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On the role of body size for life-history evolution

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Abstract. 1. Body size is a central element in current theories of life-history evolution. Models for optimal age at maturity are based on the assumptions that there is a trade-off between development time and adult size and that larger size provides a reproductive advantage.

2. The results of large, replicated experiments with the water strider *Gerris buenoi* (Heteroptera: Gerridae) contradict both these assumptions. Individual rearings under field conditions showed that there is a negative, not a positive, correlation between development time and adult size. The physiological basis of growth, with stretch-induced moulting, may provide a partial explanation for this correlation.

3. This study examined a number of fitness components for their correlations with female size: lifetime fecundity, reproductive life span, average volume per egg, total volume of eggs laid, and the proportion of eggs hatched. None of these traits was correlated with female size.

4. The data on water striders suggest an alternative scenario for life-history evolution, in which size is not an adaptive trait, but evolves as a correlated response to selection on other traits. This expands the range of possible models, and opens life-history theory to the debate about adaptation and optimality.

Key words. Body size, development time, fecundity, Gerridae, growth, life history, optimality, trade-off.

Introduction

Body size has been considered traditionally a key determinant of an organism's ecological and physiological properties. Numerous theoretical and empirical studies have explored its connections to other life-history traits, such as development time and reproduction (e.g. Peters, 1983; Calder, 1984; Reiss, 1989; Roff, 1992; Stearns, 1992). Most models of life-history evolution rest on assumptions about trade-offs between reproductive benefits of size and costs of long growth periods, e.g. through mortality.

A strong positive correlation between development time and adult size is commonly assumed, 'for one must grow for a longer time to get larger' (Stearns, 1992: 127). Some models for optimal age and size at maturity incorporate size explicitly (Roff, 1981, 1984; Kusano, 1982; Ludwig & Rowe, 1990; Rowe & Ludwig, 1991; Abrams *et al*., 1996). Most of these models link development time and adult size either by assuming an allometric relation (Roff, 1981), by using von Bertalanffy growth curves with fixed parameters (Roff, 1984), or by some other growth curve assumed to be constant throughout the population (Kusano, 1982). All these models assume that fecundity is strictly determined by size, most often through an allometric or linear relation (Roff, 1981, 1984; Kusano, 1982; Ludwig & Rowe, 1990; Rowe & Ludwig, 1991). Similar reasoning has been applied in models of latitudinal variation in life-history strategies (Roff, 1980).

Another class of optimization models is based on the assumption that either fecundity increases or offspring mortality decreases as a function of age at maturity (Stearns & Crandall, 1981; Stearns & Koella, 1986; Stearns, 1992). Such fecundity benefits of later maturation are most likely a consequence of size (Fig. 2 in Stearns & Koella, 1986); except in species with parental care where experience results in a reproductive benefit, it is unclear how a delayed first reproduction may lead to an increase in reproductive success unrelated to parental size. Likewise, offspring mortality may decrease as maturity is delayed because larger maternal size increases offspring size and survival (see Stearns & Koella, 1986: 895); again, other explanations that do not involve size assume parental care. Therefore, although Stearns and colleagues do not incorporate size explicitly, their models make crucial implicit assumptions about the role of size, or otherwise only apply to a narrow spectrum of species with parental care. Reaction norms are derived from these models by optimizing age and size at

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maturity within a series of environments differing in their growth parameters (Stearns & Koella, 1986; Berrigan & Koella, 1994). These models are closely related to those described in the preceding paragraph, despite some biological and mathematical differences, because the optimization is based on a trade-off between fecundity benefits of increased size and associated costs through a prolonged growth period before maturity. Although the models are mostly framed in terms of age, body size plays a central role, and the assumptions about its relationships to other life-history parameters are essential for the applicability of the models.

Despite the crucial importance of these assumptions, surprisingly few studies have examined their empirical basis and generality critically (e.g. Gotthard *et al*., 1994). Studies of vertebrates and laboratory studies of *Drosophila* make up a large part of the data supporting the models (reviewed by Roff, 1992; Stearns, 1992). Other groups have not been investigated comparably and few in-depth studies of invertebrates have been undertaken under field conditions (but see Banks & Thompson, 1987). While a considerable number of studies focus on the correlations between size and either development time or fecundity, most do not assess fully whether the assumptions of life-history models are met, as they do not include both aspects simultaneously. Moreover, the published studies may be biased in favour of the models because correlations reported as supporting evidence are often weak, albeit statistically significant, and their biological importance and generality are thus questionable, especially if weak contradictory results are not published.

This study attempts an empirical validation of the key assumptions made in these models (Oreskes *et al*., 1994). It reports the results from a series of experiments, replicated in several generations, with the water strider *Gerris buenoi* Kirkaldy (Heteroptera: Gerridae). Rearing experiments in the field and several measures of female reproductive performance consistently revealed relationships contradicting those generally assumed in life-history models. These findings show that much of the size variation occurring within natural populations may be selectively neutral. An alternative framework for understanding associations among life-history traits, in which size does not play an adaptive role, is presented.

Material and Methods

Study organisms

The water strider *Gerris buenoi* Kirkaldy is widespread in North America and occurs abundantly in a range of pond habitats (Spence, 1989). At the study site in central Alberta, Canada, this species has two generations per year. Overwintered adults, which all have fully developed wings, appear on ponds in spring to mate and produce a first (‘spring’) generation offspring. The spring generation partly consists of individuals that breed in the same year and do not overwinter, some of which are wingless. These direct breeders produce a second (‘summer’) generation offspring, which are invariably long-winged and reproduce only after overwintering.

Study site and rearing experiments

This study was carried out from 1992 to 1994 at the George Lake Field Site, about 100 km north-west of Edmonton in central Alberta, Canada. Rearing experiments took place on two artificial ponds (Experiment Pond in 1992; Meadow Pond in 1993 and 1994; see Spence, 1986, 1989). On these ponds, *G. buenoi* co-occurs naturally with the gerrids *Limnoporus dissortis* (Drake and Harris) and *Gerris comatus* Drake and Hottes.

Most of the results are from individual rearings (only in 1992 a part of the bugs, of the same hatching date, were reared in groups). Each larva was placed separately into a bottomless plastic container (diameter *c*. 10 cm, rim *c*. 6 cm above water), which was kept afloat on the water surface by a ring of plastic foam glued around its outside. Groups of these containers were protected from predators in enclosures screened on all sides (see Spence, 1986). In 1993 there were problems with discharges of methane gas from the pond sediment, which had accumulated under the bottom screen and occasionally burst up through the enclosure, overturning containers. Thus, in 1994 a sheet of plastic was added under each enclosure, separated from the bottom screen by a wooden strut, to ensure that gas bubbles came up outside the enclosure. Each water strider was checked daily for moults and fed *ad libitum* with frozen insects from a nearby light trap or, if light-trap catches were insufficient (summer, 1993 only), with frozen flesh flies (*Neobelliera bullata* [Parker]) reared on pork liver in the laboratory.

Within 24 h after the final moult, the emerging adults were collected, sex and wing morph recorded, and the size of each bug measured. In 1992 and 1993, bugs were killed, dried to constant mass at 60 °C, and weighed on a microbalance (resolution: 1 μg). In 1993 and 1994, total body length was measured to the nearest 0.1 mm.

A separate experiment in the summer generation 1994 examined whether the standard rearing procedure caused any biases in the correlations among life-history traits, rendering them unrepresentative of the natural population. To assess the effect of the feeding regime, individual rearings with *ad libitum* regime (the ‘standard’ treatment, see above) were compared with a treatment with reduced food levels (‘food limitation’), in which each larva received a limited quantity of frozen insects every other day only (e.g. 2–3 chironomid midges; this was severe enough to increase development time and reduce adult size significantly). An additional treatment (‘triplet’), with three larvae per container instead of one, allowed social interactions and competition among larvae. Only total body length was measured as a size variable.

To correct for variation in temperature, development times were calculated in degree-days based on air temperatures recorded 1–10 cm from the pond surface with a Ryan model 10 recorder located in the shore vegetation (this was not possible in 1992 due to incomplete temperature records, and in the experiment of summer 1994). The underlying linear model of temperature dependence, although it may not be biologically realistic, gives results highly correlated with those from more complex non-linear models (Lamb, 1992), and is thus appropriate for this study focusing on variation within a population. Because growth thresholds differ between instars (Spence *et al*., 1980), they were computed separately for each of the five instars (L1–L5) using data from this study population (J. R. Spence, unpublished data). Thresholds computed by linear regression (± bootstrap standard errors) are 7.4 ± 0.6 °C for L1 ($n = 58$), 10.1 ± 0.5 °C for L2 ($n = 95$), 9.4 ± 0.6 °C for L3 ($n = 57$), 10.0 ± 0.4 °C for L4 ($n = 71$), 9.1 ± 0.3 °C for L5 ($n = 111$). Accumulated degree-days were computed for each of these thresholds from daily minima and maxima, updating values twice daily with a sine-wave interpolation (e.g. Pruess, 1983). Total degree-days are the sum of the values accumulated during each instar.

Product-moment (Pearson) correlations between development time and size were computed separately for each generation, sex, and wing morph. The bootstrap was used to compute 95% confidence intervals with the BC_a method (Efron & Tibshirani, 1993). For each confidence interval, 5000 bootstrap iterations were performed.

Breeding design and measures of female reproduction

For the experiment in 1992, direct-breeding adults were caught in the field and kept in a laboratory mass culture for mating and oviposition. Larvae were transferred to field enclosures within 2 days of hatching. In 1993 and 1994, offspring of isolated breeding pairs were used. For the spring generations, parental bugs were collected in the field as overwintered adults immediately after snowmelt. Mating does not occur in the first few days of activity in spring, ensuring that the breeding females were virgins; none of these females laid fertile eggs when isolated in the laboratory. Larvae were transferred to field enclosures within 24 h of hatching. A randomized list was used to allocate a position in one of the enclosures to each larva. The parental bugs for the experiments in the summer generations of 1993 and 1994 were direct-breeding bugs collected in the field as fifth-instar larvae and immediately separated by sex. Matings were arranged according to a half-sib design (Falconer, 1989). In 1993 each male was mated to two females, and in 1994 to three females. Males were switched between the females allocated to them three times weekly (1993) or daily (1994).

Breeding pairs were kept under long-day conditions (19L : 5D) in the laboratory at 20 °C (1993) or in a climate chamber at the field site at 23 °C (1994). Each female or pair was fed a frozen flesh fly three times per week (1993) or either a flesh fly or house fly (*Musca domestica* L.) daily (1994). As these flies are of similar size or larger than the water striders, and remain on the water surface for several days as a potential food source, this constitutes an *ad libitum* regime. The females were provided with styrofoam strips for oviposition, which were exchanged at intervals ranging from a week to 10 days. For each female, the total body length (to the nearest 0.1 mm) and dry weight were measured after death (1993 only).

An experiment with direct-breeding females in summer 1993 examined the influence of the feeding regime on the relationship between body size and reproduction. Females were either given a permanent source of food (a frozen flesh fly that was exchanged three times weekly) or a scarce food regime, allowing access to a fly only once a week for 8 h.

Oviposition strips were kept at room temperature in separate containers for hatching. After a period of at least 4 weeks, which exceeds the incubation time of *G. buenoi* (Spence *et al*., 1980), the empty eggshells left by hatching larvae and the eggs that failed to develop on all styrofoam strips were counted. Parental bugs were kept in the laboratory until they died; egg counts therefore represent lifetime fecundity. Reproductive life span was defined as the time interval from the first egg to the death of the female, because recently laid eggs were present when most females died, and dissections showed that most females still had developing and mature eggs in their ovaries after death. The length and width of ten eggs from the first two batches of each female were measured (thereby controlling for possible variation of egg size related to female age), and from these the volume of the eggs was calculated as rotation ellipsoids, which correspond fairly well to the shape of gerrid eggs (see also Solbreck *et al*., 1989).

For correlations involving egg size, the methods had to be adjusted to take into account that fewer than ten eggs were measured for some females. Weighted correlations were therefore used, with the number of eggs measured as the weighting factor. Confidence intervals were computed with the bootstrap, using the BC_a method and 5000 bootstrap iterations (Efron & Tibshirani, 1993).

Estimates of heritabilities and genetic correlations

In the spring generations of 1993 and 1994, heritabilities of developmental time, total body length, and dry weight (1993 only) of teneral adults were estimated. Complete data were available for 513 offspring from eighty-one dams and forty-four sires in 1993, and for 643 offspring from 135 dams and forty-four sires in 1994. Data were log-transformed before the analysis to reduce skewness. The statistical model included sex and wing morph as fixed effects, and sire and dam (nested within sire) as random effects. To estimate variance components, the restricted maximum likelihood (REML) method was used (Shaw, 1987), as implemented in the SAS procedure VARCOMP (SAS Institute, 1988). Genetic correlations were computed from the variance components for each character and for their sum. Approximate standard errors for heritabilities and genetic correlations were calculated from the variances and covariances of parameter estimates provided by SAS, using formulas given by Bulmer (1980: 86) and Falconer (1989: 317).

Results

Development time and final size

There was a negative association between development time and adult size in all experiments (Fig. 1). Bugs with a longer larval period tended to be smaller in both body length and dry weight than those that developed more quickly. The estimated

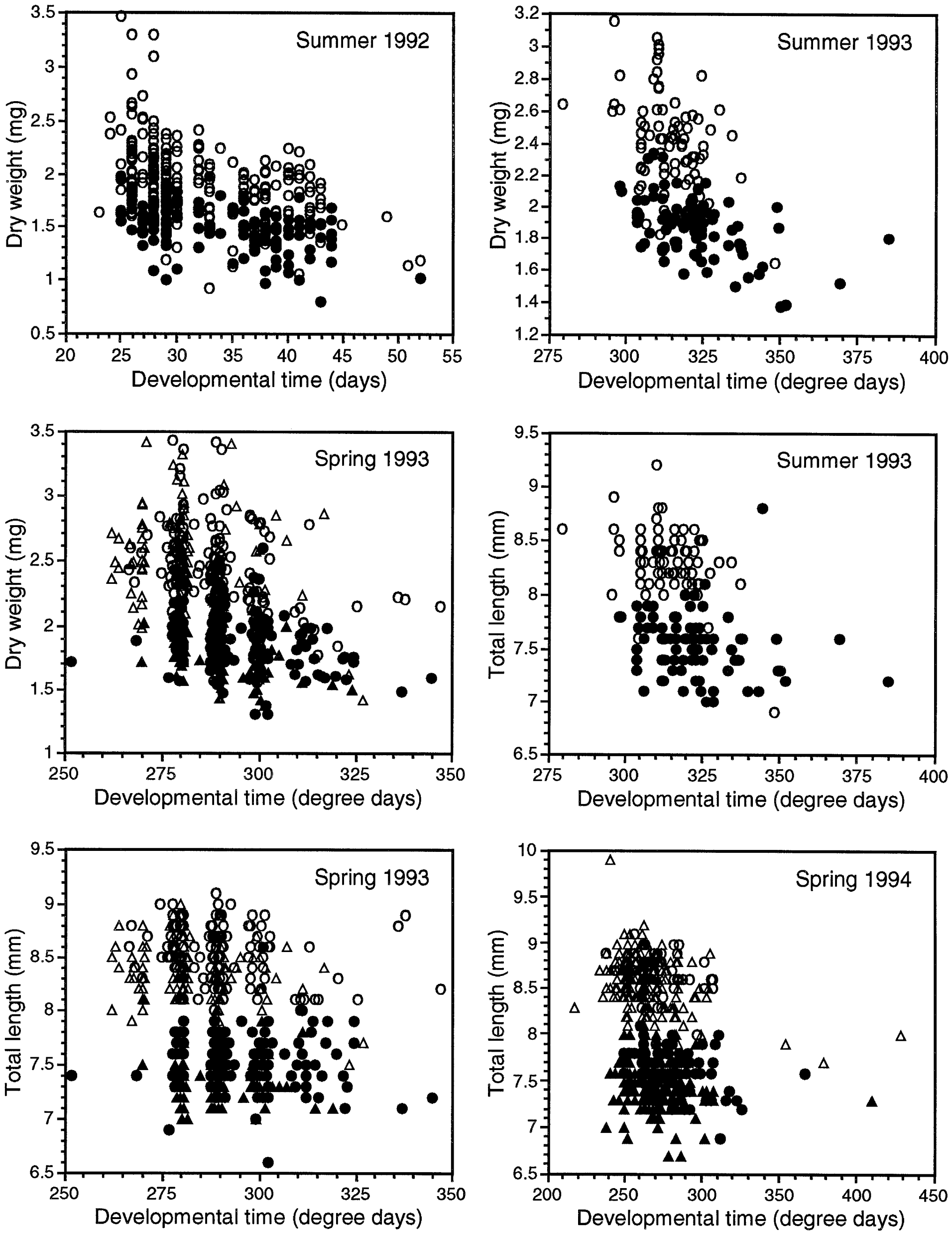

Fig. 1. Relation between development time and final size. Size measures are total body length and dry weight of teneral bugs. Solid symbols represent males, open ones females. In the spring generations, there are both long-winged (circles) and wingless bugs (triangles).

correlations between development time and adult size were negative for both size measures, in all experiments, and in each sex and wing morph (Table 1). The confidence intervals of the correlation coefficients included zero in only two of the eighteen correlations (length, male long-winged bugs in the spring and summer generations of 1993; Table 1); all others were significantly negative.

Heritabilities (± standard errors) computed from half-sib correlations, i.e. using the sire component to estimate additive variances, were 0.50 ± 0.20 for length, 0.11 ± 0.13 for dry weight, and 0.26 ± 0.14 for development time in 1993. The corresponding genetic correlations were 0.11 ± 0.55 between dry weight and development time and –0.18 ± 0.32 between body length and development time. Genetic correlations computed from full-sib correlations, which also include dominance and maternal effects, were –0.43 ± 0.25 and −0.39 ± 0.18, and thus corresponded more closely to the phenotypic correlations. These estimates, however, have to be interpreted cautiously, as suggested by the large standard errors, and because the REML analysis produced a zero estimate for the between-dam component of the sum of length and development time. Despite the larger sample size and increased

Table 1. Correlations between development time and adult size. Correlations are Pearson correlation coefficients, and bootstrap 95% confidence intervals were computed with the BC_a method (Efron & Tibshirani, 1993). Variables are dry weight (W), total length (L), and development time in days (1992) or in degree-days (1993 and, 1994). Abbreviations of wing morphs are lw for long-winged and ap for wingless (apterous).

Size measure	Sex	Wing morph	Correlation coefficient	Confidence interval	Sample size
Summer generation 1992:					
W	F	lw	–0.44	[–0.53, –0.35]	217
W	M	lw	–0.50	[–0.61, –0.37]	149
Spring generation 1993:					
W	F	lw	–0.37	[–0.47, –0.24]	145
W	F	ap	–0.42	[–0.59, –0.18]	125
W	M	lw	–0.26	[–0.38, –0.12]	168
W	M	ap	–0.42	[–0.59, –0.19]	75
L	F	lw	–0.23	[–0.40, –0.02]	145
L	F	ap	–0.36	[–0.56, –0.08]	125
L	M	lw	–0.05	[–0.22, 0.14]	168
L	M	ap	–0.33	[–0.53, –0.09]	75
Summer Generation 1993:					
W	F	lw	–0.41	[–0.58, –0.19]	83
W	M	lw	–0.50	[–0.64, –0.32]	88
L	F	lw	–0.37	[–0.62, –0.09]	83
L	M	lw	–0.17	[–0.39, 0.10]	87
Spring generation 1994:					
L	F	lw	–0.30	[–0.49, –0.06]	54
L	F	ap	–0.37	[–0.49, –0.22]	249
L	M	lw	–0.29	[–0.49, –0.08]	101
L	M	ap	–0.19	[–0.28, –0.09]	239

number of families in 1994, a zero value was estimated for the between-sire component of body length, and half-sib correlations therefore could not be used for this variable. The heritability of development time based on half-sib correlation was 0.18 ± 0.13, and the heritabilities based on full-sib correlations were 0.31 ± 0.08 for length and 0.29 ± 0.07 for development time. The genetic correlation, also based on full-sib correlations, was –0.46 ± 0.14, and therefore similar to the estimate of the previous year. A combined analysis of both years, with year as an additional fixed effect, gave results very similar to those from the 1994 experiment alone. These estimates of genetic correlations are in general agreement with the phenotypic ones (Table 1), and clearly contradict the widespread assumption that there is a strong positive association between development time and final size.

Phenotypic correlations between development time and adult size in water striders reared under food limitation or in small groups were similar to those in bugs from the standard rearing procedure (Table 2). The negative correlations between development time and adult size are therefore not an artefact of the specific experimental conditions, but most likely apply to free-living water striders as well.

Female size and reproduction

This study considered several measures of female reproductive performance and their relations to the size of the female. Lifetime fecundity showed no relation to female size (Fig. 2). The differences in lifetime fecundity between females of the same generation in different years may reflect differences in laboratory conditions. Correlation coefficients were close to zero in all generations and wing morphs, and confidence intervals were fairly narrow and included zero (Table 3). As another measure of total reproductive effort, the total volume of the eggs laid by a female was estimated as her lifetime fecundity multiplied by the average volume of her eggs. In the experiment of spring 1994, the scatter of total egg volume vs. female length closely resembled the pattern for lifetime

Table 2. Effect of food limitation and competition on correlations between development time and adult size. Development time is measured in days, and the size variable is total body length. Water striders in the standard treatment were reared in isolation and fed daily; those under food limitation were only fed every other day; and in the ‘triplet’ treatment, three bugs were reared in each container, thus allowing social interactions and competition among them. Correlations are Pearson correlation coefficients, and bootstrap 95% confidence intervals were computed with the BC_a method (Efron & Tibshirani, 1993).

Sex	Correlation coefficient	Confidence interval	Sample size
Standard:			
F	–0.79	[–0.92, –0.35]	30
M	–0.60	[–0.84, –0.12]	43
Food limitation:			
F	–0.53	[–0.69, –0.27]	21
M	–0.55	[–0.74, –0.15]	23
Triplet:			
F	–0.59	[–0.76, –0.35]	87
M	–0.46	[–0.62, –0.24]	80

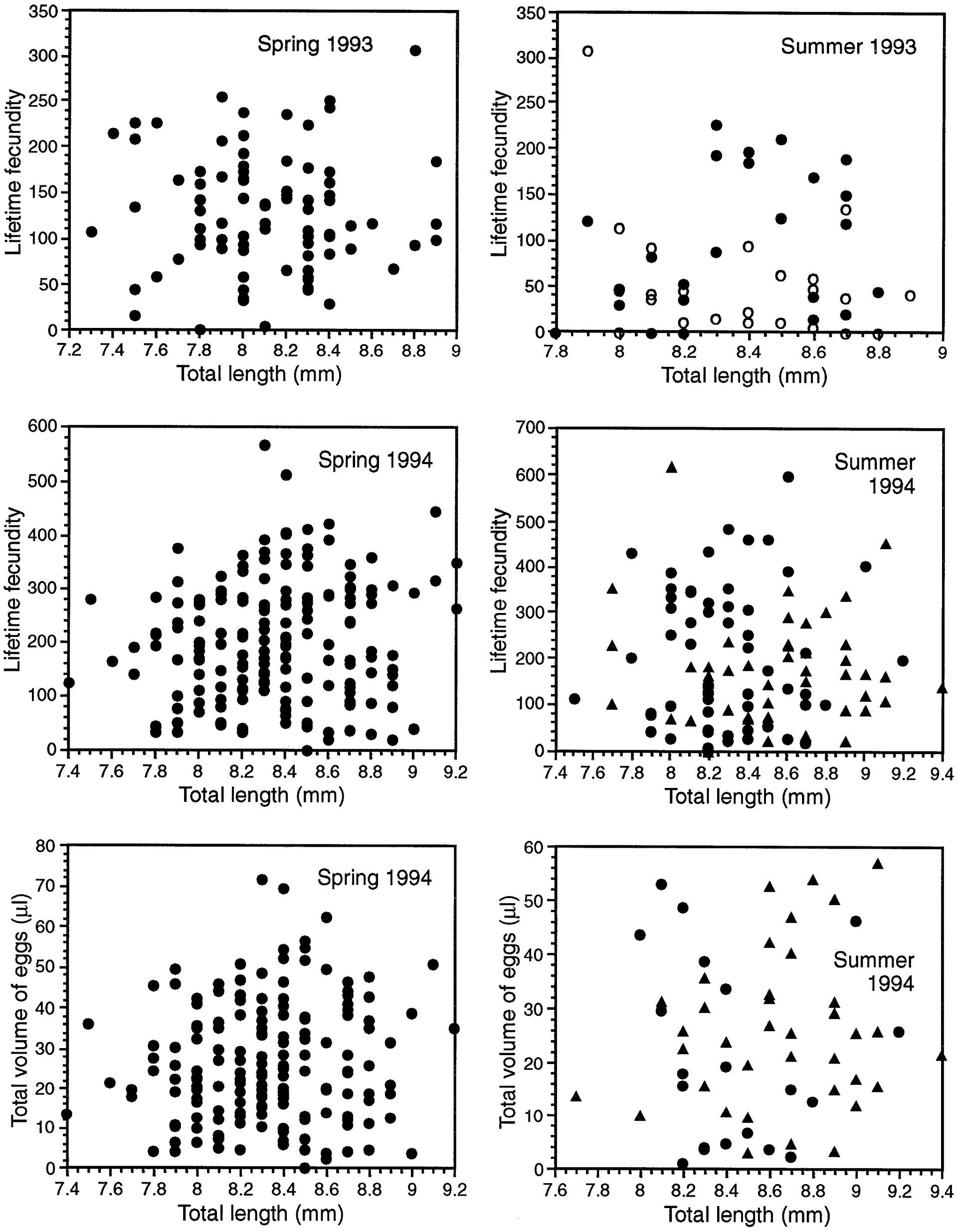

Fig. 2. Relation between female size and measures of reproductive output. Reproductive output is characterized by lifetime fecundity (top four panels) and the estimated total volume of eggs laid by a female (only in 1994; bottom row). In the experiment of summer 1993, some females were fed *ad libitum* (solid circles) and others at a reduced level (open circles). For the 1994 summer generation, circles stand for long-winged females, and triangles for wingless females.

fecundity, but less so in summer (Fig. 2). Again, correlations were low and all confidence intervals included zero (Table 3). These correlations indicate that these two measures of reproductive effort are independent of a female's body size.

Likewise, reproductive life span appears to be independent of female size. In summer 1994, however, large females tended to survive for only a relatively short time (Fig. 3), giving rise to negative correlations for both wing morphs (Table 3). These contrast with the very weak correlations found in the other two generations (with larger sample sizes), and therefore should be interpreted cautiously.

To assess whether larger size may benefit females through the quality of their eggs, egg volume and the proportion of eggs hatched were considered (Fig. 4). The volume per egg appears to be unrelated to female size, as correlation coefficients were close to zero and all confidence intervals included zero (Table 3). There were two cases where the correlations of the proportion of eggs hatched with size were statistically

Table 3. Correlations between female size and reproduction. Correlations are Pearson correlation coefficients, and bootstrap 95% confidence intervals were computed with the BC_a method (Efron & Tibshirani, 1993). Size measures are total length (L) and dry weight (W) after natural death of the female. Abbreviations of generations are OW for overwintered (diapause) and DB for direct-breeding bugs, and wing morphs are denoted lw for long-winged and ap for wingless (apterous).

Size measure	Generation	Wing morph	Year	Correlation coefficient	Confidence interval	Sample size
Lifetime fecundity:						
L	OW	lw	1993	0.002	[–0.24, 0.18]	89
W	OW	lw	1993	0.15	[–0.06, 0.35]	84
L	OW	lw	1994	0.09	[–0.06, 0.22]	179
L	DB	lw	1994	0.05	[–0.19, 0.27]	61
L	DB	ap	1994	–0.03	[–0.32, 0.33]	46
Reproductive life span:						
L	OW	lw	1993	–0.06	[–0.27, 0.18]	81
W	OW	lw	1993	–0.14	[–0.33, 0.05]	80
L	OW	lw	1994	–0.06	[–0.19, 0.08]	176
L	DB	lw	1994	–0.27	[–0.43, –0.08]	60
L	DB	ap	1994	–0.44	[–0.64, –0.14]	46
Average volume per egg:*						
L	OW	lw	1994	–0.01	[–0.17, 0.15]	163
L	DB	lw	1994	–0.11	[–0.44, 0.25]	20
L	DB	ap	1994	–0.07	[–0.36, 0.20]	38
Total volume of eggs:*						
L	OW	lw	1994	0.13	[–0.02, 0.26]	163
L	DB	lw	1994	–0.14	[–0.60, 0.39]	20
L	DB	ap	1994	0.17	[–0.09, 0.41]	38
Proportion of eggs hatched:†						
L	OW	lw	1993	0.16	[–0.09, 0.36]	87
W	OW	lw	1993	0.28	[0.05, 0.43]	82
L	OW	lw	1994	–0.03	[–0.21, 0.13]	164
L	DB	lw	1994	0.35	[0.03, 0.58]	36
L	DB	ap	1994	0.09	[–0.23, 0.36]	41

* For traits involving egg measurements, correlations are weighted by the number of eggs measured for each female.

† Breeding pairs without any hatched eggs are excluded to ensure all females were mated to a fertile male.

significant. These were the spring experiment 1993, with dry weight as a size variable, and the long-winged bugs in summer 1994. Conversely, the largest sample (spring 1994) produced a correlation very close to zero. Although these data suggest that larger size is correlated with the proportion of fertile eggs in some replicates, this correlation does not hold generally for any size measure, generation or wing morph (also note that there are 21 correlations in Table 3, and that there was no Bonferroni adjustment to control table-wide significance levels).

There is a possibility that the experiments described above missed an important benefit of body size, as larger size of females may improve their reproductive performance only under food stress, but not under an *ad libitum* feeding regime. An experiment, using direct breeding females in summer 1993, examined whether there was any such effect of nutritional status on female reproductive traits. Under food stress, correlations of size with any of the reproductive traits were not higher or were only slightly higher (more positive) than in the high food regime (Table 4). Contrary to expectations, several of the correlations were even lower (more negative) when food was scarce. While the small sample sizes make it difficult to assess the biological importance of the latter result, the experiment clearly showed that there are no benefits of larger body size under a low-food regime.

Discussion

These experiments, replicated in several generations in the same population, showed a consistent negative correlation between development time and adult size but did not reveal any clear relationship between female size and several measures of reproductive performance. The fairly narrow confidence intervals clearly indicate that the samples were sufficiently large to provide adequate statistical power for characterizing phenotypic correlations.

The negative correlations between development time and adult size suggest that there is unexpected variation in overall vigour. Some individuals have a substantially shorter larval period and also tend to grow larger than others. The additive genetic correlations seem to be in line with the phenotypic ones, although the large standard errors suggest that these estimates are unreliable. Genetic correlations estimated from full-sib correlations, which include some of the variation due to dominance and maternal effects, closely match the

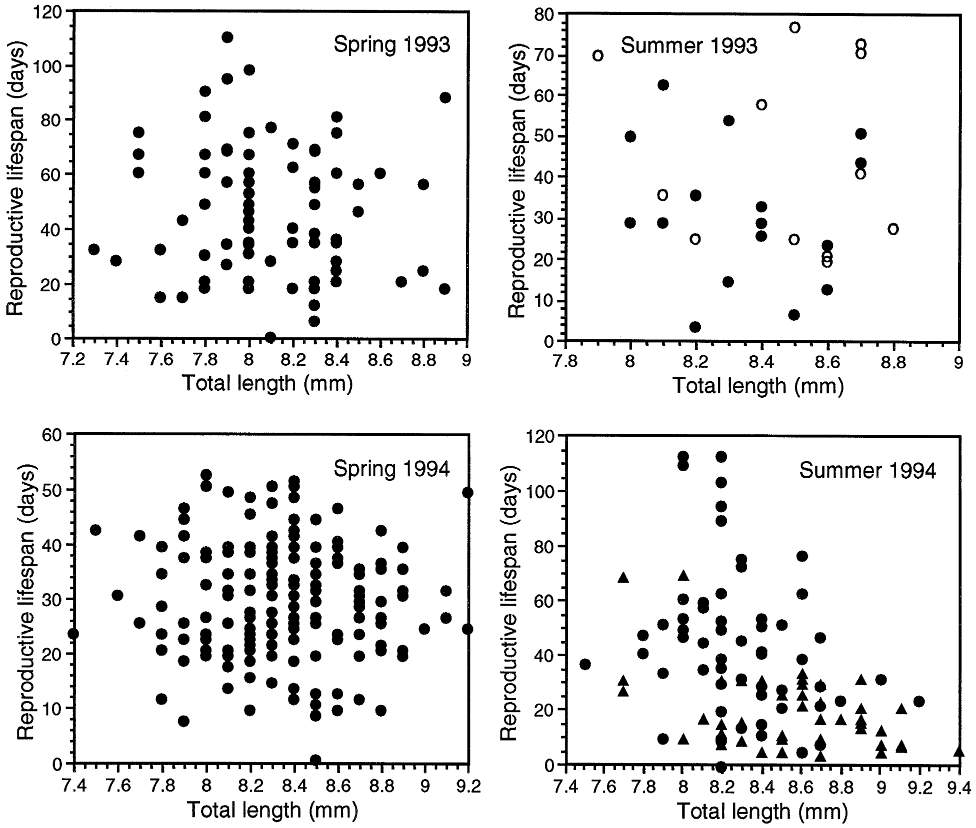

Fig. 3. Relation between female size and reproductive life span. Symbols are as in Fig. 2.

phenotypic correlations. The absence of strong genetic correlations provides flexibility for independent evolutionary changes of adult size and development time, as has been observed in comparisons among several water strider species (Fairbairn, 1990; Klingenberg & Spence, 1993).

Negative correlations between development time and adult size have often been reported for experiments in which animals were exposed to a range of environments varying in suitability, e.g. different food regimes, both in water striders (Blanckenhorn, 1994) and other insects (e.g. Dixon, 1985; Gebhardt & Stearns, 1988, 1993; Solbreck *et al.*, 1989; Roff, 1992; Stearns, 1992; Panizzi & Saraiva, 1993; Sota, 1993). Variation in food availability, however, cannot be the source of negative correlations in the experiments described here, because correlations were calculated only within experimental treatments; for each correlation estimate, all larvae were either fed *ad libitum* or the same reduced regime. Infection by protozoan parasites, which can affect the physiological condition of gerrids (Arnqvist & Mäki, 1990), also must be ruled out as a possible cause for these results (Klingenberg *et al.*, in press). As the larvae for each experimental replicate were reared simultaneously on the same pond, other environmental factors are unlikely to have had a major effect on variation within generations. Moreover, these negative correlations are not a result of the favourable conditions used in the standard rearing procedure, but also occur in experiments under food limitation and in group-reared larvae. Because this range of experimental conditions approximates those found in natural habitats of this species, negative correlations between development time and final size can also be expected in natural populations. On average, fast-developing individuals also grow larger than less vigorous ones with longer development period as well as smaller adult size. Therefore, intrinsic variation in growth rates of the water striders far exceeds the influence of a possible trade-off between development time and adult size (van Noordwijk & de Jong, 1986; Houle, 1991).

In experiments with another species of water striders, Firko (1986) and Blanckenhorn & Fairbairn (1995) found a similar negative correlation between development time and adult size within populations. Within constant environments, negative correlations between development time and final size have also been found in *Drosophila* (Gebhardt & Stearns, 1993), in the southern green stink bug (McLain, 1991), and most clearly in breeding and selection experiments with milkweed bugs (Hegmann & Dingle, 1982; Palmer & Dingle, 1986; Dingle *et al.*, 1988). In the butterfly *Pararge aegeria*, development time and pupal weight are uncorrelated (Gotthard *et al.*, 1994). These studies show that variation in growth rate and overall vigour, i.e. joint variation in the rate of moulting and the extent of growth, is also dominant in a number of other species, rather than the trade-off between development time and adult size generally assumed by life-history theory (Roff, 1992; Stearns, 1992).

The physiological processes of moulting control in insects

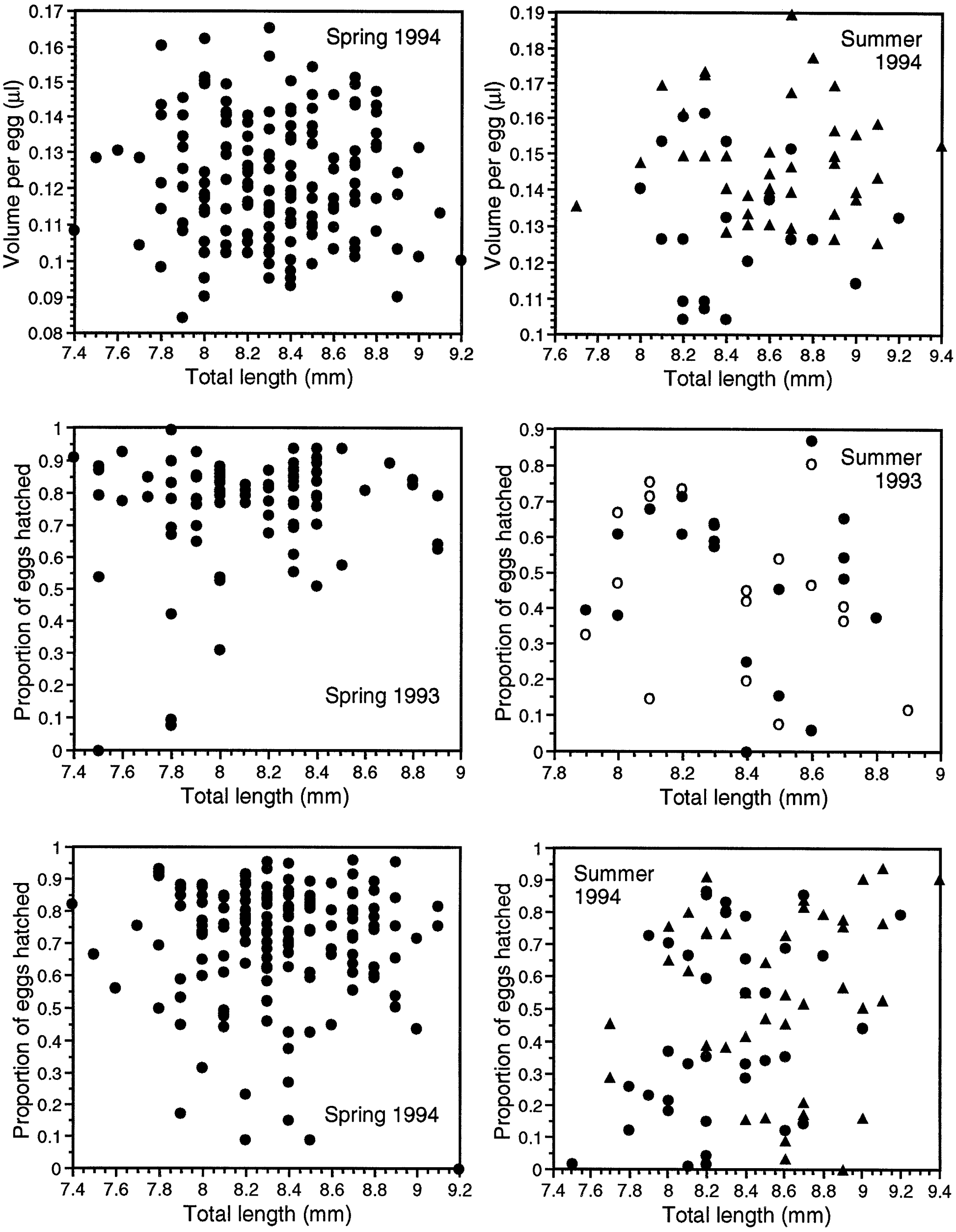

Fig. 4. Relation between female size and measures of egg size and quality. Egg size is the average volume in a sample of eggs from each female (top two panels). Egg quality is given as the proportion of each female's eggs that hatched (bottom four panels). Symbols are as in Fig. 2.

may cause or at least reinforce these negative correlations. In Heteroptera, which are particularly well studied, and in other insects, the initiation of moulting cycles is strongly size-dependent and occurs only after a larva has reached a critical size (e.g. Blakley & Goodner, 1978; Nijhout, 1979, 1994; Woodring, 1983; Sehnal, 1985). Moreover, this size threshold itself depends on the size at the outset of the instar, because the new moulting cycle is triggered by the abdominal distension resulting from growth of internal organs during the instar (Nijhout, 1979). Because this mechanism most likely involves receptors responding to stretch (Nijhout, 1984) or pressure on the body wall (Chiang & Davey, 1988), the critical size will be a multiple of the size at the start of the instar (examples in Nijhout, 1994). Conversely, the temporal sequence and duration of the moulting cycle (from reaching critical size to ecdysis) is fairly constant irrespective of growth rate or feeding regime (Bennet-Clark, 1971; Blakley & Goodner, 1978; Woodring, 1983). As the period after the initiation of the moulting cycle can take up a substantial portion of the whole instar duration, growth during this time is a major determinant of size in the following instar (Bennet-Clark, 1971; Blakley & Goodner, 1978; Nijhout, 1979; Woodring, 1983). More importantly, the

Table 4. Influence of food levels on correlations between female size and reproduction. At the high food level, females had permanent access to food (a frozen flesh fly renewed three times per week), whereas at the low food level, they had the opportunity to feed only for 8 h per week. Correlations are Pearson correlation coefficients, and bootstrap 95% confidence intervals were computed with the BC_a method (Efron & Tibshirani, 1993). Size measures are total length (L) and dry weight (W) after natural death of the female.

	High food level (*ad libitum*)			Low food level		
Size measure	Correlation coefficient	Confidence interval	Sample size	Correlation coefficient	Confidence interval	Sample size
Lifetime fecundity:						
L	0.12	[–0.26, 0.52]	21	–0.35	[–0.65, 0.30]	22
W	0.52	[0.14, 0.77]	21	0.10	[–0.72, 0.58]	22
Reproductive life span:						
L	–0.11	[–0.62, 0.40]	13	–0.15	[–0.63, 0.40]	16
W	0.33	[–0.28, 0.78]	13	–0.66	[–0.90, –0.20]	16
Proportion of eggs hatched:*						
L	–0.13	[–0.49, 0.22]	19	–0.31	[–0.81, 0.18]	18
W	–0.24	[–0.53, 0.09]	19	–0.08	[–0.46, 0.32]	18

* Breeding pairs without any hatched eggs are excluded to ensure all females were mated to a fertile male.

old cuticle serves as a template when the new epicuticle is laid down, and stretch by food or the growing internal organs therefore leads to increased size of the next instar (Bennet-Clark, 1971). Together, stretch-induced initiation and constant duration of the moulting cycle can generate a negative correlation between development time and size. Individuals with a slower growth rate attain the critical size later and thus have a longer instar duration, but those that grow faster have a larger size increment during the instar because they grow more between reaching the size threshold and the actual moult (Fig. 5). If this process occurs in all instars, the negative correlations it generates between development time and size are expected to be stronger from instar to instar. Whereas it is likely that this explanation applies to the correlations reported for species of *Oncopeltus* (Hegmann & Dingle, 1982; Palmer & Dingle, 1986; Dingle *et al*., 1988), for which physiological studies were carried out, it is unclear whether it can be extrapolated to water striders, because the only other Heteroptera studied are two species of reduviids (Nijhout, 1984, 1994).

The physiology of moulting control, however, is not the only possible explanation for the observations described in this article. Blakley (1981) searched for adaptive explanations of size-triggered moulting itself, and the theoretical studies of Ludwig & Rowe (1990), Rowe & Ludwig (1991), and Abrams *et al.* (1996) explained a negative correlation between development time and final size as the optimal reaction norm resulting from a trade-off of juvenile mortality and emergence time vs. final size and fecundity. In contrast, the physiological mechanism proposed here is a possible alternative to explain the observed life-history patterns through intrinsic properties of the organisms. This explanation accounts for the negative correlation between adult size and development time as a developmental 'constraint' rather than by invoking adaptation (Gould & Lewontin, 1979; Maynard Smith *et al*., 1985).

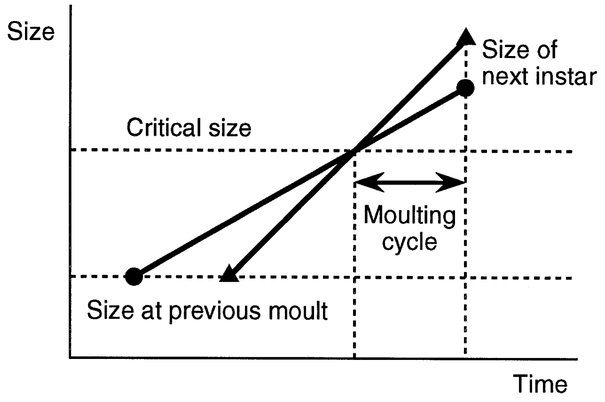

Fig. 5. Size-triggered moulting as an explanation for the negative correlation between development time and final size. The bold lines represent growth of two individuals, shifted along the time axis so that they attain the critical size simultaneously, and along the size axis so that they have the same initial size. Logarithmic transformation of the size axis accommodates multiplicative growth and the mechanism of moulting control, which responds to abdominal stretch or internal pressure. The negative correlation results because the slower-growing individual (dots) takes longer to reach the critical size than the faster-growing one (triangles), which also has the larger size increment because it grows at its higher rate during the moulting cycle (i.e. from reaching critical size to ecdysis). Because the fast-growing insect enters the next instar with a larger size, the gaps in development time and size widen in every instar, as long as the growth rates, the duration of a moulting cycle, and the properties of stretch or pressure receptors remain constant.

All five measures of reproductive performance considered here appear to be unrelated to female size. The highest correlations tended to occur in replicates with relatively small samples (Table 3). Given that twenty-one correlations were computed, the four for which the 95% confidence intervals did not include zero should be interpreted cautiously. Besides this concern about statistical significance, there is the question of biological importance of these associations. Even in the replicate with the highest correlation coefficient (between female length and the proportion of eggs hatched for long-winged direct breeders in, 1994; Table 3), size would only account for approximately 12% of the total variability in that reproductive trait. Any trade-off based on these relationships would be equally weak.

These findings closely agree with other data from *G. buenoi*. Rowe & Scudder (1990) found that body size accounted for less than 5% of the variation of several reproductive traits including lifetime fecundity. Fairbairn (1988) reported positive correlations between female body length and the number of eggs carried in the ovaries for *G. buenoi* and two other water striders. Although these were statistically significant, body size explained 11% or less of the variation, and it is therefore unclear how important body size is relative to other factors. In *Aquarius remigis*, Firko (1986) found some strong correlations of body size with lifetime fecundity and reproductive life span, but as these were very inconsistent between food treatments or study populations, he concluded that size did not account for a significant portion of the variation (p. 95); Blanckenhorn (1994), Blanckenhorn & Fairbairn (1995), and Blanckenhorn *et al.* (1995) reported similar results.

Because a female's greater body reserves may be the main advantage of larger size, experiments under *ad libitum* conditions may not reveal size effects important under food limitation. The experiment with two different food levels indicates that size does not provide a reproductive benefit even under food stress (Table 4). This agrees with the results of similar experiments reported by Firko (1986), Rowe & Scudder (1990), and Blanckenhorn (1994). Because the method of food delivery in the low-food treatment differed from study to study (e.g. small amounts of food permanently available vs. large amounts accessible for a restricted time), the temporal pattern of food availability can be ruled out as a factor itself. The lack of a clear positive correlation between size and reproductive performance is therefore real, and not an artefact of the *ad libitum* regime used in the experiments.

Because these experiments provided only estimates of phenotypic, but not of genetic, correlations between size and reproductive performance, one might suppose that a positive genetic correlation could exist. This would imply, however, that the positive genetic covariances must be compensated by similarly large negative environmental covariances to add up to the observed phenotypic covariances near zero. In more concrete terms, this means that individuals with an environmentally induced size advantage (e.g. by better nutrition) would suffer a penalty of reduced reproduction. We cannot imagine any physiological or ecological mechanism that might produce such a negative environmental covariance, and therefore rule out this possibility.

A number of studies in other arthropods are consistent with the results presented here and report the lack of correlations between female size and fitness components, such as lifetime fecundity (Slansky, 1980; Boggs, 1986; Leather & Burnand, 1987; Johnson, 1990; Spence *et al.*, 1996), female life span (Slansky, 1980; Boggs, 1986; Leather & Burnand, 1987), and egg size (Boggs, 1986 [except for unusually large or small females]; Banks & Thompson, 1987; Leather & Burnand, 1987; Solbreck *et al.*, 1989). Some studies even found negative correlations of female size with fitness components (clutch size: Banks & Thompson, 1987; fecundity and survival: Larsson, 1989). In the majority of published studies, however, correlations between female size and female fitness components are positive, including those for fecundity (e.g. Solbreck *et al.*, 1989; Marshall, 1990; Kasule, 1991; Honek, 1993; Messina, 1993), longevity (e.g. Banks & Thompson, 1987; McLain, 1991), and egg size (e.g. Marshall, 1990; Yafuso, 1994). It is difficult to assess the generality and biological importance of these relationships, as the correlations are variable, although most are stronger than those reported for water striders (see above). The literature, largely from applied entomology, is probably biased to a certain degree against cases where reproduction is independent of size: if there is no need to consider size as a covariate, authors may not even mention it. Moreover, various reproductive traits are related to each other in ways that can be complex and sometimes counter-intuitive; for instance, the proportion of eggs hatched declines with increasing egg size in the moth *Parapediasia teterrella* (Marshall, 1990). Altogether, the relationships between size and reproductive traits reflect the ecological and physiological diversity of insects; robust generalizations are unlikely (see also Leather, 1988).

A referee of an earlier version of this paper suggested that sexual selection, especially in males, might constitute a benefit for individuals of larger size. Yet, the literature on sexual selection in water striders is ambiguous or openly contradictory (reviewed by Arnqvist, 1996). In *G. buenoi*, Fairbairn (1988) found significant mating advantages of both large *and* small males in replicate samples, but no overall effect; likewise, there was no significant overall mating advantage for large females. In *A. remigis*, the best-studied species, some authors reported no significant overall effect of size (Rubenstein, 1984; Fairbairn, 1988), another study found sexual selection favouring large males (Fairbairn & Preziosi, 1994), whereas Fairbairn (1993) and Blanckenhorn *et al.* (1995) reported selective advantages of small males. Thus, the published evidence does not suggest any clear advantage through sexual selection for large gerrids.

It is not clear if there are other benefits of larger size, although several factors could possibly play a role. It is unlikely that size differences among individual *G. buenoi* affect their ability to escape predation, because the spectrum of prey sizes taken by predators far exceeds within-instar variation of gerrids (e.g. Zimmermann & Spence, 1989); between-instar differences in predation intensity would manifest themselves as selection on development time, rather than on size. Further, large size does not increase survival, even under starvation (Fig. 3, Table 4; because pre-oviposition period of direct-breeding females is short, reproductive life span comprises most of the adult life span). Overwinter survival is probably an important factor because of the high mortality during diapause in water striders (Spence & Andersen, 1994); however, Blanckenhorn (1994) found no advantage of large individuals in *A. remigis*. In sum, none of these factors appears to favour large size in water striders.

The relationships of size with other life-history traits in *G. buenoi* clearly contradict the assumptions made in conventional models and therefore suggest an alternative scenario for life-history evolution (Fig. 6). Whereas the

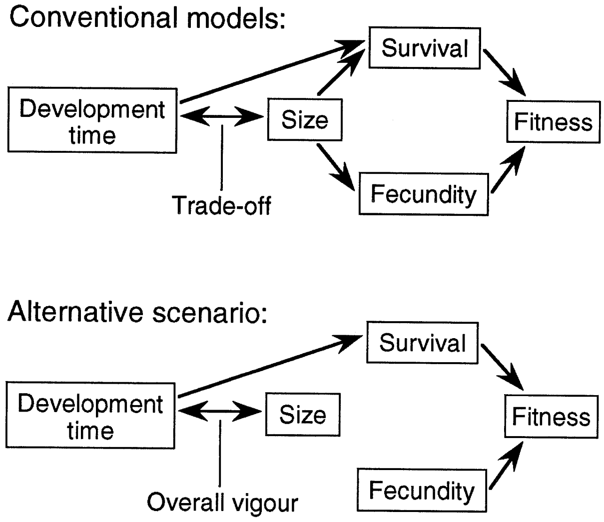

Fig. 6. Relationships among life-history traits in conventional models and an alternative scenario for *Gerris buenoi*. Size is central to conventional optimization models, because they depend on a trade-off between development time and size that is coupled to reproductive benefits of increased size. Moreover, survival may also be a function of size, although this is often not incorporated in life-history models. In *G. buenoi*, size is unrelated to reproductive traits, and is only correlated with development time through variation in overall vigour of larvae.

optimality models for age and size at maturity assume a trade-off between development time and adult size, the data presented here suggest that the correlation between these traits is due to variation in overall vigour of growth and possibly coupled with the effects of stretch-induced moulting. In *G. buenoi*, there is no positive relationship between size and several reproductive traits that provides the benefits of larger size assumed in optimality models. Within the limits of natural variation in the study population, size therefore appears to be selectively neutral, rather than an adaptive trait. It may evolve as a correlated response to selection for dispersal (Vepsäläinen, 1978; Spence, 1989), with which it may be positively correlated (Dingle, 1991), or for short development time, although the low genetic correlations should limit this latter possibility in this population. In contrast, the variation among species reflects adaptive evolution, as size and life histories of water striders are correlated with habitat use (e.g. Vepsäläinen, 1978; Spence, 1981, 1983, 1989; Andersen, 1982: 331–344).

The relations among life-history traits for a natural population of *G. buenoi* are inconsistent with current theories of life-history evolution. These data, combined with information on moulting physiology of other Heteroptera, suggest an alternative model of the relationships among life-history traits. Clearly, such an alternative will not supplant the models now accepted for well-studied organisms such as *Drosophila*, fish, and mammals. One must expect, however, that numerous patterns of associations and trade-offs among life-history traits occur in nature, and that variables other than those commonly studied may play a role. To explore this diversity, detailed empirical studies of additional species are needed that consider multiple life-history traits simultaneously.

Moreover, the results suggest that the range of theoretical models should be expanded to include new combinations of correlations and constraints, as well as neutral evolution. This opens the theory of life histories, currently an exclusive domain of adaptationist models (Partridge & Harvey, 1988; Roff, 1992; Stearns, 1992), to the debate about adaptation and optimality (Gould & Lewontin, 1979; Reeve & Sherman, 1993; Orzack & Sober, 1994). Optimization models consider an adaptive landscape with ‘peaks’ corresponding to optimal phenotypes, ‘ridges’ depicting optimal reaction norms, or gentle ascents towards a boundary set by the assumption of a trade-off. Instead, this study suggests that the adaptive landscape has a flat ‘plateau.’ On this plateau all phenotypes have approximately equal fitnesses, whereas natural selection presumably would occur on the surrounding ‘slopes,’ which are beyond the bounds of variation in the study population. Delimiting such domains of neutral and of adaptive evolution and characterizing their spatial and temporal variation will broaden the scope of both empirical and theoretical life-history studies.

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