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Survival cost of an intrasexually selected ornament in a damselfly

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SUMMARY

Ornaments could evolve as honest indicators of fighting ability, provided they have costs that make deceptive signalling unprofitable. I tested for such costs by manipulating the size of the intrasexually selected wing spots of male rubyspot damselflies (*Hetaerina americana*) and monitoring survival in the field. Males with enlarged spots had higher mortality rates than both unmanipulated and sham-manipulated controls. Natural wing spot size correlated positively with longevity, which suggests that higher quality males develop larger spots.

1. INTRODUCTION

Colour patches and other ornaments influence the outcome of contests for resources in diverse species (reviewed in Andersson 1994; Grether 1996*a*). Unlike weapons, ornaments do not affect fighting ability directly, but could function as fighting ability indicators. To signal fighting ability reliably over evolutionary time, ornaments must have costs that keep individuals with low fighting ability from benefiting by signalling high fighting ability (Zahavi 1977; Andersson 1982; Parker 1982; Nur & Hasson 1984; Zeh & Zeh 1988; Grafen 1990). I tested for such costs by manipulating the size of the red spots on the wings of male rubyspot damselflies (*Hetaerina americana*) and monitoring their survival in the wild.

The American rubyspot is one of 37 sexually dichromatic damselflies in the genus *Hetaerina* (Garrison 1990). Males bear a large red spot at the base of each wing that fits the description of a classic secondary sexual character (Darwin 1871; Grether 1995). Previous observational and experimental studies have shown that wing spots are sexually selected through contest competition, not female choice (Grether 1996*a,b*), and may reduce foraging efficiency (Grether & Grey 1996). Males with naturally larger wing spots mated at higher rates because they held territories for a greater proportion of their reproductive lives (Grether 1996*a,b*). Males with experimentally enlarged wing spots held territories more often and, consequently, mated at higher rates than both sham-manipulated and unmanipulated controls (Grether 1996*a,b*). Females given male-like wing spots showed prey capture rates similar to unmanipulated males and substantially below that of control females, suggesting that the male-like colour made them more conspicuous

to their prey (Grether & Grey 1996). The purpose of the present experiment was to determine whether wing spot enlargements reduce male survival.

2. METHODS

The experiment was conducted on a creek in the Coastal Range of California (Grether 1996*b*). A 2 km stretch of the creek was flagged at 10 m intervals and divided into six contiguous sections. Adjacent sections were separated by pools that rubyspots seldom cross (Grether 1995), and the sections farthest up and downstream were bordered on the outside by long pools (> 100 m). My assistants and I marked males on six consecutive days (30 June–7 July 1993), spending each day in a different section (see table 1). Sexually mature males with mature-coloured wing spots (Grether 1995) were marked on the left hindwing with a unique three digit number (Grether 1996*b*) and given one of three treatments: wing spots enlarged with red ink, wing spots sham-enlarged with clear ink, or unmanipulated (see Grether 1996*b* for details). To ensure a balanced experimental design and to avoid experimenter biases, males were assigned to treatment groups in a predetermined alternating order. The red ink provided a close match to the natural wing spot colour, as judged by both human eyes and spectroradiometry (Grether 1996*b*). The clear ink contained the same ingredients as the red ink, except the pigments (Grether 1996*b*), and contributed a similar amount of weight to the wings (Grether & Grey 1996). At marking, we also recorded wing wear (five levels) and characters used for estimating age (Grether 1996*b*). There were no significant chance differences among treatment groups in wing wear (Kruskal–Wallis test, $p < 0.2$) or estimated age at marking ($F_{2,933} = 1.80$, $p > 0.15$; overall mean age = 20.3 d, s.e. = 0.2, $n = 936$).

All creek sections were censused at the same intervals, starting from different marking dates (see table 1). The goal during censuses was to find all marked males. In total, 361 person-hours were devoted to this task, for a mean of 7.52 ± 0.36 h per census ($\pm$s.e., $n = 48$). Judging from the number of unmarked males sighted on day 2, about 90% of the sexually mature males present in the study area on day 0

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Table 1. *Wing spot manipulation experimental design and census results*

(This table cannot be used to exactly reproduce the survival times used in the survival analysis presented in figure 1 and table 2, because males that moved between sections were last sighted between census intervals. The downstream sequence (and length) of the creek sections was as follows: 1 (310 m), 4 (130 m), 5 (410 m), 2 (320 m), 3 (150 m), 6 (210 m).)

creek section (marking date)	wing spot treatment	males remaining *vs* days post-marking								
		0	2	4	7	10	13	16	19	22
1	unmanipulated	69	63	60	51	42	31	26	21	18
(30 Jun)	sham-enlarged	69	61	57	50	37	21	16	15	6
	enlarged	69	53	47	41	33	24	13	9	8
2	unmanipulated	67	55	39	36	30	24	18	15	13
(1 Jul)	sham-enlarged	67	54	44	39	30	24	20	17	12
	enlarged	67	50	39	36	27	23	17	15	10
3	unmanipulated	60	54	49	45	33	28	23	20	9
(2 Jul)	sham-enlarged	60	57	54	44	32	25	21	18	13
	enlarged	60	53	50	42	39	30	20	15	5
4	unmanipulated	34	27	26	20	18	16	12	7	4
(3 Jul)	sham-enlarged	34	32	29	25	20	19	18	12	6
	enlarged	34	27	23	18	15	11	11	9	3
5	unmanipulated	31	30	24	20	16	14	10	8	6
(4 Jul)	sham-enlarged	31	28	25	21	14	12	11	6	5
	enlarged	31	28	21	17	12	10	6	3	2
6	unmanipulated	51	45	45	38	32	22	15	11	7
(5 Jul)	sham-enlarged	51	45	42	36	27	24	21	12	7
	enlarged	51	46	43	40	32	27	22	19	13
total		936	808	717	619	489	385	300	232	147

Table 2. *Mortality rate as a function of wing spot treatment, age, wing wear, dispersal status, and creek section (Cox proportional hazards model)*

(The dependent variable in this model is $\log_e$ mortality rate. Hence, the $100(e^b-1)$ column shows the percentage increase in the mortality rate with a one unit increase in an explanatory variable. Regression coefficient subsets (e.g. age and age^2) were tested for significance using the likelihood ratio method (Dixon 1992); Wald and score function tests gave similar results. With the age^2 term removed, wing wear effects became significant, but otherwise the results remained unchanged and the overall fit of the model was lower. Since wing wear scores increased with age at marking ($r_s = 0.29$, $n = 936$, $t = 8.98$, $p < 0.0001$), the lack of a significant wing wear effect in the full model may be a statistical artefact of the stronger measurement scale for age. An accelerated failure time model using the Weibull distribution (Dixon 1992) gave results qualitatively the same as those shown here.)

explanatory variable	coefficient, b (s.e.)	$100(e^b-1)$	probability
wing spot treatment (enlarged *vs* controls)	0.209 (0.076)	23.3	< 0.01
age at marking	−0.151 (0.078)	−14.0	
age at marking-squared	0.006 (0.002)	0.6	< 0.0001
wing wear			
light (1–2)	0.114 (0.149)	12.0	
heavy (3–4)	0.169 (0.096)	18.4	> 0.1
dispersal status (time dependent)	−0.052 (0.108)	−5.1	> 0.7
creek section 1	0.303 (0.119)	35.3	
2	0.387 (0.120)	47.3	
3	0.032 (0.123)	3.3	
4	0.064 (0.152)	6.6	
5	0.236 (0.147)	26.6	< 0.005

were marked. Males not resighted were assumed to have died, since males that left one section would soon have been sighted in another (Grether 1996*b*).

The effect of the wing spot enlargement on mortality rate was estimated by the Cox proportional hazards program in BMDP 2L (Dixon 1992). This standard survival analysis model was used because resighting probabilities in this study were high (0.945 ± 0.005, mean±s.e.) and did not differ significantly among treatment groups (Kruskal–Wallis test, $p > 0.9$). Wing wear and age at marking, dispersal status, and creek section were entered in the model as covariates. Wing wear scores were collapsed to three levels (0, 1–2, 3–4) and dummy coded. Dummy coding was also used to include creek section as a categorical variable. Examination of the data suggested that the mortality rate was a curvilinear (J-shaped) function of the estimated age at marking, so both age at
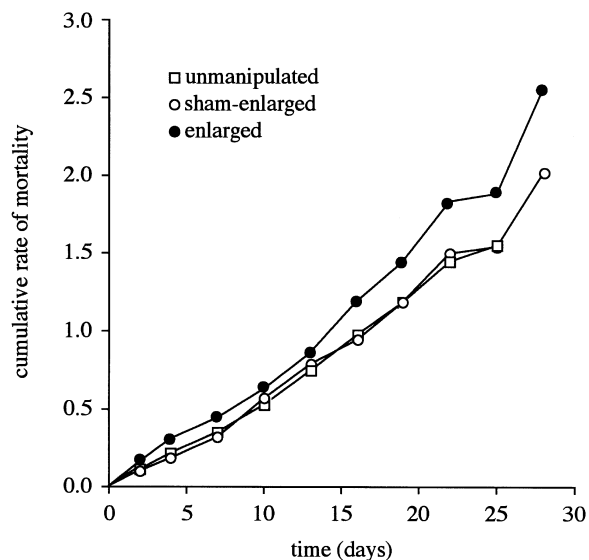
Figure 1. Cumulative rate of mortality stratified by wing spot treatment, estimated by the Cox proportional hazards program in BMDP 2L (Dixon 1992). See text for analysis details.

marking and age at marking squared were entered as covariates (Lee 1992). Dispersal status was entered as a time-dependent covariate (Dixon 1992; Lee 1992) with an initial value of zero and a post-emigration value of one. Survival times for 158 males (16.9%) that outlived the study were coded as censored (Lee 1992).

3. RESULTS

Males with enlarged wing spots had mortality rates 23% higher than the pooled controls, after controlling for age, wing wear, creek section, and dispersal (see figure 1; table 2). Control group mortality rates differed, nonsignificantly, by 0.39% ($t = 0.04$, $p > 0.5$). These results could not be attributed to relatively high rates of undetected dispersal among males with enlarged spots. There was no significant difference among treatment groups in the number of males that left their original section (53 unmanipulated, 66 sham-enlarged, and 50 enlarged; G-test, $p > 0.2$), or in the distance moved by males between marking and final sighting (ANCOVA controlling for survival time, $F_{2,932} = 0.42$, $p > 0.6$; dispersal distance was $\log_e(x+1)$ transformed and survival time was square root transformed for this analysis, to meet parametric assumptions).

4. DISCUSSION

The increased mortality rates of males with enlarged wing spots may be a consequence of increased conspicuousness to visually orienting predators (e.g. dragonflies, birds, lizards). Alternatively, or additionally, the increased mortality may be an effect of increased conspicuousness to visually orienting prey (e.g. caddisflies, mayflies, midges). Indirect evidence for the latter effect was provided by an experiment in which some females were given male-like wing spots

(Grether & Grey 1996). The manipulated females caught fewer prey per minute and per capture attempt than control females, yet experienced normal rates of agonistic interference (Grether & Grey 1996). Reduced hunting efficiency could translate into starvation when food is scarce or increased exposure to predators resulting from compensatory hunting (rubyspots hunt on the wing and are usually taken by predators while in flight).

In any case, the advantage of large wing spots in territory competition (Grether 1996a) appears to be counteracted by a survival cost. Natural wing spot size, however, correlates positively with longevity (Grether 1996b). These superficially contradictory results conform well to signalling theory. For an ornament to evolve as an honest indicator of fighting ability, the cost of a given size of the ornament must be higher for lower quality (hence lower fighting ability) males (Zahavi 1977; Andersson 1982; Parker 1982; Nur & Hasson 1984; Zeh & Zeh 1988; Grafen 1990). Under these conditions, higher quality males should develop larger ornaments (Zahavi 1977; Andersson 1982; Parker 1982; Nur & Hasson 1984; Zeh & Zeh 1988; Grafen 1990), as the positive correlation between longevity and natural wing spot size suggests.

Positive correlations with longevity appear to be the rule for sexually-selected ornaments (Price 1984; Conner 1988; Göransson *et al.* 1990; Alatalo *et al.* 1991; Hill 1991; Møller 1991; Petrie 1992; Borgia 1993). This implies that high quality males tend to under invest, i.e. develop smaller ornaments than required to reduce their survival to the level of low quality males. Under current theory, however, exact investment (zero correlation) and over investment (negative correlation) could also be evolutionarily stable (Grafen 1990; Price *et al.* 1993). The empirical prevalence of under investment suggests that theoreticians have a new puzzle to solve.

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