Fig. 2; range of signed differences = −0.94–0.74), including selection for increased dimorphism, decreased dimorphism, and no change in sexual dimorphism. However, mean difference in signed female selection differential minus male differential, averaged across all episodes of selection, was zero (mean = 0.00, SD = 0.07, t 30 = 0.07, P = 0.93, one-tailed t-test against zero), indicating that there was no net selection for increased or decreased sexual dimorphism over the 15-year study period.

Intergenerational Response to Selection

Sex-specific selection resulted in predictable intergenerational shifts in sexual dimorphism. Thus, differences in selection on spine number between adult males and females in generation 1 were correlated with differences in sexual di-

TABLE 1. Relative frequency of the six main spine phenotypes in Boulton Lake before (%B) and after (%A) seasonal bouts of selection (W, winters; S, summers; for details see Reimchen and Nosil 2002) in males (M) and in females (F). Also shown are sample sizes in each sex and sample (*n*) and directional selection differentials on total spine number (*s*; statistically significant differentials from Reimchen and Nosil 2002 are in bold). The episodes of selection depicted in Figures 2 and 4 are denoted in parentheses beside the date (e.g., W77–78 (1) is episode 1).

				3 dorsal 0 pelvic		3 dorsal 1 pelvic		3 dorsal 2 pelvic		2 dorsal 0 pelvic		2 dorsal 1 pelvic		2 dorsal 2 pelvic	
Spine phenotype	Sex	*n*	*s*	%B	%A	%B	%A	%B	%A	%B	%A	%B	%A	%B	%A
Juveniles															
W77–78 (1)	M	159	0.11	13.2	7.4	2.2	1.5	2.2	7.4	63.7	51.5	5.5	17.6	13.2	14.7
	F	161	−0.03	21.9	12.5	1.9	5.4	5.7	5.4	41.0	44.6	9.5	16.1	20.0	16.1
W78–79 (2)	M	99	0.13	11.4	17.9	0.0	3.6	2.3	1.8	61.4	55.4	9.1	8.9	15.9	12.5
	F	95	−0.26	36.1	25.4	5.6	8.5	5.6	3.4	36.1	50.8	11.1	6.8	5.6	5.1
W80–81 (3)	M	226	**0.34**	11.7	10.0	1.5	4.4	2.9	10.0	66.4	54.4	10.2	10.0	7.3	11.1
	F	198	**0.49**	25.8	20.0	4.3	8.6	4.9	14.3	52.1	31.4	4.9	8.6	8.0	17.1
S82 (4)	M	92	−0.28	13.1	12.9	1.6	0.0	1.6	0.0	50.8	64.5	19.7	6.5	13.1	16.1
	F	52	0.07	32.1	20.0	0.0	0.0	10.7	16.0	35.7	40.0	10.7	16.0	10.7	8.0
W82–83 (5)	M	324	0.25	10.9	8.5	1.2	4.9	0.0	2.4	65.6	58.5	14.2	11.0	8.1	14.6
	F	280	−0.05	19.9	7.7	2.0	2.6	2.8	5.1	52.8	64.1	12.6	7.7	9.8	12.8
W83–84 (6)	M	137	0.23	12.4	10.0	6.2	7.5	2.1	0.0	66.0	57.5	9.3	7.5	4.1	17.5
	F	138	0.17	23.7	12.5	0.9	8.3	4.4	8.3	47.4	50.0	14.9	8.3	8.8	12.5
S84 (7)	M	70	**0.29**	16.3	3.7	0.0	0.0	0.0	7.4	74.4	70.4	2.3	11.1	7.0	7.4
	F	73	−0.52	17.5	20.6	0.0	5.9	12.5	0.0	47.5	67.6	17.5	2.9	5.0	2.9
W84–85 (8)	M	90	0.05	15.4	23.	3.8	5.1	3.8	5.1	51.9	46.2	7.7	2.6	17.3	17.9
	F	103	−0.16	24.6	18.4	3.1	0.0	6.2	0.0	33.8	34.2	9.2	23.7	23.1	23.7
W85–86 (9)	M	318	0.48	27.0	10.8	2.7	7.0	2.7	6.3	51.4	41.6	13.5	15.7	2.7	18.5
	F	155	0.39	30.3	14.3	6.1	7.1	6.1	14.3	42.4	34.1	9.1	11.1	6.1	19.0
S86 (10)	M	396	−**0.43**	19.3	13.6	5.2	2.3	3.0	0.40	46.7	66.3	11.1	10.2	14.8	7.2
	F	529	−**0.37**	19.2	27.2	9.6	4.0	9.2	4.0	37.5	52.3	15.0	7.6	9.6	5.0
Subadults															
W70–71 (11)	M	87	−**0.50**	8.6	13.5	0.0	3.8	2.9	0.0	45.7	67.3	11.4	5.8	31.4	9.6
	F	68	−0.20	5.3	13.3	2.6	3.3	5.3	10.0	28.9	46.7	21.1	6.7	36.8	20.0
W76–77 (12)	M	107	−**0.87**	10.8	4.3	2.7	4.3	8.1	0.0	21.6	61.4	27.0	18.6	29.7	11.4
	F	158	−0.13	12.8	18.9	6.4	4.5	8.5	5.4	36.2	36.9	14.9	15.3	21.3	18.9
S77 (13)	M	208	−**0.58**	9.4	11.9	6.3	1.7	15.6	2.3	34.4	51.7	12.5	15.9	21.9	16.5
	F	224	0.06	3.6	10.2	0.0	4.6	3.6	5.1	42.9	45.9	28.6	16.3	21.4	17.9
S78 (14)	M	141	−0.05	7.4	9.6	1.5	5.5	7.4	1.4	51.5	56.2	17.6	6.8	14.7	20.5
	F	170	−0.04	12.5	18.4	5.4	3.5	5.4	8.8	44.6	43.0	16.1	14.0	16.1	12.3
S79 (15)	M	265	−0.18	17.9	14.2	3.6	1.9	1.8	2.4	55.4	62.6	8.9	10.4	12.5	8.5
	F	241	0.25	25.4	21.4	8.5	7.7	3.4	7.7	50.8	44.5	6.8	7.7	5.1	11.0
W79–80 (16)	M	133	**0.75**	8.6	17.3	2.9	3.1	0.0	3.1	77.1	48.0	5.7	18.4	5.7	10.2
	F	129	0.35	23.6	25.0	2.2	7.5	6.7	5.0	58.4	37.5	3.4	12.5	5.6	12.5
S82 (17)	M	201	0.02	16.1	10.0	2.7	3.3	1.8	3.3	54.5	52.2	10.7	20.0	14.3	11.1
	F	148	−0.13	20.0	22.7	9.2	0.0	4.6	4.5	49.2	50.0	6.9	13.6	10.0	9.1
W82–83 (18)	M	126	0.18	12.9	5.2	0.0	4.2	0.0	2.1	64.5	57.3	6.5	13.5	16.1	17.7
	F	70	−0.35	20.0	13.3	0.0	4.4	16.0	4.4	40.0	57.8	16.0	8.9	8.0	11.1
S83 (19)	M	126	−0.12	8.5	12.5	4.9	4.2	2.4	2.1	58.5	62.5	11.0	10.4	14.6	8.3
	F	69	0.26	7.7	22.6	2.6	0.0	5.1	0.0	64.1	38.7	7.7	16.1	12.8	22.6
S84 (20)	M	127	−**0.33**	10.0	15.6	7.5	0.0	0.0	3.3	57.5	71.1	7.5	6.7	17.5	3.3
	F	94	−0.39	12.5	16.9	8.3	1.4	8.3	1.4	50.0	54.9	8.3	16.9	12.5	8.5
W84–85 (21)	M	114	−0.27	3.7	18.2	0.0	0.0	7.4	2.3	70.4	67.0	11.1	9.1	7.4	3.4
	F	117	0.39	20.6	24.7	5.9	4.7	0.0	3.5	67.6	48.2	2.9	10.6	2.9	8.2
S85 (22)	M	59	−0.14	23.1	15.0	5.1	0.0	5.1	5.0	46.2	60.0	2.6	5.0	17.9	15.0
	F	65	0.12	18.4	25.9	0.0	7.4	0.0	7.4	34.2	29.6	23.7	18.5	23.7	11.1
S86 (23)	M	510	0.15	10.8	15.0	7.0	3.8	6.3	4.7	41.6	48.3	15.7	13.2	18.5	15.0
	F	234	−0.06	14.3	15.7	7.1	6.1	14.3	10.4	34.1	36.5	11.1	12.2	19.0	19.1
W86–87 (24)	M	323	**0.49**	13.6	9.8	2.3	6.6	0.4	4.9	66.3	54.1	10.2	9.8	7.2	14.8
	F	320	−**0.45**	27.2	27.2	4.0	4.0	4.0	4.0	52.3	52.3	7.6	7.6	5.0	5.0
Adults															
W76–77 (25)	M	253	−0.06	13.1	7.7	3.7	10.3	4.7	5.1	51.9	59.0	13.1	10.3	13.6	7.7
	F	230	0.02	22.8	6.9	5.9	10.3	6.9	6.9	38.1	44.8	7.4	13.8	18.8	17.2
W77–78 (26)	M	247	0.13	11.9	8.5	1.7	0.0	2.3	4.2	51.7	47.9	15.9	15.5	16.5	23.9
	F	221	**0.60**	10.2	4.0	4.6	12.0	5.1	12.0	45.9	28.0	16.3	8.0	17.9	36.0
W78–79 (27)	M	262	0.10	9.6	12.7	5.5	4.2	1.4	4.8	56.2	47.6	6.8	15.9	20.5	14.8
	F	220	0.25	18.4	11.1	3.5	6.5	8.8	13.0	43.0	38.0	14.0	10.2	12.3	21.3
S80 (28)	M	196	−**0.31**	17.3	11.2	3.1	2.0	3.1	1.0	48.0	63.3	18.4	14.3	10.2	8.2
	F	68	−0.19	25.0	25.0	7.5	3.6	5.0	3.6	37.5	42.9	12.5	17.9	12.5	7.1
W80–81 (29)	M	195	0.19	15.3	16.8	0.0	0.8	2.8	4.0	70.8	59.2	4.2	9.6	6.9	9.6
	F	95	0.10	32.5	19.6	0.0	5.4	7.5	5.4	40.0	41.1	10.0	19.6	10.0	8.9
W83–84 (30)	M	156	−0.07	12.5	8.3	4.2	2.8	2.1	0.0	62.5	66.7	10.4	11.1	8.3	11.1
	F	57	−0.03	22.6	25.0	0.0	0.0	0.0	7.1	38.7	42.9	16.1	14.3	22.6	10.7
W85–86 (31)	M	249	0.22	15.0	14.1	0.0	5.6	5.0	6.0	60.0	41.5	5.0	17.9	15.0	15.0
	F	144	0.11	25.9	19.0	7.4	4.1	7.4	10.7	29.6	33.9	18.5	9.9	11.1	22.3

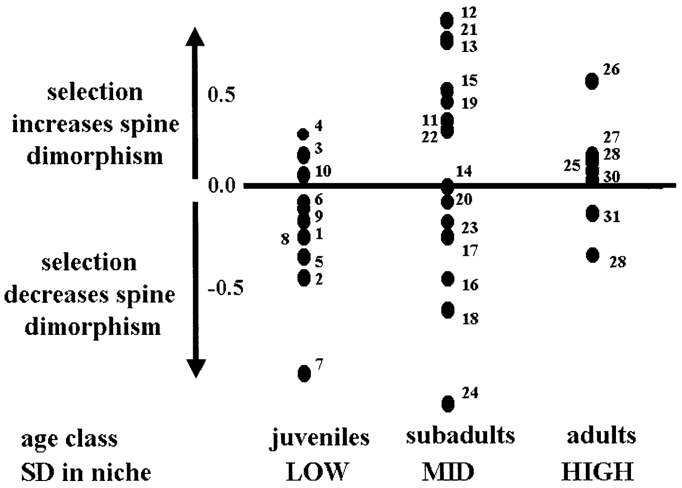

FIG. 2. Differences between the sexes in selection on spine number were dependent on the age class observed ($\chi^2 = 2.95$, df $=1$, $P < 0.05$, linear-by-linear association; each data point represent the difference between female and male selection differentials for a paired episode of selection). Females in the Boulton Lake population exhibit greater spine number than males, thus positive values on the y-axis indicate that selection acted to increase levels of sexual dimorphism (SD) (i.e., would act to increase spine expression in females versus males), zero values indicate selection did not influence levels of dimorphism, and negative values indicate selection tended to decrease dimorphism (i.e., would act to increase spine expression in males relative to females). Selection tended to decrease dimorphism in juveniles, was random with respect to contemporary levels of dimorphism in subadults, and tended to increase levels of dimorphism in adults. Thus, variability in sex-specific selection was positively associated with ontogenetic shifts in habitat, diet, and parasite load differences between the sexes. Numbers beside each data point denote the episode of selection (see Table 1).

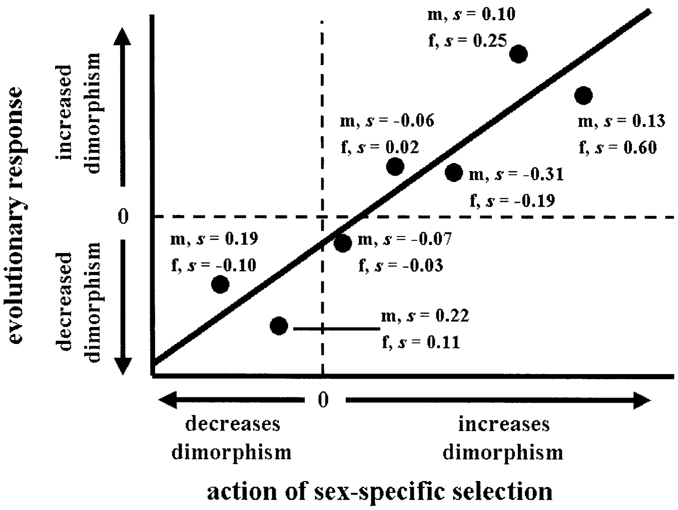

FIG. 3. The evolutionary response to sex-specific natural selection was predictable. Differences between the adult sexes in selection differentials (female differential minus male differential, ''action of sex-specific selection'') were correlated with intergenerational shifts in the magnitude of sexual dimorphism (SD) observed in adults versus juveniles from the next generation (SD in generation 2 minus SD in generation 1, ''evolutionary response''). Shown beside each datapoint is the selection differential on spine number (s) for adult males (m) and for adult females (f). For illustrative purposes, the data points represent rank-order associations ($r = 0.69$, $P = 0.043$, $n = 7$, bivariate correlation).

morphism observed between adults (generation 1) versus juveniles from the next generation (generation 2) (Fig. 3; $r = 0.69$, $P = 0.043$, $n = 7$, bivariate correlation). Moreover, for the three different cohorts where successive estimates of juvenile, subadult, and adult survival were available within a single generation, the rank order of additive sex differences in selection was perfectly associated with the rank order of intergenerational shifts in sexual dimorphism in spine number between juveniles from the two successive generations (for the three yearly cohorts; sex differences in selection differentials averaged across the ontogenetic bouts of selection, 0.11, 0.09, −0.36; differences in sexual dimorphism between successive generations of juveniles, 0.12, 0.02, −0.06).

Shifts between the Sexes in Ecology and Selection on Spine Number

Ontogenetic and temporal differences between the sexes in the magnitude of ecological divergence provide a unique opportunity to test for associations between sex-specific ecology, sex-specific selection and sexual dimorphism. Consistent with prediction, the direction of sex-specific selection is dependent on the age class examined (Fig. 2; chi-square = 2.95, DF = 1, $P < 0.05$, linear-by-linear association) such that selection acts to increase dimorphism only in the life-history stage where the sexes are most differentiated. Specifically, sex-specific selection tends to decrease sexual dimorphism in juvenile fish, is random with respect to existing levels of dimorphism in subadults, and tends to increase dimorphism in adults (Fig. 2).

Additionally, temporal shifts in ecological differences between the sexes were correlated with the mode and strength of sex-specific selection for both diet and *S. solidus* infection (Fig. 4; benthic macroinvertebrate consumption; $r = -0.63$, $P = 0.035$, n = 9; *S. solidus* infection, $r = 0.46$, $P = 0.019$, $n = 21$; *C. truncatus* infection, $r = 0.11$, $P > 0.10$). Selection acted to increase levels of sexual dimorphism when ecological differences between the sexes are pronounced and in the expected direction (i.e., when benthos consumption is strongly male biased and *S. solidus* infection is highly female biased; Fig. 4). Conversely, selection acted to decrease existing levels of dimorphism when males and females exhibit reversals in ecological niche (i.e., time periods where benthos consumption is female biased and *S. solidus* infection is male biased). Finally, when the sexes exhibit similar diet and parasite load, selection acted similarly on each sex and thus did not influence dimorphism. These associations were independent of age class (tests for homogeneity of slopes, all $P > 0.20$, ANCOVA).

DISCUSSION

We detected sex-specific selection acting on spine number in Boulton Lake stickleback, as well as a predictable evolutionary response to selection. Shifts in the direction and magnitude of selection acting on each sex were correlated with shifts in ecological differences between the sexes such that (1) selection acted to increase dimorphism when females experienced pelagic conditions and males experienced the

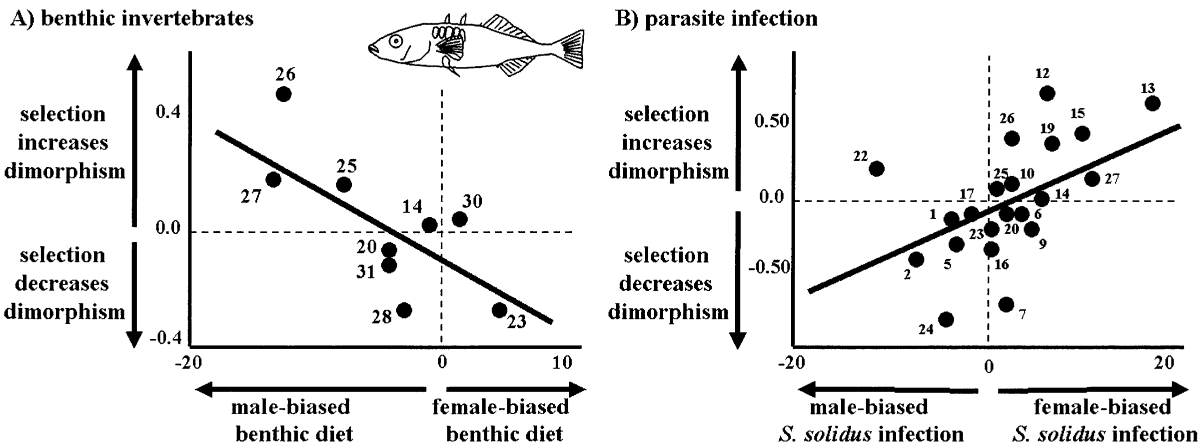

FIG. 4. Differences between male and female stickleback in selection on spine number were correlated with temporal shifts in the degree of ecological differentiation between the sexes. The y-axis represents female minus male selection differential. Females in the Boulton Lake population exhibit greater spine number than males, thus positive values on the y-axis indicate that selection acted to increase levels of dimorphism (i.e., would act to increase spine expression in females versus males), zero values indicate selection did not influence levels of dimorphism and negative values indicate selection tended to decrease dimorphism (i.e., would act to increase spine expression in males relative to females). Numbers beside each data point denote the episode of selection listed in Table 1 and sample sizes for ecological data gathered for each episode of selection are given in Table 2. (A) Dietary differences (x-axis represents female minus male percent benthic macroinvertebrate consumption; $r = -0.63$, $P = 0.035$, $n = 9$). (B) Parasite load (x-axis represents female minus male percent *Schistocephalus solidus* infection; $r = 0.46$, $P = 0.019$, $n = 21$).

TABLE 2. Sample sizes for ecological analyses. Shown are the number of males and females examined within an episode of selection (numbers refer to the episode of selection denoted in Table 1) for diet and for *Schistocephalus solidus* infection.

Episode	Males	Females
Diet		
14	76	54
20	63	47
23	128	51
25	90	130
26	43	28
27	45	42
28	82	70
30	13	15
31	21	17
S. solidus		
1	29	29
2	44	36
5	109	99
6	18	19
7	94	105
9	5	4
10	135	240
12	189	235
13	55	105
14	302	256
15	347	365
16	176	227
17	257	235
19	130	65
20	98	106
22	131	123
23	302	128
24	433	404
25	324	237
26	150	83
27	136	93

opposite benthic conditions; (2) selection did not affect existing levels of dimorphism when the sexes exhibited similar ecological niches; and (3) selection acted to decrease dimorphism when sex reversals in ecological niche occurred. Collectively, these results indicate that strong sex-specific selection occurred, but only during life-history stages and time periods in which pronounced ecological differences between the sexes result in differential exposure to divergent predation regimes. Such ecological causes for temporal variation in dimorphism within populations are rarely documented as their detection requires extended monitoring of natural populations. However, our results are consistent with previous investigations on sexual dimorphism and niche partitioning in birds (Selander 1966; Radford and du Plessis 2003) and snakes (Shine 1991) and with the observation that sexual differences in trophic morphology (an indicator of ecological niche) occur among both invertebrate and vertebrate taxa (for review, see Shine 1989).

Variability between the sexes in ecology and selection on spine number occurred across two temporal scales; among life-history stages and among time periods within life-history stages. First, selection acted to increase dimorphism only in the life-history stage in which the sexes are most differentiated. Specifically, sex-specific selection tended to decrease sexual dimorphism in juvenile fish, is random with respect to existing levels of dimorphism in subadults, and tended to increase dimorphism in adults. This result is consistent with the suggestion that contrasting selection pressures between age classes and life-history stages can exert a strong influence on adaptive evolution in general (Schluter et al. 1991), and in the evolution of sexual dimorphism in particular (Badyaev 2002; Schulte-Hostedde et al. 2002). Second, sex-specific selection occurred only during time periods and seasons in which pronounced ecological differences between the sexes results in differential exposure to the two, divergent predation regimes, and this latter effect was independent of age class of stickleback. Collectively, these data show that contrasting life-history pressures and temporal shifts in ecology can exert a strong influence on the evolution of sexual dimorphism.

Notably, we inferred differential exposure to divergent predation regimes indirectly, using differential habitat use. Thus, there are several potential alternative explanations for habitat specific selection. Firstly, reduced spine number might be favored if subadult and adult stickleback evade vertebrate predators by hiding in mud substratum as suggested by Nelson (1969) for spine loss in *Culaea inconstans*. Alternatively, reduced spine number might facilitate movement through weeds in the benthic zone. As well, there are mortality factors other than predation that may be nonrandom with respect to spine phenotype and habitat use such as differential parasitism (Reimchen and Nosil 2001). However, there is no direct evidence that these alternative processes reduce spine number whereas consideration of functional design, geographic surveys, and controlled experimental results all indicate that grappling benthic invertebrate predators produce selection favoring spine reduction (Reimchen 1980, 1983; Reist 1980; Ziuganov and Zotin 1995; Vamosi 2002; see also Conclusions below).

Selection on a character of one of the sexes causes not only a direct response of the character in the selected sex, but also a correlated response of the homologous character in the opposite sex (i.e., due to pleiotropy and linkage of genes affecting characters of both sexes, Lande 1980; Price 1984; Merila et al. 1998). Thus, sex-specific selection acting on one sex will not necessarily lead to, or maintain, sexual dimorphism. However, ecological differences between the sexes can result in contrasting selection regimes between the sexes and, in theory, should result in the evolution of sexual dimorphism (Selander 1966; Slatkin 1984; Shine 1989). In Boulton Lake, the mean difference in female selection differential minus male differential, averaged across all episodes of selection, was zero and thus sex-specific selection will not act to decrease sexual dimorphism. More likely, selection contributes to the maintenance of sexual dimorphism in this population, as occurs for selection that fluctuates among adult life-history stages in water striders (Preziosi and Fairbairn 2000). This suggestion is consistent with the observation that levels of sexual dimorphism did not differ between the beginning and end of the 15-year study period, despite variable natural selection both within and between the sexes.

Studies of fossil stickleback have revealed that spine number can exhibit long-term stasis for tens of thousands of years (Bell 1988). Our results, coupled with those of Reimchen and Nosil (2002), shed light on these fossil studies as they indicate that such stasis could result from rapid and fluctuating shifts in directional selection, rather than from an absence of directional selection or from consistent stabilizing selection. However, these fossil studies have also shown that spine number can vary between sample periods spanning several thousand years. For example, in one fossil population of freshwater stickleback 65% of the pelvic reduction that followed colonization from the ancestral marine habitat occurred within three thousand years (Bell 1988). Our results show substantive shifts in spine phenotype frequencies between successive generations, indicating that the evolution of spine reduction can occur more rapidly than detectable through analyses of the fossil record. Similarly, rapid evolution has been observed in the lateral plate complex of stickleback (Reimchen 1995; Bell 2001).

The origin of the relatively well-known habitat differences between the sexes in stickleback remains obscure, other than that male-dominated parental care occurs in benthic and littoral habitat from which females are excluded. However, once sex-specific habitat differences do occur it is possible that variable exposure to divergent predation regimes can also account for the origin of sexual dimorphism in mean spine number. The ancestral marine form of stickleback is sexually monomorphic for spine number (all males and females have a full spine complement; Wootton 1976) and thus, whenever colonization of freshwater lakes is accompanied by niche partitioning between the sexes, it is likely that strong selection for increased sexual dimorphism occurs. To the extent that females exhibit a more pelagic niche than males, they will, on average, be exposed to a different predation regime than individuals in littoral and benthic habitats (Reimchen 1994). This process could cause the evolution of a sexual dimorphism from an initially monomorphic ancestral population. Data on the factors influencing the evolution of sexual dimorphism in independently derived freshwater stickleback populations would provide comparative tests of this hypothesis. For example, comparative analysis revealed ecological causes of sexual dimorphism in *Anolis* lizards (Butler et al. 2000).

Conclusions

Our results illustrate how niche partitioning between the sexes can lead to ontogenetic and temporal shifts in selection and thus drive the evolution of sexual dimorphism. Although differential exposure to invertebrate versus avian predators is the likely mechanism causing sex-specific selection in Boulton Lake, we stress that our most general conclusion that shifts in ecology drive shifts in sex-specific selection allows for any mechanism of habitat or niche-specific selection. Our work parallels recent studies of adaptive radiation in stickleback, in which divergent selection and differential adaptation to benthic and limnetic lake habitats has contributed to the origin of stickleback species (Rundle et al. 2000; Schluter 2000; Vamosi 2002). A notable difference is that the evolution of sexual dimorphism is strongly affected by genetic correlations between the sexes and thus our understanding of the evolution of sexual dimorphism in stickleback will benefit from further studies of the genetic architecture of adaptive traits (Peichel et al. 2001). Our results compliment recent theory indicating that sexual dimorphism and speciation can be driven by similar processes but that the outcome of such processes is affected by genetic correlations between the sexes (Bolnick and Doebeli 2003). Collectively, these findings emphasize the role of ecological processes in driving evolutionary diversification both within and among populations.

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