

Alternative oviposition tactics in *Zygonyx torridus* (Kirby) (Odonata: Libellulidae): modes and sequential flexibility

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Georg Rüppell, my teacher for many years, has always insisted that there is more to odonate behaviour than one would assume. I herewith dedicate a long-lasting study to him, which proves this very passion.

Zygonyx torridus inhabits waterfalls, rapids and riffle sections. Males patrol over these sites. After copulation the partners perform an extensive search while flying in tandem over a wide range. Behavioural studies in Mauritius 1997 and 2014 showed that there is considerable plasticity in oviposition behaviour. Three main modes could be distinguished: (A) egg-laying in tandem during flight; (B) the female placing the eggs while dipping in flight without physical contact with the male; and (C) the female placing the eggs when settled without physical contact with the male. On several occasions two modes, and in a single case all three types, were observed within one oviposition sequence. In odonates, such a high degree of plasticity in reproductive behaviour was not reported previously.

Keywords: Odonata; dragonfly; *Zygonyx*; alternative reproductive tactics; mate guarding; mating system; oviposition; egg-deposition

Introduction

Odonata show a diverse range of reproductive behaviours. There are several approaches to classifying and categorizing reproductive patterns (e.g. Buskirk & Sherman, 1985; Conrad & Pritchard, 1992; Corbet, 1999; Fincke, Waage, & Koenig, 1997; Paulson, 1969; Rowe, 1988). However, to date the behaviour of most Afrotropical dragonflies is unknown (Martens, 2003).

The occurrence of alternative reproductive tactics is an active area of investigation in behavioural and evolutionary ecology (Olivera, Taborsky, & Brockmann, 2008). Morphological as well as behavioural alternative tactics are used to maximize fitness in intrasexual competition within a population (Taborsky, Oliveira, & Brockmann, 2008).

In Odonata, the major focus has been into male alternative tactics in two different contexts: (1) territorial males versus satellites or sneakers; and (2) males guarding their mates in contact versus those guarding in non-contact modes. So far, the female perspective is under-represented (Fincke, 1997). Here I have tried to examine the variability of reproductive behaviour described from both male and female perspectives.

Zygonyx torridus (Kirby) is a large libellulid, having a black body with yellow markings in both sexes. The species is widely distributed in Africa, and reaches the southern Iberian

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peninsula, Sicily and the Levant. The range includes the Arabian peninsula, and arid parts of Iran, Pakistan and India. It is also known from African islands such as the Canary and Cape Verde Islands, Soqotra, the Comoros and Mascarenes (Wildermuth & Martens, 2014).

There are only brief descriptions of the reproductive behaviour of *Z. torridus* (cf. Grand, 2004, 2010; Miller & Miller, 1985). A first general description in Wildermuth & Martens (2014, pp. 729–730) is based on the data analyzed here in detail.

Localities and methods

Studies on reproductive behaviour were carried out in Mauritius in 1997 and 2014. Observations were carried out between 10.00 h and 14.30 h local time (09.40 to 14.10 solar time), at open sites with plain ground and short grass at the banks.

The first study site, the Rivière du Poste de Flacq between Centre de Flacq and Poste de Flacq (20°10'S, 57°43'E; 41 m asl), was observed over nine days, between 31 March and 11 April 1997, for a total 26.5 h of recording. The data referring to oviposition was gathered on a single 15 m long stretch. Observations were mostly by voice recorder, assisted with some video recording. Forty-six egg-laying sequences were registered. A total of 26 males were individually marked with coloured wing bands using waterproof pens (Staedler Lumocolour).

The second study site was at the Rivière Coignard, between Centre de Flacq and Bramsthan (20°12.5'S, 57°43,7'E; 57 m asl; 3.4 km distant from location 1), in a slope of about 30 m in length (Figure 1), for four days between 5 and 9 March 2014. In a total of 9.5 h of recording, 24 full sequences were observed. All photos of ovipositing dragonflies in this paper were made in this period.

Additional observations were made at several localities in Réunion (1996), Mauritius (1997–2014), Namibia (2000–2007) and Santo Antão, Cape Verde (2010). Several attempts to observe



Figure 1. Central part of the study site in 2014. Riffle section of the Rivière Coignard between Centre de Flacq and Bramsthan, Mauritius.



Figure 2. Male of *Zygonyx torridus* hovering at a rapid.

the adult behaviour more intensively failed, because the sites were cluttered and adults could not be followed over longer distances.

In the field, it was hard to distinguish between oviposition site searching flight in tandem and tandem oviposition (Figure 2). We defined oviposition as a sequence after the first visible physical contact of the female's abdomen tip with the water surface. In most cases, following the first touch the female touched the water surface at regular intervals, in other cases it did so only irregularly. Egg release without touching the water surface could not be excluded. The number of dips could be defined and counted easily in the middle and end of the period, but only sometimes at the beginning.

Taxonomic remarks

When Pinhey (1976) recorded the species as new for the fauna of Mauritius he remarked on the smaller size and a tendency to show amber in the wing bases in his specimens. On the basis of these specimens, three males collected by himself in May 1976, Pinhey (1981) described a new subspecies, *Z. torridus insulanus* (as *Z. torrida insulana*). At that time the presence in Mauritius seemed to be highly isolated, and no records were known from islands between Mauritius and the African continent. In order to establish the taxonomic status of this population we collected several males in 1997, 1998 and 1999. Their size varied between the years but most were within the full range of the nominate form, as given by Pinhey (1981). Also, other characters distinguishing them from continental individuals were missing. Dijkstra (2007), who checked the type of *Z. torridus insulanus*, also declared it as representing a small individual. The form from La Réunion, the next island in the west, is said to be the nominate form (Couteyen, 2009). *Z. torridus* is known to have a strong tendency to behave as a migrant (Suhling, Martens, & Marais, 2009). So, there is no further reason to give the Mauritian *Z. torridus* a subspecific rank of its own. The Mauritian population belongs to the nominate form of *Z. torridus*. Because of the strong migratory tendency of *Z. torridus* and a good ability to cross large unsuitable areas such as deserts or oceans, the subspecies *Z. torridus isis* Fraser, 1924, found in and around the Thar Desert of Pakistan and India, also needs re-evaluation.

Results

Mate finding and copulation

Males patrolled in continuous flight over fast flowing unshaded river sections (Figure 2). The patrol flight showed a high proportion of hovering and gliding. Males used roughly the same

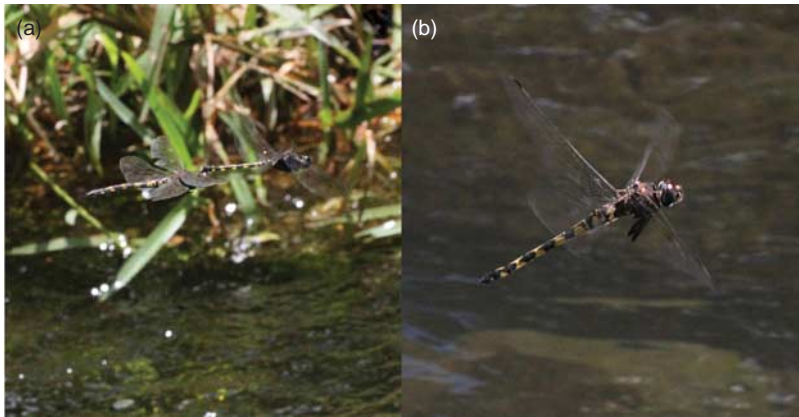


Figure 3. *Zygonyx torridus* ovipositing in flight: (a) tandem; (b) female.

flight paths which extended over about 3 to 11 m at a flight level of about 0.5 to 0.9 m over the water surface. On seven occasions males settled for a short time. Settling occurred mostly at the end of the patrol activity or when there were cool phases with clouds. Males grasped vertical or overhanging stems and held their abdomen between vertical and diagonal. Only two of the 26 marked males returned to the site, both on the date of marking. These individuals patrolled twice and three times in the course of that day, for between 90s and 14 minutes ($n = 5$, data from 1997).

At an oviposition site most pairs arrived in tandem and previous copulations at these sites were rare (1997: 42 tandem arrivals versus four copulations; 2014: 24 versus two). Only a small number of copulations took place in the immediate vicinity of the oviposition site; on five occasions a male grasped a female directly after she appeared at water or during her attempt to oviposit alone. In three cases a rival male succeeded in taking a female, which was released from tandem while ovipositing in flight.

When a male recognized a female at the water he immediately flew to her. The female was seized and the pair formed a copulation wheel in flight. During copulation (duration: 62 s, 126 s and 131 s; $n = 3$) the pair settled in a tree, bush or on a reed. Afterwards the pair flew in tandem along the stream in an altitude of between 0.3 m and 2.5 m.

In tandem the pair mostly undertook a wide-ranging flight, generally by following the stream up and/or down. In most cases at both study sites pairs were seen approaching the stream section in tandem.

Tandems appearing at the observation site of the stream showed no clear change in their flight behaviour. During tandem flight the females did not grasp the male's abdomen with their legs (Figure 3a). Mostly pairs reduced their altitude and speed and started to hover near the vegetated shoreline; others flew up and down a stretch of about 4 m without remarkable changes or showed a transition between forms.

Oviposition types

Three distinct types of oviposition behaviour were observed (Figure 4). During the same bout of oviposition a change from one type to another was observed several times (Table 1; Figure 5).

Oviposition in flight, in tandem

The tandem flew up and down and dipped back and forth in irregular fashion over broken water, mostly in the middle of the stream. In some cases of that swinging flight the tip of the female's

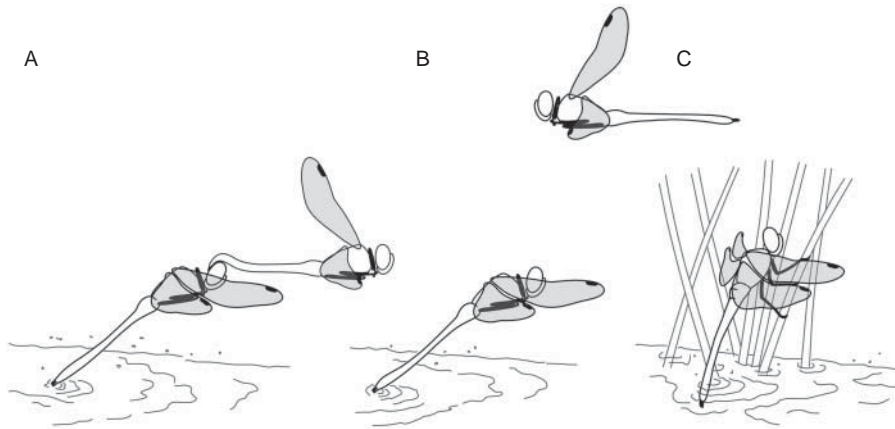


Figure 4. General types of oviposition in *Zygonyx torridus* A. in tandem; B. non-contact guarding, female in flight; C. non-contact guarding, female clinging to stems. (drawings: S. Marci).

Table 1. Oviposition behaviour of *Zygonyx torridus*. Comparison of the observed behavioural elements during two different studies in 1997 and 2014 in Mauritius.

Type or sequence*	1997	2014
A	20	8
A and pair leaving the site	6	4
B	(2)	1
C	6	4
A B	5	2
A C	3	2
B C	1	1
A B C	3	1
A C C	0	1
B C B	(1)	0
Total	46	24

*(A) tandem oviposition; (B) female oviposition in flight; (C) female ovipositing while sitting. In the cases given in brackets the sequence was interrupted by a rival male.

abdomen did not touch the water surface. Video recordings revealed a strong variance of time between two dips (2–10 s). The mean dip frequency 11.24 ± 7.00 dips per minute ($n = 13$; data from pure tandem ovipositions). The maximum duration was 420 s and the recorded maximum number of dips was 61 (Figure 6). Finally, the male released the female and she left the water ascending rapidly, along the way pursued by her mate. The dip frequency was significantly lower (7.00 ± 3.27 dips per minute, $n = 7$), when the female continued with oviposition after release.

Oviposition in flight, female without physical contact to a mate

After separation of the tandem, either after exploration behaviour or after tandem oviposition, the female hovered before beginning with dipping movements. The male accompanied her very closely. Females dipped (Figure 3b) closer to the bank, never in the middle of the water. They dipped with a high frequency and were more localized.

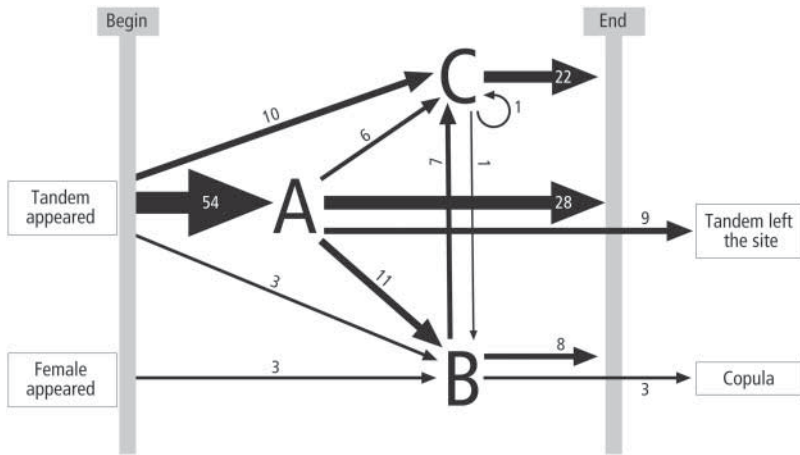


Figure 5. Flow diagram: behaviour of *Zygonyx torridus* at the oviposition site. The number on the lines and the relative thickness of the lines indicate the number of encounters following a particular pathway. Summary of the data from 1997 and 2014 (cf. Table 1).

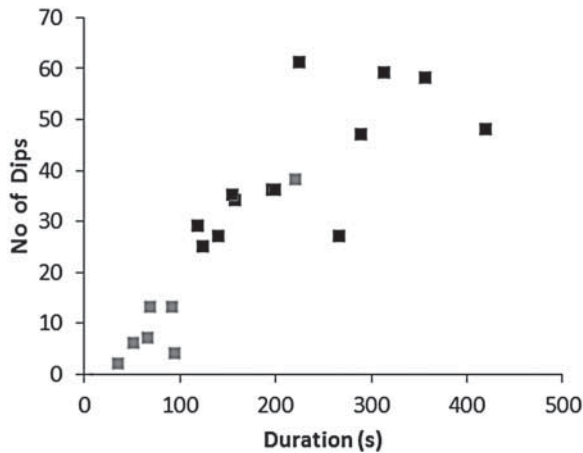


Figure 6. Relation between number of dips and duration of tandem oviposition in *Zygonyx torridus*. A distinction is drawn between tandem oviposition to the end (black, $n = 13$) and tandem oviposition when the female continued egg-laying after release by the male (grey, $n = 7$).

Oviposition while sitting

After separation of the tandem several females settled on vegetation, either immediately or after a brief hovering phase. Females grasped stalks of taro and remained motionless while holding the tip of their abdomen in the water (Figure 7a–d). In other cases females were seen sitting on a floating mat of *Elodea canadensis*. After a stay of 42 s to 279 s (median = 133 s; $n = 10$), the female abruptly flew off and disappeared without any interference by males. After the female settled, the male continued in patrolling above the site without specially approaching or inspecting her landing spot.

Diurnal patterns

Male patrol activity started around 10.00 h and ended between 13.00 and 14.00 h. The first oviposition was observed at 09.58 h solar time, the last at 13.58 h. In 1997, on sunny days the



Figure 7. Females of *Zygonyx torridus* ovipositing while settled; in various characteristic postures (see text). white arrow indicates position of female in c.

maximum of number of ovipositions per day at one site was 10 (within 4.3 h); in 2014, 14 (within 2.2 h). On cloudy days or those with strong wind, only single ovipositions were recorded. At both sites in addition to the tandems which started oviposition, many other tandems passed. The relative numbers changed from day to day. In total, there were 56 passing tandems (resighting could not be excluded) to 67 ovipositing tandems.

Interactions with rival males and males of other odonate species

During tandem flight at water the pairs were regularly attacked by rival males. In 1997, special attention was paid to that topic. In 15 of 21 recorded cases, egg-laying tandems were approached by a conspecific male. The median number of attacks during egg-laying in-tandem was five (maximum = 14). Several times they forced the tandem to change the flight path. Several times newly appearing tandems left the site. When two tandems met in flight they interfered significantly. In both observed cases, the tandem males behaved aggressively to the conspecific pair holding their partners with their claspers in tandem.

At both Mauritian streams other anisopteran species were also present at or near the turbulent stretch of the water. Males of *Anax imperator* Leach and *Tramea limbata* (Desjardins) flew continuously above the water, and *Orthetrum brachiale* (Palisot de Beauvois) and *Trithemis annulata* (Palisot de Beauvois) operated from perches. Males of these species regularly approached or attacked the searching or ovipositing tandems of *Z. torridus*. The most intensive interspecific interactions were forced by *A. imperator* (in 1997, 10 of 21 tandems were attacked, some repeatedly up to seven times). Males of the other Anisoptera also attacked *Z. torridus* tandems, but with lower intensity (*T. limbata* attacked six of 21 tandems; *O. brachiale* five, and *T. annulata* five; nearly all tandems were attacked only one time by those males). On 8 March 2014, an

A. imperator male grasped a *Z. torridus* female from a flying tandem and flew away with its prey to a treetop. This pair was successfully attacked while hovering above taro, searching for an oviposition site.

Discussion

The reproductive behaviour of *Zygonyx torridus* is wide-ranging, diverse, and very dynamic. At several other sites, in Mauritius and elsewhere, attempts to observe imagines failed because the site was cluttered and the adults could not be followed over larger distances. In most cases only short episodes could be observed.

Territoriality of males and rendezvous

Males patrol above open turbulent stretches of running water, mostly at riffles, rapids and waterfalls. These sites only partially include parts of the species' oviposition sites; at several rapids during long observation periods only patrolling males were seen. Therefore the main rendezvous (site) is unknown. One possibility is that all rapid sections along the stream act as rendezvous sites whereas oviposition is restricted to some selected sites. Rendezvous at foraging habitats or other terrestrial habitats cannot be excluded.

Mate-guarding intensity in relation to rival presence or density

In contrast to my study on *Zygonyx natalensis* (Martin) (Martens, 1991) no significant influence of the territorial male or pursuing rival on the proportion of tandem-males releasing their mate could be detected. In the case of *Z. torridus* and *Z. natalensis*, male density may partly explain the different intensities of mate-guarding, as reported by Ueda (1979) in the classic study on *Sympetrum parvulum* (Bartenev). However, (a) it is difficult to measure density in a species with a wide home range; and (b) the risk of take-over is simply dependent on the presence/absence of a rival, and in the case of the inconspicuous sedentary oviposition by the female the period during which takeover is likely is only that just after her release.

Alternative oviposition tactics and the consequences for distribution and predation of eggs

To maximize fitness, females should choose oviposition sites favouring egg and larval survivorship (Fincke et al., 1997; Rowe, 1988). An in-tandem female *Z. torridus* drops the eggs at several different spots in the middle of the stream, where there is the strongest current. In flight, a female not gripped by the male drops the eggs more locally and closer to the margin. Settled females release eggs from a single spot with slow current. In *Zygonyx* the eggs do not become sticky on contact with water (Martens, 1991). Therefore, the spot where the female drops the eggs and the place where the eggs are eventually attached to the final substrate, should differ significantly along a gradient from female control in still water to predominance of the physical current in fast water). We do not know where the eggs are actually deposited. However, risk spreading by switching from one oviposition mode to another is evident. Using only one spot for egg release is disadvantageous when small egg-feeding fish are present. In that case, oviposition in flight could be of adaptive significance.

Sedentary oviposition in Libellulidae

In Libellulidae, oviposition in flight is common, but there are some exceptions. Paulson (1969) reported that females laid eggs while settled in some species of *Micrathyria*. In the African

members of *Tetrathemis* females fixed the eggs on plant material above water while sitting (Clausnitzer & Lempert, 1998). Another known case is *Orthetrum nitidinerve* Selys, where the sitting female lays an egg string (Khelifa, Zebsa, Kahalerras, & Mahdjoub, 2012; Khelifa et al., 2013; Wildermuth & Martens, 2014, 638 ff.). In several other cases sedentary oviposition is considered as a flexible response to male harassment (Krüner, 1977; Martens, 1991; Pajunen 1966; Rüppell, 1989). In the present case it is obvious that – when the female is ovipositing in flight but not in tandem – there is a high risk or chance of take-over by a rival male whereas a female hidden in the vegetation is well protected against male interference.

Taxonomic relationships

Recent records of alternative mate-guarding tactics within a distinct taxonomic group on a worldwide scale show that this aspect of behavioural plasticity is not restricted to Libellulidae. For example, in the genus *Anax* (Aeshnidae) there is also a high degree of variability with contact-guarding, non-contact guarding and non-guarding (Martens, Günther, & Suhling, 2012).

It is noteworthy that, in contrast to *Z. natalensis* (Martens, Grabow, & Hilfert, 1997), the females of *Z. torridus* do not grasp the male's abdomen with their legs in tandem flight. Therefore, that distinct and very special behavioural feature is not characteristic for all members of the genus *Zygonyx*, although it is also seen *Tramea* spp.

So far, some New Zealand corduliids, with up to five different modes within one species (Rowe, 1988), are the odonates with the highest known numbers of different oviposition tactics. Members of *Zygonyx* seem to have the strongest sequential flexibility within a single bout in Odonata. It must be noted that all these categories are human constructs and the reproductive behaviour of most of the odonate species of the world is still unknown.

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