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Author(s): Gregory F. Grether
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SEXUAL SELECTION AND SURVIVAL SELECTION ON WING COLORATION AND BODY SIZE IN THE RUBYSPOT DAMSELFLY *HETAERINA AMERICANA*

Gregory F. Grether[1]
Animal Behavior Group, Division of Environmental Studies, University of California, Davis, California 95616

Abstract.—I review methodological problems that can lead to false evidence for selection on secondary sexual characters and present a study of selection in rubyspot damselflies (*Hetaerina americana*) that avoids these pitfalls. Male rubyspots have a large red spot on each wing that grows to a terminal size after sexual maturity. Selection gradient analyses revealed evidence for positive sexual and survival selection on both terminal wing spot size and body size. Phenotype manipulations confirmed that wing spot size was subject to direct sexual selection, but showed that the positive slope of survival on wing spot size was an indirect effect of selection on unmeasured traits. This study provides the strongest evidence yet for sexual selection on coloration in Odonata, but also provides clear examples of why phenotypic selection statistics must be calculated and interpreted cautiously.

Key words.—Field experiment, natural selection, Odonata, ontogeny, phenotype manipulation, selection differential, selection gradient.

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Darwin (1871) introduced the theory of sexual selection to explain an unusual class of traits that he called secondary sexual characters. While the evidence for sexual selection is impressive, studies reporting sexual selection vary greatly in methodological rigor (Andersson 1994). Secondary sexual characters have special properties that can lead to false evidence for selection (see below), and studies that fail to detect sexual selection may not be published (Andersson 1994). These caveats are probably irrelevant for extensively studied taxa, but most taxa are represented by a small number of studies (see Andersson 1994). In this paper, I review methodological problems that can lead to false positives in studies of selection on secondary sexual characters and report the results of a study on damselflies in which I attempted to avoid these pitfalls.

Neither observational nor experimental data alone can provide convincing evidence for sexual selection. The basic problem with observational data is well known: correlations between particular characters and mating success may be caused by mutual correlations with other variables. This problem may be mitigated by including all measured characters in a multiple regression against relative mating success (Lande and Arnold 1983). Partial regression coefficients from such a model provide estimates of the sexual selection gradient on each character (Lande and Arnold 1983; Arnold and Wade 1984a,b). Nevertheless, selection gradient estimates assume that all relevant variables have been included in the analysis (Lande and Arnold 1983; Endler 1986; Mitchell-Olds and Shaw 1987). This requirement is difficult to satisfy, in practice, especially since many secondary sexual characters are condition dependent (reviewed in Andersson 1994; Hill 1995). Individuals in better condition may mate at higher rates for reasons unrelated to secondary sexual characters (e.g., Zamudio et al. 1995). Unless phenotypic condition is controlled for, selection gradient estimates may be inflated.

Additional problems may arise for characters that continue to develop after sexual maturity (Lande 1982; Lande and Arnold 1983; Arnold and Wade 1984b; Endler 1986). Many secondary sexual characters fall into this "late maturing" category (Darwin 1871). Including data on sexually immature individuals in the analysis of a late maturing character will obviously inflate that character's selection gradient estimate. For the same reason, analyses using data only on sexually mature individuals may yield inflated selection gradient estimates if mating competency increases with age beyond sexual maturity. This caveat applies not only to short term studies but also to studies of lifetime fitness because the characters of relatively short-lived individuals may be more likely to be measured before they reach maximum (or asymptotic) expression.

Dispersal biases may also lead to false evidence for selection on late maturing characters if predispersal data on emigrants are included in the analysis. For example, relatively unsuccessful animals may be more likely to disperse (Moore and Ali 1984; Beletsky and Orians 1987; Gavin and Bollinger 1988) and less likely to be measured after their secondary sexual characters reach maximum expression. Both this and the previous problem may be avoided by measuring only fully developed individuals, by measuring all individuals at the same age, or by estimating selection on growth parameters rather than on the character measurements themselves (Lande 1982; Lande and Arnold 1983; Arnold and Wade 1984b; Endler 1986).

Experimental manipulations of secondary sexual characters side-step the problems above, but may introduce others. Since secondary sexual characters are often species specific, sex limited, and late maturing (Darwin 1871), they are likely to be integral parts of species, sex, and age-class recognition mechanisms (Butcher and Rohwer 1989; Andersson 1994). Phenotype manipulations that approach or exceed the limits of natural variation may disrupt one or more of these mechanisms (for possible examples, see Jacobs 1955; Peek 1972; Barnard 1990). Experimental reductions are especially problematic, because conspecifics may misclassify manipulated animals as reproductively or competitively immature (Barnard 1990; Andersson 1992). Reduction experiments may

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[1] Present address: Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106. E-mail: grether@lifesci.lscf.ucsb.edu.

reveal whether selection would oppose drastic and sudden reductions of a trait, but cannot provide evidence that selection is directional or stabilizing near the population mean. Experimental enhancements are less problematic, but may also reveal selection that does not occur under natural conditions (Andersson 1992).

The insect order Odonata (damselflies and dragonlflies) is an example of a sizable taxon on which evidence for sexual selection is meager. The subject of the present study, the American rubyspot, is one of 37 strikingly sexually dichromatic damselflies in the genus *Hetaerina* (Garrison 1990). Males have metallic red exoskeletons and a large red spot at the base of each wing. Females, in contrast, have faint amber wing spots and cryptically patterned bodies that vary from brown to green (see Dunkle 1990; Grether 1995). Male wing spots are displayed both during territorial contests and in precopulatory interactions with females (Johnson 1962). The primary goal of this study was to measure selection on male wing spots, while controlling for the potentially confounding factors described above.

MATERIALS AND METHODS

Study Site and Species

Hetaerina americana ranges from northern Central America to southern Canada (Johnson 1973; Garrison 1990). This study was carried out at Bear Creek in the Coastal Range of Colusa County, California (39°01′N, 122°23′W, elev. 260 m). Adults emerged continuously from April through November, with peaks in June and August.

Both study site and species were chosen, in part, to make it possible to obtain good estimates of lifetime mating success. *Hetaerina americana* is unusual among odonates, in that both sexes spend their entire lives within a few meters of a stream (Kellicott 1899; Williamson 1923; Johnson 1962; Bick and Sulzbach 1966; Weichsel 1987; pers. obs.). Matings occur exclusively at streams and, in comparison to other calopterygid damselflies, they occur infrequently (Weichsel 1987; in the present study, sexually mature males mated 0.064 ± 0.005 times per day [mean ± SE], or once every 15.7 d [$n = 444$]). These characteristics made it possible to monitor the mating activity of a large number of animals simultaneously.

The work described below centered on an 88 m section of Bear Creek referred to as the study area. No other bodies of water used by rubyspots were within several kilometers of the study area, thereby limiting dispersal to other parts of Bear Creek.

Marking and Aging

Animals were marked on the left hindwing with a unique combination of three letters and digits using a black Sharpie pen. Through binoculars these numbers were readable at a distance of several meters. First day tenerals (newly emerged adults) cannot be marked safely with a number, but ink dots gently applied to teneral wings have no ill effects. I therefore gave tenerals unique dot patterns and later converted these to numbers. This provided a sample of males with ages known to within one day.

I obtained an equation for aging males marked after the day of emergence by regressing the log-transformed age at recapture of the known-age males on four characters that change with age: eye darkening (2 levels), thorax sheen (2 levels), wing stiffness (2 levels), and middorsal carina darkening (12 levels, expanded from Weichsel 1987). To check the accuracy of this technique, I used an equation based on a random half of the recaptured known-age males ($n = 73$) to predict the ages at last capture of the other half ($n = 73$). The correlation between actual and predicted ages was 0.98, the mean ± SE absolute difference between actual and predicted ages was 1.2 ± 0.1 d, and the maximum difference was 4.7 d. The actual ages ranged from 2 to 41 d with a mean ± SE of 9.8 ± 1.0 d. The accuracy of the age estimates decreased with increasing age, but males used in the selection analyses were marked at estimated ages of 6 d or younger (see below), so their age estimates were likely to be at least as accurate as indicated above. Hereafter, I refer to both known and estimated ages simply as age.

Morphometrics

Morphological data were collected at night and in the early morning, when rubyspots are inactive and incapable of flight. Thorax width and left forewing length and width were measured with digital calipers (all repeatabilities ≥ 0.96; $n = 47$). Male tenerals have an area with pink veins and clear cells at the base of their forewings; elsewhere on the wing, veins are brown and cells are clear. Most, but not usually all, of the cells with pink vein borders fill in with red pigment as males mature. The area with red cells reaches a terminal size by about 14 d postemergence (Grether 1995). I used the length × width of the area with red cells as a measure of the *realized* wing spot size, and the length × width of the area with pink veins as a measure of the *potential* wing spot size. To avoid ambiguity, I refer to the former as wing spot size and to the latter as pink vein area. For males 14 d or older, wing spot size was as repeatable as pink vein area ($r = 0.96$ and 0.95, respectively; $n = 72$).

Wing spots also vary with respect to three additional characters: fullness, continuity, and homogeneity. Fullness is defined as the proportion of cells with pink vein borders that contains red pigment. This was estimated by counting the number of clear cells with pink veins, dividing this by an estimate of the total number of cells with pink veins, and subtracting the quotient from one. Some wing spots were interrupted by patches of clear cells. Continuity is defined as the negative square root of the number of such patches. Wing spots were given a homogeneity score of one if they looked homogeneous in color and zero if they did not. Fullness was extremely left-skewed, requiring an X^6-transformation to meet the parametric assumption of normality (Sokal and Rohlf 1981). The repeatabilities of these variables for males 14 d or older were as follows: fullness $r = 0.98$, $n = 63$; continuity $r = 0.90$, $n = 61$; homogeneity $r = 0.77$, $n = 63$.

Lifetime Mating Success Study

To measure selection on the characters described above, in 1991 I gathered lifetime mating success (LMS) data on a cohort of males. I began with approximately 240 immature males (i.e., < 6 d old, see below) marked in the study area over a four week period. For the duration of the study (67 d), I censused the 88 m study area, and 30 m up and downstream of it, daily. I also censused 300 m up and downstream, on alternate days, at hours in which rubyspots do not mate. Out of 391 males marked within the study area and alive during this study, 378 (96.7%) remained within 100 m of the study area, and only one (0.2%) was found within 100 m of the regular population census boundaries. Hence, the probability of even one cohort male dispersing beyond the census boundaries without being detected en route was minute. Disappearances were therefore classified as deaths.

One hundred eight of the original cohort males reached sexual maturity and remained within the study area until their deaths. These males were recaptured and measured up to two times per week until their terminal wing spot size was obtained (n = 51), or they died (n = 57). In the field, wing spots were considered terminal when they stopped growing between captures or greater than 95% of the area with pink veins contained red cells. Once age estimates and ontogenetic data were available, an age criterion was applied to avoid biasing the sample towards males with relatively large wing spots: only the 51 cohort males last measured at 14 d or older were used for estimating selection on the wing spots. Because the terminal spot size of some males was measured repeatedly, mean values were used in the analysis. Mean wing spot size and mean measurement age were not significantly correlated among these males (r = 0.08, n = 51, $P > 0.5$), confirming the absence of residual ontogenetic effects.

Starting several days before the first mating of a cohort male and ending when the last of these males died, I patrolled the study area continuously during all hours that rubyspots mate (ca. 1000–1900 h), attempting to find and follow all mating pairs that originated in the study area. Mating pairs fly in tandem until the male releases the female and she submerges to oviposit into underwater vegetation (Johnson 1961; Bick and Sulzbach 1966; Weichsel 1987). I considered a mating successful from the male's standpoint if the female copulated with him, submerged, and began probing the vegetation with her ovipositor (Weichsel 1987). Tandem pairs perform a continuous jerking behavior after, but not before, copulation, which enabled me to infer that copulation had occurred when I missed it. Unsuccessful matings were those aborted before (n = 49) or after (n = 2) copulation, or in which copulation never occurred (n = 2; both cases involved a female that appeared unable to copulate). I followed all matings, not just those of cohort males, to avoid biasing LMS estimates in favor of long-lived cohort males. The number of successful matings observed ranged from 2–22 per day, for a mean ± SE of 9.0 ± 0.6 per day and a total count of 552.

Reproductive life span (RLS) was estimated as age at death minus five, because 6 d was the youngest age at which males mated in 1991 (n = 245). LMS was estimated as the observed number of successful matings, with an adjustment for multiple mating by females (explained below). Rubyspots were reproductively active on every day of the study (there was no adverse weather), so mating rates were calculated simply as LMS divided by RLS.

On days that females oviposit, they often lay eggs at more than one site (Bick and Sulzbach 1966; Weichsel 1987). Between oviposition sites, a female may be clasped by a different male than she started with. If so, she almost invariably recopulates (Bick and Sulzbach 1966; Grether, unpubl. data). In such cases, I gave each male that copulated with the female an equal fractional share of one mating credit. Of 478 total mating credits, 55 (11.5%) were divided among two males and 3 (0.6%) were divided among three. The assumption behind these estimates is that the last male to copulate with a female before she lays a batch of eggs fertilizes most of them. This assumption is probably correct, because males remove 80-100% of the sperm of previous males in the calopterygid damselflies examined thus far (Waage 1984, 1986). Moreover, the penis morphology and copulatory behavior of *H. americana* closely resembles those of the known sperm removers (Weichsel 1987).

TABLE 1. Loadings of characters on the first two factors and the percent of total variance explained by the factors, from principal component analyses with varimax rotation (bold type indicates dominant loadings).

Character	Sample 1 (n = 51) Factor 1 (body size)	Sample 1 (n = 51) Factor 2 (wing spot)	Sample 2 (n = 72) Factor 1 (body size)	Sample 2 (n = 72) Factor 2 (wing spot)
Wing width	**0.91**	−0.11	**0.92**	−0.09
Wing length	**0.88**	−0.06	**0.90**	0.06
Thorax width	**0.83**	0.01	**0.86**	0.03
Pink vein area	**0.91**	0.08	**0.90**	0.15
Wing spot size	0.46	**0.74**	0.41	**0.80**
Wing spot fullness	−0.10	**0.91**	0.02	**0.89**
Wing spot continuity	−0.09	**0.66**	−0.05	**0.67**
Wing spot homogeneity	−0.03	**0.67**	−0.04	**0.76**
Percent of variance	41.6	28.4	44.4	29.1

Selection differential estimates were calculated as the covariance of characters with relative fitness components (Arnold and Wade 1984a; Falconer 1989). Selection differentials measure the direct effects of selection on a character plus the indirect effects of selection on correlated characters. Selection gradients, in contrast, estimate only the direct effects by controlling for other characters in the analysis. Due to the small sample size and large correlations among characters, it was necessary to reduce the number of characters before calculating selection gradients (Lande and Arnold 1983; Endler 1986; Mitchell-Olds and Shaw 1987; Crespi and Bookstein 1989; Anholt 1991). I extracted the first two principal components from the eight characters listed in Table 1 (PC3 had an eigenvalue of less than 0.75). Varimax rotation simplified the loading matrix, so I used this solution (Tabachnick and Fidell 1989). The resulting factors were readily interpretable as a body size factor and a wing spot factor (see Results). Factor scores were estimated by the regression method (Tabachnick and Fidell 1989).

Three fitness components were used in the selection analyses: LMS, RLS, and mating rate. These correspond to total selection during the reproductive phase, survival selection during the reproductive phase, and sexual selection. Sexual selection is sometimes equated to the covariance of characters with LMS, but this confounds sexual selection with survival selection (see Discussion). Mating rate may also include a survival component if age-specific mating rates vary with age. In this study, age-specific mating rates increased with age up to about 25 d and decreased thereafter (based on all 108 cohort males; quadratic regression model for ages 6–49 d: mating rate $= -0.023 + 0.0103$ (age) $- 0.0002$ (age^2); $R^2 = 0.30$; $P < 0.001$, $n = 44$ age intervals). Life-span adjusted mating rates were obtained by summing age-specific mating rates up to the age of death, subtracting this sum from the observed number of matings, and dividing the difference by RLS.

Since the survival and mating "episodes" (Arnold and Wade 1984a) of selection occurred simultaneously, I calculated selection statistics for each episode separately. Consequently, the selection differentials for mating rate and RLS do not sum to the total LMS selection differential, as they would if the episodes were sequential (discussed in Arnold and Wade 1984a; Koenig and Albano 1987). Directional selection gradients were estimated from multiple regressions of the form:

$$w_i = \beta_o + \beta_1 x_{i1} + \beta_2 x_{i2} + \epsilon_i, \qquad (1)$$

where $w_i = W_{i/\bar{W}}$, and x_{i1} and x_{i2} are the body size and wing spot factor scores, respectively, for individual i (Lande and Arnold 1983; Neter et al. 1985). Multiple regression was used, even though the factors were orthogonal, because this provided an overall R^2 for each fitness component and the correct number of degrees of freedom for the parametric significance tests (for an alternative approach, see Anholt 1991). Stabilizing/disruptive selection gradients were estimated with quadratic multiple regression (Lande and Arnold 1983; but see Mitchell-Olds and Shaw 1987; Schluter 1988; Schluter and Nychka 1994).

Selection statistics were calculated using two samples of males. *Sample 1* comprised the 51 cohort males with terminal wing spot measurements. *Sample 2* included *sample 1* plus 21 cohort males last measured between 6–14 d of age, that is, after sexual maturity but before wing spot maturity. *Sample 1* provided the best estimates of selection on the wing spot characters, whereas *sample 2* provided the best estimates of selection on the body size characters. I also used *sample 2* to examine the consequences of (incorrectly) including measurements of incompletely developed wing spots in the wing spot selection analysis.

Temporal variation in population demography could have biased the selection gradient estimates by causing indirect selection on characters that covaried with emergence date, or by causing spurious correlations between mating rate and characters correlated with longevity. To test for demographic effects, I represented the average demographic condition experienced by a given male as the mean of the daily demographic statistics that occured during his reproductive life span. Three demographic statistics were examined: total population density, sex ratio among sexually mature adults, and per capita mating rate (number of matings per sexually mature male per day).

Mating rate and LMS and their residuals were approximately normally distributed (kurtosis and skewness < 1.0), but RLS and its residuals were not. Since the wing spot and body size factors were orthogonal, I used rank correlations (corrected for ties) to test the significance of the RLS selection differentials and directional selection gradients (Lande and Arnold 1983). In addition, I checked all P-values smaller than 0.10 by bootstrapping (Simon 1992). Bootstrap and conventional tests gave identical results with respect to significance at the 95% confidence level.

Manipulation Experiment

The LMS study controlled for wing spot ontogeny and body size, but other factors could lead to an indirect relationship between wing spots and mating success. To determine whether wing spot size affects mating rate directly, in 1992 I enlarged the forewing spots of a sample of males with red ink (Berol Prismacolor Marker-3). I applied clear ink (Berol PM-121) to the same region of the wings on a second group of males, to control for the extra handling and the addition of weight to the wings, and left a third group of males unmanipulated. On the average, wing spots of the enlarged group ($n = 81$) were lengthened by 37.0 ± 1.0% (6.5 SD) and widened by 25.1 ± 0.7% (3.5 SD). Wing spots of the sham group ($n = 77$) were "lengthened" by 38.9 ± 0.9% (6.8 SD) and "widened" by 25.3 ± 0.8% (3.5 SD). Both Berol markers contain a normal propanol base and meleic modified resin binder; the red marker also contains solvent dyes (T. DeBietro, Empire-Berol USA, pers. comm.).

To human eyes, Berol PM-3 provides a close match to the natural forewing spot color. No data are available on the spectral sensitivity of damselfly eyes, but Endler (1990) has developed a color comparison method that is independent of the properties of particular visual systems. This method may detect differences that damselflies cannot, but it eliminates the problems associated with relying on human vision (Endler 1990, 1991; Bennett et al. 1994). I scanned the natural and artificial wing spots of 18 mature males in Endler's lab with a quantum spectroradiometer using the beam method (Endler 1990). Hue and chroma were calculated from reflectance spectra over wavelengths 350–700 nm (i.e., ultraviolet to red) using the segment classification method (Endler 1990).

Males in the enlarged and sham groups were painted and measured at night, when rubyspots are inactive. These treatments were assigned by random lot to sexually mature males observed in the study area during the day and found at night. The unmanipulated group included all other sexually mature males that were observed in the study area during the day for two or more days (i.e., long enough to be manipulated and subsequently observed). A completely randomized design would have reduced the sample size substantially because most males were not found at night. The night roosting sites of mature males are not correlated with their age, territorial status, wing spot size, or mating success (Grether, unpubl. data). All males were ≥ 9 d old at the time they entered the study; by 9 d, wing spots reach about 90% of their terminal size (Grether 1995).

To obtain mating rate estimates, I searched the study area for mating pairs continuously from 24 September to 24 October 1992. I followed pairs only to copulation because matings were rarely aborted after copulation in the LMS study (2 of 554 pairs). Eighteen pairs broke up before copulating and 365 appeared to copulate successfully. Mating rates were calculated as in the LMS study, but only for the portion of a male's life that he was present in the study area after age

TABLE 2. Directional selection differential estimates, calculated as the covariance of characters with relative fitness components using the sample of cohort males with mature wing spot measurements (sample 1; $n = 51$).

Character	Fitness component: Reproductive life span (survival)	Mating rate (sexual)	Lifetime mating success (total)
Wing width	0.020	0.027	0.043§
Wing length	0.010	0.087	0.087
Thorax width	0.008	0.019	0.025§
Pink vein area	0.519§	0.984*	1.282**
Wing spot size	0.527§	1.720**	1.958***
Wing spot fullness	0.020	0.052*	0.059**
Wing spot continuity	0.032	0.034	0.082
Wing spot homogeneity	0.050*	0.089§	0.120**

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.02$; *** $P < 0.01$.

7 d (the earliest age at first mating for males in 1992 was 8 d; $n = 196$). There were five cloudy days during the study on which the air temperature dropped below the 21 degrees C minimum for reproductive activity in rubyspots (Grether, unpubl. data). I corrected the mating rates of males present on those days by subtracting 1/6 d from the mating rate denominator for each hour during the 6 h reproductive period that the temperature fell below 21 degrees C.

I tested for treatment effects using ANCOVA with the log number of days males were in the study as a covariate. There was no significant treatment × covariate interaction ($F_{2,362} = 1.12$, $P > 0.3$), so this term was removed from the model (Neter et al. 1985). Mating rate was square-root transformed for this analysis to reduce heteroscedasticity and improve the fit to normality (Sokal and Rohlf 1981).

RESULTS

Lifetime Mating Success Study

Principal Components.—The character correlation matrices revealed a clear separation between characters that are fixed at emergence (wing width, wing length, thorax width, pink vein area) and those that develop after emergence (wing spot size, fullness, continuity, and homogeneity). PCA extracted two factors with large eigenvalues; I interpret the first as a body size factor and the second as a wing spot factor (Table 1). Pink vein area correlated more strongly with the body size characters than with wing spot size and therefore loaded mainly on the body size factor (Table 1). Apparently, pink vein area is a relatively invariant function of body size, and only a crude predictor of wing spot size (contra Johnson 1963). In *sample 1*, neither the wing spot factor nor the body size factor correlated significantly with log age (spot factor $r = 0.16$, $n = 51$, $P > 0.25$; size factor $r = 0.01$, $P > 0.9$). In *sample 2*, the wing spot factor correlated significantly with log age ($r = 0.23$, $n = 72$, $P < 0.05$) but the body size factor did not ($r = 0.17$, $P > 0.15$).

Wing Spot Selection (Sample 1).—All 24 selection differential estimates were positive, and several for the wing spot characters were significant (Table 2). Directional selection gradients on the wing spot factor were positive and significant for all three fitness components (Table 3). Neither RLS nor mating rate had significant selection gradients on the body size factor, but the total selection gradient on the body size factor was significant (Table 3). Selection gradient estimates calculated with life-span adjusted mating rates were significant for both the wing spot factor ($P < 0.02$) and the body size factor ($P < 0.05$). Hence, both characters appeared to be subject to directional sexual and survival selection (but see Discussion).

TABLE 3. Directional selection gradient estimates ($\beta \pm$ SE) and adjusted R^2, from linear multiple regressions of relative fitness components on the body size and wing spot factor scores using the sample of cohort males with mature wing spot measurements (sample 1; $n = 51$).

Fitness component	Character: Body size factor $\beta_1 \pm$ SE	Wing spot factor $\beta_2 \pm$ SE	R^2_{adj}
Reproductive life span	0.08 ± 0.05	0.10 ± 0.05**	0.09*
Mating rate	0.18 ± 0.09§	0.23 ± 0.09**	0.13**
Lifetime mating success	0.23 ± 0.10*	0.29 ± 0.10***	0.20***

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.02$; *** $P < 0.01$.

Quadratic multiple regression revealed no evidence for stabilizing or disruptive selection. None of the quadratic coefficients approached significance by the least squares method (all $P \geq 0.25$), and the total R^2 of the quadratic models was the same or lower than that of the corresponding linear models. Cubic spline estimates of the selection surface (Schluter 1988; Schluter and Nychka 1994) further suggested that selection on both wing spots and body size was purely directional (Fig. 1).

Body Size Selection (Sample 2).—The forgoing analysis was restricted to the sample of cohort males with terminal wing spot size measurements (*sample 1*). This restriction was necessary for estimating selection on the wing spots, but it biased the sample towards long-lived males and reduced the variance in relative fitness. Mean RLS for the 51 males with terminal wing spot measurements was 27.3 ± 1.4 d, versus 10.1 ± 1.5 d for the 21 males that died before their terminal wing spot size was measured (Mann-Whitney test, $z = 6.01$, $P < 0.001$). With the latter group of males added to the data set, the variance in relative fitness increased from 0.13 to 0.28 for RLS, from 0.51 to 0.85 for mating rate, and from 0.57 to 1.00 for LMS. Since variance in relative fitness sets the upper limit for selection (Crow 1958; Arnold and Wade 1984a), the combined data set provided a greater opportunity for detecting selection on body size.

Selection differential estimates for the body size characters were greater in magnitude, relative to the first analysis, and most were significant (Table 4). Directional selection gradients on the body size factor were significant for all three fitness components (RLS $\beta_1 \pm$ SE $= 0.17 \pm 0.06$, Spearman $P < 0.02$, $n = 72$; mating rate $\beta_1 \pm$ SE $= 0.27 \pm 0.10$, $t = 2.61$, $P < 0.02$; LMS $\beta_1 \pm$ SE $= 0.33 \pm 0.11$, $t = 3.08$, $P < 0.01$). The life-span adjusted mating rate selection gradient for the body size factor was also significant ($P < 0.05$). Stabilizing and disruptive selection gradient estimates were nonsignificant (all $P > 0.5$).

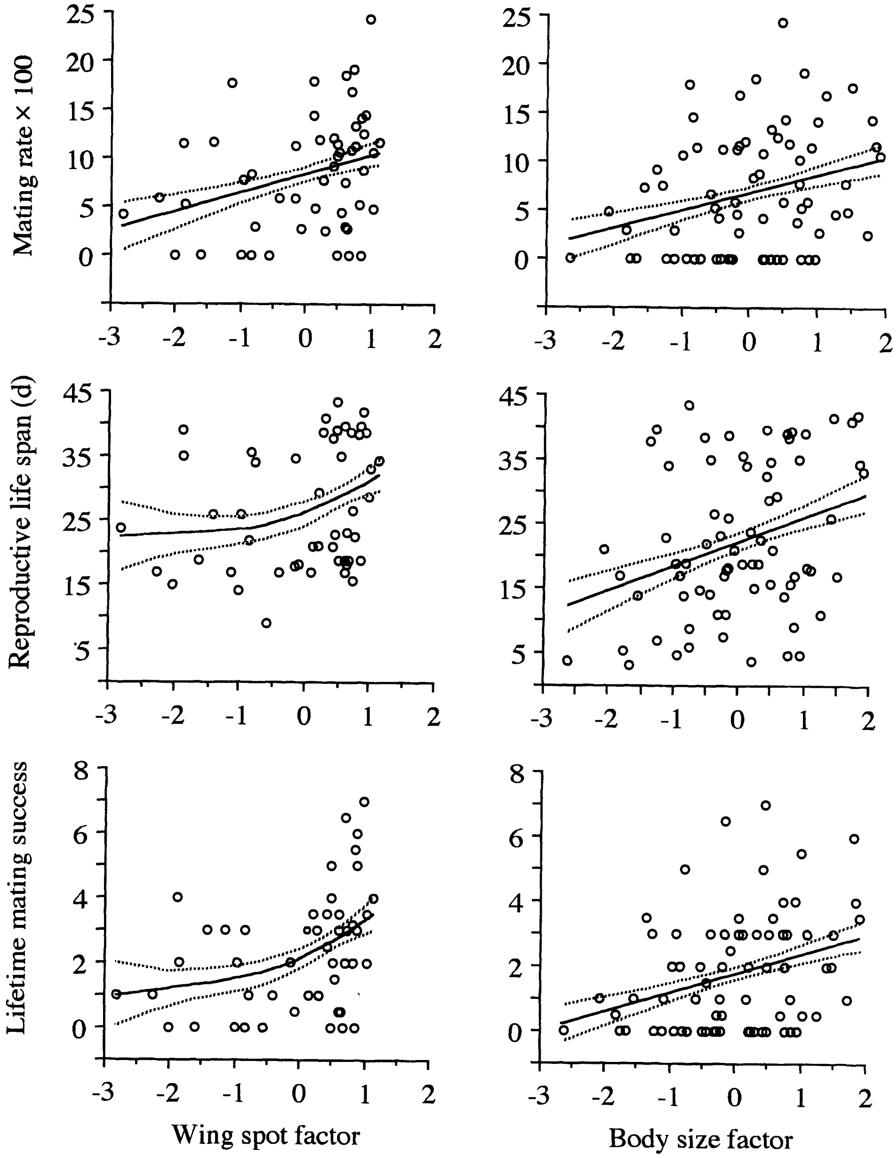

FIG. 1. Fitness components versus wing spot and body size factor scores for males in the lifetime mating success cohort. Sample sizes are $n = 51$ and $n = 72$ for wing spots and body size, respectively (see text). Solid lines represent fitness functions, as estimated by the nonparametric cross-validated cubic spline method (Schluter 1988). Dotted lines represent standard errors of the fitness functions, calculated from 1000 bootstrapped replicates of the data set.

TABLE 4. Directional selection differential estimates for the ontogenetically fixed characters, calculated as the covariance of characters with relative fitness components using the full sample of cohort males measured after sexual maturity (sample 2; $n = 72$).

	Fitness component		
Character	Reproductive life span (survival)	Mating rate (sexual)	Lifetime mating success (total)
Wing width	0.037*	0.044§	0.065**
Wing length	0.093§	0.163*	0.186*
Thorax width	0.023***	0.038**	0.044***
Pink vein area	0.843**	1.323***	1.683***

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.02$; *** $P < 0.01$.

Ontogenetic Effects (Sample 2).—I removed ontogenetic effects from the wing spot selection coefficient estimates by restricting the analysis to males measured after their wing spots were fully developed (see above). This approach would not have been possible if age estimates and ontogenetic data were unavailable. To examine the consequences of failing to exclude measurements of incompletely developed characters, I calculated wing spot selection differential estimates for *sample 2*. In comparison to the *sample 1* estimates, the *sample 2* selection differential estimates for wing spot size and fullness were highly inflated (Table 5). In contrast, most selection differential estimates for wing spot continuity and homogeneity were deflated (Table 5). These differences appear to reflect the relationship between the characters and measurement age (in *sample 2*). Whereas wing spot size and fullness

TABLE 5. Percentage change in selection differential estimates after measurements of immature wing spots were included in the analysis. Characters above (but not below) the dashed line correlated positively with measurement age (see text).

Wing spot character	Fitness component Reproductive life span (survival)	Mating rate (sexual)	Lifetime mating success (total)
Size	197	54	64
Fullness	140	46	59
Continuity	−9	9	−11
Homogeneity	−10	−36	−16

increased significantly with log measurement age ($r = 0.34$ and 0.35, respectively, both $P < 0.01$, $n = 72$), wing spot continuity and homogeneity did not ($r = -0.02$ and 0.12, both $P > 0.3$, $n = 72$). The simplest explanation for the inflated RLS selection differentials is that shorter-lived males were more likely to be measured before their wing spots reached maximum size and fullness. The mating rate selection differentials apparently were inflated because males with preterminal wing spots mated at low rates. On the average, males with terminal wing spot measurements mated 3.0 times more often than males with preterminal wing spot measurements ($t = 3.78$, $P < 0.001$, df = 71).

Emergence Date Effects.—Body size at emergence varies seasonally at this site, with spring and fall peaks and a summer trough (Grether 1995). Selection on emergence date could therefore have caused indirect selection on body size (Anholt 1991; Michiels and Dhondt 1991), but there was no evidence for selection on emergence date during this study (selection differentials $P > 0.25$ for all three fitness components, $n = 72$). Moreover, the range of emergence dates covered in this study (28 d) was sufficiently narrow that seasonal variation in size was negligible. None of the eight characters correlated significantly with log emergence date ($r = -0.02$–0.14; all $P > 0.25$, $n = 72$). Neither the body size factor ($r = 0.07$) nor the wing spot factor ($r = -0.01$) correlated significantly with log emergence date (both $P > 0.5$, $n = 72$). Hence, temporal variation in size at emergence was not a confounding factor in this study.

Longevity Effects.—Population density increased with time through most of the study, while the sex ratio (F:M) decreased (Grether, unpubl. data). Consequently, the mean population density experienced by cohort males increased with RLS ($r = 0.44$, $P < 0.001$, $n = 72$), while the mean sex ratio and the mean per capita mating rate decreased with RLS (sex ratio $r = -0.50$, $P < 0.001$; per capita mating rate $r = -0.26$, $P < 0.05$; $n = 72$). Longer-lived cohort males therefore experienced poorer average conditions for mating. This could have deflated the mating rate selection gradient estimates, but there were no significant correlations between the mean demographic variables and either the body size factor (density $r = 0.12$, $P > 0.4$; sex ratio $r = -0.11$, $P > 0.3$; per capita mating rate $r = -0.22$, $P = 0.07$; $n = 72$) or the wing spot factor (density $r = 0.04$, $P > 0.7$; sex ratio $r = 0.01$, $P > 0.9$; per capita mating rate $r = 0.17$, $P > 0.2$; $n = 51$). Although the correlation between body size and mean per capita mating rate approached significance, including mean per capita mating rate as an independent variable in the mating rate selection gradient model increased the body size coefficient by only 1.9%. Hence, temporal variation in population demography did not significantly bias the mating rate selection gradient estimates.

Manipulation Experiment

The spectroradiometer measurements indicated that the artificial (ink) wing spot color provided a close, albeit imperfect, match to the natural wing spot color. Reflectance of the natural color ranged from 48.9 to 73.4 (mean ± SE, 64.5 ± 1.3) versus 43.2 to 68.1 (56.8 ± 1.7) for the artificial color. Hue-angle of the natural color ranged from 0.6 to 2.4 (1.4 ± 0.1) versus 1.9 to 12.4 (5.2 ± 0.6) for the artificial color. Chroma of the natural color ranged from 0.61 to 0.78 (0.70 ± 0.01) versus 0.43 to 0.74 (0.60 ± 0.03) for the artificial color.

Males with enlarged wing spots mated at significantly higher rates than both sham and unmanipulated controls ($F_{2,364} = 7.77$, $P < 0.001$; post-hoc pairwise Bonferroni tests, both $P < 0.001$; Fig. 2). There was no significant difference between the mating rates of the control groups (Bonferroni test, $P > 0.7$), nor was there a significant difference between the mating rates of males in the enlarged and sham treatment groups *before* their wings spots were painted ($F_{1,122} = 0.04$, $P > 0.8$; Fig. 2).

DISCUSSION

Selection on Wing Coloration

The results of this study provide strong evidence for direct sexual selection on male wing coloration. Selection differential estimates suggested that wing spot size and fullness were subject to net sexual selection (Table 2). Selection gradient estimates showed that selection on the wing spot characters was not a correlated effect of selection on body size (Table 3, Fig. 1). Finally, the wing spot manipulation demonstrated a causal relationship between wing spot size and mating rate (Fig. 2).

Three previous studies on odonates reported sexual selection on male coloration. Jacobs (1955) removed a secondary sexual character from mature male white-tailed dragonflies (*Plathemis lydia*) by painting their abdomens black. Blackened males had low mating rates, relative to white-painted controls, apparently because they were mistaken for immature males and had difficulty repelling territory intruders (Jacobs 1955). Jacobs's experiment should be replicated using less drastic manipulations to determine whether abdomen color influences mating rates within or near the natural range of color variation. Moore (1990) reported directional sexual selection on the wing coloration of another libellulid dragonfly (*Libellula luctuosa*), but did not separate survival selection from sexual selection (see below), and was unable to rule out ontogenetic effects (Moore 1989, 1990). Thompson and Banks (1989) found evidence for stabilizing sexual selection on male abdomen coloration in a coenagrionid damselfly (*Coenagrion puella*), but also did not rule out ontogenetic effects. Waage's classic study of character displacement in *Calopteryx* damselflies provided evidence for sexual

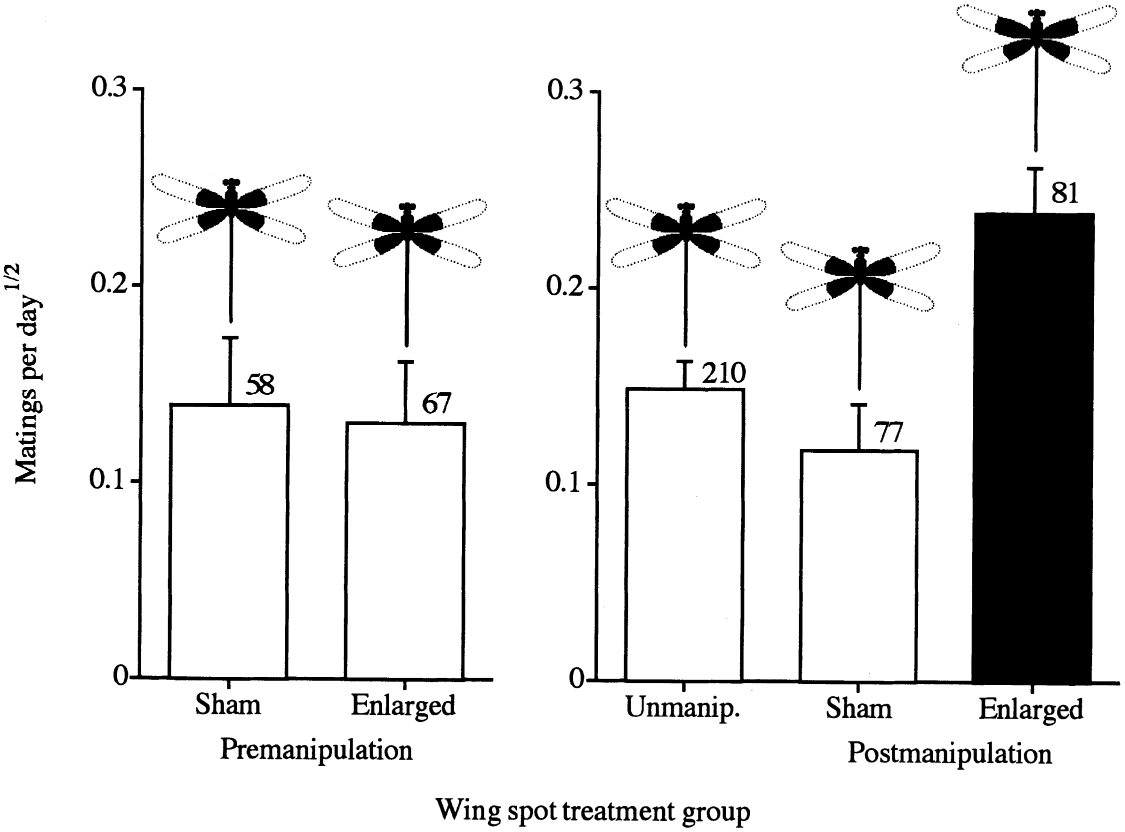

FIG. 2. Mean (± SE) mating rates classified by wing spot treatment group: (a) premanipulation mating rates; (b) postmanipulation mating rates. Pre- and postmanipulation means were adjusted in separate ANCOVAs using log number of days in the study as a covariate. Mating rate was square-root transformed to reduce heteroscedasticity. The numbers above the bars are the sample sizes for each group. Premanipulation data were only available for a subset of the males. Statistics are given in the text.

selection, but in this case the data suggest that female coloration evolved in response to male choice (Waage 1979).

Most models of sexual selection assume that secondary sexual characters have negative effects on survival (e.g., Darwin 1871; Fisher 1930; Zahavi 1975; Lande 1981; Grafen 1990a), but numerous studies, including this one, have reported positive correlations between sexual traits and survival (e.g., Price 1984; Conner 1988; Göransson et al. 1990; Alatalo et al. 1991; Hill 1991; Møller 1991; Petrie 1992; Borgia 1993). Either these traits lack survival costs (Göransson et al. 1990; Hill 1994), or individuals developing larger values of the traits live longer in spite of the costs (Parker 1982; Nur and Hasson 1984; Zeh and Zeh 1988; Grafen 1990a,b; Møller 1991). I tested for survival costs of wing spots in a scaled up version of the manipulation experiment reported here (Grether, unpubl. data). Males with enlarged wing spots had mortality rates 23% higher than controls, after controlling for age, wing wear, and dispersal; control group mortality rates differed, nonsignificantly, by less than 0.5%. Hence, the true survival selection gradient on wing spot size appears to be negative. Males with larger natural wing spots apparently survive longer despite this cost.

This study provides a clear example of why phenotypic selection measures must be interpreted cautiously (see also Lande and Arnold 1983; Arnold and Wade 1984b; Endler 1986; Koenig and Albano 1987). The positive selection differential of reproductive life span on wing spot size was apparently an indirect effect of survival selection on unmeasured characters. The evolutionary response to selection depends not only on the heritability of the character of interest, but also on the magnitude of its genetic correlations with all other directly selected characters (Lande 1979; Lande and Arnold 1983; Arnold and Wade 1984a). Even if we could assume that the correlations between wing spots and the unmeasured characters were purely phenotypic, however, the results presented in this paper are insufficient to predict the *direction* of the evolutionary response. This is because the total (i.e., LMS) selection gradient estimate was inflated by an indirect positive relationship between wing spots and survival.

Selection on Body Size

Body size selection in odonates is apparently quite variable among species (Fincke 1982, 1988, 1992; Buskirk 1987; Kasuya et al. 1987; Koenig and Albano 1987; Thompson and Banks 1989; Moore 1990; Anholt 1991; Gribbin and Thompson 1991; Michiels and Dhondt 1991; Harvey and Walsh 1993), and perhaps within species as well (Harvey and Walsh 1993). Unfortunately, however, most studies report only the correlation between body size measures and number of mates (as opposed to mating rate). This practice confounds sexual selection with survival selection. Whether sexual selection for larger male body size is the rule or the exception in odonates therefore remains an open question.

Unfortunately, the use of mating success to measure sexual selection is prevalent throughout the literature. This may be an unintended legacy of a seminal paper by Arnold and Wade (1984b), which demonstrated the application of the selection partitioning techniques derived in Arnold and Wade (1984a). In each of the examples provided, sexual selection was equated to the covariance of characters with relative mating success, that is, number of mates divided by the mean number of mates. Nevertheless, mortality may have been negligible in the first example (Howard 1979); if so, mating success approximately equaled the per season mating rate. In the second example, the authors acknowledged that survival and sexual selection were confounded (Arnold and Wade 1984b, p. 727), and in the third, mating success was measured as an instantaneous rate (0 or 1 at the time of capture). These nuances appear to have been overlooked by many of the researchers applying Arnold and Wade's (1984a,b) techniques. Several authors have argued that the variance in relative mating success is a poor measure of the opportunity for sexual selection (e.g., McCauley 1983; Banks and Thompson 1985; Koenig and Albano 1987; Brown 1988; Michiels and Dhondt 1991). Ironically, the practice of using the covariance of characters with relative mating success as a measure of the sexual selection differential has largely escaped criticism.

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