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Trophic ecology of a tropical aquatic and terrestrial food web: insights from stable isotopes (^{15}N)

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Abstract: We used stable isotope analysis (^{15}N/^{14}N) to characterize the trophic relationships of consumer communities of an aquatic food web (a permanent pond) and the adjacent terrestrial food web (secondary dry dipterocarp forest) from a seasonal tropical field site in north-eastern Thailand. In general, isotopic signatures of aquatic vertebrates were higher (δ^{15}N range = 4.51–9.90‰) than those of invertebrates (δ^{15}N range = 1.10–6.00‰). High ^{15}N signatures identified water snakes and swamp eels as top predators in the pond food web. In the terrestrial food web ^{15}N signatures of saprophagous litter invertebrates (diplopods, earthworms), termites, ants and beetle larvae were lower than in those of predatory invertebrates (scolopendrids, scorpions, whip spiders). Predatory terrestrial frogs and caecilians had lower ^{15}N signatures than snakes, indicating that snakes are among the top predators in the terrestrial web. Based on the distribution of isotopic signatures, we estimated five trophic levels for both the aquatic and terrestrial food web. The food chains of a seasonal tropical site studied were rather short, which implies similarities to the structure of temperate food webs.

Key Words: aquatic, food web, invertebrates, ^{15}N, seasonality, stable isotopes, terrestrial, trophic level, vertebrates

INTRODUCTION

The organismal biodiversity of many tropical ecosystems is high compared with temperate counterparts (Wilson 1992). A high species richness of, for example, tropical animal communities has been revealed in amphibians, reptiles (Barbault 1991, Inger & Colwell 1977), birds (Terborgh *et al.* 1990) and mammals (Heaney 2001). However, only few studies focused on food-web structure (Harrison 1962, Jepsen & Winemiller 2002, Reagan *et al.* 1996). A recent study on the food web of a tropical rain forest dominated by amphibians and reptiles using the classical approach of gut-content analysis revealed high consumer diversity with complex feeding relationships (Reagan *et al.* 1996).

It has been proposed that the number of trophic levels increases with productivity and resource availability by increasing population density at higher trophic levels (Persson *et al.* 1992, but see also Post 2002a, Post *et al.* 2000). On the other hand, theoretical considerations suggest that since nutrient-poor systems (e.g. tropical forests) are species rich, the large number of interactions between species result in a higher number of trophic levels (Vander Zanden *et al.* 1999). Indeed, Reagan *et al.* (1996) found evidence for at least five levels of consumers in a tropical rain forest in Puerto Rico and also reported long food chains (mean 8.5, max 19 links). In contrast, Ponsard & Arditi (2000) and Scheu & Falca (2000) identified only two and three to four trophic levels, respectively, in temperate forest soil food webs.

The present study investigates the trophic relationships between vertebrate and invertebrate consumers of an aquatic and an adjacent terrestrial food web of a seasonal tropical site (Mekong valley, north-eastern Thailand) using stable isotopes (^{15}N). Food web studies attempt to characterize the trophic relationships of animals and plants (Pimm & Lawton 1978, Post 2002b). Stable signatures of ^{15}N can be used to determine the trophic

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position of animals and plants within a food web (DeNiro & Epstein 1981, Minegawa & Wada 1984, Post 2002b). An increasing number of studies have used stable isotope analyses to characterize trophic relationships in freshwater (Post *et al.* 2000, Vander Zanden & Rasmussen 1999), marine (Pinnegar & Polunin 2000) and terrestrial animal communities (Ponsard & Arditi 2000, Scheu & Falca 2000). Recently, stable isotopes have been used to analyse tropical fish communities (Jepsen & Winemiller 2002), terrestrial termite (Tayasu *et al.* 1997) and ant communities (Blüthgen *et al.* 2003). However, the trophic structure of tropical animal communities of adjacent aquatic and terrestrial habitats, including animal species, which switch between the two habitats, such as amphibians is poorly known. Isotope studies on amphibians and reptiles are extremely rare (Pilgrim *et al.* 2003), as has just been pointed out in a recent review on vertebrate diets using stable isotopes (Dalerum & Angerbjörn 2005). Another aim of the study was to compare the trophic level of the respective animal taxa obtained from this study with the few literature data available on the feeding biology of those taxa (see also Pinnegar & Polunin 2000). We would expect that both systems, the aquatic and the terrestrial community in the Mekong river plain, a seasonal tropical site, differ from those of temperate regions in the number of trophic levels and we also expected long food chains, based on the findings of Reagan *et al.* (1996).

METHODS

Study site

The study area is located in the Isan region of far north-eastern Thailand (Mekong valley, Khemmarat District, Ubon Ratchathani Province, 16°02′–16°05′N, 105°03′–105°06′E). Isan is a plateau with elevations from 100 to 300 m asl formed by sand sedimentation during the Mesozoic. The region is bordered by the river Mekong to the north and east, the Petchabun mountain ridge to the west, and the Phanom Dongrak mountains to the south (Arbhabhirama *et al.* 1988). The Mekong river plain harbours different types of aquatic habitats, ranging from rivers and streams to ponds and pools harbouring a huge diversity of fish and amphibian wildlife. The former forest vegetation has been removed recently and the region is now largely used for rice farming. In the study area only small patches of primary forest remained near rivers and brooks. A secondary mixed dry deciduous forest now dominantes (Sahunalu & Dhanmanonda 1995). The climate is tropical and strongly influenced by alternating monsoon and dry seasons. The mean annual precipitation is around 1500 mm.

Sampling

We attempted to sample representatives of major animal groups inhabiting the aquatic pond and the adjacent terrestrial site (see the full taxon list in the Appendix). The pond had a surface area of about 100 m^2 and a maximum depth of 1.5 m. In the shallow-water zone about 40 m^2 were occupied by a dense vegetation of floating grasses. Aquatic invertebrates were collected by dip-netting. Freshwater fish were captured by funnel traps. Aquatic larvae of caecilians were dug out from the mud and aquatic frogs were collected by hand. Terrestrial fauna were sampled from a secondary monsoon forest at a maximum distance of 20 m to the aquatic habitat. Litter invertebrates and vertebrates were collected by hand. Soil macrofauna, caecilians, fossorial frogs and snakes were dug out of the soil to a depth of 30 cm. Collections were carried out in May and June 2001 and in November 2001.

Stable isotope analysis

White muscle samples were taken for analysis of reptiles, amphibians and fishes. Invertebrate taxa were analysed as whole animals. The animals were cut into small pieces and dried at 60 °C. The samples were then ground to powder and transferred to tin capsules. Samples were stored in a desiccator until analysis. ^{15}N concentrations in the samples were determined by a coupled system consisting of an elemental analyser (NA 1500, Carlo Erba, Milan) and a gas isotope mass spectrometer (MAT 251, Finnigan, Scientific Instrument Services, NJ, USA). The computer-controlled system allows on-line measurement of ^{15}N (Reineking *et al.* 1993). Isotope natural abundance is expressed using the δ notation with δ^{15}N (‰) = $(R_{\text{sample}}\_\ R_{\text{standard}})/R_{\text{standard}}\_\ 1000$. R_{sample} and R_{standard} refer to the ^{15}N/^{14}N ratio in samples and standard, respectively. Nitrogen in the air was used as standard and acetanilide (C_8H_9NO, Merck, Darmstadt) for internal calibration. Samples were prepared to contain 10–200 μg N; the mean standard deviation of samples in this range was shown to be 0.2‰ (Reineking *et al.* 1993). If possible, at least two replicates were measured. We attempted to collect replicates of all taxa involved, but this was not always possible. Replicates of larger taxa (all vertebrates, larger invertebrates) represented single individuals, whereas replicates of smaller invertebrate taxa (e.g. ostracods, termites) were prepared by aggregating several individuals.

To facilitate the grouping of consumers in different trophic levels we set the baseline similar to the study of Schneider *et al.* (2004). From that and other studies (Vanderklift & Ponsard 2003) it appears that primary decomposer animals, feeding on litter material, are not enriched in ^{15}N by 3.4 delta units per trophic level as are

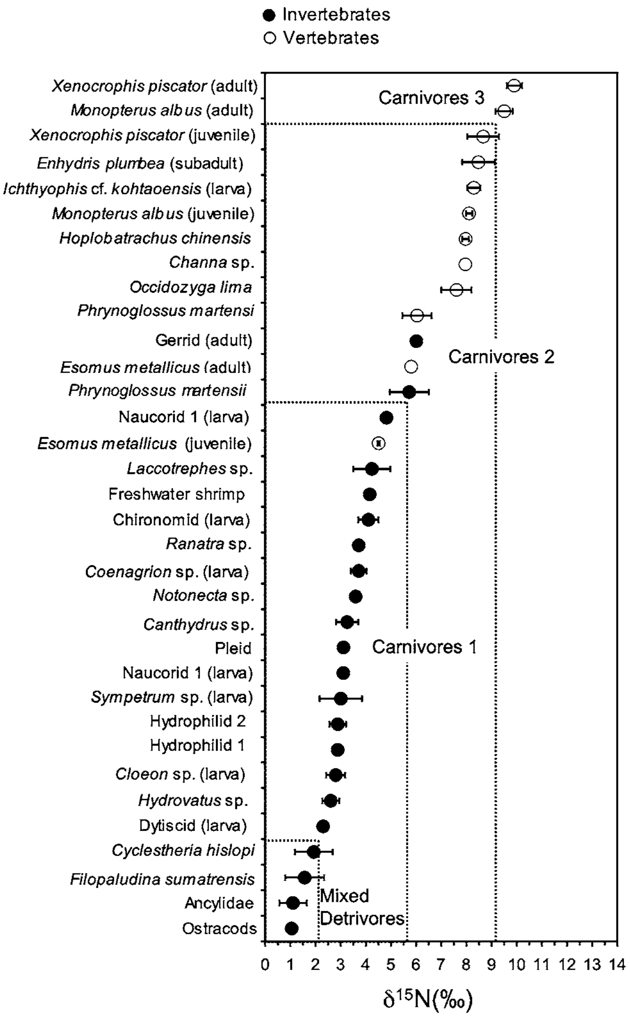

Figure 1. $\delta^{15}N$ signatures of invertebrates and vertebrates from a permanent tropical pond. Single measurements and means of two to five replicates with SD. Taxa were sorted according to increasing $\delta^{15}N$ signatures. Dotted lines indicate estimated trophic levels, assuming a trophic level fractionation of 3.4 δ units. See Appendix for further details on sample size and animal species.

other consumers. Therefore, the signatures of the primary decomposers were assumed to vary around those of their resource (± 1.7‰).

RESULTS

Aquatic food web

The distribution of isotopic signatures of ^{15}N in aquatic consumers formed a continuous gradient ranging from 1.02 to 10.1‰, i.e. spanned over nine δ units. Invertebrates such as ostracods, ancylid gastropods and the viviparous gastropod *Filopaludina sumatrensis* represented primary consumers (Figure 1). The first group of carnivores included invertebrate taxa such as water beetles, water bugs and dragonfly larvae. The next group (carnivores 2) included vertebrate taxa (fishes, frogs and larval caecilians) and some larger invertebrate species (e.g. large dytiscids and water striders). $\delta^{15}N$ signatures of riparian and aquatic frogs (*Hoplobatrachus chinensis*, *Phrynoglossus martensii* and *Occidozyga lima*) ranged from 5.62 to 8.65‰. Among amphibians the $\delta^{15}N$ signatures of larval *Ichthyophis* cf. *kohtaoensis* were the highest (8.29 ± 0.26‰). Isotope signatures were also high in juvenile aquatic snakes, $\delta^{15}N$ of 8.48 ± 0.65‰ in *Enhydris plumbea* and $\delta^{15}N$ of 8.66 ± 0.63‰ in *Xenocrophis piscator*. The highest $\delta^{15}N$ signatures of 9.90 ± 0.31‰ were recorded in adult *X. piscator* and in adult swamp eels *Monopterus albus* (9.50 ± 0.34‰).

Terrestrial food web

In terrestrial animals ^{15}N ratios ranged between 0.79 and 12.2‰, i.e. spanned over 11 δ units (Figure 2). The basal trophic groups were xylophagous termite worker castes of *Macrocerotermes crassus* ($\delta^{15}N = 0.79 \pm 0.14$‰) and *Globitermes sulphureus* (1.50 ± 0.34‰). $\delta^{15}N$ signatures were higher in workers (2.81 ± 0.03‰) and soldiers of *Odontotermes* cf. *feae* (3.07 ± 0.18‰). Termites, scarabaeid beetle larvae, diplopods, ants, crickets and juvenile and adult frogs (*Rana macrodactyla*) constituted the second group, comprising of animals using various food sources including detritus and animal prey (carnivores 1). The second group of predators (carnivores 2) included vertebrates (frogs, lizards, fossorial snakes and caecilians) and some larger invertebrate taxa such as scolopendrids, scorpions and whip spiders (Figure 2). Juvenile caecilians (*Ichthyophis* cf. *kohtaoensis*) had lower $^{15}N/^{14}N$ ratios (6.87 ± 0.13‰) than adults (8.83 ± 0.30‰). $^{15}N/^{14}N$ signatures of fossorial snakes ranged between 8.14 ± 0.28‰ in *Ramphotyphlops braminus* and 8.62 ± 0.47‰ in subadult *Cylindrophis ruffus*. The highest $^{15}N/^{14}N$ ratios were detected in two predatory snakes, 10.1‰ in the common racer *Ptyas korros* and 10.5 ± 2.42‰ in the elapid snake *Calliophis maculiceps*.

DISCUSSION

In the pond food web, animal $^{15}N/^{14}N$ ratios differed strongly spanning over a gradient of 9 $\delta^{15}N$ units. Based on the empirical evidence from other food web studies (Post 2002b, Vander Zanden *et al.* 1999) this suggests the existence of five trophic levels including algae and detritus as basal trophic level. Surprisingly little information is available on the organization of food webs of ponds and puddles (see Warren 1989). Most studies using stable isotopes for analysing the trophic structure of freshwater

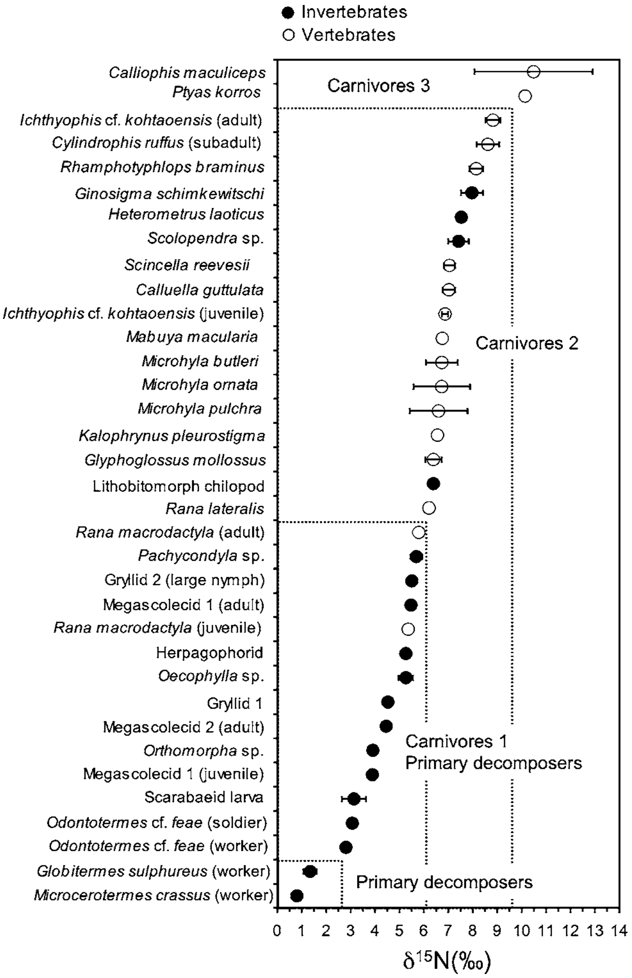

Figure 2. $\delta^{15}N$ signatures of invertebrates and vertebrates collected from a tropical gallery forest. Single measurements and means of two to five replicates with SD. Taxa were sorted according to increasing $\delta^{15}N$ signature. Dotted lines indicate estimated trophic levels, assuming a trophic level fractionation of 3.4 δ units. See Appendix for further details on sample size and animal species.

communities have been carried out in lakes and streams (Post 2002b, Vander Zanden *et al.* 1999). The size of the pond investigated in this study was about 150 m^3. We estimated five trophic levels with snakes (*Xenochrophis piscator*) and swamp eels as top predators, which suggests a short food chain length. In large freshwater systems such as lakes, Post *et al.* (2000) found evidence that larger systems support food webs with longer food chains and higher numbers of trophic levels, i.e. that ecosystem size and the length of food chains are positively correlated.

$^{15}N/^{14}N$ ratios of terrestrial animals showed a strong gradient ranging over 11 $\delta^{15}N$ units. This implies that the terrestrial food chains are slightly longer than those of the aquatic system. Based on the assumption that adjacent trophic levels differ by 3.4 $\delta^{15}N$ units (Minegawa & Wada 1984, Post 2002b, Vander Zanden *et al.* 1999), we estimated five trophic levels for the terrestrial food web including plants as basis. However, an additional trophic level may exist which includes medium-sized mammals preying on snakes. Interestingly, the results suggest that the number of trophic levels does not exceed those of temperate forest systems (Ponsard & Arditi 2000, Scheu & Falca 2000). It has been postulated that the number of trophic levels in food webs is correlated with either productivity or habitat complexity (Persson *et al.* 1992), with low-productivity systems having fewer trophic levels (Havens 1991). However, the number of trophic levels ascribed to terrestrial food webs may not reflect the actual situation due to the low resolution of trophic species (Martinez 1991). Using stable isotopes (^{15}N) the number of trophic levels in terrestrial food webs in tropical and temperate systems has been shown to be rather similar, usually 3–4 levels (Ponsard & Arditi 2000, Scheu & Falca 2000). This suggests that productivity and energy flow do not significantly affect the number of trophic levels.

Tetrapods such as amphibians and reptiles were highly abundant in the studied systems but large herbivores (e.g. elephants), carnivores (e.g. tigers) and most large bird species are lacking. A high abundance of amphibians and reptiles was previously reported from other tropical terrestrial ecosystems such as tropical evergreen (Reagan *et al.* 1996, Ziegler 2002) and dry dipterocarp forests (Inger & Colwell 1977) and savannas (Barbault 1991). Ectothermic amphibians and reptiles have higher conversion efficiencies than mammals and can support a higher biomass (Pough 1983). Reagan *et al.* (1996) reported long food chains (mean 8.5, max. 19 links) in a tropical rain forest dominated by ectotherms and suggested this to be due to high conversion efficiencies. The findings of longer food chains were contradictory to assumptions of previous food web models (Pimm & Lawton 1978). The terrestrial habitat studied here is a ‘fluctuating environment’, which undergoes strong seasonal variation in rainfall and humidity. In fluctuating environments the chain lengths are predicted to be short which is consistent with our data.

We are aware of the evidence that invertebrates with N-poor diets do not conform to the same rules of trophic fractionation as predators (see McCutchan *et al.* 2003). In invertebrates, ^{15}N signatures vary strongly with life stage (Adams & Sterner 2000), diet quality (Webb *et al.* 1998) and with the type of nitrogen excretion (Vanderklift & Ponsard 2003).

The estimates of trophic positions of aquatic and terrestrial consumers determined by stable isotope analysis fit well with the trophic classifications based on classical analysis of gut contents (see Appendix). Vertebrate predators had much higher ^{15}N signatures than invertebrates, their potential prey. Our data support previous stable isotope studies (Pinnegar & Polunin 2000, Vander Zanden & Rasmussen 1999). The grouping of the animals into functional groups has to be considered with care.

There is no objective way to adjust the lines that separate trophic groups. We used the present knowledge of the ecology of the species, partly data on ^{15}N signatures of consumers from temperate sites and evidence from other studies to group the animals into different feeding guilds.

Isotope signatures of riparian and aquatic frogs (*Hoplobatrachus chinensis*, *Phynoglossus martensii* and *Occidozyga lima*) ranged over three $\delta^{15}N$ units and identified them as one feeding guild. The trophic ecology of larval caecilians is poorly known (Himstedt 1996). A recent gut content study on larval *I.* cf. *kohtaoensis* revealed feeding on detritivorous water invertebrates, such as clamp shrimps, but also on predatory insects such as dragonfly larvae (Kupfer *et al.* 2005). In the present stable isotope study the average $\delta^{15}N$ signature of these prey groups was 5.91‰ lower than in larvae of *I.* cf. *kohtaoensis*, indicating that the larvae predominately feed on prey higher up in the food chain, presumably dytiscid and naucorid larvae. This characterizes *I.* cf. *kohtaoensis* larvae as trophic-level omnivores (as defined by Pimm & Lawton 1978). Synbranchid swamp eels are known to feed on various water insects, crabs and fishes but also benthic algae and organic debris were detected among intestine contents (Rainboth 1996, Yang *et al.* 1997). The high isotopic signatures found in this study strongly suggest *Monopterus albus* to be a predator in freshwater ecosystems.

The two water snakes, *Enhydris plumbea* and *Xenochrophis piscator*, had high isotopic signatures characterizing them as top predators. An additional trophic level might include birds, which prey on snakes, but these were not sampled in this study.

Stable isotope data suggest that the microhylid frogs *Glyphoglossus*, *Calluella* and *Kalophrynus* use similar food resources as *Microhyla* ssp. which are known to feed on ants and termites (Kuzmin & Tarkhnishvili 1997, Ziegler 2002). Recent detailed studies on the diet of terrestrial caecilians identified them as generalist predators feeding mainly on soil invertebrates (Kupfer *et al.* 2005, Measey *et al.* 2004). The $\delta^{15}N$ signatures of juvenile and adult *I.* cf. *kohtaoensis* corroborate their status as predators. Interestingly, it seems that there is a diet shift by *I.* cf. *kohtaoensis* when becoming adult. The caecilian amphibian obviously feeds higher in the food web as an adult; the stable isotope signatures of the juveniles (in aquatic and terrestrial systems) are around 7 to 8‰ whereas adults have stable isotope signatures of about 9‰.

The snakes *Cylindrophis ruffus* and *Ramphotyphlops braminus* are adapted to burrowing in soil (Taylor 1965). *Cylindrophis ruffus* is known to feed on relatively large prey such as other snakes and caecilians (Kupfer *et al.* 2003), suggesting that their $\delta^{15}N$ signatures are high. However, the $^{15}N/^{14}N$ ratios of subadult *C. ruffus* (total length of less than 200 mm) were lower than those of *Calliophis maculiceps* and *Ptyas korros*, indicating that it might also feed on soil invertebrates lower in the food chain. *Calliophis maculiceps* and *P. korros* had the highest $^{15}N/^{14}N$ ratios suggesting that they constitute top predators in the studied food web and that both snakes likely prey on other vertebrates. However, an additional trophic level above snakes may exist because terrestrial top carnivores such as little civet cats (*Viverricula indica*) and mongooses (*Herpestes javanicus*) are abundant at the study site (A. Kupfer, *pers. obs.*), but were not sampled in this study. Both species are known to prey on snakes (Lekagul & McNeely 1977).

Interestingly, large carnivorous invertebrates, such as scolopenders, whip scorpions and scorpions had $\delta^{15}N$ signatures similar to some vertebrate taxa. Probably, large carnivore invertebrates also feed on vertebrates, as reported from other tropical food webs (Reagan *et al.* 1996).

In summary, the stable isotope approach used in the present study proved to be highly effective for the characterization of relative trophic positions of two complex animal communities including herbivores, carnivores and omnivores. We found about five trophic levels appear to exist in both the aquatic and the terrestrial food web. We only investigated $^{15}N/^{14}N$ ratios of aquatic and terrestrial consumers at a single date, i.e. June and November 2001. Stable isotope ratios of animals may fluctuate over the year due to changes in food resources. There is some evidence from studies on temperate systems that stable isotope ratios change slowly (Schmidt *et al.* 1999) and that $^{15}N/^{14}N$ ratios of soil animal species vary little between seasons (Ponsard & Arditi 2000). Therefore, we assume that our data likely reflect the trophic structure of the animal community of the two sites studied. However, seasonal aspects of stable isotope ratios of tropical consumers are poorly investigated (Tayasu *et al.* 1997) and should remain the focus of future studies.

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Appendix. Names of taxa and number of replicates of the aquatic and terrestrial food web. The trophic classification of consumers is based on literature.

Animal group/family	Species	n	Trophic classification
Aquatic food web			
Vertebrates			
Snakes			
Colubridae	*Xenocrophis piscator* (Schneider 1799), adult	2	Predator[1,2]
	Xenocrophis piscator (Schneider 1799), subadult	3	Predator[1,2]
	Enyhdris plumbea (Boie 1827), subadult	3	Predator[2,3]
Caecilians			
Ichthyophiidae	*Ichthyophis* cf. *kohtaoensis*, larva	3	Predator[4]
Frogs			
Ranidae	*Hoplobatrachus chinensis* (Osbeck 1765)	2	Predator[2,5]
	Phrynoglossus martensii Peters 1867	2	Predator[2,5]
	Occidozyga lima (Gravenhorst 1829)	3	Predator[2,5]
Fishes			
Synbranchidae	*Monopterus albus* (Zuiew 1793), subadult	3	Predator[6]
	Monopterus albus (Zuiew 1793), adult	3	Predator[6]
Channidae	*Channa* sp.	1	Predator[6]
Cyprinidae	*Esomus metallicus* (Ahl 1923), subadult	2	Predator[6]
	Esomus metallicus (Ahl 1923), adult	1	Predator[6]
Invertebrates			
Water beetles			
Dytiscidae	*Cybister* sp.	4	Predator[7]
	Hydrovatus sp.	3	Predator[7]
	Dytiscid larva	1	Predator[7]
Noteridae	*Canthydrus* sp.	6	Detrivore[7]
Hydrophilidae	Hydrophilid 1	1	Detrivore[7]
	Hydrophilid 2	2	Detrivore[7]
Dragonflies			
Libellulidae	*Sympetrum* sp., small larva	2	Predator[7]
Coenagrionidae	*Coenagrion* sp.	3	Predator[7]
Water bugs			
Nepidae	*Laccotrephes* sp.	3	Predator[7]
	Ranatra sp.	3	Predator[7]
Gerridae	Gerrid	1	Predator[7]
Belostomatidae	Bellostomatid	1	Predator[7]
Notonectinae	*Notonecta* sp.	3	Predator[7]
Pleidae	Pleid (dwarf water boat men)	1	Predator[7]

Appendix. Continued.

Animal group/family	Species	n	Trophic classification
Diptera			
Chironomidae	Chironomid larva	3	Detrivore[8]
Ephemeroptera			
Baetidae	*Cloeon* sp., larva	5	Detrivore[8]
Crustaceans			
	Malacostraca (freshwater shrimp)	2	Predator[7]
Cyclestheriidae	*Cyclestheria hislopi* (Baird 1859)	5	Detrivore[7]
	Ostracods	1	Detrivore[7]
Molluscs			
Viviparidae	*Filopaludina sumatrensis* (Dunker 1852)	3	Detrivore[7]
Ancylidae	Ancylid snail	2	Detrivore[7]
Terrestrial food web			
Vertebrates			
Snakes			
Elapidae	*Calliophis maculiceps* (Günther 1858)	2	Predator[1]
Cylindrophiidae	*Cylindrophis ruffus* (Laurenti 1768)	2	Predator[9]
Typhlopidae	*Ramphotyphlops braminus* (Daudin 1803)	3	Predator[2,3]
Lizards			
Scincidae	*Scincella reevesii* (Gray 1838)	3	Predator[2,3]
	Mabuya (Eutropis) macularia (Blyth 1853)	1	Predator[2]
Caecilians			
Ichthyophiidae	*Ichthyophis* cf. *kohtaoensis*, subadult	2	Predator[4]
	Ichthyophis cf. *kohtaoensis*, adult	3	Predator[4]
Frogs			
Ranidae	*Rana macrodactyla* (Günther 1858), subadult	1	Predator[5]
	Rana macrodactyla (Günther 1858), adult	1	Predator[5]
	Rana lateralis Boulenger 1887	1	unknown
Microhylidae	*Glyphoglossus mollossus* Günther 1869	3	unknown
	Calluella guttulata (Blyth, 1856)	3	unknown
	Kalophrynus pleurostigma Tschudi 1838	1	unknown
	Microhyla butleri Boulenger 1900	3	Predator[2]
	Microhyla ornata (Duméril & Bibron 1841)	2	Predator[2,5]
	Microhyla pulchra (Hallowell 1861)	5	Predator[2]
Invertebrates			
Scorpions			
Thelyphoninae	*Ginosigma schimkewitschi* Tarnani 1894	2	unknown
Scorpionidae	*Heterometrus laoticus* Couzin 1981	1	unknown
Chilopods			
Scolopendridae	*Scolopendra* sp.	3	unknown
Lithobiidae	Lithobiid chilopod	1	Predator[10]
Diplopods			
Paradoxosomatidae	*Orthomorpha* sp.	2	Decomposer[10]
Harpagophoridae	Harpagophorid	1	Decomposer[10]
Termites			
Macrotermitinae	*Odontotermes* cf. *feae*, soldier	3	Decomposer[11]
	Odontotermes cf. *feae*, worker	3	Decomposer[11]
Termitinae	*Globitermes sulphureus* (Haviland, 1989), worker	3	Decomposer[11]
	Microcerotermes crassus Snyder 1934, worker	2	Decomposer[11]
Ants			
Formicinae	*Oecophylla* sp.	3	Mixed diet[12]
Ponerinae	*Pachycondyla* sp.	2	Predator[13]
Ground beetles			
Scarabaeidae	Scarabaeid larva	2	Decomposer[10]
Crickets			
Grillidae	Gryllid 1, small larva	1	Mixed diet[10]
	Gryllid 2, large larva	1	Mixed diet[10]
Earthworms			
Megascolecidae	Megascolecid 1, subadult	3	Decomposer[10]
	Megascolecid 1, adult	3	Decomposer[10]
	Megascolecid 2, adult	1	Decomposer[10]

Key to references: [1]Taylor 1965, [2]Ziegler 2002, [3]Cox *et al.* 1998, [4]Kupfer *et al.* 2005, [5]Kuzmin & Tarkhnishvili 1997, [6]Rainboth 1996, [7]Warren 1989, [8]Vander Zanden & Rassmussen 1999, [9]Kupfer *et al.* 2003, [10]Reagan *et al.* 1996, [11]Tayasu *et al.* 1997, [12]Blüthgen *et al.* 2003, [13]Leal & Oliveira 1995.