

CRITICAL APPRAISAL

Critical appraisals allow the analytical review of existing knowledge on current topics of significance in ecological entomology. They should assess the worth or quality of the work in the field and suggest areas for investigation.

Fitness and body size in mature odonates

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Summary. The relationship between body size and fitness components in odonates was examined using a meta-analysis of 33 published studies. There was a positive and significant overall effect of body size on mating rate and lifetime mating success among males. There was also a weaker but still significant positive effect of body size on survivorship of males. The relationship between body size, mating rate, longevity, and lifetime mating success differed significantly between males of territorial and nonterritorial species. The effect of body size was significant for all fitness components in territorial species but significant only for longevity and lifetime mating success in nonterritorial species. Effect sizes appeared to be strongest on longevity in both sexes, and on male mating rate in territorial species. Other effect sizes, even when significant, were small. Despite a much smaller data set, female fitness also increased significantly with body size. Both clutch size and longevity showed a significant positive relationship with body size. These results suggest that there is a general fitness benefit to large size in odonates. Nevertheless, significant heterogeneity is apparent in this effect, which can be attributed to sex, mating system, and fitness component. Finally, these analyses point to inadequacies in the current data that need further study before the potentially rich patterns in size effects on fitness can be explored more thoroughly.

Key words. Damselflies, dragonflies, fitness components, meta-analysis, size effects.

Introduction

Fitness is generally believed to be an increasing function of body size in animals (Clutton-Brock, 1988; Reiss, 1989), and particularly among insects (Thornhill & Alcock, 1983; Honek, 1993). Among insects, a positive correlation between female body size and fecundity has been demonstrated in several orders (Elgar & Pierce, 1988; Partridge, 1988; Berrigan, 1991; Kasule, 1991; Peckarsky *et al.*, 1993; but see Leather, 1988). Studies of territorial species of insects have shown that larger males have a clear advantage in obtaining and defending territories to which

females are attracted (Alcock, 1981; Severinghaus *et al.*, 1981; Crespi, 1986). Similarly, female choice for large males is widespread among insects (reviewed in Thornhill & Alcock, 1983; Choe & Crespi, 1997). Upon this foundation, a large body of theory in sexual selection and life-history evolution rests on the assumption that one or more components of fitness is an increasing function of body size (e.g. Roff, 1992; Stearns, 1992; Andersson, 1994). Although strong positive effects of body size on fitness are widespread, there is a growing list of studies reporting no effect or even negative effects of body size on fitness components (Clutton-Brock, 1988; Andersson, 1994).

Notably, even studies of closely related species often diverge in their conclusions. Recent research on water striders illustrates these points. Fairbairn (1988) reported significant interspecific variation in the effects of size on fitness components for both females and males among closely related species of water striders. Moreover, analogous studies of fitness components in

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the same species often lead to divergent conclusions. Klingenberg and Spence (1997) were unable to find any effect of female body size on fecundity following an exhaustive study of the water strider *Gerris buenoi*. On the other hand, Fairbairn (1988) reported significant positive effects of size on fecundity in the same species, and no effect of male size on the mating success of *G. buenoi*. Rowe and Arnqvist (1996), however, found a strong effect of size on male mating success in the same species. In such cases as these, it is not immediately clear whether any general statement about the relationship between size and fitness is possible!

There may be true differences in body size effects among species or even populations. Alternatively, the effects of body size may be so weak that only large studies can detect them reliably. Similarly, body size effects may truly vary between sexes and fitness components, but only direct comparison will reveal these differences. One way out of the mire is to analyse these many separate studies in a single statistical analysis using the tools of meta-analysis (Rosenthal, 1984; Gurevitch *et al.*, 1992; Cooper & Hedges, 1994; Arnqvist & Wooster, 1995). Such a meta-analysis has been conducted for the case of body size effects on male mating success in water striders (Arnqvist *et al.*, 1996). The effect of body size was found to be weakly positive across the group, highly variable, and statistically significant. Variation among individual studies could only be attributed to inter-population differences, not to differences among species or higher taxonomic levels (Arnqvist *et al.*, 1996).

The data regarding size effects on fitness of damselflies and dragonflies (Odonata) are analogous to water striders in their variability, generally weak effects, and therefore a need for synthesis. Several studies have reported significant positive correlations between body size (or a correlate) and a fitness component in both males and females (e.g. Banks & Thompson, 1985, 1987; Harvey & Corbet, 1985; Harvey & Walsh, 1993; Cordero, 1995). Other studies have reported weak negative effects or no effect of body size on fitness components (e.g. Fincke, 1986, 1988; Anholt, 1991; Richardson & Baker, 1997). The potential sources for these conflicting results include differences between males and females and differences between males of territorial and nonterritorial species.

Variance in female fitness may be partitioned into several factors such as variance in longevity, clutch size, clutch production rate, and clutch number. Banks and Thompson (1987) found that variance in longevity explained most of the variance in female fitness (70%) in a damselfly *Coenagrion puella*, with variance in clutch production rate explaining 20%, and variance in clutch size explaining 10% of the variance. Thus, to a great extent, the overall effect of body size on female fitness may depend on which fitness component is measured. Variance in male lifetime mating success, which is a good measure of fitness in male odonates (Banks & Thompson, 1985), may be partitioned similarly into variance in longevity and variance in mating rate.

Size effects on mating rate are believed to be less important in nonterritorial (scramble competition polygyny) male dragonflies (e.g. Banks & Thompson, 1985; Anholt, 1991, 1992, 1997; Anholt *et al.*, 1991). The differences in the effect of body size

between territorial and nonterritorial males should be particularly pronounced in mating rate. Body size is expected to have a positive effect on territorial male mating rate due to the advantages of size in obtaining and defending territories to which females are attracted, but may have a negative effect on nonterritorial male mating rate because of the importance of agility in searching for mates (Banks & Thompson, 1985; Anholt *et al.*, 1991). Variance in lifetime reproductive success may also be associated closely with variance in longevity (Banks & Thompson, 1985, 1987; Leather, 1988), so even among nonterritorial males, where larger size may not confer any advantages in mating rate, larger males may have higher reproductive success because of a longer reproductive lifespan.

In the study reported here, a meta-analysis was conducted of the effect of body size on fitness components in odonates. The effect sizes were contrasted between males and females and between males of territorial and nonterritorial species. Further, an attempt was made to determine which component of fitness was affected most by body size and how it contributes to the relationship between overall fitness and body size. The analysis points to several weaknesses in the current data set that need to be addressed before a more complete understanding of the relationship between odonate size and fitness can be achieved.

Methods

Thirty-three published studies on the relationship between body size and a fitness component were compiled to form the data set (Appendix, Tables A1 and A2). Where there were multiple estimates of body size effects on a single variable in a single population, each measure was converted into a *z*-transformed correlation, and these were averaged to produce a single effect size. Specific *a priori* predictions were tested by partitioning this data set. The data set was first partitioned by sex. The male data set was then partitioned into four subsets: longevity, mating rate, lifetime mating success, and territory defence success. Each data set was analysed separately. A second set of analyses was conducted based on another *a priori* prediction: that the heterogeneity in the components of male fitness could be explained by differences in effect size between territorial and nonterritorial males. The first three subsets were therefore partitioned further into territorial and nonterritorial groups for comparison. The female data set was partitioned into four subsets for further analyses: longevity, clutch production rate, clutch number, and clutch size. Because the sample size for each female data set was very small, these studies that examined separate components of fitness were combined into a single analysis to estimate the overall effect of size on female fitness. Estimates of the correlation between body size and fitness in separate populations of the same species (e.g. Cordero, 1995) were treated as separate samples.

The following method was employed in the analysis of each data set. If the statistic describing the effect of size in a single study was not reported as a correlation, an effect size (*d*) was computed from the reported statistic (Siegel, 1956; Rosenthal, 1984). The effect size (*d*) was then converted into a correlation through the following equation (Rosenthal, 1984):

$$r = \frac{d}{\sqrt{d^2 + 4}} \quad (1)$$

The correlations were then transformed to Fisher's $z(r)$:

$$z_{r(i)} = \frac{1}{2} \ln \left[\frac{1+r}{1-r} \right] \quad (2)$$

The meta-analysis was performed by computing a weighted mean effect size. This was accomplished by multiplying the effect size [$z(r)$] of each study with the inverse of the variance of the effect size. For z -transformed correlations, the variance is related to the sample size of the study and is equal to $1/[(\text{the sample size}) - 3]$ (Cooper & Hedges, 1994). The effect sizes of all studies multiplied by the inverse variance of the effect size of that study were then summed and divided by the sum of the inverse variances, yielding the weighted mean effect size.

$$\bar{z}_r = \frac{\sum (n_i - 3) z_{r(i)}}{\sum (n_i - 3)} \quad (3)$$

A Z statistic, testing whether the weighted mean effect size was significantly different from 0, was computed through eqn 4, and a one-tailed P -value was obtained from a Z-distribution table (Cooper & Hedges, 1994). Large body size advantage was initially proposed so all tests were one tailed:

$$Z = \frac{\bar{z}_r}{\sqrt{\frac{1}{\sum (n_i - 3)}}} \quad (4)$$

Finally, to test the assumption of the meta-analysis, that the effect sizes of all studies are drawn from a normal distribution, a chi-squared test with $k - 1$ degrees of freedom was computed:

$$\chi^2 = \sum \frac{(z_{r(i)} - \bar{z}_r)^2}{\frac{1}{(n_i - 3)}} \quad (5)$$

A chi-squared test was also performed to test the hypothesis that the weighted mean correlation between body size and longevity, mating rate, and lifetime mating success differed between studies of territorial and nonterritorial males. All calculations were performed on Microsoft Excel, 6.0 (Microsoft Corporation, Redmond, Washington).

Results

Males

Analysis of the entire data set revealed that male longevity was an increasing function of body size (Table 1, Fig. 1a), however a chi-squared test of the homogeneity of the data set revealed that the data set had some heterogeneity. A further analysis separating nonterritorial and territorial samples revealed that the differences between the two groups explained

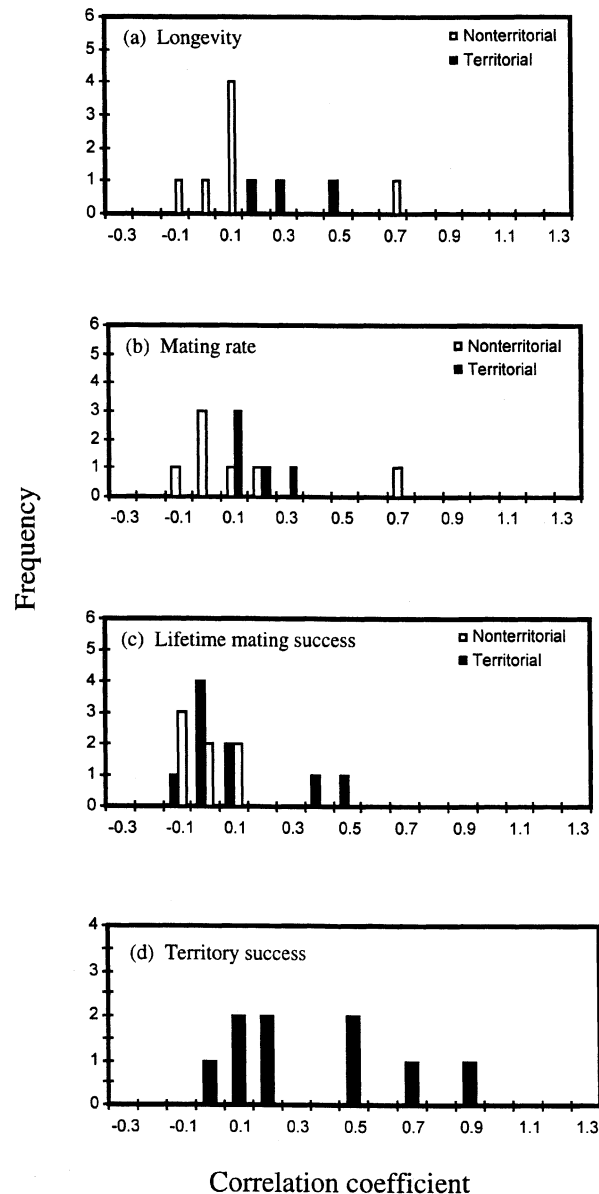


Fig. 1. Frequency distribution of correlations between male body size and (a) longevity, (b) mating rate, (c) lifetime mating success, and (d) territoriality success. (a)–(c) give separate distributions for territorial and nonterritorial males.

most of the heterogeneity of the data set (Table 2, Fig. 1a), with a single study in nonterritorial males (Forbes & Baker, 1990), which had a very large effect size, being the source of the remaining heterogeneity. The mean effect of body size was significant in territorial and nonterritorial males (Table 2). When the Forbes and Baker (1990) study that contributed the remaining heterogeneity in the nonterritorial sample was removed, the effect of body size on longevity was still significant in nonterritorial males [$z(r) = 0.039$, $P = 0.05$, $n = 6$].

The effect of body size on mating rate was significantly positive and highly variable (Table 1, Fig. 1b). Inspection of

Table 1. Results from meta-analyses on the relationship between male fitness components and body size. For male mating rate, the reported results refer to the analysis that excluded the Conrad (1992) study.

	Male longevity	Male mating rate	Male lifetime mating success	Male territoriality success
Mean effect size $z(r)$	0.059	0.091	0.070	0.401
Variance of mean	0.0005	0.0006	0.0003	0.0015
Upper 95% CI	0.081	0.115	0.086	0.44
Lower 95% CI	0.036	0.066	0.053	0.36
Z of mean effect size	2.57	3.74	4.22	10.36
P-value of Z	0.010	<0.001	<0.001	<0.001
Chi square (heterogeneity)	28.609	23.84	63	92
P-value of chi square	<0.005	<0.01	<0.005	<0.005
d.f.	9	11	15	8

Table 2. Results from meta-analyses on the relationship between body size and fitness components in territorial and nonterritorial males.

	Male longevity		Male mating rate		Male lifetime mating success	
	Territorial	Nonterritorial	Territorial	Nonterritorial	Territorial	Nonterritorial
Mean effect size $z(r)$	0.27	0.047	0.16	-0.005	0.15	0.047
Variance of mean	0.01	0.0006	0.0010	0.0014	0.0012	0.0004
Upper 95% CI	0.37	0.07	0.19	0.037	0.18	0.066
Lower 95% CI	0.17	0.023	0.13	-0.042	0.11	0.029
Z of mean effect size	2.67	2.01	5.04	-0.12	4.21	2.52
P-value of Z	0.004	0.022	<0.001	0.452	<0.001	0.006
Chi square (heterogeneity)	2.13	21.9	3.99	8.42	41.53	15.24
P-value of chi square	>0.25	<0.005	>0.25	>0.1	<0.005	<0.025
d.f.	2	6	4	5	8	6
Chi square (territorial vs. nonterritorial)	4.6		11.44		6.23	
P-value of chi square	<0.05		<0.005		<0.025	
d.f.	1		1		1	

Table 3. Results from meta-analyses on the relationship between female fitness components and body size.

	Female longevity	Female clutch production rate	Clutch number	Clutch size	Female fitness
Mean effect size $z(r)$	0.11	-0.037	0.013	0.34	0.076
Variance of mean	0.0021	0.0047	0.0019	0.007	0.0008
Upper 95% CI	0.16	0.03	0.057	0.43	0.104
Lower 95% CI	0.07	-0.105	-0.031	0.26	0.047
Z of mean effect size	2.52	-0.54	0.292	4.1	2.618
P-value of Z	0.006	0.295	0.385	<0.001	0.004
Chi square (heterogeneity)	5.82	2.104	11.23	8	26.078
P-value of chi square	>0.1	>0.1	<0.005	<0.025	<0.005
d.f. ($k-1$)	3	1	2	2	8

the data (Fig. 1b) revealed that a single study (Conrad, 1992), which had a very large effect size, was responsible for most of the variability. When this study was removed, there was still a significant size effect on mating rate. The remaining heterogeneity in the data set could be explained by differences between the territorial and nonterritorial subsamples (Table 2, Fig. 1b). A separate analysis of territorial and nonterritorial

samples revealed that there was no effect of body size on mating rate in nonterritorial males (the Conrad study was excluded) but that body size had a significant effect on mating rate in territorial males (Table 2).

When all studies on lifetime mating success were examined, the analysis showed that body size had a significant effect on lifetime mating success (Table 1, Fig. 1c). The data set also

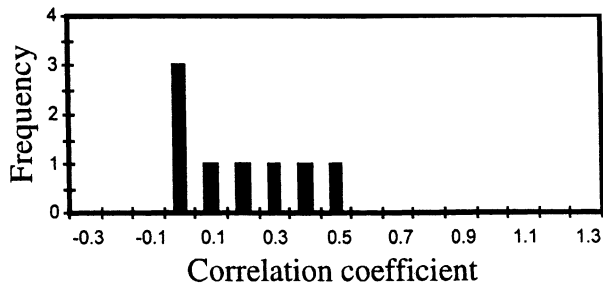


Fig. 2. Frequency distribution of correlations between female fitness components and body size.

contained heterogeneity (Table 1). An analysis showed that differences between territorial and nonterritorial males explained only some of this variability (Table 2). The effect of body size on lifetime mating success in territorial males was greater than in nonterritorial males, although the effect was significantly positive in both cases (Table 2). This result suggests that the positive effect of body size on longevity may be largely responsible for the positive effect of body size on lifetime mating success in nonterritorial males, because size had no effect on mating rate in nonterritorial species.

The mean effect size between body size and territory defend and contest success was positive, although the data set was highly variable (Table 1, Fig. 1d). Thus, body size is correlated positively with territorial defence, longevity, mating rate, and lifetime reproductive success in territorial males, whereas in nonterritorial males, body size is not correlated with mating rate, but is correlated positively with longevity and lifetime reproductive success.

Females

In females, body size was significantly positively correlated with clutch size and longevity but not correlated with clutch number or clutch production rate (Table 3). The data were not split into species with territorial and nonterritorial mating systems because there were no *a priori* hypotheses regarding effects of mating system and because the data set was very small. To get an overall picture of the effects of size on lifetime reproductive success, all the separate studies that examined the relationship between body size and the various fitness components were combined into a single data set for analysis. If any study measured more than one fitness component, only the mean effect size of these components was entered into the analysis. Not surprisingly, the data set was variable, but the mean effect size was positive and significant (Table 3, Fig. 2).

Discussion

This study supports the view that large size is associated with increased lifetime reproductive success in odonates of both sexes. In territorial species, larger males live longer, have greater mating rates, and therefore greater lifetime mating

success. Although large males in nonterritorial species do not have greater mating rates, they do tend to have longer reproductive lifespans and therefore greater lifetime mating success. Female fitness was similarly an increasing function of size, however the data set was too small to draw strong conclusions regarding any more specific hypotheses.

Male size and fitness

Clear support was found for the hypothesis that large size is associated more closely with male mating rate in territorial species than in nonterritorial species (Banks & Thompson, 1985). When the data set on mating rate was partitioned by mating system, effect size increased and remained significant for territorial males but the effect was lost for nonterritorial males. Mating rate and body size may however be confounded by age, as older males tend to have a higher mating rate (Banks & Thompson, 1985) and may be larger because large males often emerge earlier in the season (Richardson & Baker, 1997; Johansson & Rowe, 1999). This may be so particularly for territorial males with long residency periods, where older and larger males may pre-empt younger and smaller males from prime territories. In this data set, some studies, such as those by Koenig and Albano (1985, 1987) and Grether (1996), controlled for age or date of release into the population. Other studies, such as those by Harvey and Corbet (1985) and Fincke (1992), measured only the size differences between mated and unmated males and did not control for age. In the data sets where age was accounted for, body size remained significant [$z(r)=0.15$, $P<0.001$, $n=3$]. The effect of size on mating rate therefore appears to be real.

A significant, positive correlation between body size and longevity was found in both territorial and nonterritorial males. In territorial males, this contributed to the strong effect of body size on lifetime mating success, whereas it appears to have accounted wholly for the body size effects on lifetime mating success in nonterritorial males. How body size affects longevity is unclear. For example, there is no reason to expect that there is size-selective predation on adults; body size may simply be a correlate of overall individual condition (Andersson, 1994; Johnstone, 1995; Rowe & Houle, 1996), where condition is linked directly to survivorship.

Some remaining variance in the effects of size on fitness in territorial males may result from the diversity of types of territorial mating systems (Anholt *et al.*, 1991). Some species defend territories that act as oviposition sites for females; in other species, males defend territories in which mating occurs. This variation may change the relative benefits of intense territorial contests and therefore the fitness benefits of large size. The remaining variance in the relationship between body size and lifetime mating success in nonterritorial males may be explained by changing ecological circumstances. For example, warm and dry conditions may favour the survival of large males whereas wet and cool conditions may affect the survival of males of all sizes (Anholt, 1991). There is also evidence that a much stronger relationship between survival and body size may exist under conditions of food deprivation (Forbes & Baker,

1990; Leung & Forbes, 1997). Finally, density would be expected to affect the costs of territoriality through increased male–male competition.

Female size and fitness

This analysis indicates that fitness is an increasing function of body size in female odonates. Both clutch size and longevity were affected positively by large size in females although more data are required in order to confirm this relationship. It has been suggested that female size at emergence in odonates may have little effect on fecundity because feeding can take place in the adult as well as in the larval stage (Anholt, 1992; McPeck & Peckarsky, 1998). In such organisms, realised fecundity could depend largely on feeding in the adult stage. In contrast, data from this study suggest that size has some effect on fecundity. This effect may be modulated by adult feeding success. For example, female size could be important under low to intermediate food conditions, but under more benign conditions, smaller females may *catch up* in energy reserves. More research is required to clarify the relationship between size, adult feeding, and female fecundity.

Conclusions and future directions

This study is the first to attempt to synthesise statistically the published data on body size and fitness in odonates. This analysis provides considerable evidence of positive correlations between size and fitness for both males and females in territorial and nonterritorial species. The data set is small, and effect sizes, though significant, are often weak. Nevertheless, positive body size signals still appeared, and even small effects can have evolutionary significance. Analyses such as these are regarded as an essential first step towards making generalisations regarding size and fitness in odonates.

Three shortcomings of the current data set point to needs in future studies of body size and fitness in odonates. First, the data set is relatively small and limited to a few species; more data are needed. Second, the data set is biased towards one family, the Coenagrionidae; more studies of the remaining families are required. When these data are available, a phylogenetically controlled analysis of effect sizes would allow determination of whether effect sizes depend, in part, on membership in a given clade. Relatively few such phylogenetically controlled meta-analyses have been published to date, however the techniques are available (e.g. Arnqvist *et al.*, 1996). Finally, the study is limited to sexually mature individuals. Given that the processes that lead to the evolution of adult body size are by no means restricted to those occurring during the adult stage, more studies that explicitly link juveniles to adult stage are needed (e.g. Anholt, 1991; Johansson & Rowe, 1999).

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Appendix

Table A1. Correlations of all studies involved in the meta-analysis.

Study no.	Species	Mating system	Location	Fitness component	Population correlation	Sample size	Fisher's $z(r)$	Variance in $z(r)$
1	<i>Lestes disjunctus</i>	NT	Ontario	MR	-0.047	73	-0.047	0.0143
2	<i>Ischnura graelsii</i>	NT	Spain	ML	0.040	571	0.040	0.0018
2	<i>Ischnura graelsii</i>	NT	Spain	ML	0.100	275	0.100	0.0037
2	<i>Ischnura graelsii</i>	NT	Spain	LMS	0.030	571	0.030	0.0018
2	<i>Ischnura graelsii</i>	NT	Spain	LMS	0.042	275	0.042	0.0037
3	<i>Ischnura graelsii</i>	NT	Spain	FL	0.441	50	0.474	0.0213
4	<i>Ischnura verticalis</i>	NT	Ontario	Fecundity*	0.000	55	0.000	0.0192
5	<i>Enallagma ebrium</i>	NT	Ontario	MR	0.161	72	0.163	0.0145
5	<i>Enallagma ebrium</i>	NT	Ontario	MR	0.059	245	0.059	0.0041
6	<i>Enallagma hageni</i>	NT	Michigan	LMS	-0.030	512	-0.030	0.0020
7	<i>Enallagma hageni</i>	NT	Michigan	ML	-0.070	489	-0.070	0.0021
7	<i>Enallagma hageni</i>	NT	Michigan	LMS	-0.003	489	-0.003	0.0021
7	<i>Enallagma hageni</i>	NT	Michigan	CN	-0.090	298	-0.090	0.0034
8	<i>Sympetrum rubicundulum</i>	T	Pennsylvania	LMS	0.063	443	0.063	0.0023
9	<i>Sympetrum danae</i>	NT	Belgium	LMS	0.170	332	0.172	0.0030
9	<i>Sympetrum danae</i>	NT	Belgium	CPR	0.000	165	0.000	0.0062
10	<i>Sympetrum danae</i>	NT	Belgium	ML	0.108	263	0.108	0.0038
10	<i>Sympetrum danae</i>	NT	Belgium	FL	0.086	362	0.086	0.0028
11	<i>Coenagrion puella</i>	NT	England	CN	0.219	174	0.223	0.0058
12	<i>Coenagrion puella</i>	NT	England	MR	-0.168	186	-0.169	0.0055
12	<i>Coenagrion puella</i>	NT	England	ML	0.113	186	0.113	0.0055
12	<i>Coenagrion puella</i>	NT	England	LMS	-0.027	186	-0.027	0.0055
13	<i>Coenagrion puella</i>	NT	England	MR	0.065	87	0.066	0.0119
14	<i>Coenagrion puella</i>	NT	England	LMS	0.144	492	0.145	0.0020
15	<i>Nannophya pygmaea</i>	T	Japan	ML	0.500	17	0.549	0.0714
16	<i>Platthemis lydia</i>	T	New York	LMS	0.062	30	0.062	0.0370
17	<i>Platthemis lydia</i>	T	California	MR	0.125	41	0.126	0.0263
17	<i>Platthemis lydia</i>	T	California	ML	0.110	41	0.110	0.0263
17	<i>Platthemis lydia</i>	T	California	LMS	0.060	41	0.060	0.0263
17	<i>Platthemis lydia</i>	T	California	CN	-0.092	55	-0.092	0.0192
17	<i>Platthemis lydia</i>	T	California	CS	0.120	13	0.121	0.1000
18	<i>Platthemis lydia</i>	T	California	MR	0.130	502	0.131	0.0020
19	<i>Platthemis lydia</i>	T	California	LMS	0.100	38	0.100	0.0286
19	<i>Platthemis lydia</i>	T	California	LMS	0.112	65	0.113	0.0161
20	<i>Libellula luctuosa</i>	T	Colorado	LMS	0.574	108	0.654	0.0095
20	<i>Libellula luctuosa</i>	T	Colorado	TD	0.557	108	0.628	0.0095
21	<i>Hetaerina cruentata</i>	T	Mexico	LMS	0.042	13	0.042	0.1000
21	<i>Hetaerina cruentata</i>	T	Mexico	TD	0.133	35	0.133	0.0313
22	<i>Hetaerina americana</i>	T	California	MR	0.361	51	0.378	0.0208
22	<i>Hetaerina americana</i>	T	California	ML	0.300	51	0.310	0.0208
22	<i>Hetaerina americana</i>	T	California	LMS	0.447	51	0.481	0.0208
23	<i>Argia vivida</i>	NT	British Columbia	MR	0.764	491	1.005	0.0020
24	<i>Pyrrhosoma nymphula</i>	T	England	CS	0.185	90	0.187	0.0115
25	<i>Pyrrhosoma nymphula</i>	T	England	MR	0.240	155	0.245	0.0066
25	<i>Pyrrhosoma nymphula</i>	T	England	TD	0.240	155	0.245	0.0066
26	<i>Pyrrhosoma nymphula</i>	T	England	LMS	-0.072	115	-0.072	0.0089
27	<i>Calopteryx maculata</i>	T	New York	TD	0.086	24	0.086	0.0476
28	<i>Megaloprepus corulatus</i>	T	BCI	MR	0.134	239	0.135	0.0042
28	<i>Megaloprepus corulatus</i>	T	BCI	TD	0.532	33	0.593	0.0333
28	<i>Megaloprepus corulatus</i>	T	BCI	TD	0.152	206	0.153	0.0049
28	<i>Megaloprepus corulatus</i>	T	BCI	TD	0.976	12	2.202	0.1111
29	<i>Orthetrum chrysostigma</i>	T	Kenya	TD	0.795	77	1.084	0.0135
30	<i>Orthetrum japonicum</i>	T	Japan	TD	0.226	45	0.230	0.0238
31	<i>Enallagma ebrium</i>	NT	Ontario	ML	0.192	32	0.194	0.0345
31	<i>Enallagma ebrium</i>	NT	Ontario	FL	0.400	33	0.424	0.0333

Study no.	Species	Mating system	Location	Fitness component	Population correlation	Sample size	Fisher's $z(r)$	Variance in $z(r)$
32	<i>Enallagama ebrium</i>	NT	Ontario	ML	0.710	20	0.887	0.0588
33	<i>Enallagama boreale</i>	NT	British Columbia	MR	0.000	78	0.000	0.0133

*Richardson and Baker (1997) measured the relationship between body size and fecundity over a portion of the female reproductive lifespan. MR, male mating rate; ML, male longevity; LMS, male lifetime mating success; TD, territorial defence; FL, female longevity; CS, clutch size; CN, clutch number, CPR, clutch production rate.

Table A2. Studies involved in the analysis.

Study no.	Reference
1	Anholt, 1997
2	Cordero, 1995
3	Cordero, 1991
4	Richardson and Baker, 1997
5	Forbes, 1991
6	Fincke, 1982
7	Fincke, 1988
8	Van Buskirk, 1987
9	Michiels and Dhont, 1991
10	Michiels and Dhont, 1989
11	Banks and Thompson, 1987
12	Banks and Thompson, 1985
13	Thompson and Banks, 1989
14	Harvey and Walsh, 1993
15	Tsubaki and Ono, 1987
16	Marden, 1989
17	Koenig and Albano, 1987
18	Koenig and Albano, 1985
19	Koenig, 1991
20	Moore, 1996
21	Córdoba-Aguilar, 1995
22	Grether, 1996
23	Conrad, 1992
24	Gribbin and Thompson, 1990
25	Harvey and Corbet, 1985
26	Gribbin and Thompson, 1991
27	Marden and Waage, 1990
28	Fincke, 1992
29	Miller, 1983
30	Kasuya <i>et al.</i> , 1997
31	Leung and Forbes, 1997
32	Forbes and Baker, 1990
33	Anholt, 1991