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SPATIAL VARIATION IN SELECTIVE REGIMES: SEXUAL SELECTION IN THE WATER STRIDER, *GERRIS ODONTOGASTER*

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Abstract.—Studies of phenotypic selection in natural populations are often concerned with simply detecting selection. In adopting a more mechanistic approach, this study compares the sexual selection regimes in natural populations of the water strider *Gerris odontogaster* with a priori predictions of selection, based on a number of previous field and laboratory studies of the behavioral mechanisms of selection. In this species, a general reluctance of females to mate allows for intersexual selection for ability to subdue reluctant females in males. Female reluctance to mate has been shown to decrease with increasing population density, suggesting that sexual selection should be weaker in high density populations. Three different populations with large differences in population density were studied. A number of traits including parasite load, body mass, body size and male abdominal process length were found to experience significant sexual selection. The investigated populations differed considerably with regard to the total strength of selection on the measured traits and the form of selection on single traits. In general, males in the population with the highest density experienced the weakest selection for grasping ability. This pattern is ascribed to density-related alterations of female mating behavior. Selection for male grasping ability, as reflected by selection on male abdominal process length, is reduced in high-density populations where reluctant females are more easily subdued. Further, the studied populations differed significantly in mean phenotype and phenotypic variance for male abdominal process length. It is suggested that interpopulational differences in selective regimes may generate local adaptations with respect to male abdominal process length, and that gene flow may contribute to the maintenance of the high genetic variation in this trait. It is further suggested that more empirical effort should be made in quantifying and understanding spatial and temporal variation in selection in natural populations, since this may provide information on the prevalence of local adaptations in metric traits and on the mechanisms of selection.

Key words.—Density-dependent selection, *Gerris,* local adaptation, mechanisms of selection, parasite load, phenotypic selection, selection coefficient, selective regimes, sexual dimorphism, sexual selection, Trypanosomatidae.

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The study of phenotypic selection in natural populations has been given considerable attention in recent years. Regression methods have been developed for measuring selection when selection acts simultaneously on a set of phenotypically correlated characters (Lande and Arnold, 1983; Manly, 1985; Endler, 1986), and for analyzing temporal variation in selection by partitioning the total effect of selection into several selection episodes related to different fitness components (Arnold and Wade, 1984*a*, 1984*b*; Conner, 1988; Moore, 1990). Although many empirical studies have demonstrated selection in natural populations, the mechanism of selection is known only in a few cases (see Endler, 1986; for a review). Recently, several authors have stressed that a correlational approach is insufficient for inference of causal patterns of selection, and that a more mechanistic approach (i.e., a thorough knowledge of the biology of the study organism in concert with studies of selection at the population level) may provide a priori predictions about the outcome of selection and about the factors affecting the mechanisms of selection (Endler, 1986; Mitchell-Olds and Shaw, 1987; Wade and Kalisz, 1990).

The recognition that selection typically varies temporally and spatially has received considerable theoretical attention, because heterogeneous environments may promote the maintenance of heritable variation in traits related to fitness (Felsenstein, 1976; Nevo, 1978; Falconer, 1981; Grant and Price, 1981; Maynard Smith, 1989). However, theoretical models suggest that while temporal variation in selection may be of limited importance in maintaining genetic variation, spatial variation (linked with a moderate gene flow) may play a more important role (see Felsenstein, 1976; Hedrick et al., 1976; Endler, 1977; Hedrick, 1986; for reviews). This suggests that more empirical effort should be made to quantify spatial variation in selection and local adaptation in natural populations (Endler, 1986; Hedrick, 1986). Although multivariate methods for analyzing phenotypic selection in natural populations only "helps to reveal the targets of selection . . . without identifying the selective agents" (Lande and Arnold, 1983), they may prove very useful when applied in a broader conceptual framework where a mechanistic approach is adopted in studies of spatial variation in selective regimes.

In this study, the sexual selective regimes of three natural populations of *G. odontogaster* are compared with a priori predictions of selection based on several field and laboratory experiments. Because sexual selection is predicted to be inversely density-dependent (Arnqvist, 1992*a*; see below in *Predictions of Selection*), the populations were chosen because of their large differences in population density. Sexual selection was measured using standard univariate and multivariate methods, and estimates of selection are reported on several morphological traits including male secondary sexual characters. In addition to selection on morphology, sexual selection on trypanosomatid gut parasite load was also measured, because these parasites are known to decrease the viability and vigor of water striders (Arnqvist and Mäki, 1990).

Background.—In the water strider *G. odontogaster* (Zett.), matings are initiated by males that pounce on females and attempt forced copulation. Females are reluctant to mate and try to dislodge males by repeatedly performing backward somersaults at the water surface (Arnqvist, 1989*b*, 1992*a*). Both sexes mate multiply, frequently several times every day (Vepsäläinen, 1974*b*; Arnqvist, 1989*b*). Because the last male to mate a female typically fertilizes the majority of the subsequent progeny in water striders (Arnqvist, 1988; Rubenstein, 1989), males can increase their reproductive success by multiple matings. In contrast, females are able to store viable sperm and experience several costs in mating in terms of increased predation risk and energetic expenditure (Arnqvist, 1989*b*). Further, variation in female reluctance behavior has been shown to be consistent with predictions of a model of sexual conflict over the mating decision (Arnqvist, 1992*a*), suggesting that female reluctance represents a general reluctance to mate rather than an adaptive mate assessment strategy.

Reluctance of *G. odontogaster* females to mate allows for a form of intersexual selection for ability to subdue reluctant females (cf. Kence and Bryant, 1978; McCauley, 1981; Thornhill, 1984). The species *G. odontogaster* is sexually dimorphic, with males having a grasping apparatus consisting of two abdominal processes (Arnqvist, 1989*a*). The abdominal processes are essential for males to succeed in mating. Arnqvist (1989*a*) demonstrated that the length of male abdominal processes is correlated with a male's ability to clasp the female and thus to endure female reluctance behavior during the precopulative struggle. Further, as has been shown to be the case for some intersexually selected traits in other insect species (e.g., Simmons, 1987; Hedrick, 1988), the length of the processes was shown to have high heritability. Thus, abdominal processes were subjected to sexual selection in a natural population (Arnqvist, 1989*a*).

The mechanism of sexual selection for male grasping ability in *G. odontogaster* (general reluctance to mate in females) is known to be affected by environmental variation. In a series of experiments, Arnqvist (1992*a*) demonstrated that female reluctance varies with both the operational sex ratio and population density. Females fight less intensely to dislodge males attempting copulation as the sex ratio becomes male biased and/or the population density increases. Consequently, the relative importance of long abdominal processes in terms of acquiring mates has been shown to decrease with increasing sex ratio (Arnqvist, 1992*b*).

Predictions of Selection.—To attain a mate, a *G. odontogaster* male has to (1) actively search for a solitary female, and (2) subdue the female by grasping her during precopulative struggle (i.e., avoid being dislodged). Both of these factors are affected by population density. Search costs should

TABLE 1. Characteristics of the investigated populations and their habitats at the sampling occasion, on 4–9 June 1989.

Name of pond	Location	Emergent vegetation	Infection rate of gut parasites	Population density (mean ± SD; inds./m^2)	Proportion of males mating	Sex ratio (males : females)
#1 Kattögeltjärn	63°44′N 20°10′E	*Carex, Sphagnum, Potamogeton.*	48% ($N = 318$)	5.50 ± 2.4	34%	1:0.69
#2 Trehörningsmyran	63°47′N 20°22′E	*Carex, Nuphar.*	67% ($N = 308$)	8.17 ± 2.6	31%	1:0.48
#3 Gimonäsdammen	63°48′N 20°19′E	*Carex, Potamogeton.*	95% ($N = 315$)	31.25 ± 12.1	38%	1:0.49

be smaller in dense populations, and the strength of selection for male grasping ability should decrease with increasing population density as a result of females being less reluctant to mate (Arnqvist, 1992*a*). Hence, based on results from previous field and laboratory experiments, it may be predicted that sexual selection in *G. odontogaster* males should be inversely density-dependent. This pattern of selection should be especially pronounced for characters relating to grasping ability (i.e., length of the abdominal processes).

MATERIALS AND METHODS

The Study Animals.—Water striders are semiaquatic predatory insects (Heteroptera: Gerridae) that inhabit water surfaces of ponds and lakes, both as adults and as larvae. In temperate regions, adults overwinter on land in a prereproductive state (see Andersen, 1982). The reproductive activities, including mating and egg laying, start in late April or early May after a period of gonad maturation, and continue for one to two months until the overwintered adults die. Eggs are deposited on floating objects, such as leaves (Arnqvist and Byström, 1991).

Field and Laboratory Methods.—Three different populations of *G. odontogaster* situated in the area around Umeå, northern Sweden, were compared using identical sampling procedures in all populations. All populations studied were univoltine and monomorphic macropterous. The main predators of water striders, fishing spiders *Dolomedes fimbriatus* and backswimmers *Notonecta* sp., occurred at all three sites. To estimate population density, sex ratio, and the proportion of mating and single males in the populations, a number of quadrat counts were made. The method suggested by Spence (1980) was used; a 1.0 × 1.0 m sampling aluminum frame with styrox floating elements was gently dropped into the water. The number of mating pairs and single individuals "captured" within the enclosure were first recorded visually, and subsequently determined by collecting all water striders within the enclosures. In each population, 15 replicate quadrat counts were performed between noon and 2:00 P.M. three days prior to the selection analysis sampling (see below). The quadrat counts were made near the shoreline in the belt of emergent vegetation, within a range of ap-

TABLE 2. Means and standard deviations of various male characteristics in the three populations. Linear measures are given in millimeters.

Number of ind.	Weight ($g \times 10^{-3}$)	Length of pronotum	Width of pronotum	Length of fore femur	Length of midleg (total)
#1 $N = 159$	7.92 (0.78)	2.65 (0.09)	0.99 (0.04)	1.86 (0.06)	11.52 (0.34)
#2 $N = 154$	7.70 (0.65)	2.66 (0.09)	0.98 (0.03)	1.83 (0.06)	11.54 (0.39)
#3 $N = 157$	7.86 (0.63)	2.63 (0.10)	0.99 (0.03)	1.83 (0.08)	11.49 (0.41)
ANOVA[1]	$F = 4.08$ $P = 0.018$	$F = 4.22$ $P = 0.015$	$F = 6.93$ $P = 0.001$	$F = 11.76$ $P < 0.001$	$F = 0.86$ $P = 0.426$

[1] All measurements (cube root for weight) were ln-transformed prior to ANOVAs for tests of differences in mean phenotype between the populations.

[2] H represents test statistic of the Kruskall-Wallis nonparametric ANOVA.

proximately 30 m, in each of the study sites. The estimated densities may thus be said to reflect local densities in a representative part of water strider habitat in each of the sites. The characteristics of the populations are described in Table 1.

To measure sexual selection in the three populations, mating males and solitary males were sampled with a hand net at the same sites as the quadrat counts were made in each of the ponds. The populations were sampled between noon and 2:00 P.M. on 7, 8, and 9 June 1989, respectively, and mating males were assigned an absolute fitness of 1 and solitary males an absolute fitness of 0. Consequently, the data on which subsequent selection analysis was based were cross-sectional (Lande and Arnold, 1983; Arnold and Wade, 1984*a*, 1984*b*; Endler, 1986). To estimate accurately selection coefficients from cross-sectional data, mating and solitary males should be sampled in proportion to their actual representation in the population (Arnold and Wade, 1984*a*, 1984*b*; Zuk, 1988). Thus, the two groups of males were sampled in proportion to their relative abundance in each population, as estimated by the quadrat counts, and a total *N* of 150–160 males were collected from each population (see Table 2). All animals collected were frozen immediately in the field, and were kept frozen until examination in the laboratory.

The water striders were subsequently thawed in the laboratory, and nine linear measurements were made on each individual with a micrometer eyepiece on a stereo microscope. The measured characters were body size (pronotal length and width), leg length, pigmentation (pronotal spot), and secondary sexual characteristics (see Appendix). All individuals were also weighed (wet weight to ±0.05 mg) with a Mettler® AE50 balance. Finally, the water striders were dissected to determine the intensities of trypanosomatid gut parasite infections. The mid- and hindgut were teased in 0.8% NaCl solution and examined in Vaseline-sealed coverslips under a microscope. The parasite loads were ranked according to a five degree scale; (0) uninfected individuals, (1) light infections, (2) moderate infections, (3) heavy infections, and (4) very heavy infections (gut occluded by parasites). To assess whether assortative mating by size occurred, the length of the pronotum was also measured on females in the mating pairs. All laboratory work was performed by a laboratory technician who had no detailed knowledge of the aim of the study.

TABLE 2. Extended.

Length of pronotal spot	Length of abdominal process	Parasite load (rank index)
0.38 (0.08)	0.197 (0.024)	0.60 (0.76)
0.38 (0.07)	0.183 (0.020)	0.84 (0.80)
0.40 (0.09)	0.173 (0.026)	1.64 (0.93)
$F = 2.03$	$H^2 = 76.4$	$H^2 = 105.9$
$P = 0.133$	$P < 0.001$	$P < 0.001$

Differences in mean phenotype between the populations were tested with ANOVAs for all traits. For traits found to have nonhomogeneous variances (Bartlett's test for homogeneity of variances performed on ln-transformed values), the Kruskall-Wallis nonparametric ANOVA was used for comparison between the populations.

Estimation of Selection Coefficients.—When measuring phenotypic selection in natural populations, several different statistical approaches may be adopted (Manly, 1985; Endler, 1986). The method used here was introduced by Lande and Arnold (1983) and allows measurement of selection acting on several traits simultaneously. It involves the calculation of univariate selection differentials and multivariate selection gradients using multivariate regression analysis (see below).

On the basis of the phenotypic correlation matrix (see Appendix), the four measures of the mid-leg were joined to total mid-leg length, thus reducing the number of phenotypic traits from 11 to 8. This was done to reduce the effects of multicollinearity, which may present a serious problem in multivariate statistical analysis (see below; Belsley et al., 1980; Mitchell-Olds and Shaw, 1987). All linear phenotypic measures (cube root for weight) were transformed to natural logarithms prior to analysis. Further, all traits were standardized to a mean of zero and unit variance. All selection coefficients reported are thus standardized selection coefficients (Lande and Arnold, 1983; Endler, 1986). Individual measures of absolute fitness were transformed to relative fitness (w), with a mean value of one within each population (Lande and Arnold, 1983; Endler, 1986).

The selection differentials are univariate estimates of the direct effect of selection on a given trait as well as of the indirect effects of selection on correlated characters (Lande and Arnold, 1983). The directional selection differentials (s′) were estimated as the covariance of relative fitness and linear measures of single traits, while the quadratic selection differentials (C′) were estimated as the covariance of relative fitness and quadratic deviations of the traits from their mean (Price, 1970; Lande and Arnold, 1983; Endler, 1986). Significance testing of selection differentials was made with Spearman rank correlation tests (Lande and Arnold, 1983).

While selection differentials measure all direct and indirect effects of selection, the selection gradients measure only the direct effects of a given character on relative fitness, adjusting for the effects of indirect selection on the statistically correlated characters included in the analysis (Mitchell-Olds and Shaw, 1987; Phillips and Arnold, 1989). The method applied in this study largely follows the multiple regression approach suggested by Lande and Arnold (1983), where the selection gradients equal the partial regression coefficients in a standard multiple regression of relative fitness on the characters. The directional selection gradients (β') were estimated in a multiple regression model of relative fitness on linear measures of all traits ($w = a + \Sigma(\beta_i)z_i$). The quadratic selection gradients (γ') were estimated as the partial regression coefficients of the quadratic components in a model of relative fitness involving all linear, quadratic, and correlational trait components ($w = a + \Sigma(\beta_i)z_i + \Sigma(\gamma_i)z_i^2 + \Sigma(\gamma_{ij})z_iz_j$). By using separate regressions to estimate linear and quadratic selection gradients, the problem of deviation from multivariate normality is reduced (see Phillips and Arnold, 1989; p. 1219).

Following Phillips and Arnold (1989; Table 1), C and γ will be termed "quadratic selection" coefficients rather than "stabilizing selection" coefficients, and the term "nonlinear selection" will be used for nonzero C and γ rather than "stabilizing selection" (cf. Lande and Arnold, 1983). Under this definition, stabilizing and disruptive selection are special cases of nonlinear selection (see Mitchell-Olds and Shaw, 1987; Schluter, 1988; Phillips and Arnold, 1989; for a discussion of terminology).

A common computational problem when analyzing selection on a suite of phenotypically intercorrelated traits is the standard multiple regression problem of multicollinearity (Lande and Arnold, 1983; Endler, 1986; Schluter and Smith, 1986; Mitchell-Olds and Shaw, 1987). In the presence of severe multicollinearity, the most widely adopted strategy is simply to reduce the number of predictor variables, for example, by excluding or summing characters or by the use of principal components in the regression (Endler, 1986; Mitchell-Olds and Shaw, 1987; Anholt, 1991). Because at least some of the components in most multiple regression models are intercorrelated to some extent, the decision of when collinearity in a data matrix becomes severe may in itself be a problem (Belsley et al., 1980). There are several diagnostic tools that can be used to assess the presence of collinearity in data matrices. In this study I use the condition index to assess the degree of collinearity. In general, a condition index greater than 15 indicates a minor problem and one greater than 30 suggests a severe problem with multicollinearity in a data matrix (see Belsley et al., 1980; for details).

In multivariate analyses of selection, the dependent variable (fitness component) is often discrete and binary (e.g., surviving/nonsurviving, mating/nonmating) thus violating a general assumption of ordinary multiple regression techniques with least-square minimization. Although this does not pose any serious problem for parameter estimation of selection gradients (Lande and Arnold, 1983; Endler, 1986), it may bias the tests of significance of selection gradients (e.g., Mitchell-Olds and Shaw, 1987). In this study, I used binary probit regression analysis for all tests of significance of single partial regression coefficients and for total models, although this procedure gave essentially the same results as ordinary *F*-tests.

The probit analysis used involves the method of maximum likelihood (using iteratively reweighted least squares; see Wilkinson, 1985) and is appropriate for estimating multiple regression models when the dependent variable is binary (McFadden, 1982; McCullagh and Nelder, 1983; Price, 1984; Schluter and Smith, 1986; Mitchell-Olds and Shaw, 1987; Smith, 1990). Total regression models were tested with the likelihood-ratio test of H_0: all regression coefficients (except a) are equal to zero. This test is analogous to an overall F-test in standard regression analysis (see Kleinbaum et al., 1988; p. 499).

The selection differentials for the different populations were compared in a binary probit regression model where all populations were pooled. Population number was introduced as a categorical variable (1, 2, 3) and recoded into dummy variables. Test of significance of differences among the populations in selection differentials was tested with a t-test of the interaction term between group and trait (e.g., pond and body weight), which makes the procedure equivalent to a test of parallelism (equal slopes) in an ordinary least-square ANCOVA with partial F-test (Kleinbaum et al., 1988; p. 302). However, the probit regression procedure is more appropriate because the dependent variable is binary (cf. Anholt, 1991; p. 1096). Comparisons of selection differentials were restricted to the traits where at least one of the differentials was significantly different from zero. Following the same basic procedure, selection gradients were compared using multiple probit regression on the pooled data matrix. Test of significance was made with a t-test of the interaction terms between traits and the categorical group variable, again making the procedure equivalent to a test of multivariate parallelism in ANCOVA (Kleinbaum et al., 1988; p. 305).

To assess the relative overall importance of quadratic and correlational selection in each population, a series of likelihood-ratio tests was performed. These tests evaluate the increase in statistical fit when adding a group of new parameters to the probit regression model, and are analogous to multiple-partial F-tests in standard regression. However, the likelihood-ratio test statistic (here denoted LR) will have an approximate chi-square distribution (see Kleinbaum et al., 1988; p. 493; for test procedure). Due to problems of multicollinearity (see Results section), the analysis was restricted to the five traits found to be involved in any significant selection. To assess the importance of quadratic selection, models involving linear trait components were compared only with models involving linear and quadratic components. Correlational selection was evaluated by comparing models involving linear and quadratic trait components with full models involving linear, quadratic and correlational components.

Assessments of the correctness of the probit models were made by visual analyses of deviance residuals and Pearson residuals (McCullagh and Nelder, 1983; p. 216). All statistical analyses reported in this paper were performed with the SYSTAT statistical package (Wilkinson, 1987), except for the procedure generating residuals from the probit regression models where SAS software was used (SAS Institute Inc., 1990).

Estimating Fitness Functions.—In a thorough selection analysis, visualization of selection may be of critical importance for a correct interpretation of the selection coefficients (Schluter, 1988; Phillips and Arnold, 1989). Univariate fitness functions were estimated using the nonparametric cubic spline approach of Schluter (1988). This technique is appealing because it does not assume any specific form of selection a priori, and thus provides fitness functions with a local rather than a global fit. It also enables the estimation of asymmetrical standard errors with a bootstrap resampling technique (see Schluter, 1988). Fitness functions with standard errors (based on 1,000 bootstraps) were estimated for all traits exhibiting significant selection differentials, using a FORTRAN77 computer routine provided by D. Schluter (GLMS, ver. 3).

RESULTS

The investigated populations differed significantly with respect to population density, the density in population #3 being almost six times that of population #1 (Table 1, $F = 45.45$, $P < 0.001$). The populations also differed in gut parasite prevalence (Table 1, $\chi^2 = 169.61$, $df = 2$, $P < 0.001$). The overall proportion of males mating was 30–

40% in all three populations (Table 1). There was no significant difference in sex ratio between the populations (Table 1, $\chi^2 = 1.724$, $df = 2$, $P > 0.1$).

The phenotypic correlations between male traits within the populations are presented in the Appendix. The highest correlations were found between size (length of pronotum) and weight (0.71–0.78), and the lowest correlations involved gut parasite load. While most traits exhibited significant phenotypic correlations with other traits, most correlation coefficients were low or moderate (90% in the range 0.00–0.55).

The phenotypic characteristics of the males in each population for all traits involved in the analysis of selection are presented in Table 2. There were highly significant differences among the three populations in several traits, including body size (length and width of pronotum) and male abdominal processes. The only trait found to have a significant difference in intrapopulational phenotypic variance between the populations was length of abdominal processes (Barlett's test for homogeneity of variances [ln-transformed values]; $\chi^2 = 11.17$, $df = 2$, $P = 0.004$). The coefficients of variation for abdominal process length for the populations were CV = 11.95 (#1), CV = 10.69 (#2), and CV = 14.93 (#3). The pronotal length of males and females in mating pairs was not significantly correlated in any of the three populations (#1: $r = -0.112$, $N = 54$, $P > 0.1$; #2: $r = -0.095$, $N = 48$, $P > 0.1$; #3: $r = 0.047$, $N = 60$, $P > 0.1$). Thus, there was no assortative mating by size.

Analysis of Selection

Directional Selection.—Directional selection differentials and gradients are presented in Table 3. There was significant positive directional selection for weight in all three populations. The univariate measures of selection on pronotal length were very low and nonsignificant. However, when the effects of selection on correlated characters were adjusted for, the selection gradients were found to be negative in all three populations and significant negative directional selection on pronotal length occurred in population #1. Leg lengths and pigmentation were not involved in any significant selection. There was significant directional selection for long abdominal processes in population #1, as demonstrated by both univariate and multivariate measures. Significant directional selection for low parasite load was found in populations #1 and #2.

The multiple regression models used to estimate directional selection gradients were not affected by multicollinearity in the data matrices, as indicated by condition indices for the three populations of 4.51, 3.55, and 4.01 respectively. Directional selection explained approximately 14% of the variance in relative fitness in population #1, 9% in population #2, and only 4% in population #3 (see Table 3), suggesting that directional selection on the traits involved in the analysis was strongest in population #1 and weakest in population #3.

There was a significant difference between the populations in linear selection on abdominal process length ($t = 2.302$, $df = 464$, $P < 0.05$), whereas selection on weight ($t = 0.608$, $df = 464$, $P > 0.5$), and parasite load ($t = -1.386$, $df = 464$, $P > 0.05$) did not differ significantly. Further, there was no significant difference between the populations in linear selection gradients ($t = -1.677$, $df = 464$, $P > 0.05$).

Nonlinear Selection.—The estimates of nonlinear selection are presented in Table 4. The univariate estimates of selection demonstrated significant quadratic selection differentials for pronotal width and abdominal process length in population #2. There was also significant nonlinear selection for low parasite load in population #3.

In the multivariate analysis of nonlinear selection, all fitting of multiple regression models suffered from problems of multicollinearity (condition indices 36.59, 23.37, and 30.65 respectively). Further, none of the models significantly explained any portion of the variance in relative fitness (Table 4). To reduce the effects of collinearity, quadratic selection gradients were reestimated in a reduced model, involving the linear, quadratic, and correlational components only of the five traits found to be involved in any significant selection (see Table 5). By doing this, collinearity was reduced to acceptable levels (condition indices 15.15, 13.17, and 14.05 respectively) and the total models were found to be significant for pop-

TABLE 3. Standardized directional selection differentials (s′) and standardized directional selection gradients [β' (SE)] for the three water strider populations. Directional selection gradients were estimated in a multiple regression model, involving only linear components of eight traits (see Materials and Methods).

	s′			β'(SE)		
	#1	#2	#3	#1	#2	#3
Weight	**0.186***	**0.205***	0.140	**0.381 (0.16)****	**0.448 (0.13)*****	**0.296 (0.14)***
Length of pronotum	0.030	0.049	0.053	**−0.256 (0.12)***	−0.108 (0.12)	−0.102 (0.13)
Width of pronotum	0.127	0.055	−0.007	−0.043 (0.11)	−0.127 (0.11)	−0.138 (0.10)
Length of fore femur	0.102	−0.002	0.060	0.045 (0.09)	−0.059 (0.10)	0.035 (0.12)
Length of mid-leg	0.061	0.032	0.064	−0.051 (0.11)	−0.076 (0.11)	−0.024 (0.12)
Pronotal spot	−0.005	−0.055	−0.011	−0.049 (0.08)	−0.055 (0.08)	−0.007 (0.08)
Abdominal processes	**0.249****	0.048	0.008	**0.187 (0.08)***	0.052 (0.08)	−0.001 (0.08)
Parasite load rank	**−0.197***	−0.097	−0.056	**−0.201 (0.08)****	**−0.139 (0.08)***	−0.035 (0.08)
				$R^2 = 0.145$ **LR = 26.21***** *df* = 8	$R^2 = 0.094$ **LR = 15.54*** *df* = 8	$R^2 = 0.039$ LR = 6.36 *df* = 8

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.
Significance of s′ tested with Spearman rank correlation tests. Significance of β' and of the total model tested using binary probit regression analysis (see Materials and Methods). LR represents −2 log likelihood ratio.

ulations #1 and #2 (Table 5). However, the reduction of the number of traits involved in the analysis did not alter the basic result; when the effects of selection on correlated characters were removed, only abdominal process length in population #2 and parasite load in population #3 were found to experience statistically significant nonlinear selection. As with directional selection, the regression model accounted for least of the variance in fitness in population #3 (Table 5), suggesting that selection was weakest in this population.

Incorporating quadratic trait components

TABLE 4. Standardized quadratic selection differentials (C′) and standardized quadratic selection gradients [γ' (SE)] for the three water strider populations. Nonlinear selection gradients were estimated in a multiple regression model, involving linear, quadratic and correlational components of eight traits (see Materials and Methods).

	C′			γ' (SE)		
	#1	#2	#3	#1	#2	#3
Weight	−0.086	−0.029	0.191	−0.237 (0.32)	−0.033 (0.21)	0.123 (0.19)
Length of pronotum	0.003	0.001	0.279	0.047 (0.15)	0.174 (0.15)	0.235 (0.18)
Width of pronotum	−0.071	**−0.258***	0.052	−0.183 (0.14)	−0.071 (0.15)	−0.122 (0.15)
Length of fore femur	0.007	0.033	0.118	−0.078 (0.10)	0.038 (0.11)	0.187 (0.16)
Length of mid-leg	−0.130	0.041	0.054	−0.030 (0.16)	0.098 (0.15)	−0.160 (0.17)
Pronotal spot	0.086	0.009	0.123	0.067 (0.07)	0.012 (0.07)	−0.072 (0.08)
Abdominal processes	−0.001	**0.194***	−0.298	0.089 (0.08)	**0.122 (0.07)***	0.011 (0.07)
Parasite load rank	−0.185	−0.089	**−0.197***	−0.141 (0.10)	−0.164 (0.12)	**−0.168 (0.07)***
				$R^2 = 0.323$ LR = 47.94 *df* = 44	$R^2 = 0.249$ LR = 43.02 *df* = 44	$R^2 = 0.308$ LR = 35.09 *df* = 44

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.
Significance of C′ tested with Spearman rank correlation tests. Significance of γ' and of the total model tested using binary probit regression analysis (see Materials and Methods). LR represents −2 log likelihood ratio.

TABLE 5. Standardized quadratic selection gradients [γ' (SE)] estimated in a reduced multiple regression model, involving linear, quadratic and correlational components of five traits (cf. Table 4).

	γ' (SE)		
	#1	#2	#3
Weight	0.000 (0.23)	−0.013 (0.15)	0.162 (0.15)
Length of pronotum	0.029 (0.12)	0.147 (0.12)	0.156 (0.15)
Width of pronotum	−0.110 (0.12)	−0.124 (0.12)	−0.147 (0.13)
Abdominal processes	0.036 (0.06)	**0.105 (0.06)***	−0.000 (0.05)
Parasite load rank	−0.088 (0.09)	−0.159 (0.10)	**−0.129 (0.07)***
	$R^2 = 0.213$	$R^2 = 0.188$	$R^2 = 0.125$
	LR = 39.83**	**LR = 33.29***	LR = 22.53
	df = 20	*df* = 20	*df* = 20

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.
Significance of γ' and of the total model tested using binary probit regression analysis (see Materials and Methods). LR represents −2 log likelihood ratio.

in the regression models significantly increased the statistical fit in populations #2 and #3 (linear only versus linear and quadratic; *df* = 5 in all cases; LR = 4.01, $P > 0.05$; LR = 12.70, $P < 0.05$; LR = 11.25, $P < 0.05$; respectively). However, because adding correlational components did not significantly increase the fit in any of the populations (linear and quadratic versus linear, quadratic and correlational; *df* = 10 in all cases; LR = 10.34, $P > 0.05$; LR = 7.35, $P > 0.05$; LR = 6.01, $P > 0.05$; respectively), no significant selection on the correlations between characters (γ_{ij}) were found.

There were significant differences between the populations in nonlinear selection on abdominal process length ($t = 2.049$, $df = 464$, $P < 0.05$) and width of pronotum ($t = -2.136$, $df = 464$, $P < 0.05$), while selection on parasite load did not differ significantly ($t = -1.080$, $df = 464$, $P > 0.05$). The populations differed significantly in quadratic selection gradients ($t = 2.147$, $df = 464$, $P < 0.05$; estimated in the reduced model).

The visual analyses of residuals from the probit models did not indicate any unsatisfactory variance functions or cells with extreme residuals (McCullagh and Nelder, 1983).

Fitness Functions.—Univariate fitness functions, visualizing the form of selection, were estimated for all traits experiencing significant univariate measures of selection (Fig. 1A–D). In general, the graphical analysis confirms the selection analysis based on selection coefficients. Directional selection for weight was present in populations #1 and #2, whereas the fitness function in population #3 was nonlinear and increasing only in the uppermost part of the phenotypic distribution (Fig. 1A). The significant nonlinear selection experienced in population #2

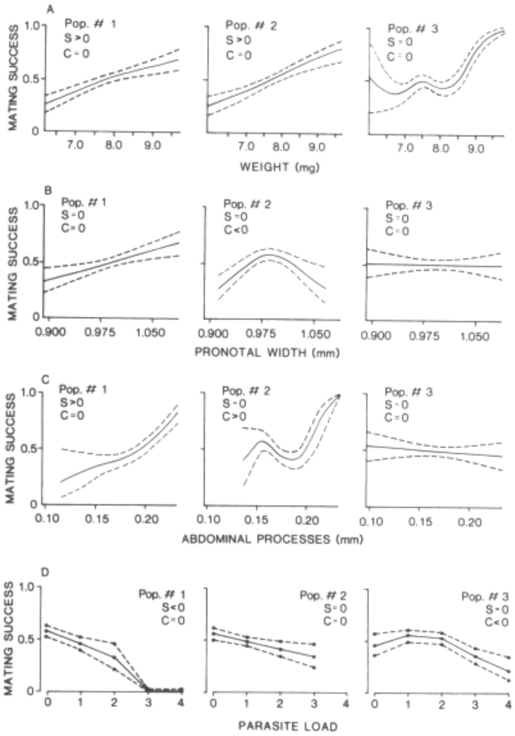

FIG. 1. Fitness functions (solid lines) and bootstrap SE (dashed lines) based on nonparametric regressions, using the cubic spline technique (Schluter, 1988), for the four traits found to experience significant univariate measures of sexual selection in the studied populations. S represents the directional selection differential, C represents the nonlinear selection differentials and equal-signs indicate nonsignificant selection differentials ($P > 0.05$).

for pronotal width, may be characterized as pure stabilizing selection because the inflection point of the fitness function is situated at the phenotypic mean (cf. Fig. 1B and Table 2). However, this pattern appears to be entirely caused by selection on correlated characters, as the estimate of selection became low and nonsignificant when indirect selection on correlated characters was accounted for (Tables 4 and 5). Significant univariate selection for abdominal process length occurred in populations #1 and #2. The fitness functions for these populations suggest that selection was moderately nonlinear and concave (sensu Phillips and Arnold, 1989) in both populations (especially in the upper phenotypic range), whereas abdominal process length was a neutral character in population #3 (Fig. 1C). Because parasite load is a categorical variable with few phenotypic values, the fitness functions should be interpreted with caution. However, the fitness functions tended to be slightly convex (Fig. 1D), suggesting that low parasite loads may have little effect whereas high loads have a relatively large effect in terms of decreased fitness.

Discussion

Selection on Traits Reflecting Condition.—The only traits that experienced significant selection in all three populations were weight and parasite load. It is reasonable to assume that a male has to have good vigor to successfully acquire matings. Arnqvist and Mäki (1990) demonstrated that gut parasite infections lower the vigor and endurance of male *G. odontogaster.* Thus, it is not surprising that parasite load was found to experience significant selection. Further, because adult water striders can consume as much as approximately 10% of their body weight in one single feeding event (Jamieson and Scudder, 1977), weight differences between individuals should to some extent be due to differences in nutritional status. This suggests that selection for weight largely reflects selection for satiation, a suggestion that is supported by the fact that the standardized estimates of selection increased when the effects of selection on correlated characters were removed (i.e., all other traits kept constant; see Table 3). In conclusion, to successfully acquire matings, a male should be in good condition and health, i.e., be well fed and free of parasites.

Due to the coevolutionary relationship between parasites and hosts, parasites have received much attention in recent theoretical and empirical studies of intersexual selection (e.g., Hamilton and Zuk, 1982; Read, 1988; Hamilton, 1990). Hamilton and Zuk (1982) proposed that male freedom from parasites and disease should be important traits in the evolution of female mating preferences. They suggested that females should prefer mating with males with low parasite loads, because this would increase the offspring fitness provided that parasite resistance has genetic components. Several studies in a wide variety of species have demonstrated that sexual selection for parasite freedom in males does occur (see Read, 1988; for a review). However, as stressed by Kirkpatrick (1987; pp. 49–50), information about the male trait alone is insufficient to understand the evolution of female mating preferences. In *G. odontogaster,* the mechanism of mating preferences (female reluctance to mate) is due to factors related to the costs of mating rather than mate assessment and adaptive mate choice (Arnqvist, 1989*b*, 1992*a*). This suggests that intersexual selection for parasite free males in *G. odontogaster* is a side effect rather than a causal evolutionary factor of female mating preferences, and hence does not lend support to the hypothesis of Hamilton and Zuk (1982).

Selection on Morphological Traits.—Previous studies of sexual selection in *G. odontogaster* have demonstrated that males are subjected to selection for grasping ability during the intersexual precopulative struggle and that males with long abdominal processes are more difficult for females to dislodge (Arnqvist, 1989*a,* 1989*b,* 1992*a*). The significant univariate and multivariate estimates of selection for process length found in this study confirm previous findings. Furthermore, the form of selection (Fig. 1C) suggests that fitness is not linearly related to process length. Rather, grasping ability seems to be increasing exponentially with process length, indicating a strong selection for long abdominal processes under certain conditions (see below).

Water striders are generally sexually dimorphic with respect to size; females are larger than males. In a recent paper, Fairbairn (1990) divided the temperate water strider species into three groups, and examined several hypotheses for the evolution of sexual size dimorphism for each of these groups. Fairbairn (1990) was able to convincingly attribute size dimorphism in two of the three groups to various selective processes. However, for the group of water strider species consisting of small, wing-polymorphic species (to which *G. odontogaster* belongs), Fairbairn (1990) was unable to account for the observed dimorphism, and concluded that "the residual variation within this group of species remains obscure" (p. 77). Fairbairn (1990) eliminated sexual selection for small size in males as a possible causal selective factor for size dimorphism, because previous studies of sexual selection in these species have found no consistent evidence of sexual selection on male size (Fairbairn, 1988; Arnqvist, 1989*a*). However, previous examinations of sexual selection in this group of water striders have considered only univariate measures of selection. The results of the current study are concordant with previous findings; none of the univariate measures of selection on male size was significant. However, when the effects of selection on correlated characters were removed in the multivariate analysis of directional selection, sexual selection for small size in males was present in at least one of the populations (Table 3). This suggests that small size in males may be favored by selection under certain circumstances, but that this pattern may be obscured by selection on correlated characters.

Although the mechanism of selection for small size in males is unclear, one possible explanation is that it may be more difficult for females to dislodge small males attempting copulation. During the precopulative struggle, females try to dislodge males on their backs with their fore legs. Small males may be more difficult to seize hold of and thus to dislodge due to physical constraints (e.g., on the mobility of female fore legs). This would then be the opposite to what is thought to be the case in the soldier beetle, where larger males have a greater ability to subdue reluctant females (McCauley and Wade, 1978; McCauley, 1981; McLain, 1982). Whatever the mechanism, sexual selection for small male size may contribute to the evolution of sexual dimorphism in small temperate water striders (cf. Fairbairn, 1990). It is worth noting that pronotal length has been found to be a heritable trait in *G. odontogaster* ($h^2 = 0.59$; Arnqvist, 1990). In conclusion, the results of this study with regard to selection on male body size illustrate the importance of using multivariate statistical techniques for the study of current selective processes contributing to sexual dimorphism (Hedrick and Temeles, 1989).

In situations where sexual selection is intense in *G. odontogaster,* selection should act antagonistically on male size and abdominal process length (e.g., population #1 in this study). While selection may favor small males, males with large abdominal processes are at selective advantage. If these characters are positively genetically correlated, selection could act to decouple the antagonistic pleiotropic linkage between the traits thus reducing the genetic correlation (Falconer, 1981). This may be the case in *G. odontogaster.* One possible explanation for the fact that the phenotypic correlations between body size and abdominal process length are remarkably low ($r = 0.13$–0.23) might be selection for a reduced genetic correlation between the traits (Cheverud, 1988; but see Willis et al., 1991).

No significant assortative mating by size occurred in the studied populations. This result is in accordance with the predictions made by Fairbairn (1988), because *G. odontogaster* closely resembles *G. buenoi* in ecology and morphology (Schaefer and Calabrese, 1980), but detailed knowledge of the behavioral causes of assortative mating in water striders is lacking (Crespi, 1989).

Spatial Variation in Selection.—In general, the investigated populations differed considerably with regard to the selective regimes. Most of the differences were quantitative; population #1 experienced the most intense selection and strongest selection for single traits, whereas population #3 experienced only very weak selection, and population #2 experienced selection of intermediate strength. Furthermore, the form of selection (directional versus nonlinear) varied between the populations for several traits. There were, however, some qualitative differences between the populations. Whereas relatively strong selection for grasping ability as reflected by selection on abdominal processes was present in populations #1 and #2, this was not the case in population #3 where abdominal process length evidently was a neutral character (Fig. 1C).

What is the mechanistic basis for spatial differences in sexual selection in water striders? Many different factors have been demonstrated to alter mating patterns in water striders: food availability (Sih et al., 1990; Rowe, 1992); predation risk (Sih et al., 1990); operational sex ratio (Wilcox, 1984; Clark, 1988; Arnqvist, 1992*a,* 1992*b*; Rowe, 1992); and population density (Arnqvist, 1992*a*) all have an impact on the mating behavior and thus potentially on sexual selection. In *G. odontogaster,* Arnqvist (1992*a*) demonstrated that the behavior that accounts for intersexual selection varies considerably with population density. The results of the current study are in agreement with the a priori predictions of sexual selection based on previous studies of the behavioral mechanisms of selection. The foremost difference between the investigated populations is population density. Sexual selection was strongest in the population with the lowest density and weakest in the high-density population. The spatial variation in selective regimes found in *G. odontogaster* is most likely caused by density-related differences in female mating behavior between the different populations. The prominent variability in mating patterns found by Fairbairn (1988) in different populations of three Nearctic water strider species may well have a similar causal basis.

Inverse density-dependent sexual selection has been demonstrated in at least two other insect species. McLain (1982) showed that nonrandom mating was more pronounced in low-density populations of the soldier beetle *Chauliognathus pennsylvanicus.* In the fungus beetle *Bolitotherus cornutus* sexual selection for long male horns has been found to be stronger at low densities (Conner, 1989). However, although the mechanism behind the density dependence is unclear in both these cases, behavioral responses in males are thought to be involved (McLain, 1982; Conner, 1989). The current study of *G. odontogaster* illustrates the importance of considering potential behavioral shifts in both females and males.

Local Adaptation.—In studies of evolutionary biology, it is critical to distinguish between selection and evolutionary response to selection (Lande and Arnold, 1983; Arnold and Wade, 1984*a*). Selection can be measured and described purely in terms of phenotypes, whereas evolutionary response to selection depends on the nature of genetic variation. If a certain trait in a population experiences phenotypic selection and the trait variation has additive genetic components, a change in the gene frequencies in the population may be the result, provided that evolutionary constraints do not prevent local adaptation (Grant and Price, 1981; Loeschke, 1987). If the selective regimes in several populations are sufficiently different (different genotypes are favored by selection), selection may lead to adjacent populations being locally adapted (i.e., having dissimilar gene pools). In this scenario, a moderate gene flow between populations would further the maintenance of genetic variation (Felsenstein, 1976; Nevo, 1978; Hedrick et al., 1976; Endler, 1977; Hedrick, 1986). Thus, to demonstrate local adaptations it must be shown that (1) natural populations differ with respect to genotype frequencies, and that (2) these differences are the result of selection rather than random processes.

The studied populations of *G. odontogaster* differed significantly both in sexual selective regimes and in mean phenotypes. It is, however, very difficult to assess to what degree the observed phenotypic differences among males also represent genotypic differences (Grant and Price, 1981). Nevertheless, one of the studied traits merits a closer examination. Arnqvist (1989*a*) demonstrated that the length of male abdominal processes was highly heritable (heritability estimate $h^2 = 1.01 \pm 0.28$ in population #3). The observed differences in process length (Table 2) should thus to some extent represent local adaptations. In support of this suggestion, the relative lengths of processes in the populations are in accordance with expectations; abdominal processes are longest in population #1 where selection for long processes was strongest, and processes are shortest in population #3 where selection was undetectable. Further, selection does not only affect the phenotypic mean, but also the phenotypic variance. In general, selection tends to decrease trait variability (Grant and Price, 1981; Endler, 1986). Again, in accordance with expectations, the population that experienced no selection for abdominal process length (population #3) exhibited highest trait variance (see Results). Because there is some gene flow between *G. odontogaster* populations during spring dispersal (Vepsäläinen, 1974*a*), genotypic exchange between locally adapted populations with different selective regimes may contribute significantly to the maintenance of additive genetic variation for length of abdominal processes.

As stressed by Endler (1986) and as illustrated in this study, assuming constant relative fitnesses of phenotypes is invalid and constitutes an example of typological thinking in evolutionary biology. Rather, the optimal phenotypes and selective regimes typically vary both spatially and temporally (Falconer, 1981; Endler, 1986; Anholt, 1991). It is very difficult to unambiguously demonstrate local adaptations in metric traits. However, the studies where this has been achieved [including studies of *Cepea* (Cain and Sheppard, 1954; Cain, 1983); *Poecilia* (Endler, 1983); and *Geospiza* (Grant and Price, 1981; Price et al., 1984)] suggest that a mechanistic and comparative approach should be adopted to elucidate complex interactions between genotypes and the environment (Endler, 1986). In empirical studies, a thorough knowledge of the biology of the organism, in terms of ecology, behavior, genetics and physiology, in concert with comparative studies of spatial and temporal variations in selective regimes at the population level, would further the knowledge of the mechanisms of selection as well as of the prevalence of local adaptations in metric traits (Grant and Price, 1981; Endler, 1986; Wade and Kalisz, 1990).

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APPENDIX. Phenotypic correlation matrix for the measured traits in male *Gerris odontogaster* from the three populations (#1–3). Correlation coefficients are Pearson product moment coefficients, except in correlations involving parasite load rank where Spearman rank coefficients are given.

		Weight	Length of pronotum	Width of pronotum	Length of fore femur	Length of mid-femur	Length of mid-tibia	Length of mid-tars. 1	Length of mid-tars. 2	Length of pron. spot	Length of abdominal processes	Parasite load rank
Weight	#1	–	0.78***	0.73***	0.52***	0.53***	0.62***	0.54***	0.33**	0.22	0.31**	−0.03
	#2	–	0.71***	0.66***	0.43***	0.45***	0.52***	0.52***	0.30*	0.11	0.13	−0.14
	#3	–	0.77***	0.61***	0.54***	0.55***	0.52***	0.57***	0.33**	0.16	0.15	−0.18
Length of pronotum	#1		–	0.58***	0.46***	0.45***	0.55***	0.46***	0.31**	0.28*	0.23	0.04
	#2		–	0.55***	0.39***	0.53***	0.50***	0.47***	0.30*	0.16	0.13	0.14
	#3		–	0.54***	0.53***	0.54***	0.56***	0.54***	0.31**	0.22	0.14	0.01
Width of pronotum	#1			–	0.37***	0.36***	0.47***	0.38***	0.28*	0.07	0.26	0.01
	#2			–	0.43***	0.31**	0.42***	0.42***	0.26	0.07	0.14	0.02
	#3			–	0.45***	0.35***	0.29*	0.33**	0.18	0.20	0.21	−0.01
Length of fore femur	#1				–	0.50***	0.49***	0.39***	0.32**	0.11	0.17	0.02
	#2				–	0.57***	0.48***	0.34**	0.35***	0.06	0.18	0.03
	#3				–	0.66***	0.54***	0.51***	0.29*	0.27	0.32**	0.06
Length of mid-femur	#1					–	0.61***	0.40***	0.20	0.09	0.06	0.03
	#2					–	0.70***	0.51***	0.37***	0.16	0.14	0.10
	#3					–	0.77***	0.55***	0.34**	0.19	0.26	0.05
Length of mid-tibia	#1						–	0.69***	0.37***	0.12	0.12	0.08
	#2						–	0.70***	0.46***	0.12	0.12	−0.08
	#3						–	0.73***	0.36***	0.10	0.13	0.10
Length of mid-tars. 1	#1							–	0.35***	0.19	0.01	0.13
	#2							–	0.44***	0.17	0.23	0.01
	#3							–	0.32**	0.13	0.14	0.09
Length of mid-tars. 2	#1								–	0.08	0.16	−0.03
	#2								–	0.02	0.04	−0.02
	#3								–	0.21	0.08	0.05
Pronotal spot	#1									–	0.07	−0.07
	#2									–	0.10	0.10
	#3									–	0.09	0.00
Abdominal processes	#1										–	−0.05
	#2										–	0.01
	#3										–	0.07
Parasite load rank	#1											–
	#2											–
	#3											–

Population #1 $N = 159$, #2 $N = 154$, and #3 $N = 157$.
* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$; all probabilities are Bonferroni adjusted within populations.