

**PLASTICITY OF MATE-GUARDING AND OVIPOSITION
BEHAVIOUR IN *ZYGONYX NATALENSIS* (MARTIN)
(ANISOPTERA: LIBELLULIDAE)**

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The African dragonfly, *Z. natalensis*, inhabits waterfalls and rapids. For oviposition at rocky river courses, current-washed mats of plant roots are of great importance. Because of strongly varying water levels and currents the oviposition sites are limited and their suitability is unpredictable. — Males hover over rapids, where the females appear. After copulation on the wing the pairs look for an oviposition site in tandem. As a rule, they separate for oviposition. Guarded by the male, the female settles on roots or stalks and allows the discharged eggs to be washed away by the current. The eggs are covered by a gelatinous secretion which expands rapidly in contact with water and causes the eggs to stick to the soil or roots. Apart from this, there are other types of oviposition: the female may stick her eggs directly to the substrate through movements of the abdomen whilst in a sitting position, or position the eggs in the main current while dipping in flight. If the searching tandem is disturbed, it frequently flies away. Disturbed tandems still manage to oviposit. In this case the male often stays in contact. Oviposition in tandem occurs only in flight and is less successful than the other 3 types. — The plasticity of oviposition behaviour is an adaptation to the high intraspecific competition between males and to the limitation and unpredictability of suitable oviposition sites. Oviposition in tandem occurs only when the risk of take-over by another male is great.

INTRODUCTION

Several examples of different types of mate-guarding behaviour within one species have been reported, but only in the genus *Sympetrum* is the behaviour well known (MOORE, 1952; UEDA, 1979; CANNINGS, 1980; SINGER, 1987; CONVEY, 1989; MICHIELS, 1989). UEDA (1979) showed that in *S. parvulum* the mate-guarding tactic is dependent on the status of the male and on population density. Territorial males always use non-contact guarding, while those

without territories use non-contact guarding at times of low density but switch to tandem guarding at times of high density, presumably in response to raised risk of take-over by other males. SINGER (1987) showed in that *S. obtusum* both types of mate-guarding occur, but he did not find a relation with population density. Tandem guarding occurred only when a high male thoracic temperature was found, this being dependent on absorbed radiant energy and wind speed. CONVEY (1989) and MICHIELS (1989), on the other hand, found that *S. sanguineum* and *S. danae* always begin oviposition in tandem. According to Convey whether they finish oviposition in tandem or whether the male switches to non-contact guarding depends on possible interruptions during the early stages of oviposition. Michiels ruled out any influence of temperature on the type of guarding found.

Zygonyx natalensis shows an example of an extreme adaptation to running water (CORBET, 1962). One type of oviposition is reported in detail. The female oviposits alone, settling in the spray zone of a waterfall, attaching eggs to the interstices of roots and Bryozoa (CORBET, 1962). FRASER (1952), on the other hand, notes that members of the genus *Zygonyx* oviposit in tandem. It will be shown in this paper that *Z. natalensis* has a very variable oviposition behaviour. I would like to draw special attention to the mate-guarding behaviour of the males when competition is strong.

MATERIAL AND METHODS

Zygonyx natalensis is a large libellulid distributed from eastern and western equatorial Africa south to Natal (PINHEY, 1985). The body is dark brown with yellow markings and shows metallic green iridescence, and the male develops a blue pruinosity on thorax and abdomen. Females have apical golden wing patches.

Observations were carried out on the Umzimkulwana River in the Oribi Gorge Nature Reserve (Natal, S.A.; 30°42'S, 30°16'E) between 22 March and 11 April, 1988. The river, despite its impoundments, is marked by strongly varying water levels. Submerged vegetation is completely missing and emergent vegetation can be found only at certain locations near the banks. Large rocks in the river cause varying currents, ranging from still-water zones to falls exceeding 1 m/s.

Observations were carried out between 09.00 h and 15.00 h. The data referring to oviposition were gathered on a 13 m long stretch of river bank, overgrown with *Juncus* sp. along its complete length. The higher part (about 5 m long) had a dense growth of *Juncus* in the region where the current struck an island of vegetation. The lower part of about 8 m length had only a narrow *Juncus* border. The massed *Juncus* roots, covered with moss and algae were permanently wet. The sections of the river bank that were washed by the current varied daily with the dynamics of the water level (daily variation between 3 and 5 cm). To make observations from the bank easier, stalks were bent over with stones. Observations were assisted by a video camera. Sixty-nine ovipositions were registered, of which 57 were filmed.

The data referring to the patrol activities of the males were gathered at two large rapids on the same section of river. A total of 65 males were individually marked with coloured wing bands using waterproof pens (Staedler Lumocolor 317 permanent). After being marked the males immediately left the river. Due to the catching and marking of males, the number of undisturbed ovipositions on this section of the river probably increased.

MALE PATROL ACTIVITY

The males patrolled over the rapids. They regularly crossed the white spray areas using roughly the same flight paths which extended over about 5 to 20 m. The flight level was always about 0.6 to 0.9 m over the actual water surface. The patrol flight pattern showed a high proportion of hovering and gliding phases. No hunting activities were noted. If a section of the river was in the shade (before 09.00 h and after 13.30 h) no patrol activity was seen. Only seldom did the males settle for a short time; of the 312 registered patrol flights such behaviour was observed only 4 times. In these cases males attached themselves with all 6 legs to vertical stems and let their abdomens hang down.

If another male appeared over the rapids a contest immediately ensued, in which two forms were distinguishable: when the contest comprised only a single, short clash, the challenger was always driven off, whereas a longer contest comprising a number of clashes often led to the challenger taking over from the challenged male (Tab. I). Contests also occurred between neighbouring, patrolling males without either of the males leaving the rapids.

Table I
Fights of patrolling males with arriving males of *Zygonyx natalensis*. — Data from marked individuals

Fight intensity	Residents win	Arrivers win
Short fights (one brief clash)	82	4
Long fights (much more than one clash)	3	5

$\chi^2 = 28.29$; $df = 1$; $P < 0.001$

Marked males patrolled for between 5 and 137 minutes over the rapids, doing so more than once in the course of the day. Without external interference a patrol was terminated on average after 52 minutes (s.d. ± 35 min; $n=6$), but after a contest, on average after 40.8 minutes (s.d. ± 39.5 min; $n=9$; $U=20$; N.S.). In addition males regularly approached the rapids and, without external interferences, flew off again within one minute. Such males accounted for between 2 and 25% of the total number appearing during the course of a day ($\bar{x}=13.8\%$; $n=10$).

When a female appeared high over the rapids the patrolling male immediately shot up towards her. The female was seized and the pair immediately formed a copulation wheel. Copulation always occurred in flight and lasted on average 31 s (s.d. ± 9.2 s; $n=14$; minimum = 19 s, maximum = 46 s). After ending the copulation wheel, the pair flew over the river in tandem at an altitude of more

than 1 m. If the tandem violated the patrol path of another male, it was pursued by that male.

OVIPOSITION SITE

Among the bare rocks of the river bed were islands of vegetation, mainly of *Juncus* sp.. The water level and the current changed daily. During high water the plants were completely covered, while at low water they lay dry, but the dense, tangled roots remained wet. At or close to such sites oviposition took place, but only when the mass of roots was lapped or covered by a shallow current. Oviposition only occurred in the sun, never in shadow.

EGGS

When the tip of the abdomen of a hand-held female briefly touched the water surface, eggs were immediately discharged; they formed a clump and remained attached to her. The next time that the abdomen touched the water the clump of ca. 20 eggs at once fell apart, the individual eggs falling to the bottom of the vessel. Further contact of the abdomen with the water resulted each time in 2-5 eggs being discharged. On contact with water the eggs immediately separated. The eggs adhered at once to the bottom of the vessel. They also adhered to one another, to stone, earth, roots of *Juncus* sp., to fine, suspended particles of a river water sample, to cellulose fibres and to glass. The eggs are ellipsoidal, with a small apex. Those preserved in 70% ethanol immediately after deposition were found to be 0.5x0.4 mm in linear dimensions. In water they developed a colourless to milky, gelatinous coat.

The first larva hatched from a sample of 25 eggs after 17 days, followed over the ensuing 8 days by 15 more. The eggs were kept under 1 cm of tap water which due to circumstances ranged between 17-29°C in temperature. An attempt to keep the larvae over a longer period was not successful.

Two sections of root mat (10x5 cm) were cut out directly after oviposition had taken place there. Among the clay-coloured tangle of roots no egg was found. On washing the samples out, however, 5 small dragonfly larvae of varying sizes came to light. Presumably these were larvae of *Z. natalensis*.

After the observation of oviposition on a *Juncus* stem, the piece with the attached eggs was taken and stored in water. However, when the stem was again examined the eggs were no longer found. On the other hand, when a piece of stem was immediately placed in 70% ethanol, the eggs with their gelatinous coat were clearly seen.

OVIPOSITION TYPES

When a tandem approached a potential oviposition site it reduced its altitude

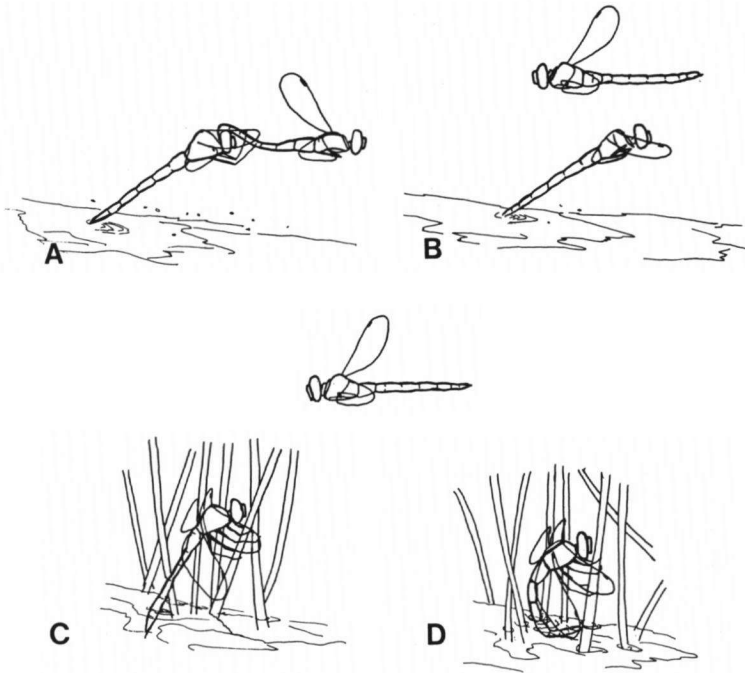


Fig. 1. Oviposition types in *Zygonyx natalensis*: (A) Tandem oviposition in flight; — (B) Oviposition in flight, non-contact guarding by hovering male; — (C) Oviposition while perched, motionless, guarding by hovering male; — (D) Oviposition while perched, with active oviposition movements, guarding by hovering male.

to between 10 and 20 cm over the water. It then remained at this height, hovering over a single or a number of sites, or else flying in a zig-zag at one position. This search flight lasted on average 53.7 s (s.d. \pm 22.3 s, $n=11$). Under certain circumstances the tandem left the site again without attempting to oviposit (see below). During oviposition I was able to distinguish 4 different types of behaviour (Fig. 1). During the same bout of oviposition there was sometimes a change from one type to another (Tab. II; Fig. 2).

TANDEM OVIPOSITION

The tandem flew over a small area where the current directly struck a mat of roots. It dipped back and forth in irregular fashion over the rough water. Only occasionally did I clearly observe the tandem making contact with the water. Towards the end of the bout the dipping movements became ill-defined. Finally, the female turned up her abdomen until the pair separated, whereupon she

immediately left the river in a fast, ascending flight. On one occasion a bout duration of 270 s was noted.

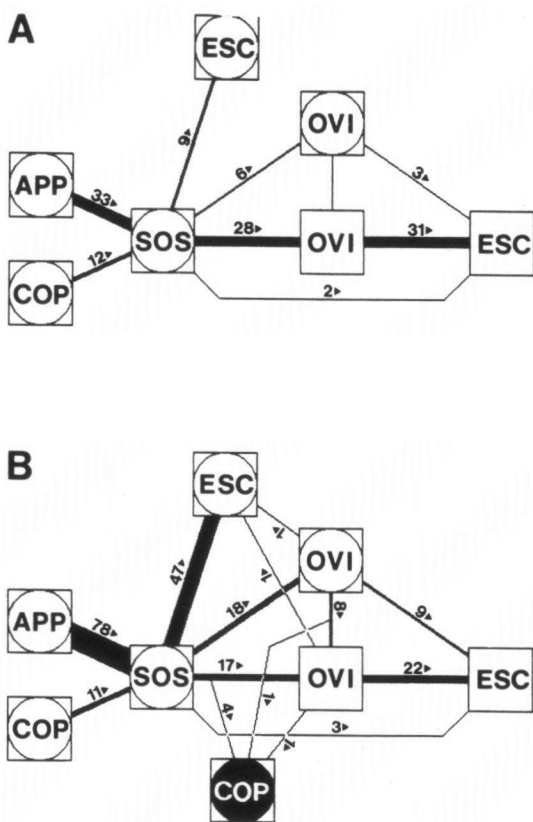


Fig. 2. Flow diagrams; behaviour of *Zygonyx natalensis* at an oviposition site: (A) Undisturbed; —(B) Disturbed by other males. — Circle within square indicates tandem actions; a square indicates female actions. The black circle indicates action of another male. Flow is from left to right and the numbers on the lines and the relative thickness of the lines indicate the numbers of encounters following a particular pathway. — [APP = Appearing at the site, COP = Copulation, SOS = Searching of an oviposition site, OVI = Oviposition, ESC = Escape].

OVIPOSITION IN FLIGHT; NON-CONTACT GUARDING BY HOVERING MALE

After separation of the tandem, the female hovered above the water before beginning the dipping movements characteristic of oviposition. She was accompanied very closely by the guarding male, and he, during the initial hovering stage, raised the tip of his abdomen.

OVIPOSITION WHILE PERCHED, WITH OR WITHOUT ACTIVE MOVEMENTS; NON-CONTACT GUARDING BY HOVERING MALE

After separation of the tandem the female generally settled immediately, within 5.3 s (s.d. \pm 5.3 s; $n=11$) at unpredictable sites: she gripped the stem of a rush or settled on a mat of roots, holding her abdomen in the water in the first case, or laying it on the roots so that it was regularly washed by the current in the second. In the process the female's wings were often wetted by waves or spray. Only seldom was an active adhesion movement of the abdomen observed. Except under strong spray, the wings were not in motion. After an average of 153.1 s (s.d. \pm 44.7 s; $n=13$), the female abruptly flew off and disappeared in the direction of the

immediately left the river in a fast, ascending flight. On one occasion a bout duration of 270 s was noted.

Table II
Changes of oviposition-type in *Zygonyx natalensis* during oviposition

Oviposition type	Change into oviposition			No change
	<i>In tandem</i>	<i>Non-contact guarded In flight</i>	<i>While settled</i>	
Oviposition in tandem	—	4	6	13
Oviposition in flight, non-contact guarded	0	—	3	3
Oviposition while perched, non-contact guarded	0	1	—	45

jungle, always without interference by guarding or other males. If only the final stage of oviposition was conducted in a sitting position its duration was shorter, lasting on average 95.0 s (s.d. \pm 54.0 s; $n=4$; $U=8$; $P<0.05$). After the female had settled, the guarding male usually patrolled the oviposition site for at least one minute, and only in 3 cases did he leave within 10 s. The male patrolled the river bank over a range of between 4 and 8 m without apparent regard to the oviposition site of the female. Rival males were engaged and driven away from the oviposition area. Guarding flight would finally extend over the rapids and often become the patrolling flight as before. When a female appeared copulation took place. One marked male was observed to copulate 3 times in this manner.

INFLUENCE OF DISTURBING MALES ON POSTCOPULATORY BEHAVIOUR

Only a small number of copulations took place in the immediate vicinity of the oviposition site. As a rule, the tandems arrived from more distant reaches of the river (Fig. 2). A rival male was able to intervene successfully only after the tandem had separated. Six observed interventions of pairs by marked rival males were successful, whereby the rival was able to grasp the female and copulate with her. At the moment of separation the rival male shot onto the scene. The female was seized as she was landing (3 times), during dipping (2 times), or immediately after landing (1 time), on average 4 s after separating from the tandem (s.d. \pm 2 s; $n=6$).

In the event of the tandem being pursued by a rival male while looking for a suitable oviposition site, another kind of behaviour was generally observed. The tandem attempted to escape from or to avoid the intruding male. A disturbed tandem separated significantly less frequently than one which remained undisturbed (Tab. III). Either it terminated its search for a site and flew off, or it began with oviposition in tandem flight. Comparing post-copulatory behaviour of disturbed and undisturbed tandems, one notes a significant tendency for distur-

Table III
Influence of approaching males on tandem separation in *Zygonyx natalensis* at a suitable oviposition site

Tandem separation	♂ presence at searching flight	No ♂ presence at searching flight
Yes	24	30
No	65	15

$$\chi^2 = 19.58; df = 1; P < 0.001$$

Table IV
Influence of approaching males on the mate-guarding type during oviposition in *Zygonyx natalensis*

Oviposition type	♂ presence at searching flight	No ♂ presence at searching flight
Non-contact guarding	17	28
Contact guarding	18	6

$$\chi^2 = 8.68; df = 1; P < 0.01$$

bed tandems to continue with oviposition in tandem (Tab. IV).

When two tandems met in flight the respective males also behaved aggressively. Flying in curves each male would attempt to seize the other tandem.

DISCUSSION

In *Zygonyx natalensis* there is a clear separation of the locations where copulation and oviposition take place. For this reason the males show no territorial behaviour at the oviposition sites, which clearly distinguishes them from other libellulid dragonflies of running waters (ALCOCK, 1987; MILLER, 1982; MILLER & MILLER, 1985; WILLIAMS, 1977). The persistent patrol flights over rapids have, perhaps, some advantages: above the spray the males are hardly visible and are thus protected against predators. The high flying females (PINHEY, 1951) can selectively approach such locations. Rapids and waterfalls from a long way off clearly mark the habitat of *Z. natalensis*, on torrential sections of river (PINHEY, 1951, 1985). Water plants are only found between boulders of the rocky river bed. These islands of vegetation, which are partly submerged, partly washed by the current, are of particular importance. The matted roots of the plants hold together fine sediment against the raging current. Here, among this substrate of living and dead roots, algae, moss and silt particles, the early larval stages live (CORBET, 1962). The frequent, short-lived and large changes in water level have little influence, since these areas are always wet owing to spray (CORBET, 1962) and the capillary action of the substrate. Any eggs here are safe from desiccation even during low water.

Owing to the irregularly changing water level, oviposition cannot take place at any time at predictable, predetermined sites. A particular site is not always washed by the current, which is necessary if the eggs are to swell and become adhesive. If the mat of roots is too deeply submerged or if the current is unfavourable, there is less chance of the discharged eggs becoming attached. Therefore, it is always necessary for a suitable oviposition site to be sought out. During a lengthy search on her own the female would have no protection against interference by rival conspecific males. Search flight in tandem protects the mated female from this kind of interference, enabling it to be of protracted duration and making possible a more thorough examination of potential oviposition sites.

For oviposition of long duration the disturbing influence of rival males needs to be kept as small as possible. Dipping females are readily recognized by such males (UBUKATA, 1983). On the other hand, females which oviposit in a settled position are hardly noticeable. The oviposition site is intricately structured and offers good cover. In their colouring females of *Z. natalensis* are also well adapted. They may not need to beat their wings or perform "adhesive" movements with their abdomens. Movements of wings and abdomen occur only under unfavourable conditions: eggs need only be actively stuck to the substrate when the current is unfavourable, and thermogenic wing vibrations are necessary only when there is a lot of spray which would have a cooling effect on the dragonfly's body. Sedentary oviposition is also considered by other authors to be a tactic for avoiding conspecific interference, for example in *Leucorrhinia dubia*, *L. rubicunda* (PAJUNEN, 1963, 1966), *Orthetrum cancellatum* (KRÜNER, 1977) and *Erythemis simplicicollis* (WAAGE, 1986).

It is only during the space of time between the tandem separating and the female landing that a rival male has the opportunity, despite the guarding male, of pursuing and seizing the female. The tandem male has two possibilities for countering a rival: (1) he can flee with the female in tandem and try to shake off the pursuer; or (2) oviposition can be begun in tandem. This he does not have to continue until the end, as he can separate from the female later and leave her to continue oviposition on her own. The male's guarding behaviour is thus dependent on interference by rival males, as CONVEY (1989) found for *Sympetrum sanguineum*. However, I would not exclude physiological causes, as put forward by SINGER (1987). The various kinds of guarding behaviour in *Zygonyx natalensis* probably have more important consequences since in-tandem oviposition is far less precise and fewer eggs land in the optimal place.

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