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LIFE HISTORIES AND ECOLOGY OF ODONATA BREEDING IN PHYTOTELMATA IN BORNEAN RAINFOREST

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Pericnemis triangularis Laidlaw (Coenagrionidae), *Indaeschna grubaueri* (Förster) (Aeshnidae) and *Lyriothemis cleis* Brauer (Libellulidae) are reported breeding in phytotelmata in the understorey of lowland mixed dipterocarp rainforest in Borneo. The pattern of utilization by the 3 spp. of phytotelmata of varying sizes is surveyed and observations are made in field and laboratory on larval behaviour, especially territoriality and intra- and interspecific predation, and developmental rates. Possible adaptations to special conditions found in phytotelmata, including low oxygen tensions, limited food and close proximity of other larvae, are discussed. Descriptions are provided for the larvae of *P. triangularis* and *I. grubaueri.*

INTRODUCTION

In tropical rainforests, phytotelmata may represent an important habitat for the development of the larval stages of Odonata. This is likely to be particularly true of situations where accumulated ground water is scarce, such as on steep, well drained slopes or on very porous soils, and species which normally breed in small pools must find alternative oviposition sites. Acceptable habitats include water collected at the base of leaf axils of various plants, in rot holes, in bamboo internodes and in depressions formed in the buttresses at the bases of large trees. CORBET (1983) reports 8 species of Anisoptera and 22 species of Zygoptera recorded as breeding in phytotelmata, mostly in tropical habitats, and to these may be added the observations of CORBET & McCRAE (1981), KITCHING (1986), and FINCKE (1992a), who identified a treehole dwelling guild of five pseudostigmatid (Zygoptera) and one aeshnid (Anisoptera) species.

In mixed dipterocarp forests in Brunei three species of odonates were commonly found breeding in various phytotelmata, especially rot holes and buttress pans in the forest understorey. These included *Lyriothemis cleis*, the larvae of which has been described from material found breeding in treeholes in Sulawesi by KITCHING (1986); *Indaeschna grubaueri* which in Java has been recorded as breeding in forest pools (LIEFTINCK, 1954) but the larva was not described, and there has been no previous record of its breeding in treeholes; and *Pericnemis triangularis* the life history of which has been hitherto totally unknown, although larvae of the related *P. stictica* are known to breed in water collected in bamboo stumps (LIEFTINCK, 1941, 1954; KOVAC, in press).

Odonate larvae living within the highly circumscribed habitat of a buttress pan or treehole experience a unique set of conditions (CORBET, 1983). Prey are highly concentrated, and at least for younger larvae may be abundant, but for larger larvae may be severely limited. Individuals are forced to live in very close proximity to one another and the potential for inter- and intraspecific competition and predation is high, and may favour territorial behaviour (CORBET, 1983). In the following I survey patterns of utilization of phytotelmata by the above three odonate species in lowland mixed dipterocarp forest in Borneo, and report also on observations of behaviour, development and general biology in the field and under laboratory conditions. Descriptions of the larvae of *I. grubaueri* and *P. triangularis* are also included.

METHODS

Between January 1992 and November 1993, 55 natural treeholes were examined for Odonata larvae and other macroinvertebrates in several sites in mixed dipterocarp forest in Brunei. These were located at Kuala Belalong and Bukit Patoi (both Temburong District), Sungei Burong (Tutong District), and in the Labi hills (Belait District). The floristic composition of the forests at these localities differed considerably, but as the same invertebrate species were found commonly breeding in treeholes, the total sample is considered homogeneous and data from all sites are combined.

The surface area of water exposed at each hole was estimated from measurements of principle diameters (see KITCHING, 1971) and from a field sketch of the shape of the hole at the water surface. Depth was measured at the deepest point and the contours of the hole were sketched roughly, enabling an estimation of volume (typically approximated by the formula 1/3 surface area × depth). Behaviour of larvae was observed at night by torchlight when they emerged from concealment. After observations were completed, as many larvae as possible were collected using a small hand net and the remainder were subsequently located by removing accumulated litter systematically and examining it in situ on a white tray. All odonates were removed to be bred in the laboratory. Litter was returned to the hole, along with non-odonate macroinvertebrates which included culicid, tipulid and scirtid larvae (ORR, in press; R.L. Kitching & A.G. Orr unpublished).

In addition, forest pools and rock pools along streams were searched to see if treehole breeding species were also utilizing these habitats in the study areas. Physical conditions were recorded in a sample of treeholes and pools including temperature, pH, and dissolved oxygen 5 cm and 10 cm below the surface.

Larvae collected in the field were reared at 26°C on ad lib food, including microcrustacea (chiefly *Daphnia*), mosquito larvae, chironomids and tadpoles. Most larvae were reared individually in wide mouthed plastic containers containing 0.5 l of water taken from the natural habitat with a small quantity of detritus in the bottom. As water evaporated it was replaced with deionized water, and any uneaten food material, especially tadpole carcasses, was systematically removed. In addition small groups of up to five larvae were reared together in dark brown plastic containers, 20 cm wide at the base, gradually expanding to 40 cm wide at the rim and 18 cm deep, containing 1.5 l of water, and roughly similar in shape and internal appearance to natural treeholes. In all cases developmental times including time of ecdysis were recorded and general habits and interactions were noted. Overall length, from head to terminalia, was measured immediately before ecdysis using vernier callipers.

SURVEY OF TREEHOLES AND HABITAT USAGE BY LARVAL ODONATES

Most of the holes, and all the larger holes, were filled to within 1-5 cm of the water surface with a dense layer of litter between 10 and 15 cm in thickness, and beneath this was a thick reddish sludge, apparently devoid of macroscopic life. Surface area therefore gave a more accurate estimate of available habitat than did volume, and is presumably also a cue used by ovipositing females.

Natural treeholes were classed as large (surface area 201-1500 cm^2) (Fig. 1), medium (surface area 51-200 cm^2) and small (surface area 5-50 cm^2). Corresponding mean volumes are listed in Table I. In holes with a deep detritus layer, oxygen tensions were very low, ranging from 0.1-0.3 ppm 5 cm below the surface to undetectable at 10 cm (5 large and 5 medium holes). Temperatures ranged from 24.3-27.1°C, with a diel range in one large hole at Bkt Patoi of 1.7°C. In three medium holes where there was little accumulation of litter, oxygen tension was much higher (2-3 ppm).

Of the 55 holes examined 25 were small, 19 medium and 11 large. Large holes were much more frequently occupied by odonates (91%) than medium (53%) or small (28%) holes (Tab. I). With one exception (at Bkt Patoi) *Indaeschna* was found only in large holes, and it was present in almost half the

Fig. 1. A large buttress pan at Bukit Patoi (60 × 25 cm), regularly inhabited by *Indaeschna grubaueri*.

large holes examined. *Indaeschna* larvae were also found commonly in forest pools and in exposed ponds near the forest margin, frequently along with *Cratilla metallica* (Libellulidae), which was also found on one occasion in a large (disturbed) treehole at Bukit Patoi. Neither *Lyriothemis* nor *Pericnemis* was ever found breeding in situations other than treeholes. Both occurred in large treeholes but only on one occasion did either coexist with *Indaeschna*: a large (1247 cm^2) hole with one half grown (28 mm) and two very young (5 mm) *Indaeschna* larvae also supported one half grown *Lyriothemis* larva and three small *Pericnemis* larvae (Fig. 2). Both *Lyriothemis* and *Pericnemis* tended to utilize large holes unoccupied by *Indaeschna* to a greater extent than they did medium and small holes, although *Lyriothemis* showed a stronger preference for medium sized holes over small holes than did *Pericnemis*. There was no other evidence for segregation of the two species.

Table I

Size distribution of phytotelmata sampled and occupancy rates by odonates, overall and by each species. Size is defined by surface area as follows: small (5-50 cm^2), medium (51-200 cm^2) and large (201-1500 cm^2)

Hole volume and occupancy	Size and number of holes Small 25	 Medium 19	 Large 11
Mean volume ± SD (l)	0.065±0.049	0.55±0.51	7.34±4.82
No. (%) occupied by odonates	6 (24.0)	10 (52.6)	10 (90.9)
No. (%) occupied by *Pericnemis*	5 (20.0)	6 (31.8)	5 (45.5)
No. (%) occupied by *Indaeschna*	0 (0)	1 (5.3)	5 (45.5)
No. (%) occupied by *Lyriothemis*	2 (8.0)	8 (42.1)	4 (36.4)

Figure 2 illustrates the relationship between hole size, as measured by surface area of water exposed, and numbers of larvae of all species. Large holes tended to contain more *Pericnemis* larvae than did small holes, but not *Lyriothemis* which was never found at a density of more than three individuals per hole. Where *Indaeschna* occurred, it was usual for three to seven individuals of approximately the same size, probably representing a single cohort, to be present. As indicated by the relatively few additional moults required for the completion of development by larvae collected from the field, most individuals of all species were relatively mature (Fig. 3), suggesting rapid growth and development in the early instars until a fairly advanced stage is reached, followed by a prolonged period of slow growth, presumably owing to food limitations. (The total number of instars for *Indaeschna* is 12 [see below] and probably a similar number for the other two species). The relative scarcity of young larvae may also result from predation by larger larvae of the same or different species.

LARVAL DESCRIPTIONS, LIFE HISTORIES AND GENERAL BIOLOGY

The following descriptions follow CORBET's (1953) terminology for characters of the labium.

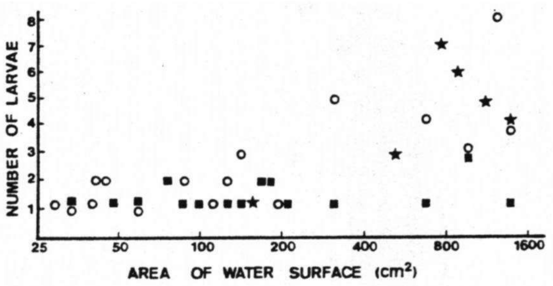

Fig. 2. Numbers of individuals found in different sized holes: ○ = *Pericnemis triangularis*; – ★ = *Indaeschna grubaueri*; – ■ = *Lyriothemis cleis*.

PERICNEMIS TRIANGULARIS LAIDLAW

Figure 4

DESCRIPTION OF LARVA. – Mature larva 17:18 mm in length excluding caudal lamellae. Facies typically coenagrionid, although overall slightly short and squat (Fig. 4a). Integument uniformly dark in colour. Prementum short, deltoid, with a single pair of setae and a row of fine spines along its lateral margins (Fig. 4b). Distal margin moderately projected, with row of fine blunt processes. Labial palps each with 6 setae, about two-thirds the length of the movable hook. Distal margin of palp with outer flattened, slightly serrated area and a strong inner hook. Serrations also occur along the inner margin of the palp opposing the toothed processes on the distal margin of the prementum. Legs relatively short. Wing sheaths reaching to posterior margin of 4th abdominal segment. Caudal lamellae 4-5 mm; thin, relatively short but very broad (Fig. 4c), the outer three-quarters being strongly pigmented blackish purple. Presumably the increased

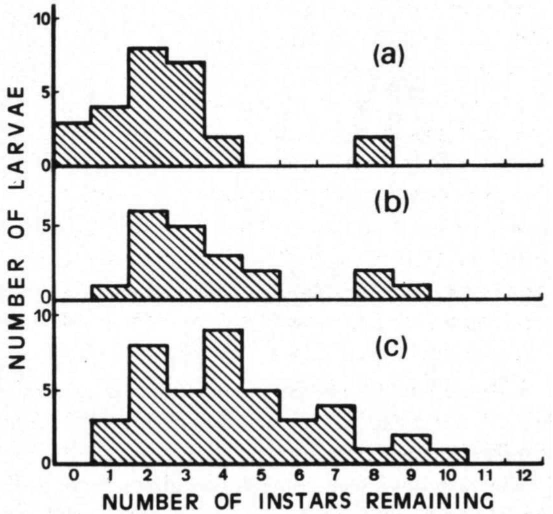

Fig. 3. Frequency distributions of relative maturity of larvae found in phytotelmata as indicated by the number of larval instars required to complete their development: (a) *Indaeschna grubaueri*; – (b) *Lyriothemis cleis*; – (c) *Pericnemis triangularis*.

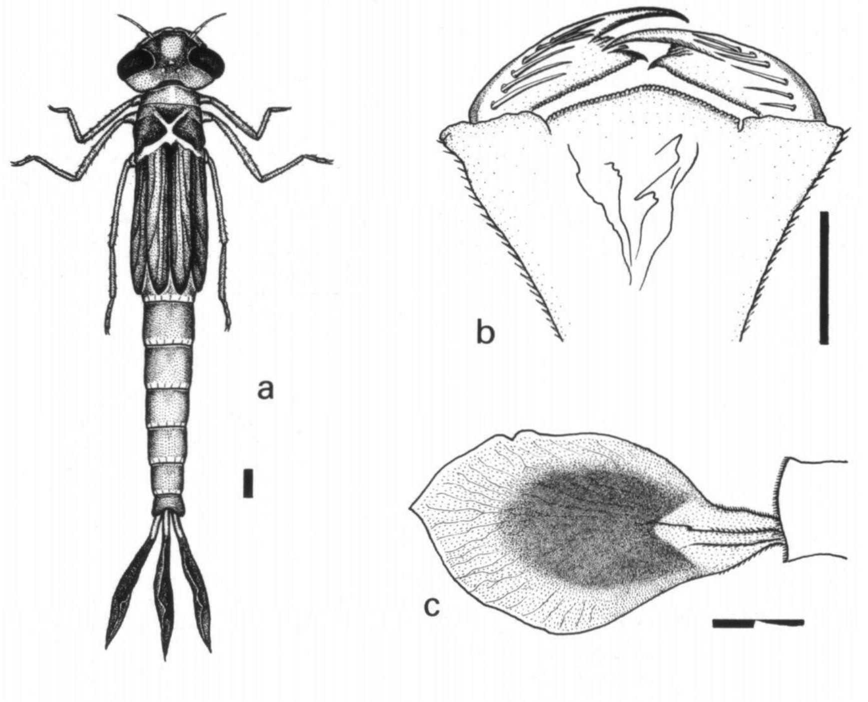

Fig. 4. *Pericnemis triangularis*: (a) final instar shortly before ecdysis; — (b) distal part of labium; — (c) lateral view of right caudal lamella. — [Scale bars = 1 mm].

area of the lamellae is a response to living in conditions of low oxygen tensions. In early instar larvae the caudal lamellae are of a shape normal in coenagrionids, elongate but not broad.

The most obvious distinguishing character of the species is the broad pigmented caudal lamellae, a feature it probably shares with the allopatric *Pericnemis stictica* (LIEFTINCK, 1954).

DEVELOPMENT. — In captivity small larvae of about 4 mm body length (excluding caudal lamellae) were raised to maturity at 26°C, on a diet of microcrustacea and mosquito larvae, in six to eight weeks. As food was not always available, this probably underestimates the maximum developmental rate at this temperature.

BEHAVIOUR. — *Pericnemis* larvae of about the same size could be maintained at relatively high density (5/litre) in captivity without any evidence of aggression toward each other. They tended to be found on the sides of the container, where they probably fed mainly on mosquito larvae, but there was no clear evidence of territoriality.

INDAESCHNA GRUBAUERI (FÖRSTER)

Figures 5-6

DESCRIPTION OF LARVA. – Larva is typically aeshnine in general form (Fig. 5a). Mature larvae range from 51-55 mm in length. The head is broader than long with 7 segmented antennae; eyes bulbous and of moderate size. Prementum long, distal margin weakly rounded and fringed with fine setae (Fig. 5b). Labial palp seruciform with a strong sharp process on the inner angle. Setae absent. Movable hooks long and broadly overlapping each other when at rest. Abdomen with well developed lateral spines on segments 6-9. Anal pyramid with paraprocts slightly longer than epiproct, which is truncated at its tip. Cerci slightly more

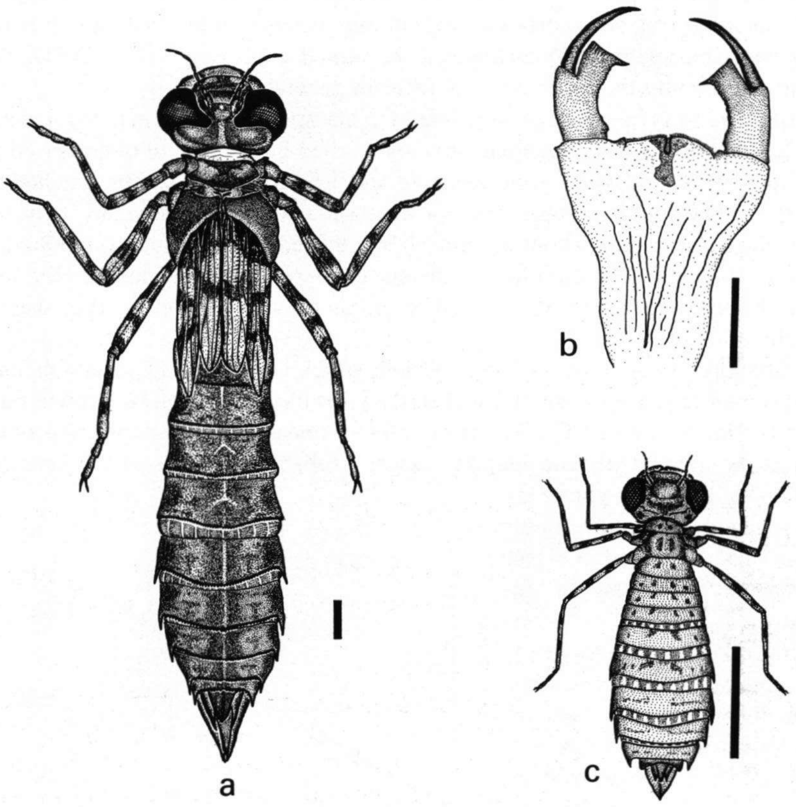

Fig. 5. *Indaeschna grubaueri* larva: (a) final instar shortly before ecdysis; – (b) distal part of labium; – (c) 4th instar larva. – [Scale bars = 3 mm].

than one third (females) to nearly half (males) length of paraprocts. Overall the integument is variably mottled and the legs are banded. The ground colour depends on habitat. Specimens from clay bottomed ponds are pale sandy brown in colour with very faint patterning, whereas those from treeholes are nearly black. Immature specimens such as the 5th instar specimen shown (Fig. 5c) resemble larger larvae, but have only five antennal segments. Mature larvae can be distinguished from most sympatric aeshnids by their size; *Anax* spp., which are of similar size and may overlap in habitat, can be distinguished by their longer head, larger eyes, absence of lateral spines on abdominal segment 6 and proportionally longer anal pyramid. Immature *Anax* are transversely banded (CORBET, 1962). *Indaeschna* differ from larvae of *Anaciaeschna* (figured by LIEFTINCK 1962; cf. VAN TOL, 1992) in having the head proportionally longer and the eyes less closely approximated. Larvae of *Tetracanthagyna* spp. and *Gynacantha* spp. are poorly known, but may occupy similar habitats. It is usual for the labial palp of *Gynacantha* to be armed with setae (TILLYARD, 1917) and presumably these genera also differ in general facies.

DEVELOPMENT. — Larvae were reared to maturity from eggs inserted in detritus in a small body of semipermanent water formed in the bottom of a disused prau (longboat). Eggs, which were elongate and 1.5-1.6 mm in length, hatched after 9 days. The prolarva stage was not observed, but was presumably very brief. Second instar larvae, about 2.2 mm in length, fed microcrustacea, moulted in 4 days. Thereafter the duration of instars grew progressively longer. By fourth instar, mosquito larvae were added to the diet and by 8th instar they were fed mainly tadpoles.

The total duration of the larval period, which comprised 12 instars including the prolarva, ranged from 107 to 126 days for three individuals. Growth curves for ad lib. food at 24°C (Fig. 6) are almost linear. The developmental time in nature is undoubtedly considerably longer, probably in excess of one year. (One cohort of four very young larvae, examined at three month intervals, developed to 8-10th instar in the course of one year).

HABITAT AND BEHAVIOUR. — *Indaeschna* were found breeding in diverse habitats, including an open pond 3 × 5 m, in which there were abundant tadpoles and daytime temperatures reached 32°C. D.O. 5.3 ppm, rock pools beside a small forest stream ap-

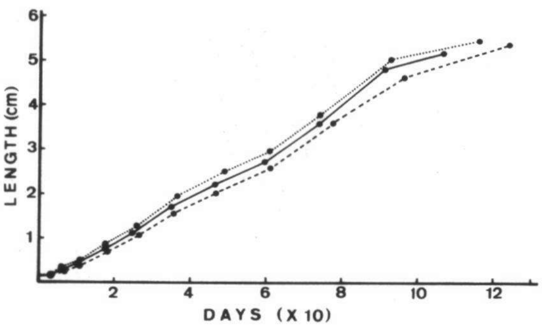

Fig. 6. Growth curves for three *Indaeschna grubaueri*, raised in captivity from egg to adulthood.

proximately 0.5-1.0 m in diameter (24-26°C, D.O. 4.1 ppm), water in the bottom of a disused boat, and large treeholes. Conditions in treeholes were at variance with those in other habitats; dissolved oxygen was very low, there was relatively little free water, and there was a shortage of prey items for larger larvae; notably there were no tadpoles. This appears to have necessitated several behavioural adaptations. Larvae in treeholes were apparently entirely nocturnal. By day they were to be found concealed among the leaves below the water surface, an area from which oxygen was almost absent (0.1 ppm) and certainly insufficient for sustained activity. At night they perched around the walls of the hole with their head downwards and the tip of the abdomen, with the caudal appendages open, just penetrating the water surface. Frequently a bubble formed around the projecting abdomen. Presumably in this way they were able to augment their oxygen supply. In one large (60 × 25 cm) hole (Fig. 1), 7 larvae were found ranging from 10-12th instar. These spaced themselves uniformly around the side of the hole, suggesting that each maintained a feeding territory. When 3 were removed from one end, the remainder respaced themselves uniformly. There was no evidence of aggression or display and such spacing may come about as much by mutual avoidance as by aggressive defense of territory.

In an experimental container with 3 final instar individuals, younger conspecifics (6-8th instar) and mature *Lyriothemis* and *Pericnemis* were attacked and eaten. At no stage did more than one individual attack a large prey item. Large larvae fed voraciously on tadpoles, but would take mosquito larvae if no larger prey was available. Small larvae swam actively, often capturing mosquito larvae from just beneath the water surface.

LYRIOTHEMIS CLEIS BRAUER

Larvae described by KITCHING (1986) were found inhabiting small rot holes in Sulawesi. This species proved more difficult to breed than the other two, mainly because it was not always possible to obtain adequate food. They ate both mosquito larvae and chironomid larvae, but not small tadpoles. Small larvae (4 mm long) were raised to maturity in 10-16 weeks. Larvae exhibited remarkable resistance to desiccation. Two half-grown larvae were kept in dry air (relative humidity 70-90%) for four days, during which time they experienced a 46% loss in weight but were still capable to walking. When they were restored to water they initially floated on the surface, but within 24 hours had rehydrated and had resumed normal activity.

Unlike *Indaeschna* and *Pericnemis, Lyriothemis* invariably remained half buried in the detritus in the bottom of the breeding container. When two or three larvae of similar size were maintained together in a small 0.5 l container for periods of one to three weeks, cannibalism occurred, usually when one individual became vulnerable during ecdysis (4 instances).

DISCUSSION

In the aseasonal tropical rainforest environment phytotelmata offer a unique set of conditions. Firstly, compared with alternative habitats they are very stable, with minimal fluctuations in physical conditions (cf. CORBET, 1983). At KBFSC, where the terrain is steep, forest pools are few and transient, and rock pools beside streams are frequently scoured by torrents following heavy rain. By contrast, no large treehole was observed to dry significantly during the study period which extended over nearly two years. This means that the time taken for larval development may be extended if this is necessary or advantageous. Secondly, most tropical phytotelmata support a rich decomposer based community of small invertebrates (KITCHING, 1987, 1990). Odonates entering this system do so as top predators. Prey are very concentrated, but total available food may be limiting, as evidenced by the fact that the biomass of predators may exceed total prey biomass (ORR, in press). In such circumstances intense inter- and intraspecific competition among the predators would be expected. Thirdly, owing to high rates of decomposition the oxygen concentration in the most productive treeholes is very low, and anatomical or behavioural mechanisms to cope with this, such as the hypertrophied caudal lamellae of *Pericnemis*, or the habit of *Indaeschna* of sitting with its rectal basket exposed directly to the air at the water surface, are likely to be advantageous.

The high rate of occupancy of phytotelmata overall (47%) and especially of large buttress pans (91%) suggests that they are important larval habitats for some odonates in the forest ecosystem. Any species which normally breeds in small forest pools probably has the potential to extend its niche space by ovipositing in the larger more open treeholes, and wherever accumulated groundwater is scarce, phytotelmata may assume considerable importance as secondary habitats for such species. At Kuala Belalong, from which about half the samples were taken, there are known to be about a dozen species of odonates, mostly Zygoptera, found only within the forest away from streams. Many of these most probably oviposit facultatively in larger phytotelmata, but the high rate of occupancy by obligate treehole breeding species may generally prevent their survival and detection.

Consideration of potential interactions raises two questions which on present knowledge can only be very incompletely answered. Do treehole specialists have the competitive advantage over non-specialists? – And if so how does *Indaeschna*, a facultative treehole breeder massive in size compared with any other treehole breeding species, succeed where other species are apparently less successful?

On the basis of general evidence there appears to be some tendency for treehole breeding species to be large, especially in comparison with related species breeding in other habitats. Examples are provided by the giant neotropical pseudostigmatids *Megaloprepus* and *Mecistogaster* (FINCKE, 1992a, b), and the Australian megapodagrionid *Podopteryx selysi* (WATSON & DYCE, 1978). The stability of the habitat would allow for a long developmental period, which would enable a larger size to be reached. Size is likely to be subject to various selective pressures acting on all stages of the insect (HARVEY & CORBET, 1985; FINCKE, 1992b), but in certain situations large size is probably advantageous in interspecific interactions among larvae (FINCKE, 1992a). Among the species considered here, *Pericnemis* is unusually large, *Lyriothemis* is probably about normal, and *Indaeschna* is large. It is probably *Indaeschna*'s size, aggression, and high rate of early development which enables it to often dominate the fauna of larger holes, but it must do so at the expense of developmental rate, which in odónates is expected to be slow in the event of limited prey (LAWTON et al, 1980; WISSINGER, 1988). Probably *Indaeschna* is better adapted to forest pools with abundant large prey such as tadpoles and higher oxygen content, but by regularly utilizing treeholes it shows itself to be very versatile indeed.

As the three species differ very greatly in size it is predicted that there should be considerable potential for ecological segregation among them, but whether this is realized within the highly circumscribed confines of a treehole is uncertain. There is some evidence from observing the feeding of *Lyriothemis* and *Pericnemis* in the laboratory that the former tends to feed more among bottom sediments, whereas the latter feeds closer to the surface, but the strongest form of segregation is probably the range of hole sizes occupied; *Pericnemis* is found in holes of all sizes, whereas *Lyriothemis* tends to occur in medium-large holes and *Indaeschna* is almost entirely confined to large holes.

The extremely close confines in which treehole communities live has special implications for interspecific interactions. As long as food is abundant the best strategy to pursue may be to avoid conflict with conspecifics, especially since there is a high probability of their being related, and the evidence from breeding *Pericnemis* and *Indaeschna* (but not *Lyriothemis*) in the laboratory suggests that this is the case. In the relatively homogeneous habitat of the treehole, where one perch is probably much the same as another, larvae are expected to space themselves out to avoid interference rather than defend any particular territory, but only in *Indaeschna* is there good evidence that this happens. Conversely, if food is in short supply cannibalism may be the best strategy. The large numbers of *Pericnemis* tolerating each other in large natural holes probably indicate that there is no extreme prey shortage. Smaller numbers in medium and small holes may be indicative of past cannibalism but may also result from females laying fewer eggs in these holes. It is harder to explain why similar numbers of the much heavier *Indaeschna* coexist. Even among larvae of the same size individuals would become vulnerable during ecdysis. However, as a facultative phytotelm breeder it may not be well adapted to this situation. *Lyriothemis* appears to minimize the number of larvae per hole either by virtue of the oviposition behaviour of the female or by larval cannibalism or both.

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