

THE COST OF MALE SECONDARY SEXUAL TRAITS:
DEVELOPMENTAL CONSTRAINTS DURING ONTOGENY
IN A SEXUALLY DIMORPHIC WATER STRIDER

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Abstract.—Natural selection is generally thought to constrain the effects of sexual selection on secondary sexual traits. In hemimetabolous arthropods, the evolution of complex secondary sexual morphologies may be constrained by interference during the molting process. This study assesses the effects of phenotypic variation in secondary sexual traits during ontogeny in the water strider *Gerris odontogaster*. In this species, males are provided with a grasping apparatus consisting of two abdominal, ventral processes. It is demonstrated that the length of the processes is positively related to the duration of the ultimate larval molt, presumably because the processes constitute a mechanical hindrance during molting. It is further shown that larvae experience a high risk of mortality from cannibalism during their ultimate molt and that this risk is density-dependent. On the basis of the assumption that cannibalistic events occur at random during molting, males with long processes will suffer higher risk of mortality during molting than will males with short processes. It is concluded that this form of developmental constraint can affect the evolution of male abdominal processes, and quantitative cost curves for the length of male abdominal processes are presented. Simulations of natural selection due to larval mortality show positive density dependence, in contrast to sexual selection in this species. It is suggested that the net effect of selection on secondary sexual traits in this species varies between negative and positive values and that net selection is zero only within a narrow range of environmental conditions. A comparison between natural populations showed that mean trait value co-varies negatively with environmental variables related to the cost of the trait in accordance with this suggestion.

In theoretical models of sexual selection, natural selection is generally thought to constrain the evolution of male secondary sexual traits (Bradbury and Andersson 1987). Sexual and natural selection are typically assumed to act in opposite directions on male traits. In models in which the male trait is assumed to be at evolutionary equilibrium, natural and sexual selection must balance such that net selection on the trait is zero (Lande 1980; Partridge and Endler 1987). In models of sexual selection based on honest signaling (Zahavi 1975; Grafen 1991), a critical assumption is that the expression of secondary sexual traits is costly. However, despite the critical importance of cost components as constraints on sexual selection, empirical evaluations of costs of secondary sexual traits are very scarce (Halliday 1987; Partridge and Endler 1987; Price 1987; Townsend 1989; Harvey and Bradbury 1991; Balmford et al. 1993). Available data are typically qualitative, namely, demonstrations of male-biased juvenile or adult mortality (Clutton-Brock

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et al. 1985; Partridge and Endler 1987; Harvey and Bradbury 1991), and there have been very few attempts to estimate quantitative cost curves for sexually selected traits (Partridge and Endler 1987; Price 1987; Schluter et al. 1991). This is partly due to methodological problems; in cases in which costs of adult secondary sexual traits are believed to be experienced in juvenile stages, for example, in terms of an increase in juvenile mortality (Clutton-Brock et al. 1985), estimations of cost functions and phenotypic selection may be difficult simply because the traits have not yet been phenotypically expressed. Nevertheless, several authors have recently stressed the need of identifying cost components in specific systems to enable evaluations of the joint effect of sexual and natural selection on sexually selected traits (e.g., Partridge and Endler 1987; Schluter et al. 1991).

Developmental constraints may be defined as limitations in phenotypic variability, arising from ontogenetic processes (Maynard Smith et al. 1985; Atchley and Hall 1991; Arnold 1992). Developmental constraints may have a variety of mechanistic bases, but they are generally thought to have important evolutionary consequences (Mayr 1983; Maynard Smith et al. 1985; Bürger 1986). However, with respect to evolutionary constraints on secondary sexual traits, developmental constraints have received little attention (Eberhard and Gutiérrez 1991; Larsen 1992).

The water strider *Gerris odontogaster* (Zett.) (Heteroptera: Gerridae) is sexually dimorphic, with males having a grasping apparatus consisting of two ventral abdominal processes (Arnqvist 1989). The length of the processes affects a male's ability to subdue reluctant females, and the processes have been shown to be subjected to sexual selection (Arnqvist 1989, 1992a). Further, as a result of alterations in female behavior, sexual selection on abdominal process length typically is negatively density-dependent (Arnqvist 1992a, 1992b, 1992c).

Several studies have shown that cannibalism and intraguild predation are important mortality factors in water strider populations (Nummelin 1989; Spence and Cárcamo 1991). As is typically the case, cannibalism in water striders is size related and adults frequently kill and eat larvae. In general, transition stages (e.g., molting individuals in hemimetabolous insects) are particularly vulnerable to cannibalism since the individuals are relatively soft bodied and defenseless (see, e.g., Dong and Polis 1992). This is true also for water striders, where larvae are at high risk during molting (Andersen 1982).

The current study addresses the possibility of developmental constraints on the evolution of secondary sexual traits in *G. odontogaster* males. I test the hypothesis that abdominal processes may interfere with the molting process, thereby increasing the risk of juvenile mortality due to cannibalism, by assessing the relation between molting duration and length of male abdominal processes. I also estimate the rate of cannibalism during molting at different adult densities.

MATERIAL AND METHODS

Relation between Morphology and Molting Duration

The male abdominal processes in *Gerris odontogaster* are exoskeletal and sclerotized and thus do not change shape or size during the adult life span. The processes are not phenotypically expressed in juveniles (Vepsäläinen and Krajew-

ski 1986; Zimmermann 1987) but arise during the initial part of the ultimate molt (i.e., from the fifth larval instar to adult). Since potential costs associated with the processes are most likely to appear during this specific molt, I studied the relation between morphology and the duration of the ultimate molt.

Water strider larvae were collected July 1, 1992, from a monomorphic long-winged population (the Gimonäs Pond, 63°48'N, 20°19'E) and brought to the laboratory. A number of fifth-instar *G. odontogaster* larvae were placed individually in 8-cm-diameter glass jars. A piece of Styrox (2 cm × 2 cm) was placed in each jar, serving as a resting site, and the water strider larvae were fed daily with three frozen *Drosophila* fruit flies per individual. The larvae were kept at 27°C and videotaped continuously (for 24 h) until they had molted. After molting, adults and their exuvia were preserved in 70% ethanol. The total body length and the length of the hind-femur were subsequently measured on each adult with a micrometer eyepiece on a stereomicroscope. In addition, the length of the abdominal processes was measured on all adult males, and the length of the hind-femur was measured on each exuvium to provide a measurement of larval size.

In water striders, the larvae become relatively immobile before the molt (see Andersen 1982). The actual molting is a rather rapid process that takes place at the water surface. During the initial phase of the molt, the larvae push the midlegs backward with jerky movements until they are extended backward almost parallel with the main body axis (the midlegs are normally held forward). Thereafter, the larval cuticle splits open along the ecdysial line, which runs through the dorsal midline of the body from the head to the first abdominal tergum. During the actual emergence, the body and the legs are pulled free from the exuvium and the adult emerges. In the current study, molting durations were determined from videotape playbacks (see above). Molting duration was defined as the time between the moment when the midlegs of the larva passed an imaginary line at right angles to the body axis and the moment when the last parts of the emerged adult (the midlegs and hind legs) were pulled free from the exuvium.

Rate of Cannibalism during the Ultimate Molt

To estimate the risk of mortality due to cannibalism during the ultimate molt, a laboratory experiment was performed in which larvae were introduced to adults kept in plastic aquaria (0.45 m × 0.25 m). Five different adult densities were used: 0, 2, 4, 8, and 16 adults per aquarium, with four replicates of each treatment. The densities used are thus equivalent to 0, 18, 36, 71, and 142 adults per m². Densities in natural populations of this species normally range between five and 40 adults per m² (Arnqvist 1992a). To produce a certain microhabitat complexity and to create potential refuges for molting larvae, pieces of floating Styrox were placed in the aquaria. Ambient temperature was 21°C ± 1°. Two fifth-instar larvae of *G. odontogaster* were introduced to the adults in each aquarium. All water striders were fed daily with two fruit flies per individual. Twice every day, I recorded whether the larvae had molted successfully or had been cannibalized, in which case they were replaced with new fifth-instar larvae. I also recorded during which phase of the molting process the cannibalized larva had been killed. The experiment was terminated after 10 d. Mean probabilities for being cannibalized during molting for each aquarium (no. of larvae cannibalized/total no. of

TABLE 1
 GENERAL LINEAR MODEL (ANCOVA) OF THE EFFECTS OF
 MORPHOLOGY AND SEX ON MOLTING DURATION

Source	df	Mean Square	F Ratio	P
Body size	1	6.101	5.681	.022
Adult leg length	1	.334	.311	.580
Larval leg length	1	4.236	3.944	.054
Sex	1	1.593	1.483	.230
Error	42	1.074		

NOTE.— $F = 3.231$, $df = 4,42$, $P = .021$.

larvae introduced) were used for subsequent statistical analysis. Hence, each aquarium was treated as an experimental unit.

RESULTS

Relation between Morphology and Molting Duration

The only general morphological trait that significantly affected molting duration was adult body size (table 1); molting duration decreased with increasing body size (fig. 1). However, there were no differences in molting duration between the sexes, either in the ANCOVA (table 1) or in a univariate test (t -test; $t = 1.440$, $df = 46$, $P = .157$). Neither did the sexes differ in the variance of molting duration (Bartlett's test for homogeneity of variances; $\chi^2 = 0.421$, $df = 1$, $P = .516$). The relation between molting duration and body size did not differ between the sexes, as shown by a lack of improvement in statistical fit by addition of an interaction term (sex \times body size) to the model in table 1 (partial F -test; $F = 0.77$, $df = 1,41$, $P > .25$). The pooled mean molting duration was 8.66 min (SD = 1.13, $N = 48$). The initial phase of the molt constituted 69%, and the actual emergence 31%, of the total molt duration ($N = 11$).

There was a significant positive relationship between the length of abdominal processes and molting duration in males (fig. 2). Controlling for potential indirect effects of body size in a multiple regression model did not reduce the effect of abdominal processes on molting duration (table 2), in accordance with expectations, since the phenotypic correlation between these two traits is very low (Arnqvist 1992a). Thus, males with long abdominal processes had significantly longer molting durations than did males with short processes. There was no apparent nonlinearity in the relation, as revealed by cubic spline regression (fig. 2).

The length of the hind-femur of exuvia and that of adults were highly correlated in both sexes ($r_p = 0.752$, $P < .001$ in males; $r_p = 0.835$, $P < .001$ in females). Thus, large larvae produced large adults.

Rate of Cannibalism during the Ultimate Molt

As expected, the rate of mortality due to cannibalism during the ultimate molt increased significantly with adult density (fig. 3; ANOVA performed on arcsine-

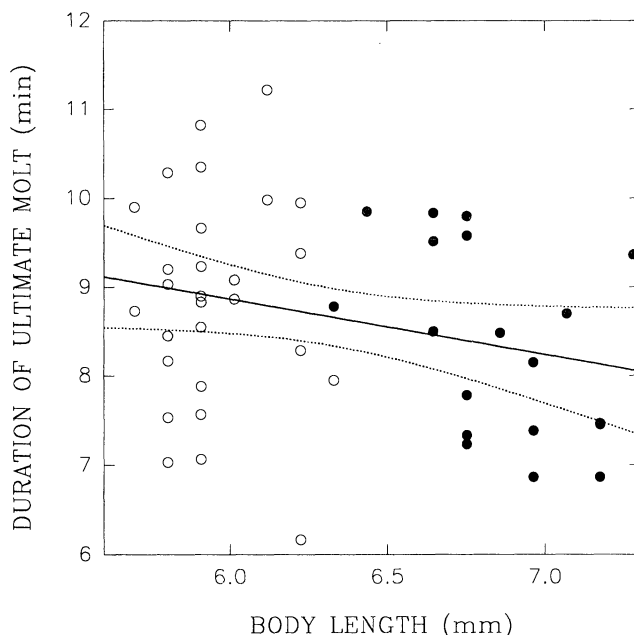


FIG. 1.—The relationship between duration of the ultimate molt and adult body size in *Gerris odontogaster*. Linear regression with 95% confidence limits is indicated in the figure (t -test of $\beta = 0$; $P = .046$, $N = 48$). Hollow circles represent males; filled circles represent females.

transformed values; $F = 14.29$, $df = 4, 15$, $P < .001$). Of a total of 78 larvae used in this experiment, 51% survived the ultimate molt. Larvae that were cannibalized were all killed during the molting process; 35% were cannibalized during the initial phase of the molt, 10% during the actual emergence, and another 4% shortly after emergence. The relative numbers of larvae killed during the initial phase of the molt and the actual emergence were not significantly different from those expected from the relative duration of these two phases of the molt ($\chi^2 = 1.085$, $df = 1$, $P > .25$).

DISCUSSION

The Cost of Male Abdominal Processes

The results of the current study demonstrate that there is a positive relation between abdominal process length and molting duration in *Gerris odontogaster*, suggesting that the abdominal processes interfere with the molting process. Although there may be several possible mechanisms explaining this pattern, a plausible explanation would be simply that the abdominal processes constitute a physical hindrance during molting. Since the abdominal processes are pointed downward and forward (see Arnqvist 1989), it seems reasonable that they have the same effect during emergence as barbs on a hook, to wit, that the abdominal

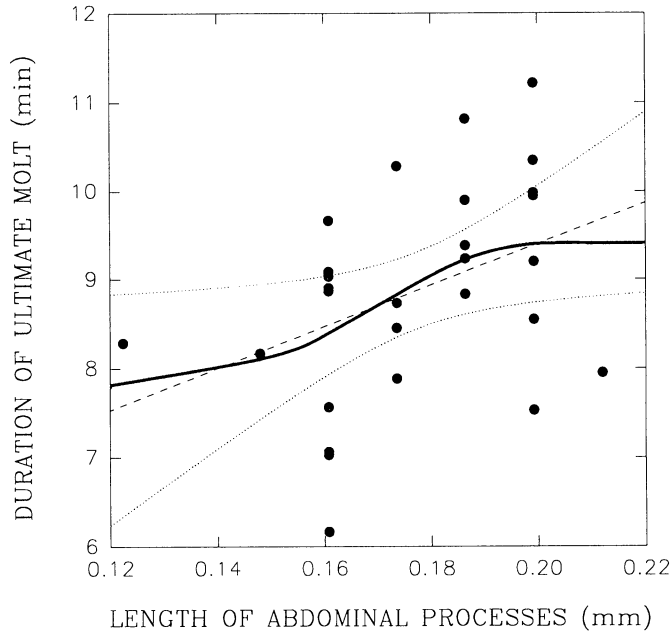


FIG. 2.—The relationship between duration of the ultimate molt and the length of male abdominal processes in *Gerris odontogaster* males. Linear regression with 95% confidence limits is indicated in the figure (t -test of $\beta = 0$; $P = .034$, $N = 28$). The solid line represents the cubic spline nonparametric regression surface, providing a more local fit to data compared with ordinary linear regression (see Schluter 1988).

TABLE 2

MULTIPLE REGRESSION ANALYSIS OF THE EFFECTS OF ABDOMINAL PROCESS LENGTH AND BODY SIZE ON MOLTING DURATION IN MALES

	β	SE	t Value	P
Body size	-1.547	1.119	-1.382	.179
Abdominal processes	23.070	10.298	2.240	.034

NOTE.— $N = 28$; $R^2 = 0.220$, $P = .044$.

processes increase the friction between the new adult cuticle and the exuvial cuticle during emergence when the abdomen is pulled free from the exuvium, and the longer the processes, the higher the friction becomes. This interpretation of the results is also supported by observations from laboratory cultures, where fifth-instar larvae in a few cases have been observed to actually get stuck in the abdominal region of the exuvium during the ultimate molt (G. Arnqvist, unpublished data).

Fifth-instar *G. odontogaster* larvae are at great risk of cannibalism and interspecific predation during molting. The cost of male abdominal processes in terms of juvenile mortality can be estimated from the relation between process length and

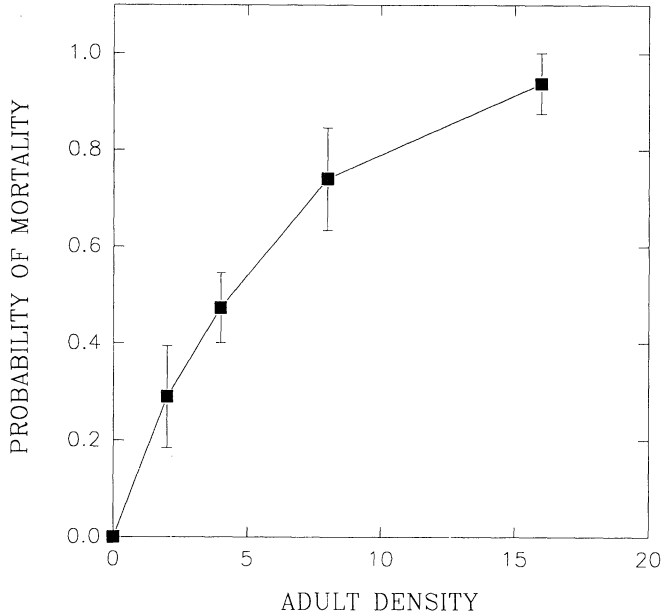


FIG. 3.—The mean probability of mortality (\pm SE) due to cannibalism for *Gerris odontogaster* larvae during the ultimate molt at different densities of adults (no. of adults/aquarium).

molting duration. Given the relatively high rates of cannibalism in water striders and the fact that molting larvae are particularly vulnerable (Riley 1922; Andersen 1982; Nummelin 1989; Spence and Cárcamo 1991; this study), an increase in molting duration should lead to a higher risk of being cannibalized. Assuming that cannibalism occurs at random over time during molting, that is, that cannibalism is a Poisson process, the probability of being cannibalized during the ultimate molt (P) for a certain phenotype is given by

$$P = 1 - e^{-\lambda t}, \quad (1)$$

where t is the average duration of the molt and λ is the rate of cannibalism. The linear approximation of molting durations for males with different lengths of abdominal processes (fig. 2) allows an estimation of the cost function for the trait. In figure 4, equation (1) has been used to produce cost functions for different values of λ . In general, the cost in terms of risk of cannibalism increases with the length of male abdominal processes, but the relative as well as the absolute costs are related to population density (i.e., the rate of cannibalism; fig. 4). Thus, assuming that predation occurs at random during molting, there is a cost of the abdominal processes in terms of increased risk mortality during the ultimate molt. The validity of this assumption is supported by the fact that larvae in different phases of the molt were cannibalized in proportion to the relative duration of these phases.

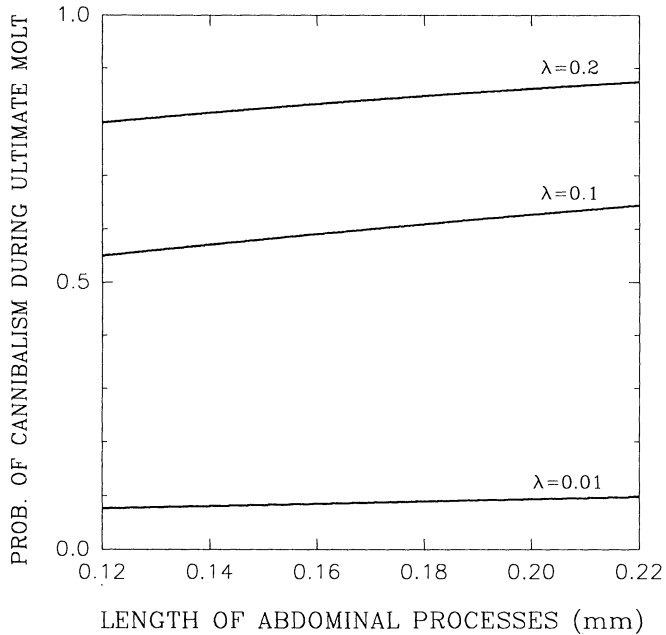


FIG. 4.—Cost functions for male abdominal processes in *Gerris odontogaster*. Estimations of the risk of cannibalism during the ultimate molt are based on eq. (1), and the figure shows cost functions for three environments differing in the rate of cannibalism (λ).

The Joint Effect of Natural and Sexual Selection

The effects of natural selection on abdominal processes cannot be measured directly in natural populations, since the trait is not expressed in the life stage at which mortality is experienced (i.e., the transition stage between fifth instar and adult). However, natural selection can be simulated from the cost functions. In a given population, each specific male phenotype will experience a mortality risk that is determined by the length of abdominal processes and the rate of cannibalism in the population. I estimated the relative fitness of each phenotypic class of abdominal processes by simulating mortality in hypothetical populations consisting of 1,000 individual males. Frequency distribution of lengths of abdominal processes were set according to previous field data (averaged from the three populations in Arnqvist 1992a; total $N = 936$ individuals). The relative mortality rates of the phenotypic classes were set according to the cost functions described above. Figure 5C and D shows simulated relative fitness functions for two different population densities (rates of cannibalism) obtained by this procedure. With the assumption of mortality occurring at random over time during the ultimate molt, there is natural selection for short male abdominal processes, and this selection becomes more intense as the population density increases (positive density dependence) within the range of densities found in natural populations. It is important to note that the absolute intensities of this form of natural selection in natural populations may be affected by a number of factors besides those included

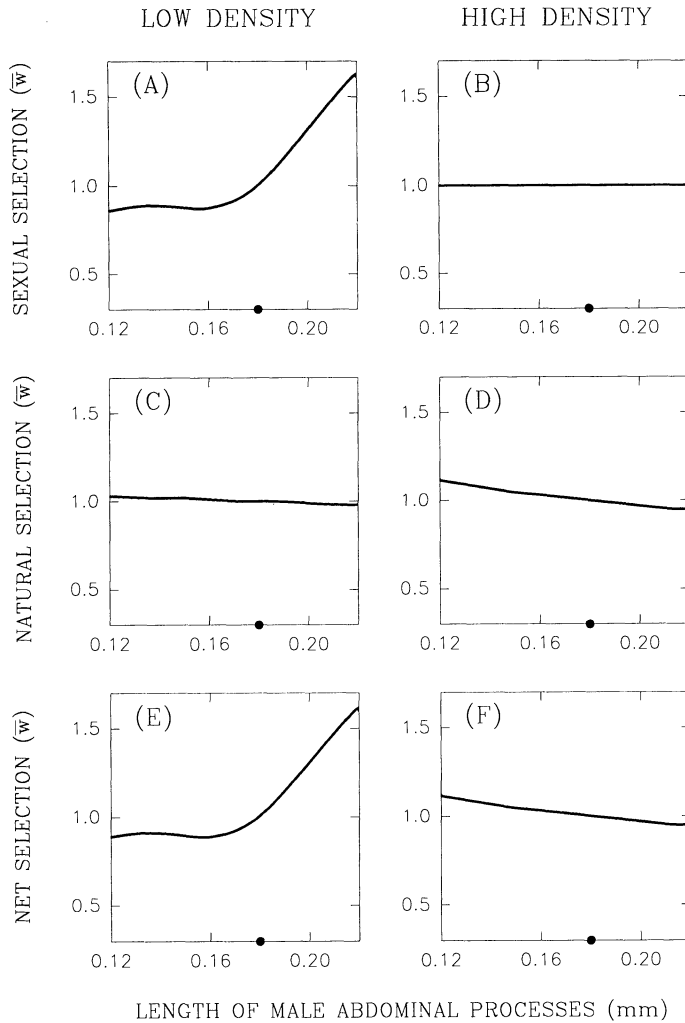


FIG. 5.—Estimates of sexual, natural, and net selection on male abdominal process length in low- (≈ 5 individuals/m²) and high- (≈ 30 individuals/m²) density populations of *Gerris odontogaster*. *A*, Estimate of sexual selection in natural low-density populations (pooled data from populations 1 and 2 in Arnqvist 1992a); and *B*, a high-density population (population 3 in Arnqvist 1992a). *C*, *D*, Simulated relative fitness functions based on differential molting duration among phenotypes during the ultimate molt (see Discussion). Rates of cannibalism per minute during the molt for low- ($\lambda = 0.009$) and high- ($\lambda = 0.059$) density conditions were extracted from the results of the experiment on rates of cannibalism for the relevant densities, i.e., 5 and 30 individuals/m², respectively. *E*, Net selection in low-density populations will be positive; *F*, net selection will be negative in high-density conditions. Relative fitness functions represent cubic spline regression surfaces (Schluter 1988), and the dot at the X-axis represents overall mean phenotypic value of the trait.

in this simple simulation. Factors other than molting duration per se may, for example, affect the probability of survival during the ultimate molt in various ways. However, even if the absolute intensities may differ, the relative intensities will remain the same, that is, there will be natural selection and this selection will be positively density-dependent.

In contrast to natural selection, sexual selection in *G. odontogaster* has been shown to be negatively density-dependent as a result of behavioral plasticity in females (see Arnqvist 1989, 1992a, 1992b, 1992c). In populations with low density, females are reluctant to mate and males are subjected to sexual selection for ability to subdue females (fig. 5A). In high-density populations, however, females are not as reluctant and sexual selection is thus weak or nonsignificant (fig. 5B).

An evaluation of the joint effects of natural and sexual selection in *G. odontogaster* is of importance since it is generally assumed that these two forms of selection are antagonistic and counterbalancing (Lande 1980). A simple extrapolation for a high- and a low-density situation (fig. 5E, F) illustrates the fact that, although these two forms of selection on male abdominal processes are antagonistic, they will not balance in either situation. Low-density conditions will produce a positive net selection, while net selection will be negative in high-density populations. Net selection can only be expected to be close to zero in a rather narrow range of environmental situations (intermediate population densities). Provided that sexual selection for grasping ability and natural selection for larval survival during the ultimate molt are the major selective mechanisms acting on male abdominal processes in *G. odontogaster*, this analysis suggests that, rather than being at an evolutionary equilibrium with zero net selection, this secondary sexual trait experiences a variety of selective regimes in different populations with local net selections ranging from negative to positive values. Thus, depending primarily on population density but also on other environmental factors, such as predator presence, food availability, and operational sex ratio (Arnqvist 1992a), local populations should form a mosaic of conflicting selective regimes. Since there is considerable gene flow between populations (Vepsäläinen 1974), abdominal processes should be in a state of evolutionary flux rather than at an equilibrium. Such spatial variability would also promote the maintenance of high levels of additive genetic variance for the trait (see, e.g., Hedrick 1986). Previous observations of differences in mean phenotype and phenotypic variance of abdominal processes between different local populations (Arnqvist 1992a) and a high heritability of abdominal process length (Arnqvist 1989) are in accordance with this scenario.

Considering the positive density dependence of natural selection and the negative density dependence of sexual selection we would predict that the mean phenotypic value (mean process length) should decrease with increasing population density (fig. 5E, F). This prediction was tested with data from seven different populations of *G. odontogaster*, in which data are available on mean male abdominal process length (sample sizes within populations ranging between 75 and 159 males), population density (estimated by quadrat counts; see Arnqvist 1992a for a detailed description of methods), and predator presence. Predator presence was measured simply as the number of predatory taxa present in the population

TABLE 3
 MULTIPLE REGRESSION ANALYSIS OF THE EFFECTS OF POPULATION DENSITY AND PREDATOR PRESENCE ON MEAN MALE ABDOMINAL PROCESS LENGTH IN NATURAL POPULATIONS OF *GERRIS ODONTOGASTER*

	β	SE	t Value	P
Population density	-.034	.012	-2.913	.043
Predator presence	-.510	.113	-4.503	.011

NOTE.— $N = 7$; $R^2 = 0.901$, $P = .010$.

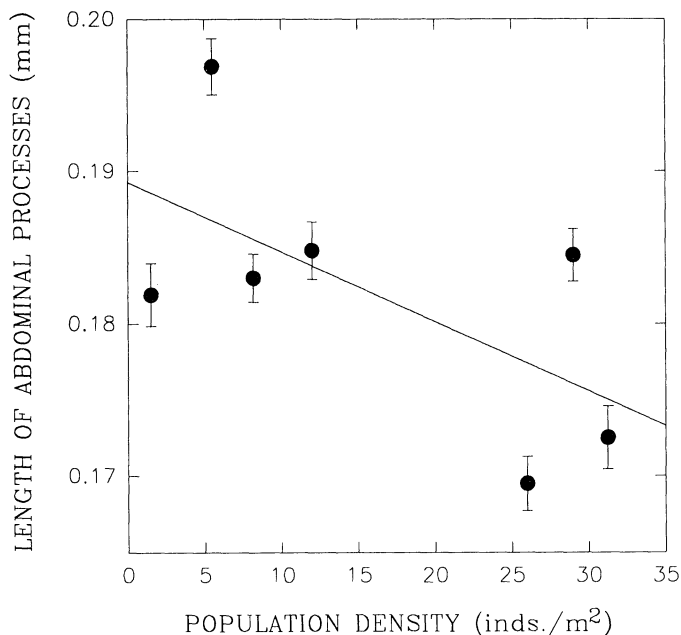


FIG. 6.—The relationship between mean length of male abdominal processes and population density among seven populations of *Gerris odontogaster* (see table 3). Errors bars represent SEM.

(potential predators were fish, *Notonecta* back swimmers, and *Dolomedes* fishing spiders). Predator presence is important, since an increasing interspecific predation risk should tend to increase the relative intensity of natural selection in a manner analogous to an increase in population density (intraspecific predation risk). Thus, population density and predator presence should both be important in determining the relative costs of abdominal processes, and we would predict both to be negatively related to average mean trait value across populations. In accordance with these predictions, mean process length was found to be negatively related to both population density and predator presence (table 3; fig. 6). Even if the number of populations included in the analysis is rather low, it is

worth noting that approximately 90% of the interpopulational variance in mean trait value was explained solely by these two factors (table 3). These results thus provide support for the scenario described above, that is, that net selection varies between populations and that this unstable balance between natural and sexual selection is determined by environmental factors.

This study demonstrates that complex morphological traits, such as secondary sexual characters, may interfere with the molting process in hemimetabolous arthropods. Such interferences may represent a general and widespread type of developmental constraint on adaptive evolution. However, since very few studies have concerned themselves with the relation between morphology and timing and duration of molting events (Nijhout 1981; Sehnaal 1985), it is at present impossible to evaluate the general importance of this type of mechanical ontogenetic constraint on the evolution of complex morphologies in hemimetabolous arthropods. An example that may potentially parallel the developmental constraints in *G. odontogaster* can be found in *Dolania* mayflies (Peters and Peters 1986). The legs of these mayflies are sexually dimorphic in form and structure. Interestingly enough, the legs of males frequently break off during the ultimate molt and get stuck in the subimaginal exuvium. Unfortunately, the functional significance of sexual leg dimorphism in *Dolania* has not been examined (Peters and Peters 1986).

The results of this study also suggest a possible novel selection pressure on body size in water striders. As indicated by the weak but significant negative relation between body size and molting duration, there may be selection for large body size in both sexes. Differential mortality among phenotypes during ontogenetic events could thus potentially not only influence the evolution of body size in general but also constrain the evolution of sexual size dimorphism in water striders (see Fairbairn 1990).

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