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INTRASEXUAL COMPETITION ALONE FAVORS A SEXUALLY DIMORPHIC ORNAMENT IN THE RUBYSPOT DAMSELFLY *HETAERINA AMERICANA*

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Abstract.—I studied the sex-limited red spots on the wings of male rubyspot damselflies (*Hetaerina americana*) in relation to territoriality and fitness in the wild. Both observational and experimental (wing spot manipulation) studies indicated that wing spots were selected through competition among males for mating territories, not through female choice or direct competition for females. Males with naturally or artificially large wing spots were more successful at holding territories and consequently mated at higher rates than males with relatively small wing spots. In contrast, sexual selection on male body size appeared to operate among nonterritorial males at the clasping stage of the mating sequence, perhaps because larger males were better at clasping females forcibly. Of four models proposed to explain the evolution of ornaments through territory competition, only the agonistic handicap model makes predictions consistent with the results of this study.

Key words.—Body size, coloration, intrasexual competition, mate choice, Odonata, sexual conflict, sexual selection.

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Following Darwin (1871), most students of sexual selection have assumed that sex differences in traits such as coloration and plumage evolve through mate choice, while sex differences in traits such as weaponry and strength evolve through intrasexual competition (reviewed in Bradbury and Andersson 1987; Kirkpatrick 1987; Pomiankowski 1988; Harvey and Bradbury 1991; Kirkpatrick and Ryan 1991; Andersson 1994; Johnstone 1995). However, this dichotomy has a long history of detractors (e.g., Fisher 1930; Huxley 1938; reviewed in Butcher and Rohwer 1989; Andersson 1994), and a host of recent empirical studies appear to contradict it. Numerous studies report intrasexual selection of male ornaments (e.g., Bakker and Sevenster 1983; Kodric-Brown 1983; Rowland 1984; Silberglied 1984; Møller 1987, 1988; Røskaft and Rohwer 1987; Collias 1990; Ligon et al. 1990; Moore 1990; Metz and Weatherhead 1992; Warner and Schultz 1992; Marchetti 1993; Olsson 1994; Savalli 1994; Zucker 1994) and at least one study reports intersexual selection of male weaponry (Göransson et al. 1990).

These new data suggest that mate choice and intrasexual competition have similar evolutionary effects, but there are reasons to remain skeptical. First, the intrasexual functions of ornaments are poorly understood (Andersson 1994). Why do traits with no effect on competitive ability influence the outcome of contests? How is this evolutionarily stable? Although several intrasexual selection models of ornament evolution have been proposed (e.g., Rohwer 1975, 1982; Zahavi 1977; Maynard Smith and Harper 1988; Grafen 1990a; Johnstone and Norris 1993), none has been tested extensively. Second, ornaments often appear to be favored by both male-male competition and female choice, or female choice alone, but very few studies reporting intrasexual selection of ornaments have convincingly ruled out mate choice (Butcher and Rohwer 1989; Warner and Schultz 1992; Andersson 1994). In theory, either mechanism of sexual selection could set the stage for the other (Johnstone and Norris 1993). Intersexually selected ornaments are often condition dependent (reviewed in Møller 1990; Zuk 1992; Nicoletto 1993; Andersson 1994; Hill 1995) and may provide information about their bearers that competitors could profitably exploit. Hence, the functions of ornaments in intrasexual competition might have evolved secondarily, after the ornaments evolved through mate choice.

In this paper, I present evidence that the sexually dimorphic wing coloration of the rubyspot damselfly, *Hetaerina americana*, is maintained by competition among males for mating territories and not by female choice. Although this result does not rule out intersexual selection of wing coloration in the evolutionary past, it strengthens the case for intrasexual competition as an independent mechanism of ornament evolution. In light of other work on this species (Grether in press, unpubl. data), the results of this study are consistent with just one of the models proposed to explain the evolution of ornaments through intrasexual competition (see Discussion).

Mature male rubyspots have red metallic exoskeletons and a large red spot at the base of each wing (Johnson 1963; Grether 1995). Females, in contrast, have faint amber wing spots and cryptically patterned bodies that vary from brown to green (Grether 1995; see Dunkle 1990). Male wing spots increase in size and chroma with age, reaching a terminal (i.e., fully developed) stage after sexual maturity (Grether 1995). They are displayed both during territorial contests and in precopulatory interactions with females (Johnson 1962).

To measure selection on a suite of male characters, I gathered data on the lifetime mating success of a cohort of males (Grether 1996). Selection gradient analyses (Lande and Arnold 1983) indicated that male wing spots and body size were independently subject to directional sexual selection for increased size, after controlling for wing spot ontogeny and seasonal size variation (Grether 1996). Experimental manipulations of wing spot size confirmed the presence of direct sexual selection on this trait (Grether 1996). The goal of the present study was to identify the mechanisms of selection on wing spots and body size at the level of male-male competition and female choice.

This species has a lek mating system (Bradbury 1985) in

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which males compete for perching sites along stream riffles where females oviposit. Females obtain no nuptial gifts or parental care from their mates and usually lay eggs outside their mate's territory (Weichsel 1987). Hence, female mate preferences, if any, are probably based on the characteristics of males themselves (see Borgia 1979; Conrad and Pritchard 1991). Territory residency carries a strong mating advantage (this paper), but is not required for mating. Thus, sexual selection of male characters could occur through territory competition, through female choice among residents or nonresidents, or though direct competition for females among residents or nonresidents. To distinguish among these possible mechanisms of sexual selection, I examined the relationship between mating rate components and both natural and experimentally manipulated wing spots.

Materials and Methods

Study Site

This study was carried out at Bear Creek, a small perennial stream in pine-oak woodland in the Coastal Range of Colusa County, California (39°01′N, 122°23′W, elev. 260 m). *Hetaerina americana* is the most abundant odonate and the only calopterygid species at this site. The work described below centered on an 88 m section of Bear Creek referred to as the study area.

Marking, Aging and Morphometrics

Methods of marking, aging, and measuring animals are described in Grether (1996). Here I provide a synopsis of those methods. Animals were marked on the left hindwing with a unique three digit number. Animals captured on the day of adult emergence are easily identified; I used recapture data on these individuals to estimate the ages of animals first captured later in life. Newly emerged males have an area with pink veins and clear cells at the base of their forewings. As males age, most of the cells in the pink vein area fill with red pigment to form the wing spot, which reaches a terminal size by about 14 d postemergence. I also measured three other characteristics of the wing spots (fullness, continuity, and homogeneity) and three body size characters (left forewing length and width, thorax width).

Lifetime Mating Success Study

Mating Rate Estimates.—In 1991, lifetime mating success (LMS) estimates were obtained for a cohort of males that remained within the study area throughout their reproductive lives (Grether 1996). Mating rates were calculated as LMS divided by age at death minus five, because 6 d was the earliest age at first mating observed among males during this study. Methods of monitoring mating success, survival, and dispersal are described in Grether (1996).

Territorial Status.—Males only defend territories during the mating period, that is, the time of the day when females mate and oviposit (Weichsel 1987; Grether and Grey in press). In late September, for example, this period begins at about 1100 h and ends by 1730 h. At other times, the behavior of residents (males with territories) and nonresidents (males without territories) is indistinguishable. All statements below refer to the mating period unless otherwise indicated.

The territorial status of males usually can be inferred from their degree of site fidelity. Residents return to defend the same site daily until they die or are evicted, as opposed to "time sharing" (Koenig 1990) or establishing new territories daily (Pezalla 1979). Except when mating or fighting, residents perch on their territories continuously (Johnson 1962). In this study, territory sizes ranged from about 1 to 4 m^2 (Grether, unpubl. data). Nonresidents are also faithful to particular stretches of creek, but range more widely than residents.

Other cues are also useful for distinguishing residents from nonresidents (except when nonresidents are challenging residents or fighting over vacant sites). Residents typically perch in direct sunlight within 20 cm of rippling or turbulent water on emergent objects or vegetation overhanging the creek (Johnson 1961). Nonresidents, in contrast, usually perch in areas with slow moving water where territorial defense is rare, or in the shade of the stream bank or on high perches over the bank within other males' territories. Residents tolerate or fail to detect intruders that remain motionless, but immediately chase mature males flying within their territory boundaries. Nonresidents, in contrast, rarely chase other males and usually behave submissively when attacked.

I monitored the territorial status of males through multiple daily records of their locations and agonistic interactions. Locations were recorded in three dimensions by reference to the stream and markers placed along the banks. I also recorded whether males were perched in sun or shade. In total, I recorded the location of males on 14,964 occasions, for an average of 226.7 records per day. These data were supplemented with 11,399 records collected outside the mating period to monitor mortality and dispersal. On average, the location of each male in the LMS cohort was recorded 3.8 ± 0.1 times per day (mean ± SE, $n = 51$).

I recognized two types of agonistic interactions. In one-way chases, the male being chased did not double back or circle his opponent. These were brief (< 3 s) and frequent. I only attempted to record one-way chases that seemed helpful for documenting changes in territory ownership. In two-way chases, two or more males flew back and forth or circled each other (Johnson 1963). These ranged from brief skirmishes between neighboring residents to prolonged interactions involving several residents and intruders. I recorded the boundaries of these fights and the identities of the males involved. In total, 249 one-way chases and 543 two-way chases were recorded.

All categories of data described in this section were combined to determine the territorial status of each male on each day of the study. Territory status assignments were based solely on these data, without knowledge of an individual's mating success or wing spot size.

Sampling Bias.—Although I tried to record all matings that occurred in the study area, I undoubtedly missed some. The analyses described below rely upon the assumption that the matings of residents and nonresidents were equally likely to be recorded. Because I could not test this assumption directly, I examined factors that could have led to sampling bias.

A complete rubyspot mating sequence is comprised of

eight distinct events: clasping, precopulatory tandem flight, copulation initiation (male flutters wings and pulls female forward), copulation (sperm removal and transfer), postcopulatory tandem flight, submergence (male releases female and she crawls under the water), probing (female probes with her ovipositor), and oviposition. After the female submerges, her mate perches in a characteristic "guarding" posture, for a variable duration, immediately above the submergence site (Johnson 1961; Bick and Sulzbach 1966; Weichsel 1987).

Variables that might have influenced the probability that I detected a mating pair include: L, the length of time the pair was in tandem; D, the distance traveled by the pair while in tandem; T, the time of day; G, guarding duration (I inferred 60 of 552 matings from the presence of a male in the guarding posture immediately above a submerged ovipositing female); and the location of the oviposition site. I obtained minimum estimates of G by subtracting the time a male started guarding from the time I last saw him guarding. Oviposition site locations were represented by two variables: X, the distance along the stream from an arbitrary point; and S, the speed of the stream current. S was scored on a three point scale, based on the degree of disturbance of the water surface: (1) smooth (slow); (2) rippling (medium); (3) turbulent (fast). These rank scores correlated well with actual current speed measurements ($r_s = 0.94$, $n = 12$, $P < 0.002$).

For each male that mated at least once during the study ($n = 272$), I calculated resident and nonresident values for each variable. When multiple measurements were available for a particular male, I used mean values of L, D, T, and G, and the last recorded values of X and S in the analysis. I tested for territory status effects on L, D, T, and G using unpaired t-tests; paired tests would have been less powerful because most males did not mate as both residents and nonresidents. Variables were log or square-root transformed for these tests, as necessary, to eliminate significant kurtosis, skewness, and heteroscedasticity (Sokal and Rohlf 1981). Sample sizes vary between tests because complete information was not available for all matings.

Mating Rate Components.—Given a particular trait z that covaries positively with mating rate, the female choice hypothesis predicts that males with larger values of the trait mate at higher rates than other males of the same territorial status. The same prediction follows from the hypothesis that z is selected through direct competition for females. In contrast, the territory competition hypothesis predicts that males mate at higher rates while holding territories than when they do not and that males with larger values of the trait hold territories for a greater proportion of their reproductive lives. To test these predictions, which are not mutually exclusive, I subdivided the mating rate of each male into three components:

$$W_m = W_{m.t}W_{p.t} + W_{m.n}(1 - W_{p.t}), \quad (1)$$

where W_m is the overall mating rate (mating credits per day; defined in Grether 1996), $W_{m.t}$ is the territorial mating rate (mating credits per day as a resident), $W_{m.n}$ is the nonterritorial mating rate (mating credits per day as a nonresident), and $W_{p.t}$ is the proportion of days during the male's reproductive life span on which he held a territory ("territory tenure," hereafter). Thus, the female choice and direct competition hypotheses predict positive covariance of z with $W_{m.t}$ or $W_{m.n}$ or both, whereas the territory competition hypothesis predicts $\bar{W}_{m.t} > \bar{W}_{m.n}$ and positive covariance of z with $W_{p.t}$. Since W_m is completely determined by $W_{m.t}$,$W_{m.n}$, and $W_{p.t}$, any of these hypotheses could be rejected if its predictions did not hold.

To further explore the mechanism of selection on characters that covaried with the nonterritorial mating rate (see Results), I divided the nonterritorial mating rate of each male into subcomponents corresponding to specific stages in the mating sequence:

$$W_{m.n} = W_{m.n.1}W_{m.n.2}W_{m.n.3}W_{m.n.4}, \quad (2)$$

where $W_{m.n.1}$ is the number of clasping attempts per day (as a nonresident), $W_{m.n.2}$ is the proportion of attempts that led to clasping, $W_{m.n.3}$ is the proportion of claspings that led to copulation, and $W_{m.n.4}$ is the number of mating credits per copulation (defined in Grether 1996). The fourth subcomponent primarily reflects a male's success in reclasping mates that resurface with unlaid eggs. When calculating subcomponents, I only included cases in which the female was 7 d of age or older, because no females were observed to mate successfully at younger ages.

The mating rate subcomponent approach (eq. [2]) has the potential to reveal the stage in the mating sequence at which a particular character is selected, but some caveats are in order. First, different mating rate subcomponents were measured with different amounts of error. All mating events were recorded on an all-observed-occurrences basis (Grether 1996), but events differed in duration and thus in the probability of detection. Failed clasping attempts were quite brief (< 5 s) and most undoubtedly were missed. Thus, the observed rate of clasping attempts, $W_{m.n.1}$, underestimates the true rate, and consequently, $W_{m.n.2}$ overestimates the rate of claspings per attempt. A second practical limitation is that statistical power diminishes as a fitness component is subdivided into multiplicative parts.

Selection Coefficients.—The covariance of a character with relative fitness is mathematically equivalent to the within generation change in the mean of the character due to directional selection, that is, the directional selection differential (Lande and Arnold 1983; Arnold and Wade 1984; Falconer 1989). When components of fitness are multiplicative and correspond to sequential "episodes" of selection, the selection differential can be partitioned into additive parts corresponding to the separate episodes (Arnold and Wade 1984). However, the mating rate components (eq. [1]) were neither multiplicative nor sequential, so I calculated selection differentials separately for each component, without adjusting for figurative shifts in the character mean at previous episodes. Selection differentials calculated in this way are not additive, but they still provide information on the relative strength of selection through different fitness components (see Arnold and Wade 1984; Koenig and Albano 1987; Conner 1988). Subcomponents of the nonterritorial mating rate (eq. [2]) were multiplicative and sequential, so I partitioned the nonterritorial selection differential into additive parts.

Selection differentials measure the direct effects of selection on a character plus the indirect effects of selection on other correlated characters. Selection gradients, in contrast,

TABLE 1. 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*).

Character	Mating rate component			
	Territory tenure w_{pt}	Nonterritorial mating rate w_{mn}	Territorial mating rate w_{mt}	Overall mating rate w_m
Wing width	−0.022	0.114***	0.012	0.027
Wing length	−0.050	0.222	0.115	0.087
Thorax width	−0.005	0.043	0.019	0.019
Pink vein area	−0.137	2.843***	0.632	0.984*
Wing spot size	1.248**	1.084	1.264	1.720**
Wing spot fullness	0.083****	−0.035	0.022	0.052*
Wing spot continuity	0.085§	−0.098	0.052	0.034
Wing spot homogeneity	0.105***	−0.005	0.073	0.089§

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.02$; *** $P < 0.01$; **** $P < 0.0001$.

measure only the direct effects by holding the other characters constant (Lande and Arnold 1983). 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. The resulting factors were readily interpretable as a body size factor and a wing spot factor (see Grether 1996). Directional selection gradients were estimated using multiple regression (see Grether 1996).

Selection coefficient estimates were calculated for two samples of LMS cohort males. *Sample 1* comprised the 51 cohort males with terminal wing spot measurements. *Sample 2* included *sample 1* plus 21 cohort males last measured after sexual maturity, but before their wing spots reached terminal size. It was necessary to use *sample 1* for measuring selection on the wing spot characters, to eliminate ontogenetic effects (Grether 1996). *Sample 2* provided better estimates of selection on the ontogenetically fixed characters (wing length, wing width, thorax width, pink vein area), due to the larger sample size and greater variance in relative mating rate (Grether 1996).

The selection coefficient estimates do not rely upon distributional assumptions (Lande and Arnold 1983), but the standard parametric significance tests assume normality of residuals (Neter et al. 1985). This assumption was not always met in this study, so I recalculated all P-values smaller than 0.10 (according to the parametric method) by resampling (Simon 1992). The parametric and resampling methods always gave identical results with respect to significance at the 95% confidence level. No parametric tests have been developed for additively partitioned selection coefficients, so I tested components of the nonterritorial selection coefficient (eq. [2]) by resampling.

Manipulation Experiment

The lifetime mating success study controlled for wing spot ontogeny and body size, but other factors could lead to an indirect relationship between wing spots and mating rate components. To determine whether wing spot size affects mating rate components 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. For further information on the experimental manipulation and method of sampling mating rates, see Grether (1996).

I tested for treatment effects on the territorial and nonterritorial mating rates in ANCOVAs with the log number of days males were in the study as residents or nonresidents, respectively, as covariates. Treatment × covariate interaction terms were not significant and so were removed from the models (Neter et al. 1985). Mating rates were square-root transformed to reduce heteroscedasticity, skewness, and kurtosis (Sokal and Rohlf 1981).

RESULTS

Lifetime Mating Success Study

Sampling Bias.—The observed mating rates of residents were higher than those of nonresidents (see below); the question considered here is whether a difference in this direction could be a spurious sampling effect. That is, was I more likely to detect the matings of residents? The results indicate that sampling biases, if any, would have led to a difference in the opposite direction. Nonresidents were in tandem significantly longer than residents (mean ± SD: nonresidents 1208.9 ± 825.1, $n = 14$; residents 647.2 ± 363.7; $n = 30$; $t = 3.34$, $P < 0.01$), so there was more time for me to find nonresidents in tandem. There was no significant difference between nonresidents and residents in the minimum guarding duration ($t = 1.16$, df = 74, $P > 0.1$), the time of day at which mating occurred ($t = 0.26$, df = 326, $P > 0.7$), the distance moved by the pair between copulation and oviposition sites (mean ± SD; nonresidents: 23.0 ± 26.3 m, $n = 21$; residents: 15.4 ± 18.5 m, $n = 50$; $t = 2.01$, $P > 0.05$), or the current speed at oviposition sites (Mann-Whitney test, $z = 0.04$, $P > 0.9$; $n = 98$ nonresidents, 120 residents). The oviposition sites of nonresidents and residents were distributed in similar fashions along the stream; both were clustered in areas with fast moving water (rank correlations between current speed and the number of pairs ovipositing in 150 one-meter sections of creek; nonresidents: $r_s = 0.45$, $P < 0.0001$; residents: $r_s = 0.43$, $P < 0.0001$). These results agree with my impression

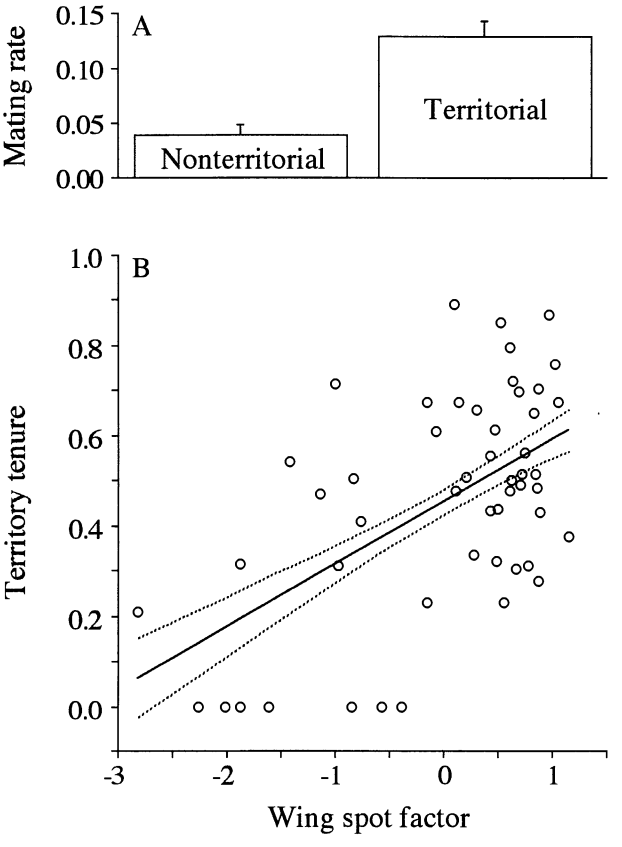

FIG. 1. Relationship between territorial status, mating rate, and the wing spot factor for the 51 cohort males with terminal wing spot measurements (*sample 1*). (A) Mating rate (mean + SE) versus territorial status. Only data on the 44 cohort males that held a territory are represented in this figure. Mating rates of the seven males that never held a territory were significantly lower than the other males' overall mating rates (unpaired *t*-test, $t = 3.07$, df = 49, $P < 0.004$) but not their nonterritorial mating rates ($t = 0.69$, df = 49, $P > 0.4$). (B) Territory tenure as a function of the wing spot factor. The solid line shows the shape of the function, as estimated by the cross-validated cubic spline method (Schluter 1988). Dotted lines represent standard errors of the function, as estimated from from 1000 bootstrapped replicates of the data set.

that the matings of nonresidents were at least as easy to detect as those of residents.

Wing Spot Selection (Sample 1).—Wing spot characters appeared to be selected through competition for mating territories and not through female choice or direct competition for females. As predicted by the territory competition model:

TABLE 3. 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).

Character	Mating rate component: Territory tenure w_{pt}	Nonterritorial mating rate w_{mn}	Territorial mating rate w_{mt}	Overall mating rate w_m
Wing width	0.010	0.138***	−0.034	0.044§
Wing length	0.058	0.300*	0.007	0.163*
Thorax width	0.017	0.063**	0.017	0.038**
Pink vein area	0.577	2.910***	−0.063	1.323***

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.02$; *** $P < 0.01$; **** $P < 0.0001$.

(1) males mated at higher rates while holding territories than when they did not (paired *t*-test, $t = 5.14$, df = 43, $P < 0.0001$; Fig. 1a); and (2) males with larger values of the wing spot characters held territories for a greater proportion of their reproductive lives (Table 1). The latter result was not an indirect effect of selection on body size: none of body size characters covaried significantly with territory tenure (Table 1), and the selection gradient of territory tenure on the wing spot factor was positive and highly significant (Table 2; Fig. 1b). In contrast to the predictions of the female choice and direct competition models, none of the wing spot characters covaried significantly with either the territorial mating rate or the nonterritorial mating rate (Tables 1 and 2).

Body Size Selection (Sample 2).—Body size also appeared to be under directional sexual selection, but the mechanism was different from that favoring larger wing spots. Each of the body size characters covaried positively and significantly with the nonterritorial mating rate, but none covaried significantly with the territorial mating rate or territory tenure (Table 3). Likewise, the nonterritorial selection gradient on the body size factor was significant ($\beta_1 \pm SE = 0.59 \pm 0.18$, $t = 3.19$, $P = 0.002$), but the territorial and territory tenure selection gradients were not (territorial, $\beta_1 \pm SE = -0.004 \pm 0.169$, $P > 0.9$; territory tenure, $\beta_1 \pm SE = 0.09 \pm 0.08$, $P > 0.2$). On the basis of these results, the territory competition hypothesis for body size selection can be rejected. It appears that larger body size gives nonresidents an advantage in acquiring mates, but not in acquiring territories. There was no evidence that larger body size provides a mating advantage for residents.

To further examine the causes of body size selection, I partitioned the nonterritorial selection differentials into additive components corresponding to consecutive stages in the

TABLE 2. 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 for the sample of cohort males with mature wing spot measurements (*sample 1*).

Fitness component	Character: Body size factor $\beta_1 \pm SE$	Wing spot factor $\beta_2 \pm SE$	R^2_{adj}
Territory tenure	−0.06 ± 0.06	0.31 ± 0.06****	0.30****
Nonterritorial mating rate	0.51 ± 0.20**	−0.08 ± 0.20	0.09*
Territorial mating rate	0.12 ± 0.11	0.21 ± 0.13	0.04
Overall mating rate	0.18 ± 0.09§	0.23 ± 0.09**	0.13**

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.02$; *** $P < 0.01$; **** $P < 0.0001$.

TABLE 4. Nonterritorial mating rate selection differentials partitioned into additive components corresponding to successive stages in the mating sequence, for the full sample of cohort males measured after sexual maturity (sample 2). Numbers in the *%S* columns indicate the percentage contribution of the subcomponent selection differential, S_k, to the total nonterritorial mating rate selection differential, *S*. Because the body size factor was orthogonal to the wing spot factor and expressed in standardized units, the body size factor selection differential is equal to the body size factor selection gradient. Selection differential estimates were tested for significance by bootstrapping.

	Nonterritorial mating rate subcomponent								
	Clasping attempts per day $W_{m.n.1}$		Claspings per attempt $W_{m.n.2}$		Copulations per clasping $W_{m.n.3}$		Mating credits per copulation $W_{m.n.4}$		Mating credits per day $W_{m.n}$
Character	S_1	%S	S_2	%S	S_3	%S	S_4	%S	S
Wing width	−0.016	−11.7	0.124§	89.8	0.009	6.9	0.021	15.0	0.138***
Wing length	−0.062	−20.5	0.266	88.6	0.054	18.0	0.042	14.0	0.300*
Thorax width	0.014	21.6	0.039	61.3	0.004	5.8	0.007	11.3	0.063**
Pink vein area	0.492	16.9	1.897	65.2	0.224	7.7	0.297	10.2	2.911***
Body size factor	−0.005	−0.8	0.464	79.1	0.053	9.1	0.074	12.7	0.587***

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

mating sequence (eq. [2]; Table 4). No selection differential components were significant ($P > 0.05$), but their relative magnitudes suggest that body size selection occurred primarily at the clasping stage (Table 4). That is, large nonresidents mated at higher rates than small nonresidents primarily because they were better at clasping females.

Manipulation Experiment

Premanipulation.—The sham and enlarged wing spot treatments were randomized successfully with respect to all measured variables. Thirty-five (43.2%) of the 81 males with enlarged wing spots were residents on the day before the night they were manipulated versus 33 (42.8%) of the 77 sham controls (*G* test, $P > 0.9$). In the subset of males for which mating and territorial data were available for one or more days *prior* to the manipulation (67 enlarged, 58 sham), there was no significant difference between treatment groups in overall mating rate ($F_{1,122} = 0.04$, $P > 0.8$), nonterritorial mating rate ($F_{1,83} = 0.18$, $P > 0.6$), territorial mating rate ($F_{1,66} = 0.06$, $P > 0.8$), or territory tenure ($F_{1,123} = 0.15$, $P > 0.7$). (Degrees of freedom differ between tests because not all males were observed as both residents and nonresidents.) There also were no significant differences between the enlarged and sham treatment groups in natural wing spot size ($F_{1,156} = 0.45$, $P > 0.5$), wing length ($F_{1,156} = 0.49$, $P > 0.4$), wing width ($F_{1,156} = 2.95$, $P = 0.09$), or thorax width ($F_{1,156} = 0.41$, $P > 0.5$).

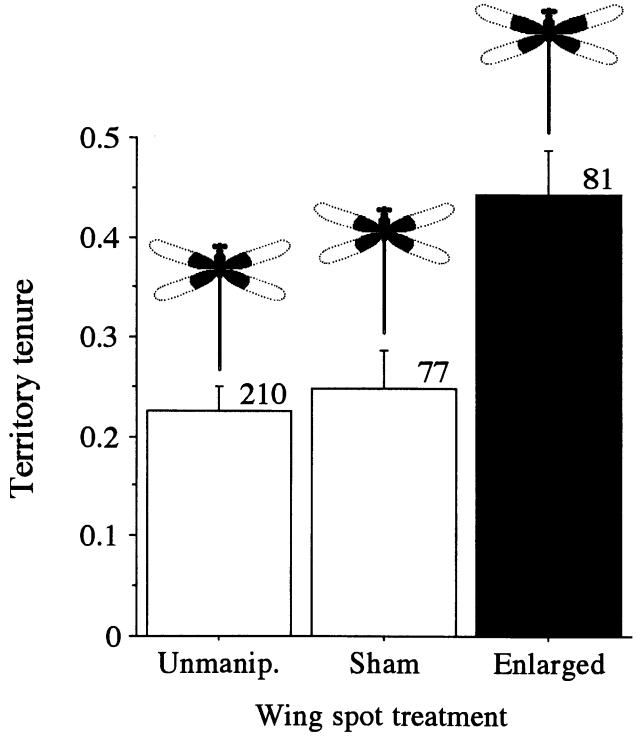

FIG. 2. Effect of the wing spot enlargement on territory tenure. Bars depict treatment group means; vertical lines represent one SE. Numbers above the columns are the corresponding samples sizes.

Postmanipulation.—The results of the manipulation experiment were consistent with the results of the LMS study. As predicted by the territory competition model, males with enlarged wing spots held territories on a greater proportion of days than both sham and unmanipulated controls ($F_{2,365} = 10.94$, $P < 0.0001$; post-hoc pairwise Bonferroni tests, both $P < 0.001$; Fig. 2). Territory tenures of the control groups did not differ significantly (Bonferroni test, $P > 0.9$). In contrast to the predictions of the female choice and direct competition models, there was no significant effect of the wing spot enlargement on the territorial mating rate ($F_{2,160} = 0.91$, $P > 0.4$) or the nonterritorial mating rate ($F_{2,318} = 1.35$, $P > 0.25$). The higher overall mating rates of males with enlarged wing spots (Grether 1996) appeared to be due to a positive correlation between the overall mating rate and territory tenure ($r = 0.22$, $n = 368$, $P < 0.0001$). That is, males with enlarged wing spots mated at higher rates than controls because they held territories on a greater proportion of days than controls.

DISCUSSION

The results provided clear evidence for contrasting mechanisms of sexual selection on wing spots and body size. Wing spots appeared to be selected through competition for mating territories (Tables 1 and 2, Figs. 1 and 2), while body size appeared to be selected through female choice or direct competition for females (Tables 3 and 4, see below).

Body size selection operated primarily among nonresidents at the clasping stage of the mating sequence (Table 4). It is not difficult to imagine how larger size could give nonresidents an advantage in clasping females. Males frequently attempt to clasp females by pinning them against the ground or vegetation (pers. obs.). Although females are significantly larger than males in some dimensions, the size distributions of the sexes overlap broadly (Grether 1995). Males on the upper end of the size distribution are larger than a greater proportion of females than are males on the lower end, and thus may be able to forcibly clasp more females. Male damselflies cannot force females to copulate (Corbet 1963), but may be able to detain them long enough to make resistance unprofitable. If so, this may be viewed as an example of body size selection through female choice, in that female resistance favors larger males, or as an example of body size selection through intersexual conflict (see West-Eberhard 1987; Arnqvist 1992; Rowe et al. 1994; Weigensberg and Fairbairn 1994). Large males may also have an intrasexual competitive advantage when several males simultaneously attempt to clasp the same female (in midair or against the substrate). Both forcible clasping attempts and clasping attempts by multiple males occur most frequently along slow stretches of creek, where nonresidents congregate and territorial defense is rare (pers. obs.).

At least four models have been proposed to explain the evolution of ornaments used in territory competition: priority, identity badge, status signaling, and agonistic handicap. Under the priority model (Butcher and Rohwer 1989), conspicuous ornaments signal territory ownership from a distance; signaling owners and receiving intruders benefit alike by avoiding unnecessary interactions (Huxley 1938; Peek 1972; Borgia 1979; Hansen and Rohwer 1986). The identity badge model (Rohwer and Røskaft 1989) supposes that novel ornaments initially give good fighters an advantage by making them more recognizable, but then spread through the population by mimicry (for similar ideas, see West-Eberhard 1983; Krebs and Dawkins 1984; Weldon and Burghardt 1984). Both of these models predict that ornament size and competitive success are uncorrelated, once the ornament has spread in the population (Butcher and Rohwer 1989), and therefore may be rejected in the present study.

Two versions of the status signaling model have been proposed: the uncorrelated asymmetry model and the correlated asymmetry model. Under the uncorrelated asymmetry model (Rohwer 1982; Maynard Smith and Harper 1988; Johnstone and Norris 1993), the size of an ornament signals aggressiveness (not fighting ability). More aggressive individuals gain priority of access to resources, but suffer higher costs of aggression. This model is only stable, however, when (1) the value of the contested resource is trivial relative to the costs of fighting; and (2) cheaters producing deceptively large ornaments are "punished" by conspecifics (Maynard Smith and Harper 1988). The first assumption seems unlikely to hold for rubyspot territories, since territory residents mated three times as often as nonresidents. The second assumption also appears to be false: males with experimentally enlarged wing spots held territories on a greater proportion of days and mated at higher rates than controls. If punishment occurred, it apparently was insufficient to offset the advantages of cheating. Moreover, the uncorrelated asymmetry model predicts that males with different sized ornaments have equal lifetime fitness (Maynard Smith and Harper 1988; Johnstone and Norris 1993). In contrast, I found that lifetime mating success increased with wing spot size (Grether 1996).

In the correlated asymmetry version of the status signaling model, individuals with high fighting ability (FA) gain greater access to resources by producing large ornaments; individuals with low FA produce small ornaments because, for them, the social costs of signaling high FA outweigh the benefits (Rohwer 1975, 1982; Maynard Smith and Harper 1988; Butcher and Rohwer 1989). This version of the status signaling model has not been formalized mathematically, but it appears to be a special case of the agonistic handicap model in which the costs of the signal are social (Grafen 1990a,b).

Under the agonistic handicap model (or agonistic indicator model; Andersson 1994), traits with no effect on FA evolve as honest indicators of FA, provided that larger values of the trait are more costly and the cost of a given value of the trait is lower for individuals with higher FA (Zahavi 1977; Grafen 1990a). Larger wing spots apparently are more costly: males with experimentally enlarged wing spots suffered higher mortality than controls (Grether, unpubl. data). The prediction that wing spot costs are lower for males with higher FA remains to be tested, but the evidence obtained thus far suggests that this prediction also holds. Males with larger natural wing spots lived longer (Grether 1996), despite the increased mortality of males with experimentally enlarged spots (Grether, unpubl. data), which implies that wing spots are condition dependent (see Møller 1990; Zuk 1992; Nicoletto 1993; Andersson 1994; Hill 1995). Thus, the applicability of the agonistic handicap model to this system hinges on the assumption that males with larger wing spots not only are more viable but also have higher fighting ability.

The agonistic handicap model is not restricted to competition for territories; it could explain the evolution of signals used in competition for resources of any type (Zahavi 1977; Grafen 1990a). To my knowledge, this is the first study to satisfy the main predictions of this model while ruling out the known alternatives.

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