

PREDATION RISKS ASSOCIATED WITH MATING AND OVIPOSITION FOR FEMALE *CROCOTHEMIS ERYTHRAEA* (BRULLÉ) (ANISOPTERA: LIBELLULIDAE)

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Observations are presented on oviposition and mate guarding in the Camargue, France. After a short copulation at the oviposition site, females immediately commence exophytic oviposition whilst being non-contact guarded by their mates, and they generally suffer a high level of interference from other males. Although a trend was found, guarded females did not have a significant advantage over non-guarded in terms of either reduced interference rates or an increased number of egg-laying dips made. Predation rates on ♂, ♀ and tandem pairs of *C. erythraea* by other dragonfly spp. were measured. Tandem pairs and ovipositing females were particularly vulnerable, providing hard evidence for a survival cost associated with reproduction.

INTRODUCTION

The Libellulidae are a behaviourally advanced family of the Odonata (see review by WAAGE, 1984). Male territoriality is common, copulation frequent and of short duration, females often oviposit within the male's territory (if present) and post-copulatory association in the form of non-contact guarding (infrequently tandem oviposition) is common. Such mating systems are likely to have been influenced by sexual selection via intense intrasexual competition (WAAGE, 1984), with the role of sperm competition being important in this context. *C. erythraea* is one of the few anisopteran species in which sperm competition has been demonstrated (SIVA-JOTHY, 1984).

The general advantages of non-contact guarding to males are clear (ability to take additional mating opportunities while guarding; maintenance of territorial

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defence; lowered risk of predation compared to tandem; (WAAGE, 1984), though all may not apply to any one species. The benefits accruing to females are different, and their interests may even be in conflict with the male's. Particularly, as females do not use their full sperm load during oviposition on one day, being mated several times within one oviposition visit is unnecessary with respect to sperm supply, and may increase the risk of damage or predation. Multiple mating does, however, carry advantages such as increasing the genetic variation of the female's offspring. Reduced interference rates from other males (i.e. reduced risk of damage and/or reduced time spent at oviposition site) has been cited as an advantage (WAAGE, 1979), as has parasitism of male guarding behaviour by non-mated females (ALCOCK, 1979; WAAGE, 1979). Unlike those endophytically ovipositing species which oviposit under water, exophytically ovipositing libellulids are not likely to become stranded on the water surface (cf. FINCKE, 1982), and rescue of floating females by their mates has not been recorded.

Crocothemis erythraea is a typical libellulid dragonfly. Females arrive at water carrying a mature batch of eggs and, unless virgin, unused viable sperm from previous matings; they commence oviposition immediately, without being copulated. In dense populations, such as the one studied here, the female is usually quickly spotted by several males, one of which succeeds in capturing her and forming the tandem position in flight. The pair often copulate in flight, but may spend most or all of the few seconds of copulation perched on emergent vegetation over the oviposition site, where they are probably less obvious to potential predators or competing males. After copulation, they separate and the female immediately commences exophytic oviposition, dipping the tip of her abdomen rapidly onto the water surface (1-2 dips each second; REHFELDT, 1991). Each dip may wash several eggs from the tip of the abdomen (or none). During oviposition the male guards his mate in flight, attempting to drive off other intruding males. If a female is not copulated, or if she is and her mate is successful in keeping intruders away, her complete egg batch will be released in one oviposition sequence (taking 2-3 minutes), after which she leaves the oviposition area. However, if the female is captured by an intruder, despite being guarded, egg release stops and she is recopulated. This may happen several times, and thus the release of the complete egg batch may be divided into several shorter oviposition sequences.

REHFELDT (1991) described mate-finding and oviposition behaviour in this species. The study reported here considers the risk and rewards of multiple mating and post-copulatory guarding in a high density population of *C. erythraea*. Most discussions of odonate mating systems have been centred on the male's role in their evolution and maintenance (e.g. CORBET, 1980; WAAGE, 1984). The question here is approached from the female's perspective, as the costs and benefits may clearly be different for the two sexes.

METHODS

Observations were made between 20 August and 11 September 1986, on the Estate of the Station Biologique de la Tour du Valat in the Camargue, France. Male *C. erythraea* were abundant over many of the areas of shallow water on the Estate between approximately 1030 and 1630 (European Summer Time) on sunny days. Females spent much shorter periods near the water, only arriving to mate and oviposit. All activity was concentrated over shallow water within 10-15 m of the shore.

Observations of copulation, egg-laying rates and male interference rates were made at one pool known as Les Garcines. Copulation time (spent in wheel formation) was measured using a stopwatch. Egg production was approximated by recording the number of egg-laying dips onto the water surface each female made after copulation. At the same time the number of interference events or copulation attempts by other males was recorded. Total batch size was obtained by capturing females after copulation and holding them with the tip of the abdomen submerged in a small vial of pond water. Release of the complete batch occurs involuntarily in this situation (McVEY, 1984), and the number of eggs, and duration of release, were recorded. It is proposed that the rate of egg release into the vials, and the total number released, approximate to those of free-flying females, as it is not possible to measure the latter directly.

During the study predation of *C. erythraea* by the larger anisopterans *Anax parthenope* (Sel.) and, infrequently, *Orthetrum cancellatum* (L.) was noted, and the class of victim (male, female, tandem) recorded. To estimate the availability of the three prey classes to predators over the oviposition site, an area of the shoreline and adjacent water of Les Garcines was selected, approximately 15 m x 15 m. Within this area a total of 84 visual scan surveys were made between 1130 and 1545 on one day, recording the number of males, females and tandems present. Only flying individuals were recorded during the surveys, as the larger species only took prey in flight (with the high local population density, few males perched at any one time; likewise, females rarely perched during oviposition and tandems perched only for the few seconds necessary for copulation).

RESULTS

BATCH SIZE

The mean number of eggs/batch was 455 (SE= 71, N= 39; Fig. 1), and mean duration of oviposition into the vials was 99.2 s (SE= 12.1 s). These figures are likely to be slight underestimates, as most females commenced oviposition immediately after separation from the wheel, and there was usually a few seconds' delay before capturing them. Eight females producing no eggs were included in the calculations above and in Figure 1, in the assumption that they would

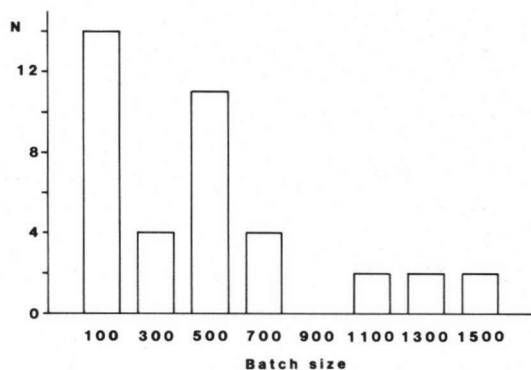


Fig. 1. *Crocothemis erythraea*: histogram of complete batch sizes produced by 39 females with the abdomen held in a vial of pond water.

not have released eggs if free-flying, so would have given their mates no immediate return. The maximum batch size and production time were 1570 eggs and 280 s respectively. The egg release rate into vials remained constant with time, at approximately 6/s, giving a highly significant regression ($n \text{ eggs} = -17.1 + 5.73 \times \text{time}$, $F_{1,28} = 144.2$, $p \ll 0.001$, $r^2 = 83.2\%$).

OVIPOSITION IN THE FIELD

Mean duration of copulation was 8.1 s (SE = 0.3 s, N = 34), with exophytic oviposition usually following immediately. Eighty-six oviposition sequences were followed with females being non-contact guarded by their most recent mate, and a further 26 of females seen ovipositing without being guarded. Cases where individual females were copulated by two or more different males were treated as separate oviposition sequences. Four females left the water immediately after copulation without any oviposition. At least two males guarded two females simultaneously, however they did not copulate with the second female, and seemed unable to distinguish them.

Although there was a trend for guarded females to manage more dips in an oviposition sequence than non-guarded (means: guarded 27.6, non-guarded 18.0), neither this nor the slight difference in interference rates (means: guarded 1.9, non-guarded 1.7 events/sequence) approach significance (Fig. 2). The distribution of number of dips per

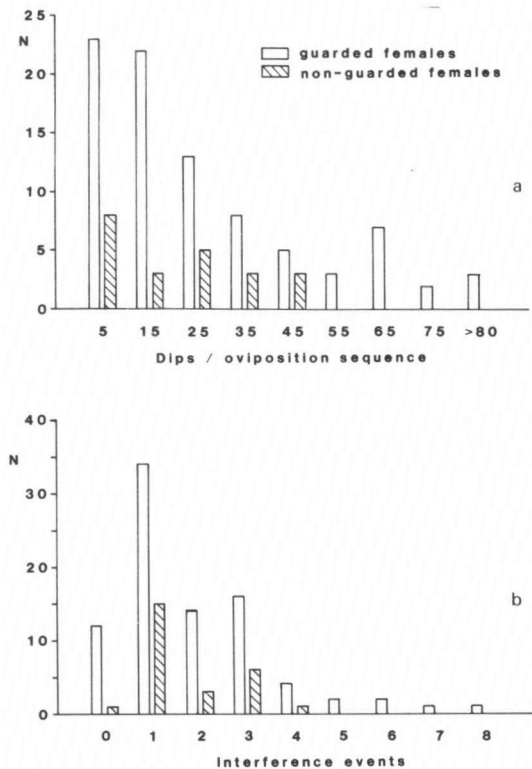


Fig. 2. *Crocothemis erythraea*: (a) The influence of the presence or absence of male guarding on female oviposition (measured as number of egg-laying dips / oviposition sequence) [Mann-Whitney U-test, $W = 5050.0$, $p = 0.189$, NS]; — (b) The influence of the presence or absence of male guarding on the number of interference events experienced by females from other males during an oviposition sequence [Mann-Whitney U-test, $W = 4891.0$, $p = 0.819$, NS].

oviposition sequence was heavily skewed, suggesting that most sequences, and hence most copulations, only resulted in fertilisation and release of a small number of the available eggs (Fig. 2a). The maximum number of dips recorded in a single sequence was 180, approximately ten times the median number. The fate of guarded and non-guarded females after commencing oviposition is shown in Table I. Again, although the figures suggest that more non-guarded than guarded females are captured by males rather than completing oviposition and leaving the water, the trend does not approach significance ($\chi^2 = 2.03$, $p > 0.1$, NS). In this population, any advantage of non-contact guarding to females is small.

Table I
The fate of guarded and non-guarded female *C. erythraea* after commencing oviposition

	Guarded N	Non-guarded N
Leave pool	23	5
Copulated by other ♂	19	10
Unknown	36	9

PREDATION RATES

Data related to predation events are summarised in Table II. In 59 of the 60 predation events recorded the predator was *Anax parthenope*, with a single event involving *Orthetrum cancellatum*. Predation occurred evenly between 1200 and 1600, with only two events recorded before 1200 and five after 1600. The visual surveys were carried out on one day, whereas predation events were recorded over the full duration of the study, however they give a reasonable approximation of the numerical availability of the different prey classes (it is purely coincidental that the numbers of females and tandems recorded in the surveys, and predated, are identical). In all of the cases of predation on females, the individuals were actively ovipositing. On at least two of the occasions of tandem predation, the

Table II

Numbers and percentages of three classes of *C. erythraea* adults (lone males, females and tandem/wheel) found in visual scan surveys of part of the oviposition area at Les Garcines, and observed as victims of predation [$\chi^2 = 236.9$, $p < 0.001$ (calculated from raw data); – percentages given in parentheses]

	N	♂	Victim class	
			♀	Tandem/wheel
Survey result	672	648 (96.4)	18 (2.7)	6 (0.9)
Observed predation	60	36 (60.0)	18 (30.0)	6 (10.0)

male escaped (the fate of the other pairs was not recorded). All successful attacks on males were of lone patrolling individuals. Females particularly, and probably also tandem pairs, were much more vulnerable to predation than lone males.

Five cases of predation of other odonate species' tandems were recorded during the study; twice, *A. parthenope* males captured an *O. cancellatum* tandem in flight; black-headed gulls, *Larus ridibundus* L., captured two *A. parthenope* tandems while in the process of endophytic oviposition; a green lizard, *Lacerta viridis* (Wolf), captured a perched *A. parthenope* wheel. No predation of single individuals of either species at water was noted.

DISCUSSION

The mating system employed by male *C. erythraea* in this study population is one of female defence polygyny (EMLEN & ORING, 1977). Although mating occurred over the oviposition area, no attempt to defend a territorial site was seen. Territorial behaviour in male libellulid dragonflies is well known (e.g. CORBET, 1980), and may occur in lower density populations of the current species (pers. obs.; FALCHETTI & UTZERI, 1974) or be influenced by changes in habitat structure (REHFELDT, 1991). WAAGE (1984) states that "all odonates known to exhibit non-contact guarding are territorial". The high population density found in this population of *C. erythraea*, combined with the small number of perch sites available at the oviposition site, is likely to have caused the breakdown of any territorial system (cf. PAJUNEN, 1966; REHFELDT, 1991).

Postcopulatory guarding by males is common among the Odonata and can be advantageous to females by reducing interference during oviposition (e.g. JACOBS, 1955; CORBET, 1962; WAAGE, 1978), accelerating the rate of egg release (MILLER & MILLER, 1985; CONVEY, 1989) or even decreasing the chance of drowning in species that oviposit underwater (FINCKE, 1982). Other studies have shown direct advantages to males by reduction or prevention of sperm competition, (e.g. WAAGE, 1979), maintenance of territorial defence and/or being able to take advantage of additional mating opportunities (WAAGE, 1984). Unusually, the results of this study suggest that any benefit of postcopulatory guarding to either sex is small (in terms of reduced interference rates or extended oviposition periods), agreeing with REHFELDT's (1991) study. As with the breakdown of territorial behaviour, this may be due to the high population density causing levels of interference great enough to reduce to insignificance the advantage from guarding. Males may not have the behavioural plasticity to alter their guarding strategy in this situation.

The risk of predation as a possible cost of reproduction is a subject which has generated recent interest (GWYNNE, 1989; MAGNHAGEN, 1991). Although an attractive theoretical idea, empirical evidence for a "survival cost" is scarce (MAGNHAGEN, 1991). In the Zygoptera, predation of ovipositing females and their guarding mates (often in tandem) has been demonstrated (WAAGE, 1972; FINCKE, 1982). A number of female damselflies spend extended periods oviposi-

ting underwater, and in such species the increased risk from aquatic predators is compounded by that of being unable to surface successfully (FINCKE, 1982). CROSS (1987) records an instance of predation of female *Libellula depressa* L. by a pied wagtail, *Motacilla alba* L., noting that successful attacks only took place on flying tandems and that only females were eaten. The current study clearly demonstrates that female *C. erythraea* suffer a large predation cost associated with copulation and oviposition, even allowing for the short time commitment these activities involve. Interference from non-guarding males may be an additional risk for females, as harassment increases the time that they spend at water, and can lead to wing damage, or even drowning. In contrast, males may incur only a slight increase in predation risk during mating and mate-guarding, as although spending several hours at water each day, they are generally very alert (searching for potential mates, competitors or predators), and are only more vulnerable for the very short period of copulation.

The risk of predation whilst away from the site of reproduction is also likely to be significant. *C. erythraea* forms an important part of the diet of bee-eaters, *Merops apiaster* L., in the Tour du Valat area (KREBS & AVERY, 1985), although no figures are available for any sex-related predation risk. Predation away from water was also noted by cattle egrets, *Bubulcus ibis* (L.), green lizards, *Lacerta viridis*, spiders and mantids (pers. obs.).

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