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Reproductive behaviour and ecology of the dendrolimnetic *Hadrothemis scabrifrons* (Odonata: Libellulidae)

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Abstract

Oviposition in water-filled tree holes and mating behaviour of *Hadrothemis scabrifrons* was observed in a lowland coastal forest in Kenya. Conforming with the predominant mode of oviposition in the Libellulidae, females of *H. scabrifrons* touch the water with their ovipositor while hovering above tree holes. Male behaviour is opportunistic: usually males perch and patrol in clearings away from tree holes but at exceptionally large tree holes males are territorial and guard mates. Larvae and adults were found in different seasons; the species seems to be non-seasonal.

Introduction

Worldwide at least 24 genera and about 47 species of Odonata are known to breed in phytotelmata (Corbet 1999), about 2/3 being Zygoptera. In the Afrotropical region larvae of only three species have been recorded from phytotelmata so far: the zygopteran *Coryphagrion grandis* Morton (Lounibos 1980) and the two anisopterans *Hadrothemis camarensis* Kirby (Copeland et al. 1996) and *H. scabrifrons* Ris (Corbet & McCrae 1981).

The first and only report of *H. scabrifrons* larvae collected from tree cavities was made by Corbet & McCrae (1981) in the Makadara Forest, Shimba Hills, Kenya. Adults have been caught usually in sunlit forest clearings, where they are reported to settle on branches or tree stumps (e.g. Pinhey 1961). The oviposition behaviour of *H. scabrifrons* has never been observed before.

Methods and study area

Coastal forests in Kenya were visited from 08 April to 24 May 2000, from 10 to 21 December 2000 and from 18 March to 15 April 2001, mainly to study the giant zygopteran *Coryphagrion grandis*. Most time was spent in the Arabuko-Sokoke Forest (03°11-29'S, 39°48'-40°00'E). Other, more briefly visited localities were Muhaka

Forest (04°19'S, 39°31'E), Buda Forest (04°26-27'S, 39°23-25'E), Gongoni Forest (04°23-25'S, 39°27-29'E), Mrima Forest (04°28-29'S, 39°14-16'E), Kombeni Forest, Rabai (03°55'S, 39°34'E) and different forest areas in the Shimba Hills (04°09-20'S, 39°16-30'E).

Most observations were made in the Arabuko-Sokoke Forest. This forest was situated a few kilometers inland of Kenya's north coast. It was the largest remaining fragment of a once-common forest of the East African coast covering an area of approximately 400 km^2. Annual rainfall varied between 900 and 1,100 mm; altitude ranged from sea level to about 210 m a.s.l. The eastern part of the forest, where the observations were made, was a mixed semi-deciduous forest on Pleistocene lagoonal sands (Fig. 1). The main tree species were *Afzelia quanzensi*, *Combretum schumannii*, *Dialium orientale*, *Drypetes reticulata*, *Hymenaea verrucosa* and *Manilkara sansibarensis* (Robertson & Luke 1993). The forest was at one time dominated by the large *Afzelia quanzensis*, but systematic logging had reduced this species drastically and during my study the forest was dominated by *Hymenaea verrucosa* and *Manilkara sansibarensis*, which did not grow very large and formed a dense understore (Fig. 1). Tree holes (Figs 2, 3) were often found in these trees close to the ground. Such tree holes were very small and in the Arabuke Sokoke Forest no big tree holes were found (see Table 1).

The forest was rich in rare and endemic wildlife and scored highest in Kenya in respect of bird importance (Bennun & Njoroge 1999). In the whole forest only few pools were permanent. In the eastern part of the Arabuko-Sokoke Forest no permanent waters existed. The only waters were seasonal pools and water-filled tree holes.

In the Arabuko-Sokoke Forest two areas had to be distinguished: the already described mixed forest (Fig. 1) with its natural tree holes (Figs 2, 3) and the forest in the Gede Ruins National Monuments. The Gede Ruins were adjactent to the Arabuko-Sokoke Forest and overgrown by dense forest. The most important difference from the main part of the Arabuko-Sokoke Forest in terms of observations on *Hadrothemis scabrifrons* were artificial ponds built with concrete (Fig. 4). These were built to supply permanent water for wildlife, e.g. monkeys, in the otherwise dry forest. All such ponds were situated under the closed canopy and were of equal size – 33 cm wide, 105 cm long, 22 cm deep –; the water depths were variable and the bottom was often covered by a thick layer of litter, mainly rotting leaves.

Another oviposition place worthy of notice was found in the Gongoni Forest (824 ha, along Kenya's south coast), where open coconut shells from an adjacent coconut-palm plantation were used as reproduction sites. The coconut shells were scattered on the forest floor close to the plantation in a random pattern, probably having been discarded and/or carried by animals into the forest. The coconut shells were checked for presence of mosquito and dragonfly larvae and their water volumes were measured.

It has to be noted, however, that my main aim was to find *C. grandis* in the coastal forests of Kenya. The tree holes sampled during this study, often small and between ground level to a height of 2 m, may not represent the optimal larval habitat of *H. scabrifrons*.

Observations on other *Hadrothemis* species are compared with the reproductive behaviour of *H. scabrifrons*. These include literature references and observations by the

Figure 1. "Mixed forest" in the Arabuko-Sokoke Forest, Kenya, 11 December 2000. In the dense understorey which is dominated by *Hymnaea verrucosa* and *Manilkara sansibarensis*, larval habitats of *Hadrothemis scabrifrons* and *Coryphagrion grandis* are often found close to the ground (Figs 2, 3).

Table 1. Presence of larval *Hadrothemis scabrifrons* and *Coryphagrion grandis* in tree holes in different coastal forests in Kenya.

Locality	*n*	mean volume [l] (range)	*H. scabrifrons* (%)	*C. grandis* (%)
Arabuko-Sokoke	28	0.50 (0.007-1.40)	10.7	53.6
Buda Forest	9	0.40 (0.030-0.95)	-	77.8
Gongoni Forest	18	0.25 (0.120-0.36)	27.7	44.4
Kombeni Forest	10	0.30 (0.050-1.00)	-	-
Makadara Forest (Shimba Hills)	10	0.92 (0.080-5.00)	10.0	70.0
Muhaka Forest	10	0.80 (0.060-4.00)	20.0	60.0
Mrima Forest	5	0.67 (0.300-2.50)	-	-

Figure 2. Typical oviposition site of *Hadrothemis scabrifrons* and *Coryphagrion grandis*, a shape of tree hole difficult for *H. scabrifrons*, because the water level might be well below the opening of the cavity, Arabuko-Sokoke Forest, Kenya, 11 December 2000. Diameter of lenscap: 5.3 cm.

author on *H. infesta* (Karsch), *H. camarensis* and *H. coacta* (Karsch) in the Budongo Forest, Uganda (1°37'-2°03'N, 31°02-26'E) in March 1999 and on *H. camarensis* in the Kakamega Forest, Kenya (0°08-24'S, 34°20-33'E) in December 1994 and January 2001.

Observations

Hadrothemis scabrifrons was recorded in all forests as larvae (Fig. 5) and/or as adults, except Mrima Forest and Kombeni Forest which were visited only briefly.

Figure 3. Typical oviposition site of *Hadrothemis scabrifrons* and *Coryphagrion grandis*, a tree hole with optimal shape for *H. scabrifrons*, Arabuko-Sokoke Forest, Kenya, 11 December 2000. Diameter of tree hole: 23 cm.

Males

Males were usually found either settled in sunlit patches in the forest, e.g. in small clearings or patrolling along linear structures, e.g. tracks in the forest not close to any potential oviposition site. On average-sized tree holes which were 7.76 cm in average diameter (2.0-19.0 cm; n = 29; Arabuke Sokoke Forest) I never found males perching at or near the tree hole. On two occasions I saw a male passing close to the ground through dense forest as shown in Figure 1.

The behaviour on larger tree holes was different. At the artificial ponds in the Gedi Ruins (Fig. 4) and a very large tree hole (diameter >1 m) in the Muhaka Forest,

Figure 4. A typical concrete pond in the Gede Ruins, Arabuko-Sokoke Forest, Kenya, 12 December 2000. Size: 33 cm wide, 105 cm long, 22 cm deep.

males were territorial and perched on twigs close to the water. Males perched only for a few minutes close to the tree hole before disappearing for several minutes to the canopy. At four of the concrete ponds seven marked males kept their territories throughout four days of observation. Although the ponds were also frequently visited by other non-territorial males, these were driven away at all times successfully by the territorial males.

Females

Oviposition was witnessed only in the Arabuko-Sokoke Forest (n = 11). Oviposition took place with the female hovering over the tree hole and touching the water surface with the ovipositor. If there was subsequent scooping, I could not confirm this. There were always drops of water scooped from the water surface; if they contained eggs and/or if this was done deliberately, I do not know. I observed three females placing eggs in tree holes similar to those shown in Figures 2 and 3. At these tree holes oviposition lasted only a few minutes before the females departed, flying close to the forest floor. Even if the opening of the tree hole was very small, e.g. as shown in Figure 3, the female hovered above the opening and then lowered herself, hovering, into the hole with the abdomen bent down and the wings held dorsally, but not extended horizontally.

The conrete ponds in the Gede Ruins (Fig. 4) were frequently visited by females which oviposited there in the same way as described above, but they came straight from, and left straight to, the tree canopy, without searching for more oviposition sites. These females were frequently disturbed by a territorial male and either flew away or were taken into tandem and shortly after that into the wheel position. After mating the male guarded the ovipositing female. On one occasion a female could be observed to oviposit in the concrete pool, washing the eggs into the water while hovering above the water surface. A stone in one corner of the concrete pond separated a small tree hole-like section from the main water body. This 'hole' was triangular in shape (8 x 11 x 15 cm) and 15 cm deep. The female hovered for some time above that 'hole', before manoeuvering herself down into it, apparently with some difficulty and then placing eggs there with the abdomen touching the water. The average wing span of *H. scabrifrons* females (n = 5) was 9.5 cm, the broadest wing being 2.0 cm wide and with a length of 5.7 cm. The female managed to move down into the 'hole' by not expanding the wings totally. From time to time the wings would scratch against the stones.

Larvae

The larvae (Fig. 5) were built like typical libellulids, but the dorsal white spots on the eyes were remarkable and unusual. F-0 larvae of *Megaloprepus coerulatus* (another tree-hole dweller) also have conspicuous white dorsal spots, though not in the same places (Ramirez 1997). The function of such spots are not yet understood. A description of the larva of *H. scabrifrons* will be prepared.

Table 1 gives an overview of the frequency with which odonate larvae were encountered in tree holes in different patches of coastal forest in Kenya. The presence of *Coryphagrion grandis* larvae is indicated in this table as well, because the occurrence of both species was negatively correlated (Spearman correlation coefficient = –0.331; n = 29; p = 0.079). The presence of *H. scabrifrons* larvae was not significantly correlated with any of the measured habitat parameters, i.e. circumference and diameter of opening, depth, water volume and height above ground, but there was a strong positive correlation with tree hole diameter (Spearman correlation coefficient = 0.3527; n = 29; p = 0.061).

In the artificial ponds in the Gedi Ruins and in the big tree hole in the Muhaka Forest more than one *H. scabrifrons* larva was found. In smaller tree holes, only one larva of either *H. scabrifrons* or *C. grandis* occurred. Several coconut shells

Figure 5. *Hadrothemis scabrifrons* larva, Arabuko-Sokoke Forest, Kenya, 12 December 2000. Length of larva: 22 mm. Note the conspicuous white spots on the upper surface of the compound eyes and the distal tip of each wing sheath.

lying on the forest floor of the Gongoni Forest were filled with water and contained mosquito and often dragonfly larvae. At most only one larva of either *H. scabrifrons* or *C. grandis* was found in such a shell. In 16 water-filled coconut shells checked on the floor of the Gongoni Forest, four contained one *H. scabrifrons* larva, six contained one *C. grandis* larva, one contained one larva of each species and five contained no dragonfly larvae.

Notes on other *Hadrothemis* species

Hadrothemis coacta was observed to reproduce in small ponds on the rainforest floor in the Budongo Forest. In that case the small ponds were muddy puddles on a car track. Males were territorial on these ponds, perching on small sticks above the water. After copulation the ovipositing females were guarded (non-contact) by the males. Females hovered above the water and touched the water surface with their ovipositor with a short downwards movement.

Males of *H. infesta* were observed patrolling above deeply shaded, small water bodies in the Budongo Forest. They were on the wing most of the time, only settling very briefly and occasionally disappearing into the tree canopy. Females were guarded (non-contact) during oviposition after copulation. As described for *H. coacta,* females hovered above the water, touching the water surface with their ovipositor with a short downwards movement.

Males of *H. camarensis* were territorial at sun-exposed tree holes in the Budongo Forest, perching close to the tree hole in the sun. In the Kakamega Forest I never observed males near tree holes, which were all in full shade, but found males perching in sunny spots of small glades which were away from potential larvae habitats.

Discussion

Although *Hadrothemis scabrifrons* reproduces in the concrete ponds (Fig. 4) in the Gede Ruins National Monuments, I would still call the reproductive habitat of this species tree holes or phytotelmata. I regard the concrete ponds as surrogate tree holes or surrogate buttress pans and not as groundwater pools. I have never observed adult males or females near any of the seasonal or permanent pools. For *H. scabrifrons*, as for *H. camarensis*, no evidence exists that they oviposit in ground pools, even when the latter are plentiful.

Mating

Large tree holes are the only places observed where males are territorial, perching next to the oviposition sites and guarding females after copulation. Average-sized tree holes (Figs 2, 3) are apparently too small to attract territorial behaviour by males. Similar observations were made for males of *Megaloprepus caerulatus* (Drury) in Panama, where males defend only tree holes containing more than one litre of water in the forest understorey (Fincke 1992a).

In most cases males of *H. scabrifrons* have little control over their mating success, thus resembling *Mecistogaster linearis* (Fabricius) and *M. ornata* Rambur from Central America (Fincke 1992b). The above-mentioned species of *Mecistogaster* invest little in offspring survivorship, but much in acquiring mates (Fincke 1992b: 111). When only small tree holes are present, the stable strategy of males of *H. scabrifrons* seems to be to maximize matings and to leave the distribution of egg clutches at many different tree holes to the female, i.e. without mate guarding. Only the presence of large tree holes makes territorial behaviour and mate guarding efficient.

An analysis of offspring survivorship in the damselfly *Megaloprepus coerulatus* showed that adults had not much influence on their reproductive success and that this was not correlated with traditional fitness estimates (Fincke & Hadrys 2001). From my observations on *H. scabrifrons* I assume that the influence of the adults on offspring survivorship is likewise somewhat limited and can be mainly triggered by females when distributing egg clusters on a large temporal and spatial scale.

Oviposition

Phytotelmata are usually not an ideal oviposition site for Anisoptera due to the latter's size and structure (Corbet 1983). In Uganda females of *H. camarensis* have been found dead in sections of an non-indigenous bamboo, where they had been apparently become trapped while trying to oviposit (Corbet 1961, 1983). Females of the related *H. coacta* and *H. infesta* oviposit like most Libellulidae while hovering, scooping the eggs into the water of rainforest pools (V. Clausnitzer pers. obs. in the Budongo Forest, Uganda; for *H. coacta* see also Neville 1960; Miller 1995). Females of *H. versuta* (Karsch) have been observed ovipositing in the mode that is predominant for most Libellulidae, touching the water with the ovipositor with subsequent scooping (Lempert 1992). Eggs are propelled in a drop of water from the water surface onto the shore or plants above the water level. The larval habitat of *H. scabrifrons* as well as that of *H. camarensis* led to discussions of alternative oviposition methods (e.g. Corbet & McCrae 1981; Corbet 1983; Copeland et al. 1996). Larvae of *H. camarensis* have been found mainly in tree holes wide enough to permit a female to hover within the hole while ovipositing, but also in tree holes too small for such ovipositing behaviour, leading to the considerations that "females... exhibit an array of alternative behaviours" (Copeland et al. 1996: 145). Corbet & McCrae (1981) found a larva of *H. scabifrons* in a tree hole where exophytic oviposition onto water while hovering would have been difficult. Maybe eggs in such small tree holes are placed when water levels are higher permitting hovering by an ovipositing female. All females I observed ovipositing manoeuvered into the hole and placed eggs by washing them from the tip of the abdomen.

Legrand (cited in Corbet 1999: 146) witnessed the dendrolimnetic *H. camarensis* ovipositing in the most common libelluline way by placing eggs into the water, with the tip of the abdomen touching the water surface (exophytic without scooping), while hovering above the water body. This corresponds to my observations on the oviposition of *H. scabrifrons* and also to the related *H. coacta* and *H. infesta*. At this stage there is no evidence that *H. scabrifrons* or *H. camarensis* oviposit while settled, either dropping the eggs through narrow openings as observed for *Davidius moiwanus taruii* Okumura (Inoue & Shimizu 1976) or placing them on the wall above the water level like *Micrathyria ocellata* Martin (Paulson 1969).

The *H. scabrifrons* females observed ovipositing in natural tree holes (Figs 2, 3) were flying close to the ground in the dense understorey of the coastal forest after finishing oviposition. I interpret such behaviour as a search for more tree holes in order to distribute the eggs in as many tree holes as possible, thus increasing offspring survivorship, as already outlined above. In most cases the offspring survivorship of an egg cluster in any tree hole is likely to be zero, e.g. if the tree hole is already occupied by a larva of *H. scabrifrons* or *Coryphagrion grandis*. Experiments and observations have shown that cannibalism among these larvae is very high and the same has been reported from other species breeding in phytotelmata (e.g. Fincke 1992a, 1992c; Orr 1994). In tree holes of under one litre in volume on Barro Colorado Island not more than one larva survived to emergence per season (Fincke 1992b).

The situation becomes different with increasing water volume and increasing leaf and twig litter in the tree holes. Multiple cohorts, i.e. several conspecific larvae of the same and of different sizes were only found in exceptionally large tree holes and in the concrete ponds (surrogate tree holes; Fig. 4).

Mating

The large tree holes were the only places observed where males were territorial, perching next to the oviposition sites and guarding females after copulation. Average tree holes (Figs 2, 3) are apparently too small to attract territorial behaviour by males. Similar observations were made for males of *Megaloprepus caerulatus* (Drury) in Panama, where males defended only tree holes containing more than one litre of water in the forest understorey (Fincke 1992a). Also the female oviposition behaviour on the concrete ponds (= artificial giant tree hole) was different from the one described for natural tree holes above. Females would come straight from and would fly back into the tree canopy, without searching for more oviposition sites.

In most cases males of *H. scabrifrons* have little control over their mating success, thus resembling *Mecistogaster linearis* and *M. ornata* from Central America (Fincke 1992b). *Mecistogaster* invest little in offspring survivorship, but much in acquiring mates (Fincke 1992b: 111). When only small tree holes are present, the stable strategy of males of *H. scabrifrons* seems to be to maximize matings and leaving the distribution of egg clutches at many different tree holes to the female (i.e. no mate guarding). Only the presence of large tree holes makes territorial behaviour and mate guarding efficient.

Conclusions and notes on the evolution of dendrolimnetic reproduction

The oviposition behaviour of the two *Hadrothemis* species reproducing in tree holes is conservative. Oviposition is exophytic into water, the ovipositor touching the water surface while the female hovers above it. No special adaptations have been developed for the habitat. This statement is supported by my own observations and the finding of trapped *H. camarensis* females in bamboo sections (Corbet 1961) too small to permit hovering oviposition, but obviously trapped while attempting to oviposit in this way.

Comparison with the oviposition behaviour of other *Hadrothemis* species allows speculations about the evolution of reproduction in tree holes. As far as I know all species of this genus except *H. camarensis* and *H. scabrifrons* reproduce in smallish pools and puddles on the rainforest floor. The distribution centre of all *Hadrothemis* species except *H. scabrifrons* is the Central African basin. *H. scabrifrons* and *H. camarensis* are the two *Hadrothemis* species with the easternmost distribution in Africa, which I regard as a result of their ability to utilize tree holes.

The Kakamega Forest, once in contact with the large rainforest areas in the Congo basin is a very dry rainforest with hardly any surface water except a few small streams. In comparison with other Guineo-Congolian rainforest areas, the Kakamega Forest is the driest one without any types of swamp forest, which are common e.g. in the Ugandan rainforests. I speculate that species of *Hadrothemis* other than *H. camarensis* have either never colonized the forest areas so far east or else have become extinct in the eastern forest areas, when the climate got drier, e.g. during the last Ice Ages. In Uganda *H. camarensis*, *H. coacta*, *H. defecta pseudodefecta* Pinhey and *H. infesta* all occur together in rainforest habitats (V. Clausnitzer unpubl.).

The coastal forests of Eastern Africa have experienced dry periods associated with the most recent Ice Ages and have been much moister prior to this time (Clarke 2000). Habitats of forest dragonflies depending on stagnant water under closed canopies may have vanished in the coastal forests rapidly during droughts and, in the case of the Arabuke Sokoke Forest, remained only as scarce seasonal swamps or seasonal forest pools. The adaptation to use tree holes as reproduction sites may have allowed *H. scabrifrons* to inhabitat the coastal forests of Eastern Africa and to colonize much larger ranges, than other coastal forest species like *Gynacantha usambarica* Sjöstedt.

H. scabrifrons seems to be non-seasonal because during all visits I found larvae consisting in several stadia, ovipositing females and emerging adults. Adults have been caught previously throughout the year as collecting dates in the collection of the National Museums of Kenya, Nairobi show.

It is worth mentioning that in the Arabuke Sokoke Forest large tree holes, which apparently provide an optimal reproduction site, are not found any more or only very scarce. The forest has been selectively logged for commercial purposes, leaving a secondary forest without hardly any large trees, as shown in Figure 1. This, together with the highly fragmented habitat and the apparently low offspring rates, make *H. scabrifrons* rather vulnerable. Urgent conservation efforts for the remaining coastal forest patches of Kenya are needed. Although several of these forests are now gazetted as forest reserves, illegal logging still continues at an alarming rate.

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