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THE FOODWEB FROM WATER-FILLED TREEHOLES IN KUALA BELALONG, BRUNEI

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ABSTRACT. - The animals inhabiting water-filled treeholes in lowland mixed dipterocarp forest around the Kuala Belalong Field Studies Centre in Brunei were studied. A minimum of 20 species of animals were found over the 52 sites studied with individual hole faunas ranging from 2 to 8 species around an average of 4. These included one or more species of anurans, dytiscid beetles, odonates, culicids, chironomids, ceratopogonids, phorids, syrphids, oligochaetes and copepods. Of special note were the three species of odonate and two of frog larvae within these habitats. The foodweb that can be inferred from the occurrence of these organisms was compared with those from other Old World tropical locations including northern Australia, Papua New Guinea and Sulawesi. The Bruneian webs were exceptional in their richness of the larger saprophagous species possibly because the relatively aseasonal, perhumid climate of the region provides a more energy rich and predictable environment than is found at the other locations.

INTRODUCTION

The habitats contained in water-holding parts of plants have collectively been termed phytotelmata (Varga, 1928). These habitats have attracted much attention from community ecologists over the years (Thienemann, 1934; Frank & Lounibos, 1983; Kitching, in press). As habitats, phytotelmata are discrete, replicated and relatively simple faunistically. These characteristics have made them ideal subjects of study for the comparative investigation of foodwebs.

Water-filled treeholes have been studied extensively in this regard (Kitching & Pimm, 1985). Foodwebs have been collated for treeholes from Germany (Rohnert, 1950), the United Kingdom (Kitching, 1971), various locations in the USA (Fashing, 1975; Snow, 1958; Woodward et al., 1988), in Australia (Kitching & Jenkins Unpublished results; Kitching & Callaghan, 1982), from New Guinea (Kitching, 1990) and Sulawesi (Kitching, 1987). The available information on such foodwebs from the moist tropical forests of the world, from

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where we would expect the most diverse and structurally complex webs, is restricted to one site each in New Guinea and Sulawesi and a number of sites in tropical Australia.

We have examined the fauna of a large set of water-filled treeholes from the lowland rainforest around the Kuala Belalong Field Studies Centre in Temburong Province of Brunei in northern Borneo. This paper presents the results of these investigations and compares the community which we found with those recorded from other sites in the Indo-Australian region. More detailed information on the Odonata from treeholes in Brunei is provided by Orr (1994).

STUDY SITE AND METHODS

The Kuala Belalong Field Studies Centre of the University of Brunei is located on the west bank of the Belalong River just south of its confluence with the Temburong (4°32' N, 115°09'E). The Centre is located in undisturbed lowland dipterocarp forest. The vegetation and botanical make-up of the forest has been described in detail by Ashton (1964) (see also Whitmore, 1975). The forest canopy is exceptionally tall reaching over 40 metres in places. The mid- and upper canopy comprises a wide range of species dominated by dipterocarps belonging to the genera *Dipterocarpus, Hopea, Shorea* and *Vatica* (Ashton, 1964). The area has a perhumid climate with monthly rainfalls varying from about 100 to 550 mm. Temperatures are relatively constant with average daily maxima varying from 30.5°C (January) to 35°C (March), and minima virtually constant at about 25°C. The general environment, biology and natural history of the area around the Field Studies Centre is described by Cranbrook & Edwards (1994).

During the period January 6th to January 14th, 1994, fifty-two water-filled treeholes were located in the forest around the Centre. The treeholes we sampled were of several basic types. Pans are holes completely lined by bark and they occurred in tree roots (11/52 holes), in buttresses (18/52) and in a curious form wherein a horizontal 'fold' of trunk growth bridged the gap between two adjacent buttresses (4/52). These last I called 'trunk pans' and are of a type I have never before recorded. In addition to these pans there were a range of holes formed by the rotting of the heartwood following branch or trunk damage. So we encountered simple rot-holes (10/52), 'pipes' (deep cylindrical holes with relatively small apertures) (5/52) and, even, water-filled hollow trees (2/52). In addition we sampled two log-holes in which watertight cavities occurred within recently fallen tree trunks. No sampling was carried out in the forest canopy.

Our sampling sites were located adjacent to the 'Ashton Trail' along the west bank of the Belalong, the 'East Ridge Trail' along the east bank of the same river, and at a location about 2 kilometres upstream from the Centre. The diameters, depth and height of each treehole were measured. A sample of water was collected from each site for later determination of the pH and then a relatively large subsample of the contents removed from each for subsequent faunal analysis. These samples comprised plant detritus and water and were collected using a simple siphon and by hand. The sample volumes were subsequently measured by displacement. They varied with the volume of the treehole itself and ranged from 45 to 2300cc. Entire contents of treeholes were not removed partly for conservation reasons and, partly, because of the magnitude of the sorting task which would have resulted.

At the field laboratory these samples were passed through a stack of Endicott™ sieves. Larger animals were picked out of the coarser sieves. The residue remaining on the finest

(355 μm) sieve was sorted using a binocular microscope. Living material was removed. Live identifications were made to the finest level of taxonomic resolution possible (usually the family or genus). Living larvae were retained and adults were collected and curated as they emerged. These adults were then identified further with the assistance of a range of specialist taxonomists (see 'Acknowledgements'). The trophic status of most 'species' was determined by inference from previous knowledge of the genera concerned.

Additional observations by one of us (AGO) preceded and followed the period of intensive study in January 1994. These observations have been incorporated into this account where appropriate.

RESULTS

The physical parameters of the treeholes sampled, and the pH values for the water they contained, are summarized statistically in Table 1. These are presented, wherever possible, as means with associated standard errors. The different classes of treehole varied in size and height (indeed some are defined in such a way that this must be the case). Rot-holes in general are located somewhat higher from the ground than are pans. Holes in general were almost full to capacity and pH values were almost always slight acidic. The only exception to this - water from hollow trees - was based on so few observations that no general statement can be made about water acidity in this case.

The species of metazoan animals encountered, their frequency of occurrence and levels of abundance are presented in Table 2. Frequencies of occurrence are calculated as the

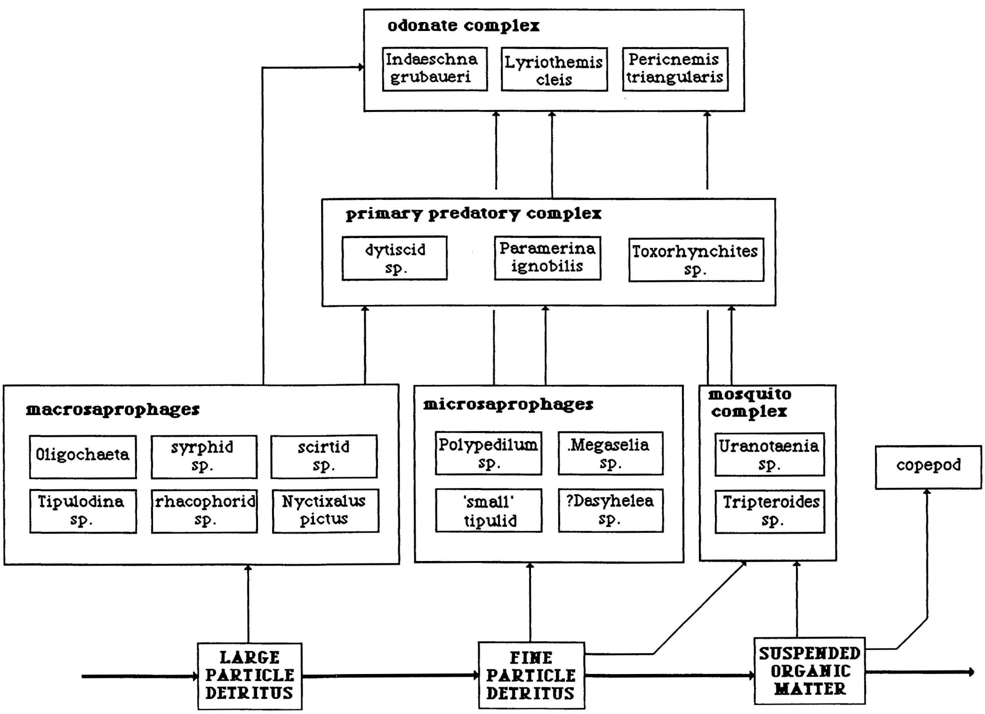

Fig. 1. The metazoan foodweb inferred from samples of 52 water-filled treeholes at Kuala Belalong Field Studies Centre, Temburong Province, Brunei.

Table 1. Physical features and environmental characteristics of water-filled treeholes in lowland dipterocarp forest at Kuala Belalong, Brunei.

Treehole Type	Number of holes	Length (mm)	Breadth (mm)	Depth (mm)	Height from ground (mm)	Proportion full	Water pH
ALL	52	243±27.3	94±10.1	184±18.3	657±89.4	0.82±0.027	4.7±0.11
Root Pans	11	241±37.5	118±28.8	103±14.3	245±57.9	0.75±0.083	4.5±0.11
Buttress Pans	18	289±44.3	85±10.7	176±28.4	401±54.2	0.86±0.045	4.7±0.20
Trunk Pans	4	363±116.5	144±63.9	226±66.3	2108±602.6	0.91±0.048	5.4±0.09
Rot-holes	10	144±21.2	72±5.6	195±54.2	842±162.3	0.81±0.038	4.5±0.17
Pipes	5	82±16.5	35±5.07	216±41.6	855±183.2	0.85±0.040	4.4±0.15
Hollow trees	2*	150	72.5	455	1035	0.65	7.7
Log holes	2*	615	230	208	545	0.94	4.4

* Variance terms not calculated because of lack of replication

Table 2. Fauna recorded from water-filled treeholes at Kuala Belalong, Brunei.

	Frequency of Occurrence n/52	Mean density (± 1 s.e.)	Maximum density	Minimum density	Coefficient of Variation (%)
OLIGOCHAETA	0.33	41.1±22.25	1120.50	0.00	3.91
CRUSTACEA					
COPEPODA	0.02	2.93	152.80	0.00	—
INSECTA					
ODONATA					
Pericnemis triangularis	0.40	3.42±1.007	40.00	0.00	3.40
Lyriothemis cleis	0.12	0.28±0.0163	7.69	0.00	1.70
Indaeshna grubaueri	0.02*	—	—	—	—
DIPTERA					
Tipulidae					
Tipulodina sp.	0.12	1.55±0.82	33.30	0.00	1.88
Tipulid sp.	0.08	1.52±0.88	40.00	0.00	1.73
Culicidae					
Toxorhynchites sp.	0.08	0.22±0.11	3.77	0.00	2.03
Others **	0.62	35.20±9.00	259.46	0.00	3.91
Chironomidae					
Polypedilum sp.	0.56	49.06±22.34	1086.21	0.00	2.20
Paramerina ignobilis	0.04	1.52±1.30	66.67	0.00	1.17
Ceratopogonidae					
?Dasyhelea sp.	0.35	11.06±3.75	131.25	0.00	2.95
Syrphidae					
Eristalinae sp.	0.02*	—	—	—	—
Phoridae					
Megaselia sp.	0.02	0.10	—	—	—
COLEOPTERA					
Scirtidae sp.	0.75	65.10±15.01	400.00	0.00	4.34
dytiscid	0.06	0.43±0.29	13.51	0.00	1.51
CHORDATA					
ANURA					
Nyctoxalus pictus	0.02	0.98	—	—	—
Rhacophoridae sp.	0.08	0.39±0.29	14.49	0.00	1.36

* not found during the primary survey; found in a single hole on previous occasions
** *Uranotaenia* sp. and *Tripteroides* sp. in an approximate 12:1 ratio

proportion of the 52 treeholes in which the particular species occurred. All abundances have been calculated as numbers per litre. The foodweb that can be inferred from these results is Figure 1.

The commonest species encountered were larvae of a species of scirtid beetle (occurring in 75% of holes), mosquitoes (62%), chironomine chironomids (56%), ceratopogonids (35%) and Zygoptera (40%).

The scirtids were not determined further as it proved impracticable to breed through to the adult stage in the available time. The larvae have the characteristic facies of phytotelm-dwelling sections of the family which includes members of the genera *Prionocyphon, Elodes, Cyphon* and *Scirtes.*

The mosquitoes comprised members of the genera *Uranotaenia* and *Tripteroides* which emerged as adults in the ratio of 12:1. Both genera are known to be phytotelm specialists. *Uranotaenia* is known from rot-holes, the axils of *Curcuma australasica*, taro and *Pandanus*, bamboo stems and pitchers of *Nepenthes. Tripteroides* is one of the sabethine mosquitoes, known worldwide as container breeders. Members of this Old World genus are recorded from treeholes, coconut shells, pitcher plants, bamboo stems and the axils of both taro and banana plants. The large predatory larvae of *Toxorhynchites* occurred in but 4 holes. The genus is known from treeholes, pitcher-plants, bromeliads, leaf axil habitats and bamboo internodes (MacDonald & Traub, 1960) in subtropical and tropical forest situations worldwide.

The Chironomidae were represented by two species. The red larvae of the chironomine, *Polypedilum* sp. were very common. Larvae of this detritivorous genus are recorded from treeholes in Australia and western North America and from pitcher plants and the axils of *Colocasia* in south-east Asia. The predatory larvae of the tanypodine *Paramerina ignobilis* occurred in two sites only. This species is widespread in south-east Asia and Australia and has been recorded from treeholes, bamboo stems and the axils of *Pandanus* leaves.

The abundant larvae of a ceratopogonid were not reared to adulthood. The genus involved is almost certainly either *Dasyhelea* or *Culicoides.* Both these genera are of worldwide distribution and breed commonly in a wide range of phytotelm habitats.

Bruneian treeholes are remarkable for the range and frequency of occurrence of their odonate fauna (Orr 1994). Larvae of the coenagrionid *Pericnemis triangularus* occurred in 40% of the holes we examined. The predatory guild within the treeholes was completed by a species of small dytiscid beetle.

Other species occurred only rarely within our samples (see Table 2).

In constructing a foodweb from the faunistic data presented in the Table we have chosen (Fig. 1) to designate trophic interactions only at a coarse scale. Our study was not protracted enough for us to be able to make firm statements about the prey choices of each of the species we encountered (although this would not be difficult to do in further study). Accordingly we have designated the three species of odonates as potential top predators. There is little doubt that large individuals of any one of the odonates prey upon smaller individuals of their own and other odonate species in addition to the suite of prey species implied in the Figure. The primary predators - the dytiscid beetle, larvae of the tanypodine chironomid and the toxorhynchitine culicid - are all generalists in terms of their known range of prey items. Larvae of *Toxorhynchites* are generally presented (usually in a biocontrol context) as predators on other species of culicid (and they are undoubtedly facultatively cannibilistic in addition). They do prey, however, on a wide range of other larvae and oligochaetes.

The set of at least eleven detritivorous organisms completes the foodweb. This should be taken as a minimum estimate of species richness as the exact number of species involved in the culicid sub-guild and among the oligochaetes has not been determined.

DISCUSSION

We raise three general points in this discussion. We view both the faunal list and the foodweb itself in a comparative context and we explore briefly the needs for further investigation of these rich and intriguing habitats. The most appropriate sets of comparative data for these analyses are those from Sulawesi (Kitching 1987), Papua New Guinea (Kitching 1990) and the lowland rainforests of Cape Tribulation in tropical Australia (Kitching & Jenkins Unpublished results).

The fauna of the treeholes we examined contained, in general, the taxa that were expected on the grounds of previous studies in New Guinea, Sulawesi and northern Australia. The odonate fauna has already been commented upon. In addition the occurrence of two species of anurans marks this web out from the others. The island of Borneo is particularly rich in rhacophorid frogs which are one of the families of Anura most likely to occur in plant container habitats in general and this is reflected in the occurrence of this taxon in treeholes (Inger 1985, 1990, Kitching In press). The faunal list is also remarkable for some of the groups that are *not* present. This is particularly noteworthy given that our sample of 52 holes represents, comparatively speaking, an extensive survey. Indeed only our studies of treeholes in northern Queensland have been based on a larger set of samples (where 76 treeholes were examined).

Returning to the specifics of the Bornean fauna we note the absence of psychodid larvae (present at Cape Tribulation and New Guinea). There were also no mosquitoes of the genera *Aedes* (Cape Tribulation, New Guinea, Sulawesi), *Culex* (Sulawesi, Cape Tribulation) or *Orthopodomyia* (New Guinea). This does not necessarily mean that these genera are absent from treeholes in our Bornean study site but again we draw attention to the extensive set of holes studied and the relative ease with which mosquitoes breed through from samples such as ours. The occurrence of the genus *Uranotaenia* stands out in comparison with other studies. It did occur at the New Guinea sites studied but, there, was restricted to the habitat offered by water-filled bract axils (Kitching 1990). The genus is also recorded from bamboo internodes in West Malaysia (MacDonald & Traub, 1960). Various specialist predators encountered elsewhere were also absent: larvae of *Culex (Lutzia)* (Sulawesi), planarians (Cape Tribulation) and namaneriine polychaetes (New Guinea) are cases in point. The absence of mites from all of these tropical webs stands in general contrast to the situation in temperate treeholes (Fashing 1975, Kitching & Callaghan 1982, Kitching In press). The particular collecting and seiving techniques used have led to the discovery of mites in comparable studies elsewhere.

The foodweb presented as Fig. 1 is summarized and compared in Table 3 with published information from elsewhere. In general the structure of the treehole community we have identified from Kuala Belalong is similar to that from other Old World tropical locations (although for various biogeographical reasons the fauna observed at the Sulawesi sites is smaller and the associated foodweb simpler than elsewhere - see Kitching, 1987 and In press, for a discussion of this point). The overall species richness is very similar to that observed in northern Australia and New Guinea as is the number of trophic levels. The number of predators and top predators in Borneo and New Guinea are similar as is the associated predator:prey ratio, and these are higher than the results observed in northern Australia. The most remarkable difference observed between the results we present here and all the other data sets alluded to is in the number of macrosaprophages present. The six species we found in our Brunei studies is at least twice that found in any of the other three data sets. This of course reflects the presence of the anurans more than anything else.

Table 3. Comparative data on the composition of treehole foodwebs from old World tropical locations. Species counted as 'top predators' may also act as primary predators.

	Cape Tribulation Australia	Dumoga-Bone Sulawesi Indonesia	Baiteta Madang New Guinea	Kuala Belalong, Brunei
No. of species	20	13	17	19
No. of predators	3	4	4	3
No. of top predators	2	1	2	3
No. of macrosaprophages	2	3	2	6
No. of trophic levels	3	3	3	3
Predator:prey ratio	0.25	0.38	0.35	0.32

Sources: Cape Tribulation - Kitching & Jenkins, unpublished; Sulawesi - Kitching 1987; Madang - Kitching 1990.

In seeking explanations for this richness of macrosaprophages in comparison with the other locations studied we note that the Brunei location is the only one of those studied which comes close to having a perhumid, aseasonal equatorial climate. All the other sites have more or less well marked wet and dry seasons. This perhumidity may be expected to have two consequences relevant to the present question. First the rate of breakdown of the allochthonous detritus which provides the basic energy source for water-filled treeholes is likely to be high and the consequent supply of food resources more or less continuous. Second and in consequence, this will mean that the treeholes in these situations represent a highly predictable environment even for those organisms, such as most of the macrosaprophages, which have relatively long life cycles.

Tree-hole breeding anurans are known to be abundant in a number of other tropical locations (eg. Phillipines, Brown & Alcala 1983; Thailand, Wassersug et al. 1981; Amazonia, Hoogmoed & Cadle 1991; parts of Madagascar, Glaw & Vences 1992) and it will be of interest to compare the predictability and seasonality of these environments as well as the presence or absence of other macrosaprophagous members of the foodwebs from these locations as further information comes to hand.

The special features of the treehole communities we have studied in Brunei and the general abundance and ease-of-access of water-filled treeholes in these locations presents opportunities for further work. In particular there is considerable scope for the investigation of within-guild processes related to inter-specific competition as the occurrence and abundance of such animals are readily manioulated experimentally. The odonate and anuran faunas in particular will lend themselves to this. The impact of the rich predatory guild (the odonates etc.) on the structure and relative abundance of the other fauna will also repay attention.

Lastly our studies were made at relatively low altitudes. There is ready (if arduous) access from the Kuala Belalong Station to higher altitudes with other forest types. Altitude-based collecting from treeholes would allow testing of hypotheses concerning the impact of the abiotic environment and forest structure on the infauna of these phytotelms.

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