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Body size and fecundity in the waterstrider *Aquarius remigis*: a test of Darwin's fecundity advantage hypothesis

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Abstract The general female bias in body size of animals is usually attributed to fecundity selection. While many studies have demonstrated a positive relationship between body size and fecundity, the most common interpretation of fecundity selection is that larger females have larger abdomens and can hold more eggs, yet the relationship between abdomen size and fecundity has rarely been examined. For the waterstrider, *Aquarius remigis*, we find a significant relationship between body size and fecundity and demonstrate that the target of fecundity selection is abdomen size. Thus, larger females have higher fecundities because they have larger abdomens and not because of their total size per se. The rate at which fecundity increases with increasing abdomen size exceeds that which would be expected due to a simple volume constraint and suggests that other factors, such as increased ability to obtain resources, may contribute to the increase in fecundity with body size. Selection intensities estimated from our data indicate that fecundity selection could be a significant selective force on both total and abdomen lengths. Previous studies have found that abdomen size increased faster than body size and thus, larger females had relatively larger abdomens. The relationship of abdomen length and thorax length in *A. remigis* is hypoallometric and indicates that larger females have relatively smaller abdomens. We hypothesize that this may reflect conservation of abdomen size in females developing under poor conditions. Finally, while egg size is not directly related to body size, we find a trade-off between egg size and number when female abdomen length is held constant, suggesting that selection on egg size may influence abdomen length only indirectly through its effects on fecundity.

Key words Sexual size dimorphism · Body size · Abdomen size · Fecundity · Egg size

Introduction

Sexual size dimorphism (a difference in body size between males and females) is common in almost all taxa of animals (Lande 1980; Slatkin 1984; Hedrick and Temeles 1989). While males are generally larger than females in homoiotherms (Price 1984), females are usually the larger sex in poikilotherms (Darwin 1874; Arak 1988; Wiklund and Karlsson 1988; Fairbairn 1990). The proposed explanation of Darwin (1874) for the general phenomenon of larger females was the relationship between female body size and increased egg production. Although fecundity selection is neither necessary nor sufficient to explain the evolution of sexual dimorphism, the "fecundity advantage" model is the most common explanation for the evolution of female biased size dimorphism [see Shine (1988) for examples from several taxa and a general critique]. There are two difficulties in using the fecundity advantage model to explain the evolution of female biased sexual size dimorphism. First, the relationship between body size and fecundity in females is most often measured as instantaneous fecundity (Leather 1988). Since body size is central to many components of the life history of organisms (Roff 1992; Stearns 1992), factors such as reproductive rate (Shine 1988) and longevity (Leather 1988) may have a strong effect on the relationship between body size and lifetime fecundity. Thus, lifetime estimates of the relationship between body size and fecundity are required to estimate the impact of fecundity advantage on the evolution of female body size. Second, the existence of a fecundity advantage is not sufficient to explain the evolution and maintenance of sexual size dimorphism since it provides no information about the size of females relative to the

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size of males (Greenwood and Adams 1987). The evolution and maintenance of sexual size dimorphism reflects differences in the net selective pressures on body size in males and females (Lande 1980; Arak 1988; Harvey 1990; Ydenberg and Forbes 1991). For female-biased dimorphism to exist at equilibrium, lifetime selection pressures must be for an optimum body size which is smaller in males than in females (Hedrick and Temeles 1989).

We are currently estimating lifetime selection pressures on both males and females in the waterstrider, *Aquarius remigis*. Here we address the relationship between female body size and lifetime fecundity as a major component of the forces affecting the evolution of female body size, and hence, sexual size dimorphism. In addition, a detailed examination of the relationship between components of female body size and measures of reproductive success (egg size, egg number) provides us with information on the mechanism of selection on body size in females and suggests the components of size that may be the actual targets of selection in natural populations.

Evidence of the reproductive advantages of body size

A number of interspecific studies have examined the relationships between body size and egg size and between body size and fecundity (e.g. Berrigan 1991; Sivinski and Dodson 1992) and in general both of these relationships are positive. However, mechanisms operating on an interspecific (or interpopulation) level may be quite different from those operating within a population and may result in divergent allometric relationships within and among populations or species (Rayner 1985). Because we are concerned with the mechanism of selection acting on individuals, we will consider only intrapopulation studies.

Within species, descriptive studies usually support the proposal of Darwin (1874) that larger females will produce more eggs. While environmental variables [e.g. temperature (Wiklund et al. 1987; Buns and Ratte 1991; Ohgushi 1991) and food quantity and quality (Buns and Ratte 1991; Blanckenhorn et al. 1995)] may have a large impact on fecundity, empirical studies generally show that fecundity increases with female body size (Thornhill and Alcock 1983; Peters 1983; Reiss 1989; Honek 1993; Roff 1992; but see Leather 1988). The functional basis for this relationship is most commonly assumed to be a space constraint (i.e. larger females have more space to hold eggs), although some authors have suggested that the constraint may be the space available to store materials used for making eggs or the size of organs necessary for egg production (Wickman and Karlsson 1989; Roff 1992).

In addition to the relationship between body size and fecundity, larger females may produce larger eggs which in turn have a higher probability of survival (Wiklund et al. 1987). Intraspecific analyses often find a positive association between female size and egg size (Roff 1992, p. 354; Nakaoka 1994; Rowe 1994; Boyle et al. 1995) although there are a notable number of studies that find no relationship (Wiklund and Karlsson 1988; Solbreck et al. 1989; Beamish et al. 1994; Haddon 1994; Thorbjarnarson 1994). Empirical support for the fitness advantage of increased egg size is limited, but the trend in animals seems to be a positive one (insects: Araujolima 1994; Babry 1994; fish: Fox 1994; Rijnsdorp and Vingerhoed 1994; see Roff 1992, p. 350 for a table of studies).

Since larger females may be at a fitness advantage either by producing larger eggs or by producing more eggs, there is a possible conflict which may obscure relationships with female body size. Smith and Fretwell (1974) assumed that there should be a trade-off between number and size of eggs when resources are limited. The limiting resource can be either storage space for eggs or materials for making eggs (Roff 1992). In general, there is empirical support for such a trade-off (Roff 1992, p. 357), although only a small number of these studies have been conducted on insects (but see Carrière and Roff 1995).

Components of body size

Estimating relationships between components of size and reproductive parameters allows us to determine whether body size itself or specific components of size are the targets of fecundity selection. Wickman and Karlsson (1989) point out that fecundity is expected to be more highly correlated with abdomen mass than with body mass, presumably because of limited space or resources in the abdomen. However, we know of only one other study which has examined the relationship between abdomen size and fecundity (Griffith 1994). Fecundity is often represented as a function of total mass or total length (Wickmann and Karlsson 1989), but other "indicator" measures of body size are also common (e.g. head width, thorax length, tarsal length, wing length). While it may seem a reasonable assumption that components of body size are all highly correlated, this is not always the case (Alpatov and Boschko-Stepanenko 1928; Banks and Thompson 1987; Fairbairn 1992; Griffith 1994). Further, some of these components of size may be targets of other types of selection. Both head width and tarsal length have been shown to be targets of trophic selection (Key 1970; Rietschel 1975; Kritsky 1977; Mason 1986) and sexual selection (Riek 1970; Atchley 1971; Popham et al. 1984; Crespi 1986).

Sexual dimorphism and fecundity selection in waterstriders

The waterstrider, *Aquarius remigis*, is both common and abundant in North America (Polhemus and Chapman 1979). In our study populations in Quebec, and in Canada in general, *A. remigis* have one generation per year, overwinter as adults and reproduce in spring (Galbraith

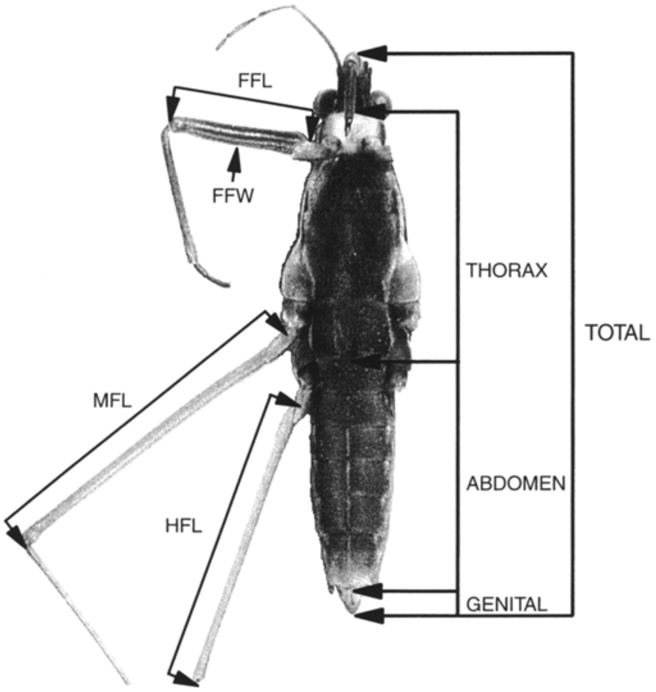

Fig. 1 Ventral view of a female *Aquarius remigis* with morphological measurements indicated (*TOTAL* total length, *ABDOMEN* abdomen length, *THORAX* thorax length, *GENITAL* genital length, *FFW* forefemoral width, *FFL* forefemoral length, *MFL* midfemoral length, *HFL* hind femoral length

and Fernando 1977; Fairbairn 1985). Female *A. remigis* are long and thin, about 15 mm long but only 3 mm across (Fig. 1; Fairbairn 1992). Total length has been shown to be significantly correlated with instantaneous fecundity in field caught waterstriders of three species of waterstriders including *A. remigis* (Fairbairn 1988). As in most animals, food availability has an extremely large effect on fecundity in waterstriders (Kaitala 1987; Rowe and Scudder 1990; Blanckenhorn 1991a; Blanckenhorn et al. 1995), but evidence exists for body size effects on fecundity even under experimentally manipulated food levels (Blanckenhorn 1991a, 1994).

One reason to suspect that selection may be acting directly on components of size in this species is the disparity in sexual dimorphism of components of size and total length. While females are only about 10% larger than males in terms of total length, the length of their abdomens is 80% larger than males (Fairbairn 1992; Preziosi and Fairbairn 1996), indicating that abdomen length is a much larger proportion of total length in females than in males. When several measures of body size were analyzed using principle components analysis, Fairbairn (1992) found that male and female *A. remigis* differ in shape independently of their difference in size. We present here a detailed examination of the statistical relationships between female body size (measured as total length), components of body size and measures of female reproductive capacity in the waterstrider *A. remigis* as a step in understanding the mechanisms and targets of fecundity selection. We examine the effects of total length and components of size on lifetime fecundity and egg size. We also test the hypothesis of a trade-off between egg size and number and describe the scaling of abdomen length with total length and thorax length.

Methods

Experiment 1: size, components of size and fecundity

A. remigis were collected from a stream near Mont-St-Bruno, Quebec (45° 39'N, 72° 33'W) in September of 1991, and overwintered *en masse* in plastic containers with sphagnum moss using the protocol of Fairbairn (1988). As soon as they were removed from diapause, 90 females were placed in individual plastic containers (37 cm by 25 cm) filled to a depth of 6 cm with tap water and equipped with an airstone. All waterstriders were kept at 20 ± 2°C and a 12:12 photoperiod. Each container was supplied with a bisected styrofoam cup and foam blocks as resting and oviposition sites. Females received half of a frozen mealworm (*Tenebrio* sp.) and six frozen *Drosophila melanogaster* per day. Old food items were removed each day. Each of the 90 females was mated to 1 of 30 males by placing the male in a female's container for 1 day in turn (i.e. each female had a male present on every 3rd day). Eggs were counted and removed daily. Females were maintained until death and then frozen. Lifetime fecundity (hereafter fecundity) was estimated as the sum of daily egg counts for each female.

An important consideration in measuring body size in insects is hypogastry, the distention of the abdomen in gravid females. While hypogastry affects both length and width of the abdomen in some species of waterstriders (Andersen 1982, p. 318), a paired comparison of total length of *A. remigis* females before and during the reproductive season showed no significant change (R.F. Preziosi, unpublished data). In contrast, abdomen width shows a large degree of variation throughout the reproductive season (personal observation). Because of this inconsistency we have used abdomen length as our measure of abdomen size when estimating lifetime fecundity.

Measurements of individuals (Fig. 1) were made using a computer digitizing system attached to a dissecting microscope: total length, defined as the distance from the point of curvature of the anteclypus to the most distal point of the last genital segment; thorax length, defined as the distance from the most anterior medial point of the prosternum to the most posterior medial point of the metasternum; abdomen length, defined as the distance from the most anterior medial point of the second abdominal sternite to the most posterior medial point of the seventh abdominal sternite; genital length, defined as the distance from the most posterior medial point of the seventh abdominal sternite to the most medial distal point of the last genital segment; forefemoral width, defined as the width at the midpoint of the forefemur; forefemoral length, midfemoral length, and hind femoral length all defined as the distance from the most proximal point of the trochanter to the most distal point of the femur. Complete sets of measurements were not possible for three of the females due to damage during handling of the frozen specimens. All analyses were conducted on the remaining 87 females. We also note that preservation, either by freezing or storage in 70% ethanol, had no significant effects on any of the measures of size in this species (Brennan and Fairbairn 1995).

Since there was no significant paternal effect on fecundity ($F = 0.85$, $df = 27$, $P = 0.675$), fathers were not considered in the analyses. Log transformed values were used for all analyses except principal components analysis (PCA) (Roff 1992). The relationships between total length and components of size and fecundity were estimated using ordinary least squares regression since we expect the error in measuring morphometric variables to be much smaller than the error in measuring fecundity (McArdle 1988), and because we are examining the data for functional relationships (Rayner 1985). Significance levels for the multiple models were adjusted using the Bonferroni procedure for multiple comparisons. Allometric relationships between morphometric traits were estimated using reduced major axis regression (RMA; Rayner 1985; McArdle 1988). PCA (based on the covariance matrix) was used as a method of examining the multivariate variability of body size components. Independent effects of size (isometric and allometric) and shape were estimated by extracting the first two principle components from the morphometric data (Manly 1986; LaBarberra 1989) and regressing fecundity on the component scores for each female. Untransformed variables were used in the PCA since standardizing the variables removes scale effects (Klingenberg 1996).

Experiment 2: size, components of size and egg size

Individuals were collected from creeks near Bromont, Quebec (45°18'N, 72°32'W) and Morin Heights, Quebec (45°57'N, 74°10'W) in May and June 1991. A total of 72 females were preserved in 70% ethanol and later measured using a digitizer attached to a dissecting microscope. Measurements of females were made according to the methods of Brennan and Fairbairn (1995) which differ slightly from the above methods in the landmarks used. Females were then dissected and all eggs removed. Eggs of *A. remigis* are cylinders with a length roughly 3 times their diameter. Unfortunately, the accuracy in measuring width of these eggs is low compared to accuracy in measuring length. Because of the measurement error in egg width, we used egg length as our only measure of egg size. Length of mature eggs (defined by the presence of a chorion) was measured using a computer digitizer and the average egg length calculated for each female. Relationships between total length, components of size, egg number and egg length were estimated as above. The trade-off between egg length and number was estimated using a partial correlation between egg length and egg number having controlled for the effects of abdomen length. All statistical models were originally run with population as a covariate. Since the population effect was never significant (all $P > 0.30$), the population term was dropped from all models to simplify interpretation and presentation.

Results

Experiment 1: size, components of size and fecundity

Summary statistics for lifetime fecundity and size measures are given in Table 1. Total length (Fig. 2A) is a significant univariate predictor of fecundity, as are thorax length, abdomen length (Fig. 2B), midfemoral length and forefemoral length (Table 2). Hind femoral length, forefemoral width and genital length were not significantly related to fecundity in univariate models (Table 2). When a multivariate model including all measures (except total length) was used, only abdomen length remained a significant predictor of fecundity (Table 2; full model $F = 3.676$, $df = 7{,}78$ $P = 0.002$, $r^2 = 0.25$).

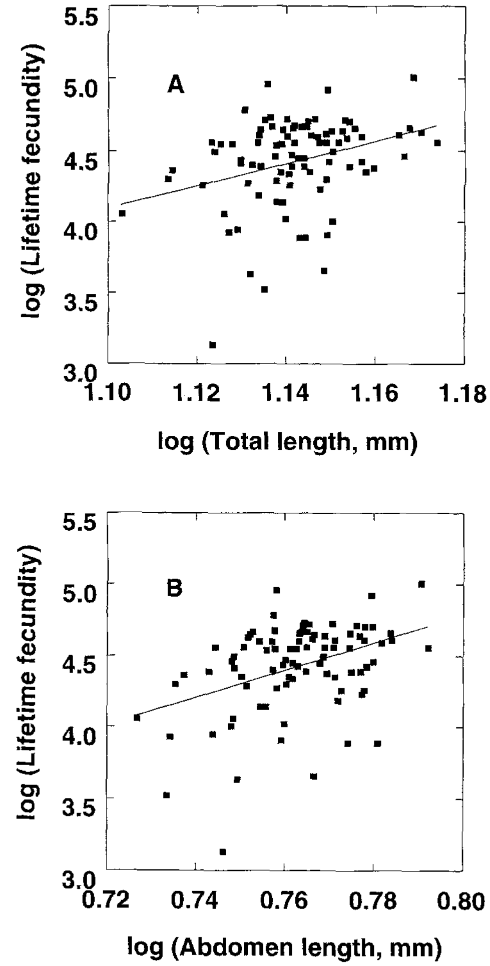

Fig. 2 Relationships between lifetime fecundity and **A** total length and **B** abdomen length. *Solid lines* are least squares regression lines

The relationship between abdomen length and total length (Fig. 3A) is not significantly different from isometry (RMA slope = 1.043, 95% confidence intervals of

Table 1 Means, SDs, and PCA loadings of female trait values; $n = 87$

Trait	Descriptive statistics		PCA loadings	
	Mean	SD	Component 1 (size)	Component 2 (shape)
Lifetime fecundity	87.29	23.5		
Total length (mm)	13.87	0.41		
Hind femoral length (mm)	8.12	0.37	0.330	–0.143
Midfemoral length (mm)	9.26	0.34	0.310	0.050
Forefemoral length (mm)	4.49	0.14	0.075	0.049
Forefemoral width (mm)	0.47	0.04	0.010	0.005
Genital length (mm)	0.72	0.12	0.011	0.013
Abdomen length (mm)	5.79	0.18	0.072	0.059
Thorax length (mm)	5.87	0.25	0.136	0.174
Eigenvalue			0.234	0.060

Table 2 Experiment 1: univariate and multivariate regression coefficients for body size measures as predictors of log(lifetime fecundity); $n = 87$.

Trait (log transformed)	Univariate coefficient	Univariate r^2	Multivariate coefficient
Total length	7.896*	0.10	–
Thorax length	4.714*	0.08	1.033
Abdomen length	9.656*	0.16	7.058*
Genital length	–0.474	0.02	–1.318
Hind femoral length	2.969	0.03	–1.476
Midfemoral length	6.539*	0.11	3.848
Forefemoral length	8.169*	0.13	3.565
Forefemoral width	1.449	0.03	0.256

* P<0.05

Table 3 Experiment 2: univariate and multivariate regression coefficients for body size measures as predictors of log (instantaneous fecundity); $n = 72$

Trait (log transformed)	Univariate coefficient	Univariate r^2	Multivariate coefficient
Total length	6.256*	0.35	–
Head and thorax length	6.383*	0.28	–0.049
Abdomen length	7.040*	0.34	4.949*
Genital length	2.151*	0.15	0.902
Abdomen width	6.797*	0.26	1.784

*P<0.05

0.872–1.214). From this result it appears that abdomen length increases at the same rate as total length. Although it is common to examine allometries by regressing traits on total size (length or weight) there is a conceptual and statistical difficulty with this method when the trait is a subset of total size. Because total length is made up, in large proportion, of abdomen length (40% on average), there is a built-in component of isometry in this relationship which obscures the relationship between abdomen length and the rest of body length. To examine how abdomen length changes as the rest of body length increases it is more informative to replace total length with total length minus abdomen length or another major component of total length such as thorax length. The relationship between abdomen length and thorax length is presented in Fig. 3B and shows significant hypoallometry (we use hypoallometry here as indicating a slope between 1 and 0, RMA slope = 0.710, 95% confidence intervals of 0.568 to 0.853). Thus, abdomen length increases at a slower rate than thorax length and larger females have relatively smaller abdomens.

Principal components analysis of morphological measures produced the loadings in Table 1. The first component (PC1) explains variability due to isometric and allometric size, while the second component (PC2) explains variability due to changes in shape that are independent of size (Manly 1986; Bookstein 1989; LaBarberra 1989). PC1 (size) explains 61.4% of the variability in body size traits and PC2 (shape) explains 15.6%. When fecundity was regressed on component scores for females, both components were significant predictors of fecundity [Log(fecundity) = 4.425 + 0.211 (PC1) + 0.324 (PC2), $P = 0.002$ and $P = 0.016$ respectively, model $r^2 = 0.16$]. Thus, the variance in fecundity among females is partially explained by differences in both size and shape.

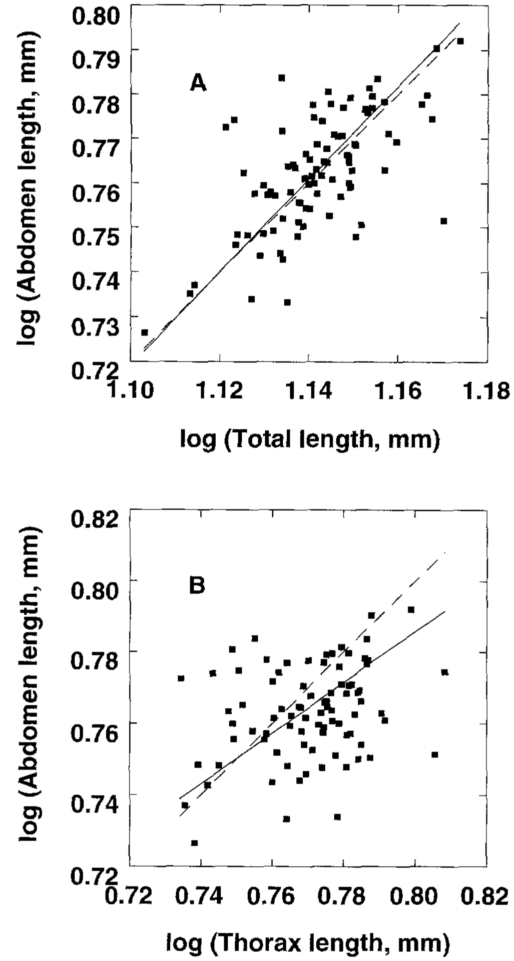

Fig. 3 Relationships between abdomen length and **A** total length and **B** thorax length. *Solid lines* are reduced major axes. *Dashed lines* represent isometry (1:1)

Experiment 2: size, components of size and egg size

As in the above analysis, several components were significant predictors of fecundity (Table 3). The multivariate model for this data set included all body size measures available: head and thorax length, abdomen length, abdomen width, and genital length. Abdomen length was the only significant predictor in the multivariate analysis (Table 3). Although egg size did differ significantly among females ($F = 13.073$, $P < 0.001$), mean egg size was not significantly related to either total length ($b = -0.036$, $df = 70$, $P = 0.651$, $r^2 = 0.003$) or abdomen length ($b = -0.066$, $df = 70$, $P = 0.469$, $r^2 = 0.008$). The trade-off between egg length and number was examined using a partial correlation between log (egg length) and log (egg number) having controlled for the effects of log (abdomen length). With abdomen length effects removed, increasing egg size had a significant negative effect on instantaneous fecundity ($r = -0.525$, $n = 72$, $P < 0.001$). The magnitude of the effect of changes in egg length on egg number (instantaneous fecundity) was estimated by interpolation using a regression of egg number on adbomen length and egg length. For an average-sized female a decrease of one SD in egg length (*c.* 66 μm) increases fecundity by 2.23 eggs. Because the average instantaneous fecundity was 18.94 (± 9.39), the effect of egg size is biologically significant.

Discussion

Fecundity increases with body size in *A. remigis*. While fecundity is expected to increase with body size in insects in general (Honek 1993), effects of environmental factors such as temperature and food quantity and quality may obscure the relationship, especially in natural populations (Leather 1988). Keeping this in mind, we can still get an idea of the selective force of this relationship by estimating selection intensity from a regression of relative fecundity on standardized total length (*sensu* Lande and Arnold 1983). The resulting selection intensity on total length (0.088) is highly significant ($P = 0.002$) and, assuming a heritability of 0.5 (Mousseau and Roff 1987) and constant variance, would be sufficient to change the mean total length by 0.5 standard deviations in 12 generations.

The association between fecundity and body size is most often interpreted as indicating that larger females have more space to store eggs and more resources to produce eggs (e.g. Howard and Kluge 1985). The target of fecundity selection under this interpretation would be abdomen size. Among the set of body size traits we examined in *A. remigis*, several components of size were significant univariate predictors of both lifetime and instantaneous fecundity, but abdomen length was the only significant predictor in either multivariate model. This suggests that fecundity selection is indeed targetted at abdomen length in natural populations. As above, we can get an idea of the effect of this relationship by estimating the selection intensity on abdomen length. With fecundity as our measure of fitness the selection intensity on abdomen length is 0.110 and is highly significant ($P < 0.001$).

If the relationship between fecundity and abdomen length is based on the fact that abdomen volume limits the number of eggs that a female can carry, we would expect the coefficient from the regression of log fecundity on log abdomen length to be 3.0 or smaller. However, the coefficient from this relationship in *A. remigis* is more than twice this value (7.040) and suggests that the increase in fecundity for larger females is due to more than a simple increase in abdomen volume. We discuss this interpretation below. This exponent is at the high end of the range that Wootton (1979) reported for fish and suggests that energy throughput may be more important than holding capacity. Other explanations for increased fecundity with increased body size may be size of particular organs or an increased ability of larger individuals to procure resources required for egg production (Roff 1992). Body size has been associated with territoriality in *A. remigis* (Rubenstein 1984; Kaitala and Dingle 1993). Blanckenhorn (1991a, b) has shown that dominant females in foraging situations had significantly higher fecundity and significantly greater weight gain. However, territoriality does not explain the results of our study since females were maintained individually and their only competitor was a male who was present only one-third of the time. An alternative explanation may be the effect of egg size discussed below.

While both total length and abdomen length are significant predictors of fecundity, the regression of fecundity on principle component scores indicates that there is an effect of shape on fecundity that is independent of size. The correlations between components and size measures indicate that the shape effect is, at least in part, an effect of relative leg and body sizes. The shape component is, by definition, independent of size and does not include measures of proportion (Bookstein 1989). We currently have no specific interpretation of this shape effect.

A cautionary note that comes from our results is that "indicator" variables of body size may be very poor predictors of fecundity. If abdomen size is the best predictor of fecundity in a species, then the use of an indicator variable (e.g. head width or tarsal length) because it is highly correlated with body size places several intermediate correlations between fecundity and the indicator variable. For example, while all of our body size measures are positively correlated, not all are significant predictors of fecundity (Table 2).

Wickman and Karlsson (1989) examined the allometry of abdomen size in three species of butterflies and one species of fly, and found hyperallometric relationships (slope significantly greater than 1) in all species. These relationships are subject to the difficulties mentioned in our methods (i.e. nonindependence of x and y). However, Wickman and Karlsson also demonstrated that proportional abdomen size was positively related to body size. Since the bias caused by regressing y/x on x would be to underestimate the slope, the positive slopes they found confirm their hyperallometric results. Wickman and Karlsson interpret this result as an increased reproductive effort in larger females. Our results for *A. remigis* differ in that abdomen length increases at a slower rate than total length, and thus, that larger females have relatively smaller abdomens. Following Wickman and Karlsson's argument, we would expect larger females would have lower reproductive efforts. However, our results indicate that larger females produced more eggs over their lifetimes than did smaller females. Thus, in *A. remigis* larger females have greater reproductive efforts even though they have relatively smaller abdomens. This is presumably because the rate at which fecundity increases with abdomen length is greater than the rate at which volume increases with abdomen length. While we did not measure abdomen volume directly, a check of this can be made using the linear abdomen measures from our second experiment and assuming a cylindrical shape of the abdomen for volume estimation. The scaling of abdomen volume on abdomen length gives a coefficient of 2.447, much less than the scaling of fecundity on total length. Fairbairn (1992) compared females within populations of *A. remigis* and found that the reduction in total length from the larger winged morph to the smaller wingless morph was explained to a much greater extent by a reduction in other components of size than by a reduction in abdomen length. One possible explanation for the hypoallometric relationship between abdomen and thorax size is that females who grow up in nutritionally poor environments may maintain abdomen size at the cost of other components of total length.

Our final consideration is the trade-off between fecundity and egg size. Smith and Fretwell (1974) modeled the evolution of optimal clutch size based on the assumption of a negative trade-off between egg size and number. Empirical evidence appears to support this trade-off, although few studies have included invertebrates (Roff 1992;, Carrière and Roff 1995; Weigensberg and Roff, unpublished work). In *A. remigis* this trade-off is present: for a given abdomen length, there is a negative relationship between egg number and egg size. Since there is no relationship between egg size and abdomen length, females may increase fecundity by reducing egg size in a manner which is, at least partially, independent of body size. Likewise, selection on egg size will influence abdomen size only indirectly through effects on fecundity. This indicates that, for *A. remigis*, estimates of female reproductive fitness based on fecundity measures alone are sufficient and the inclusion of egg size measures are unlikely to provide additional information.

The general female-biased body size of animals is assumed to be driven by the relationship between abdomen size and fecundity. While there is abundant empirical support for a positive relationship between body size and fecundity, the relationship between abdomen size and fecundity remains largely untested. Our results indicate that, for both lifetime lab estimates and instantaneous field estimates for a waterstrider, the target of fecundity selection for larger total length is actually abdomen length. In contrast to previous work, the relationship between abdomen length and thorax length in *A. remigis* is hypoallometric (i.e. larger females have relatively smaller abdomens), perhaps due to conservation of abdomen size in females which develop under poor conditions. Thus, while sexual size dimorphism is a result of lifetime selection pressures on each of the sexes, our results indicate that the evolution and maintenance of sexual size dimorphism may be strongly influenced by selection acting on abdomen size.

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