RELATIONSHIPS OF LARVAL PHENOLOGY AND IMAGINAL SIZE TO MALE PAIRING SUCCESS IN *ARGIA VIVIDA* HAGEN (ZYGOPTERA: COENAGRIONIDAE)

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The study was conducted at 2 geothermically heated sites in British Columbia, Canada. Because of different thermal regimes, the sp. has a 1-yr life cycle at Halcyon Hotsprings, and a 3-yr life cycle at Albert Canyon. At Albert Canyon, males mating early in the day did not differ significantly in size from males selected at random from the population later in the day. At Halcyon Hotsprings, males mating early in the day were significantly smaller that those selected at random later in the day. Males were also smaller, in general, at Halcyon Hotsprings than at Albert Canyon, but females were not. Differences in larval phenology may have led to changes in the relationship between male size and pairing success between the two sites. Comparative studies of lifetime mating success between populations having differing life cycles may aid in separating the effects of size, age and survivorship on mating success in nonterritorial odonates.

INTRODUCTION

The investigation of the effects of size on lifetime reproductive success of male odonates has largely been a quest without theory. Formulating hypotheses about the influence of male size on mating success in odonates is very tempting, since the size of breeding adults is fixed from the time the exoskeleton hardens at emergence. Large body size can confer an advantage in inter-male competition among insects (see BLUM & BLUM, 1979 for examples). However, for flying insects, smaller body size can confer an advantage in maneuverability and flight efficiency (McLACHLAN, 1986; CONVEY, 1989). Intersexual selection via mate choice is not likely to act directly on adult male body size in odonates, because adult size is fixed at emergence and is, therefore, unlikely to reflect adult phenotypic condition. However, large size may be favoured by intersexual

selection if it signals quality in other traits that are correlated with fitness, such as male age (BANKS & THOMPSON, 1985), or larval success (HARVEY & CORBET, 1985). In any given population, there is no a priori reason to assume large or small size will be favoured by sexual selection.

HARVEY & CORBET (1985) have shown that increased larval size leads to increased adult size and thus increased mating success in a territorial damselfly. They also noted a bimodal distribution of male size at emergence over the season. They suggested that the late emergence of particularly small individuals was the result of some larvae that did not moult to the final instar in the previous fall but were delayed until spring. The influence of adult male size on mating succ may, therefore, be influenced by the phenology of the larvae.

Argia vivida is a medium-sized damselfly that is found, in western Canada, mainly in geothermally heated waters (PRITCHARD, 1982). Depending on the thermal regime, the life cycle of *A. vivida* in these areas varies from one to three years (PRITCHARD, 1982). Different temperatures can result in different growth rates between instars and different timing of diapause stages (LEGGOT & PRITCHARD, 1985; PRITCHARD, 1989). Both of these factors should influence the relationship of emergence and male body size over the flight season.

The mating behaviour of *A. vivida* is described in detail elsewhere (CONRAD & PRITCHARD, 1988, 1990). Briefly, male capture mates either while basking at sunspots in the morning or by searching for previously-mated females ovipositing at the water in the afternoon. Pairs remain in tandem (male attached to the female's prothorax by his terminal abdominal claspers) for 1 to 2.5 hr while performing copulation and oviposition. Tandem pairs are therefore easily identified as individuals that have mated.

I sampled adult male *A. vivida* at two sites, Halcyon Hotsprings (HH), British Columbia, where the species has a one-year life cycle and Albert Canyon (AC) where it has a three-year life cycle (PRITCHARD, 1989). My intention was to determine if the influence of male size on pairing success differed between the two populations.

METHODS

The study was performed in July and August 1985 at both sites. *A. vivida* and *Amphiagrion abbreviatum* (Sel.) are the only zygopterans breeding at either site and the latter species is much less numerous than *A. vivida*.

Observations were performed in a series of 5 three-day "sessions", beginning at AC and alternating between each site. Each day, the first five copulating pairs seen were captured, individually marked, held for about 1 hr to permit voiding of their guts and then were killed with ethyl acetate and preserved in formalin. In mid-afternoon, five nontandem males were selected at random from those males at the water and were treated in the same way as the mated pairs. These specimens are referred to as the "formalin samples". The length of the left forewing of each individual was measured to the nearest 0.1 mm using dial calipers.

The left forewing length of approximately the first 100 individuals captured each session was also

measured and whether they were captured in tandem was recorded. These individuals are referred to as "field-caught" specimens. Other than the individuals collected, all damselflies encountered were individually marked on the left hindwing with indelible ink and released at the point of capture. This permitted the "recapture" of marked damselflies without disturbing them by reading the numbers using close-focus binoculars. Whether a male was in tandem was noted for each resighting. I made all forewing measurements with the same calipers. Analysis of an independent sample confirmed that forewing length was strongly correlated with constant dry mass (HH, $r^2=0.827$, df=20, p< 0.001) and presumably therefore, overall size of the damselflies.

RESULTS

Adults were found at both sites from late May (29th) to mid September (10th), suggesting that *A. vivida* is a "summer species" (cf. CORBET, 1958). *A. vivida* appeared to have a prolonged period of emergence at both sites, as judged by the long flight season and given a relatively short adult lifespan (ca 12 days; CONRAD, 1987).

For the purposes of the following analyses, field-caught individuals captured in tandem on at least one day are referred to as mated. Unmated field-caught individuals are those never captured in tandem. Individuals were captured about 1.3 days each (max. = 7 days) at each site, but only the day of first capture of an individual is used in analysis.

There were no significant correlations between date of capture and size at either site for either males or females (all $r^2 < 0.04$, all p > 0.11, smallest N = 52). As a result, no corrections for a change in size over the brief period of the study are included in the following analyses.

Both field-caught and formalin males were smaller at HH than at AC (Tab.

Table I

Forewing measurements of "formalin" and "field-caught" males from Albert Canyon and Halcyon Hotsprings. [x ± S.E., sample sizes in parentheses].

Condition	Albert Canyon	Halcyon Hotsprings
	Field-caught	
Mated	2.407±0.014 (51)	2.413±0.012 (49)
Unmated	2.424±0.007 (173)	2.370±0.009 (93)
	Formalin	
Mated	2.405±0.037 (35)	2.335±0.036 (30)
Unmated	2.413±0.033 (30)	2.403±0.029 (30)

Field-caught males, 2-way ANOVA results: Site effect F = 4.742, df = 1,362, p = 0.030; − Mating status effect F = 1.375, df =1,362, p = 0.242; − Interaction F = 7.435, df = 1,362, p = 0.007.

Formalin males, 2-way ANOVA results: Site effect F = 7.397, df = 1,121, p = 0.007; − Mating status effect F = 6.621, df = 1,121, p = 0.011; − Interaction F = 7.435, df = 1,121, p = 0.042.

I). Among field-caught males, mated and unmated males did not differ significantly at each site (Tab. I). At Albert Canyon there was no significant difference between mated and unmated formalin males (t = 0.355, df = 63, p = 0.724) but at Halcyon Hotsprings, mated formalin males were smaller than unmated formalin males (t = 3.392, df=58, p = 0.001, Tab. I).

This relationship is supported by the significance of the two-way interaction term in the analysis of formalin males. There is also a significant interaction term in the analysis of the field-caught males, suggesting that unmated males at Halcyon are smaller than males in the other groups (Tab. I). This appears to contradict the data for formalin males, but it is most likely the result of bias in my sampling program. There was a preponderance of large mated males captured in the afternoon because capturing pairs proved to be the best way to mark females. If small males mate early in the day as suggested by the formalin data, then larger males that mated later may be over-represented among field-caught males and smaller males are under-represented because they have already completed oviposition (Tab. II).

Table II

Numbers of sightings (all sightings of individuals of known size included) of small versus large mated and unmated males in morning and afternoon at Halcyon Hotsprings. Specimens captured and removed (formalin males) are not included. Small males are those less than the population median. Morning is earlier than 1130 solar time (CONRAD & PRITCHARD, 1990) or approximately 1320 Pacific Daylight Time.

Condition	Small	Large
	Morning	
Mated	0	4
Unmated	45	48
	Afternoon	
Mated	17	32
Unmated	16	16

There was no difference in the size of field-caught females between sites (Tab. III). However, mated formalin females at Halcyon Hotsprings were smaller than those at Albert Canyon.

DISCUSSION

Argia vivida at Albert Canyon were larger than at Halcyon Hotsprings. At Albert Canyon, males of the first five tandem pairs seen each day did not differ from a random sample of non-tandem males collected later in the day. At Halcyon

Table III

Forewing measurements of "formalin" and "field-caught" females from Albert Canyon and Halcyon Hotsprings. — [x ± S.E., sample sizes in parentheses].

Condition	Albert Canyon	Halcyon Hotsprings
	Field-caught	
Mated	2.554±0.015 (48)	2.545±0.013 (46)
Unmated	2.538±0.046 (12)	2.553±0.024 (6)
	Formalin	
Mated	2.552±0.032 (35)	2.506±0.032 (30)

Field-caught females, 2-way ANOVA results: Site effect $F = 0.015$, $df = 1,108$, $p = 0.902$; — Mating status effect $F = 0.021$, $df = 1,108$, $p = 0.884$; — Interaction $F = 0.198$, $df = 1,108$, $p = 0.570$. Mated formalin females, t-test results: $t = 2.244$, $df = 63$, $p = 0.028$.

Hotsprings, males in the first five pairs captured each day were smaller than non-tandem males selected at random in the afternoon. These data, when compared with the data on field-caught males, suggest that small males were able to mate earlier, and subsequently complete mating earlier in the day than large males. However, this relationship did not hold at Albert Canyon. Therefore, assuming that mating early in the day confers an advantage over an individual's lifetime, the relationship of male size to lifetime reproductive success would differ in the two populations studied.

In general, workers studying territorial species have discovered a positive correlation between adult male size and reproductive success, usually because large size confers increased resource holding potential (WALTZ & WOLF, 1984). Larger males may be territorial longer (KOENIG & ALBANO, 1987), may win more territorial disputes (HARVEY & CORBET, 1985) or may hold better territories (TSUBAKI & ONO,1987). Both MILLER (1983) and FINCKE (1984) have shown that territorial males are larger than non-territorial males in a dragonfly and damselfly, respectively. Size seems to confer some advantage to males of territorial species, even though this advantage is often accrued indirectly. In contrast, studies of non-territorial damselflies have found stabilizing selection for male body size (FINCKE, 1982; BANKS & THOMPSON, 1985).

My study cannot be compared directly with studies on lifetime reproductive success. I must assume that males that mate earliest in the day will ultimately obtain a higher lifetime reproductive success than males mating later in the day. I have argued that the morning and afternoon matings of *A. vivida* do not constitute distinct behavioural alternatives and that males mating early in the day away from the water or later in the day at the water do not neccessarily obtain different numbers of fertilizations (CONRAD & PRITCHARD, 1988, 1990). I based this

argument on the fact that mating twice in one day was extremely rare for males. At HH in 1986, of 1426 sightings of 917 marked males, 75 males were seen at least twice in one day, 24 of those were in tandem during both sightings and only one of those males was seen with two different mates. It seems unlikely that early-mating males might benefit from additional matings within a day, but I cannot completely reject this as a benefit of mating early.

The mating behaviour of *A. vivida* and the data I have presented suggest three hypotheses to explain the stabilizing selection for male size observed in this and other non-territorial species:

(1) Constraints on male ability to capture and hold mates. — In non-territorial species practicing a female-control mating strategy (CONRAD & PRIT-CHARD, 1988), extremes of size may be selected against because large males may not be agile enough to capture females and small males may not be large enough to retain them.

(2) Varying selection pressure within a day. — Small size might be favoured early in the day because small size enables males to begin mate-searching earlier. Small males would have to be more efficient flyers or perhaps warm up faster each day. Larger males could gain an advantage when competing for mates at the water later in the day, when the density of males is higher. Such a pattern is suggested by the data from Halcyon Hotsprings.

(3) Varying selection pressure over the season. — The relationship between male size and mating success might change curvilinearly with season. In this study, curves could be identical at HH and AC, but the sites could be "out of phase". Sampling then would have occurred at two different points on the curves, which would have produced the differences in the relationship between size and pairing success between sites. Overall, however, both sites would display stabilizing selection for male size over the season.

As BANKS & THOMPSON (1985) have pointed out, explanations for the relationship between male size and reproductive success in odonates are confounded by the decline in size at emergence with season and selection for early emergence. A spurious correlation between size and mating success can result when age (time since emergence) is correlated with mating success (BANKS & THOMPSON, 1985) or lifespan is negatively correlated with emergence date and lifespan is positively correlated with lifetime reproductive success. Fortunately, where the relationship between mating success and male body size is altered by changes in larval phenology, it may be possible to partition the effects of male age, size and lifespan by comparative studies between populations. Further study of the effects of male size on mating success of male odonates should take larval phenology into consideration.

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REFERENCES

BANKS, M.J. & D.J. THOMPSON, 1985. Lifetime mating success in the damselfly Coenagrion puella. *Anim. Behav.* 33: 1175-1183.

BLUM, M.S. & N.A. BLUM [Eds], 1979. *Sexual selection and reproductive competition in insects.* Academic Press, New York.

CONRAD, K.F., 1987. *Complementary male and female mating strategies of Argia vivida Hagen (Odonata: Coenagrionidae): an example of a female-control mating system.* MSc. Thesis, Univ. Calgary.

CONRAD, K.F. & G. PRITCHARD, 1988. The mating behaviour of Argia vivida Hagen: as an example of a female-control mating system (Zygoptera: Coenagrionidae). *Odonatologica* 17: 179-185.

CONRAD, K.F. & G. PRITCHARD, 1990. Pre-oviposition mate guarding and mating behaviour of Argia vivida (Odonata: Coenagrionidae). *Ecol. Ent.* 15: 363-370.

CONVEY, P., 1989. Influences on the choice between territorial and satellite behaviour in male Libellula quadrimaculata Linn. (Odonata: Libellulidae). *Behaviour* 109: 125-141.

CORBET, P.S.,1958. Temperature in relation to seasonal development of British dragonflies (Odonata). *Trans. Xth. Int. Congr. Ent.* 2: 755-758.

FINCKE, O.M., 1982. Lifetime mating success in a natural population of the damselfly, Enallagma hageni (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* 10: 293-302.

FINCKE, O.M., 1984. Giant damselflies in a tropical forest: Reproductive biology of Megaloprepus coerulatus with notes on Mecistogaster (Zygoptera: Pseudostigmatidae). *Adv. Odonatol.* 2: 13-27.

HARVEY, I.F. & P.S. CORBET, 1985. Territorial behaviour of larvae enhances mating success of male dragonflies. *Anim. Behav.* 33: 561-565.

KOENIG, W.D. & S.S. ALBANO, 1987. Lifetime reproductive success, selection, and the opportunity for selection in the white-tailed skimmer Plathemis lydia (Odonata: Libellulidae). *Evolution* 42: 22-36.

LEGGOT, M. & G. PRITCHARD, 1985. The effect of temperature on rate of egg and larval development in populations of Argia vivida Hagen (Odonata: Coenagrionidae) from habitats with different thermal regimes. *Can. J. Zool.* 63: 2578-2582.

McLACHLAN, A.J.,1986. Survival of the smallest: advantages of small size in flying animals. *Ecol. Ent.* 11: 237-240

MILLER, P.L., 1983. The duration of copulation correlates with other aspects of mating behaviour in Orthetrum chrysostigma (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 12: 227--238.

PRITCHARD, G., 1982. Life-history strategies in dragonflies and the colonization of North America by the genus Argia (Odonata: Coenagrionidae). *Adv. Odonatol.* 1: 227-241.

PRITCHARD, G., 1989. The roles of temperature and diapause in the life history of a temperate--zone dragonfly: Argia vivida (Odonata: Coenagrionidae. *Ecol. Ent.* 14: 99-108.

TSUBAKI, Y. & T. ONO, 1987. The effects of age and body size on the male territorial system of the dragonfly, Nannophya pygmaea Rambur (Odonata: Libellulidae). *Anim. Behav.* 35: 518--525.

WALTZ, E.C. & L.L. WOLF, 1984. By Jove!! Why do alternative mating tactics assume so many different forms? *Am. Zool.* 24: 333-343.