



Research Article

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Feeding strategies and competition between terrestrial *Haemadipsa* leeches (Euhirudinea: Arhynchobdellida) in Danum Valley rainforest (Borneo, Sabah)

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Abstract: Haemadipsid leeches are among the most successful terrestrial invertebrates in Bornean rainforests. They are very common ectoparasites of vertebrates, and their abundance has facilitated the conduction of numerous projects in the fields of ecology, zoogeography and taxonomy. We undertook research on two species inhabiting lowland dipterocarp forest, *Haemadipsa picta* Moore, 1929 and *Haemadipsa subagilis* (Moore, 1929), in order to address the following questions: (a) is there a difference in leech abundance between trails and off-trails?; (b) is ambush location dependent on specimen size or is species-specific?; (c) is intra- and interspecific competition limited by differences in foraging behaviours or vertical niche partitioning? Our results clearly show that *H. picta* is more abundant on trails than on off-trails and is vertically dispersed within the understory; the size of a specimen is strongly correlated with plant height. *Haemadipsa subagilis* was found not to exhibit such patterns. We suggest a possible lowering of interspecific competition between these species as a result of: (i) size-dependent dispersion of *H. picta* (together with reduction of intraspecific competition); and (ii) habitat specialisation of *H. subagilis*. Moreover, we provide new observations on their foraging behaviour.

Keywords: ectoparasites, foraging behaviour, Haemadipsidae, haematophagy, parasitism

Tropical rainforests of South-East Asia are the biodiversity hot-spot for terrestrial leeches of the family Haemadipsidae (Euhirudinea: Arhynchobdellida), which comprises over 80% of all land leech species and includes the most species-rich genus *Haemadipsa* Tennent, 1859 (see Borda and Siddall 2004, 2010, Sket and Trontelj 2008). The leech fauna of the Oriental region has received much attention since the fundamental works of Moore (1929, 1935, 1938). The tiger leech *H. picta* Moore, 1929 and two brown coloured species, namely *H. subagilis* (Moore, 1929) and *H. sumatrana* (Horst, 1883), are typical and widely dispersed elements of the Bornean lowland rainforest fauna (Sawyer et al. 1982, Govedich et al. 2004).

Many ecological aspects of the life history of haemadipsid species remain unresolved, including establishing an average life span for each species and species habitat preferences. Fogden and Proctor (1985) conducted some important studies on the feeding habits of species of *Haemadipsa*, and until now this was the only paper containing detailed data on growth after feeding and the length of time they can endure without a blood meal. In contrast, feeding strategies of aquatic leeches are better understood (Davies and Kasserra 1989, Kutschera 2003, Chin Teh et al. 2012).

The second essential work by Kendall (2012), provided insights into changes in leech species proportion in

response to environment modification and how various abiotic factors, including temperature and humidity, affect their abundance and frequencies. Statistical analyses performed by him confirmed previous assumptions that the brown leech species complex (former *H. zeylanica sensu lato*, see Borda and Siddall 2010) is more frequent in primary tropical rainforest, whereas more disturbed environments are dominated by conspicuously coloured *H. picta*.

Biotic factors, such as competition and feeding strategies of hematophagous leeches, have not been examined so far. Parasites can be an important factor influencing host mortality and, therefore, their abundance in an ecosystem (Anderson and May 1978). However, it is not possible to simply apply this theory to ectoparasites, such as leeches, which normally do not kill their hosts. Since an ecological balance between sympatric species should exist (Inger and Greenberg 1966), the co-existence of several common sanguivorous invertebrate species in rainforests raises questions about the relationship between inter- and intraspecific competition and niche partitioning.

Due to unresolved issues related to leech inter- and intraspecific ecological relationships and foraging behaviour, we conducted a study to address the following questions: (a) for as much as the inter-habitat distribution of species of *Haemadipsa* is already known (Kendall 2012),

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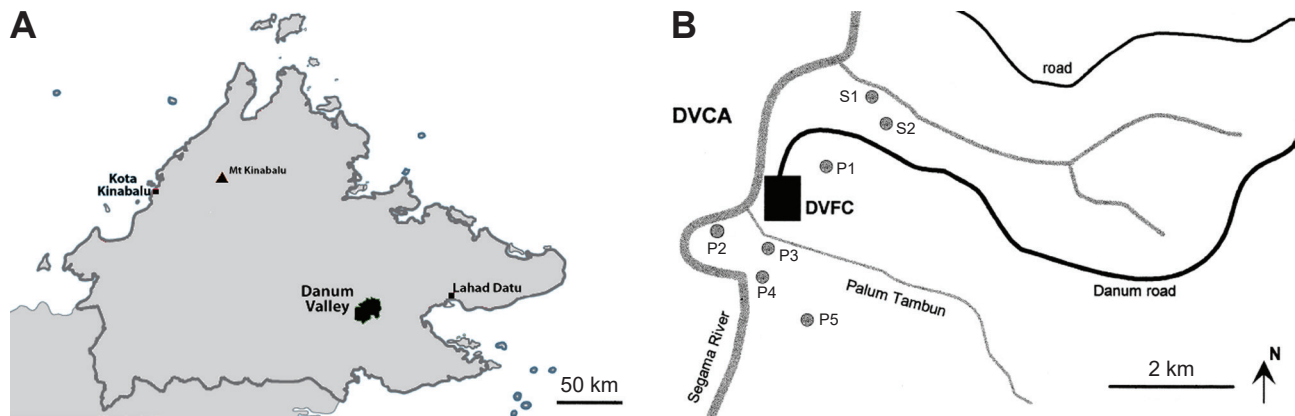


Fig. 1. A – Location of Danum Valley Conservation Area (DVCA) in Sabah (Malaysia); B – Danum Valley Field Centre (DVFC) vicinity. Grey circles signify sampling sites in the primary (P1–P5) and secondary (S1, S2) rainforest. Modified from Willott et al. (2000).

do *H. picta* and *H. subagilis* exhibit variable population densities as a result of greater host availability on trails vs off-trails?; (b) as both species can be found on the ground, i.e. amongst leaf litter, as well as on the foliage of plants up to 2 m high (although preference of the brown leech species complex for the ground and *H. picta* for growing plants was noted – see Smythies 1959); when searching for a host, does the placement of the leech (forest litter vs plant foliage) depend on body size or on species-specific preferences?; (c) do both species alter inter- and intraspecific competing changes in feeding strategies?

MATERIALS AND METHODS

The present study was carried out during a Tropical Ecology Field Course over three weeks in July 2016 in Danum Valley (Borneo, Sabah) (Fig. 1A). Two common Bornean haemadipsid species were chosen for analyses, *Haemadipsa picta* and *H. subagilis*. Taxa were identified on the basis of dorsum morphology, using the original description (Moore 1929) and the key by Govedich et al. (2004). Specimens were collected in seven sites identified after the reconnaissance, i.e. a preliminary two-day-long survey was conducted to determine localities characterised by average leech occurrence (where at least 10 leeches per half-hour were observed). Ultimately seven localities were chosen: five in the primary rainforest (P1–P5), and the other two in the secondary rainforest (S1, S2, approximately 100 m² plots). Two localities in the primary rainforest and one in the secondary rainforest were in close proximity to rivers/ streams (localities P2, P3 and S1; see Fig. 1B). Primary rainforest in Danum Valley is dominated by trees from the family Dipterocarpaceae, with predominant Euphorbiaceae present in understory (Newbery et al. 1999). Secondary rainforest has a more dense understory, commonly composed of rattan palms (mainly of the genera *Calamus*, *Daemonorops* and *Korthalsia*; Johnson 1996); the canopy layer is uneven and with dominant *Koompassia excelsa* (Fabaceae). Individuals were collected twice per day (9–12 AM and 3–6 PM) from those areas closest to the trail (defined as an area extending no more than 1 m from a path) and off-trail (an area further than 1 m and no more than 15 m from a path) at each of the seven localities. One collecting session lasted approximately one and half hours. During the first three nights collecting sessions were

Table 1. Size classes of *Haemadipsa picta* Moore, 1929 collected for this survey.

Size class (mm)	No. collected leeches			%	Age category
	Morning session	Afternoon session	Total No.		
6–13	24	25	49	24	Juvenile
14–21	13	14	27	13	Juvenile
22–29	18	11	29	14	Subadult
30–37	41	19	60	30	Adult
38–45	24	12	36	18	Adult
46–53	2	-	2	1	Adult
Total	122	81	203	100	

also undertaken between 8–10 PM, but the authors subsequently stopped data collection after dusk due to very low leech activity. Collected leeches were preserved individually in vials with 50% ethanol and labelled with all necessary information (i.e. collection time, locality, the type of habitat and approximate time since the last rainfall).

Animals were measured on the day of collection to reduce the time they were kept in ethanol to only a few hours. Leeches were pinned out to resting length using metal strand to avoid artificial deformation or lengthening of a specimen (Sawyer et al. 1982). Millimetre graph paper was used for morphometrics. Total body length was measured from the margin of an anterior sucker to the margin of a posterior sucker. Body length served as an estimator of relative body size (Ben Ahmed et al. 2009) and six size classes were distinguished for *H. picta* (see Table 1 for details). Individuals with gastric caeca filled with blood were discarded from statistical analyses.

Differences in leech abundance between habitats was assessed using two-way ANOVA. The type of habitat (trail or off-trail) and collecting time after the last rainfall (i.e. up to 5 h, or at least 12 h, after the last rainfall) were entered as fixed independent factors and the number of individuals gathered during a session as the dependent variable. The time after last rainfall, which can be treated as an estimator of humidity (higher shortly after rainfall and lower during longer periods without rain, respectively), was included in the model because it is known to affect the encounter rate of haemadipsid leeches (Kendall 2012). To examine whether

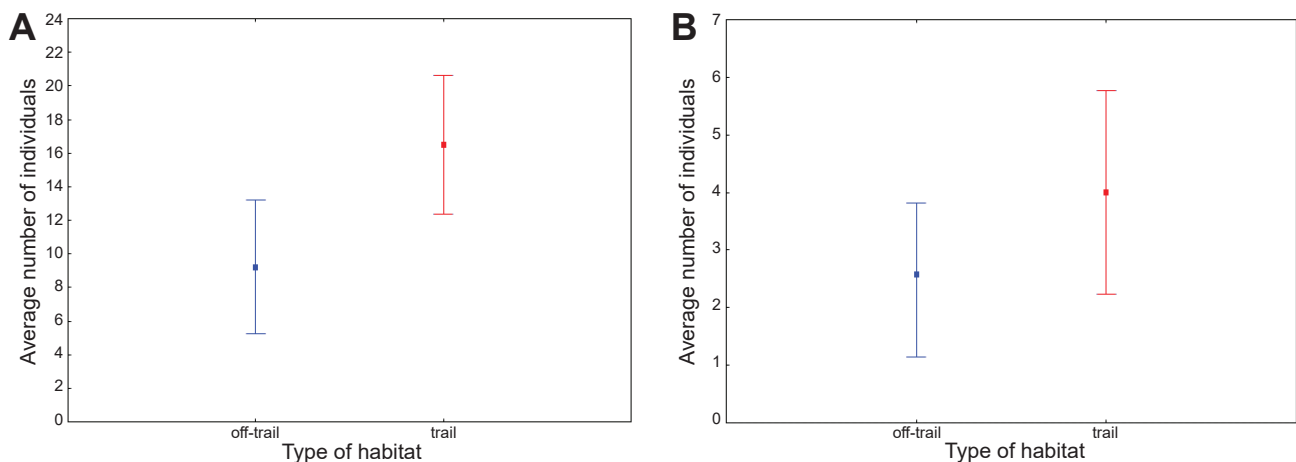


Fig. 2. An average number of individuals (found on 100 m² plot) occurring in the particular type of habitat. **A** – *Haemadipsa picta* Moore, 1929; **B** – *H. subagilis* (Moore, 1929). The line segments indicate 95% confidence intervals.

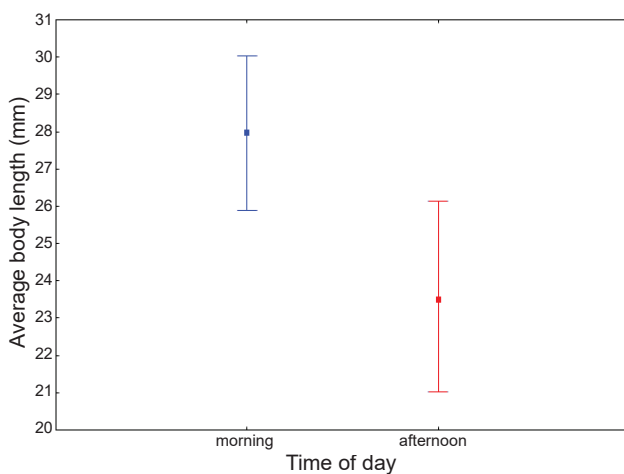


Fig. 3. An average body length (mm) of *Haemadipsa picta* Moore, 1929 individuals hunting during morning (M) and afternoon (A). The line segments indicate 95% confidence intervals.

individuals of *H. picta* of distinct body sizes preferred hunting during different times of a day, we applied one-way ANOVA with the time of a day (morning vs late afternoon) as the fixed independent factor and the body length as the dependent variable. We used Kruskal-Wallis test by ranks in the case of *H. subagilis* due to the considerably smaller sample size. To establish if there was significant dependence between size of the specimen and the height from which it attacks a host, non-parametric measure of rank correlation, Spearman's rho, was used. The best fitting curve and equation of non-linear regression were chosen to describe the character of correlation between the tested variables. Standard errors are presented after \pm mark.

RESULTS

In total 205 individuals of *Haemadipsa picta* and 54 individuals of *H. subagilis* were collected. More than 90% of *H. subagilis* were found on the ground, which prevented direct testing of the second hypothesis for this species. Two specimens of *H. picta* and one individual of *H. subagilis* were excluded from the analyses due to evident enlargement of the body after feeding.

Two-way ANOVA revealed statistically significant differences ($F = 7.18$, $p = 0.02$) in the abundance of *H. picta* between trails (average number of individuals/100 m²: $N_t = 16.5 \pm 1.9$) and off-trails ($N_o = 9.2 \pm 1.8$), indicating the understory immediately adjacent to trails richer in leeches. No disparities in the abundance of *H. subagilis* were found ($F = 2.14$, $p = 0.17$; $N_t = 2.6 \pm 0.5$, $N_o = 4.0 \pm 1.0$; see Fig. 2 for both species), and the impact of rainfall appeared non-significant ($p = 0.78$ and 0.28 , respectively).

One-way ANOVA confirmed differences in average body length (L) of *H. picta* collected during the morning ($L = 28.0 \pm 1.0$) and afternoon sessions ($L = 23.6 \pm 1.3$; $F = 6.89$, $p = 0.01$; see Fig. 3), with larger leeches (i.e. from the third size class onwards, see Table 1) hunting mainly during the morning. Kruskal-Wallis test did not reveal differences in the case of *H. subagilis* ($H = 0.51$, $p = 0.48$).

A significant positive correlation between a place of ambush (i.e. the height from which leeches fall onto their hosts or simply attach to them) and body size was discovered for *H. picta* ($\rho = 0.83$, $p < 0.001$). The best fit curve, describing these data points had a logarithmic character (see Fig. 4), and the following equation was assigned to this line: $y = 30.682 \times \log_{10}(x) - 22.7252$. No such correlation was detected for *H. subagilis* ($\rho = -0.08$, $p = 0.56$).

DISCUSSION

Inter-habitat dispersion and temporal variation in leech size

It is widely known that closely related ectoparasites can sometimes inhabit quite different environments (Siddall and Burreson 1996, Williams and Burreson 2006, Borda et al. 2008). Such a pattern is recognised in the Bornean haemadipsid genera: whereas species of *Haemadipsa* occur in very high numbers in lowland forests (Lai et al. 2011), also occur at higher elevations, i.e. above 800 m a.s.l. (Moore 1929). In contrast, members of the sister genus *Tritetrabdella* Moore, 1938 can be found mainly in mountainous areas, i.e. above 1,200 m a.s.l. (Kappes 2013, Nakano et al. 2016). However, the environmental distribution within the members of the same genus remains unclear.

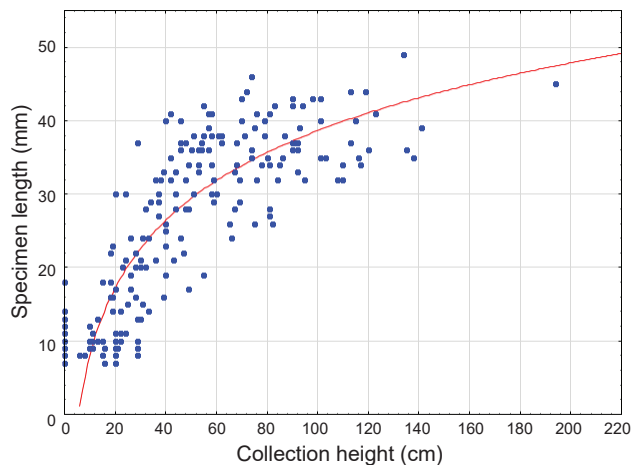


Fig. 4. The dispersion plot depicting the correlation between the length and preferred altitude of attack of *Haemadipsa picta* Moore, 1929. The best-fitting logarithmic curve is drawn and the following equation of regression is assigned to this curve: $y = 30.682 \times \log_{10}(x) - 22.7252$.

The present study shows that *H. picta* exhibits opportunistic behaviour and agglomerates in the vicinity of animal trails used mainly by mammals such as humans, bearded pigs, macaques and rodents, which logically implies an increase in hunt success ratio. The average number of collected individuals was relatively high in off-trail habitats. It is worth mentioning that host preferences for both species studies are unknown, but Schnell et al. (2015) indicated that mammals and amphibians are hosts of *Haemadipsa* and *Tritetrabdella* (see also Rocha et al. 2012 for a brief summary of records of species of *Haemadipsa* spp. parasitising amphibians).

Lai and Chen (2010) appointed mammals as predominant hosts of leeches of *Haemadipsa* and our results suggest that these leeches can be choosy in selecting particular hosts of an adequate size. In contrast, we did not find any differences in the abundance of *H. subagilis* across sampled habitats. A considerably lower sample size could have influenced this result, and higher average number of individuals found on trails suggests that significant disparities could be discovered when more leeches are collected and measured.

Demonstrated temporal variation in the size of *H. picta* means that relatively larger specimens (from the third size class onwards, referred to as 'subadult' herein) prefer hunting during the morning, whereas juveniles (first two size classes) exhibited similar activity throughout the day. Given that leech growth is saltatory, not continuous (Sawyer et al. 1981), this discovery suggests shifts in ecological preferences connected with aging, a factor previously reported as responsible for attenuating interspecific competition between sympatric species (Bashey et al. 2016). Therefore, we hypothesise that a similar mechanism could alleviate intraspecific competition within populations of *H. picta*. In contrast, no such phenomenon was detected for *H. subagilis*. This might suggest that *H. subagilis* exhibits a constant ecological preference throughout its life cycle. However, if the population density is small (e.g. during the dry season

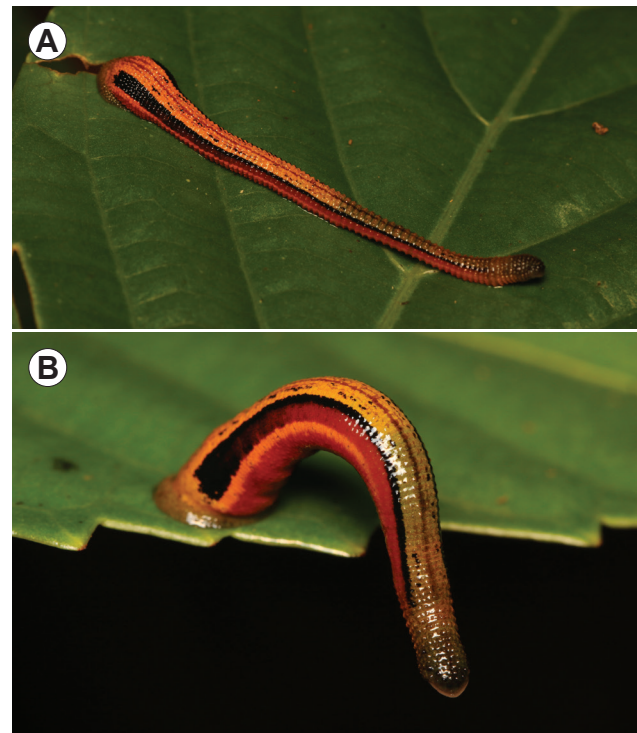


Fig. 5. Typical postures of haemadipsid leeches on the example of *Haemadipsa picta* Moore, 1929. **A** – in resting position; **B** – in attack position. Photo ©Ryszard Laskowski, used with permission.

in Danum Valley), no aggregations within a particular habitat, or temporal variation would be observed.

Spatial variation in leech size

Generally, *H. picta* exhibits visible vertical intraspecific niche partitioning. We demonstrated strong correlation between the size of *H. picta* and the height from which it attacks its hosts. The relation has a non-linear character, and is likely shaped by a compromise between (i) energy expenditure associated with foliage climbing, and (ii) the leeches' inclination to select the best place for attack. In other words, it is very profitable for small and intermediate individuals to crawl slightly higher above the surrounding ground level (ranging from 20 cm to approximately 60 cm), as this may increase the host encounter rate and balance the energy expended through movement. Big individuals do not have to climb much higher, because there are no mammalian leech hosts in Bornean rainforest which have a height, as measured at the whiskers, exceeding 2 m (the biggest, wild cattle – banteng, reaches 1.7 m).

As the vast majority of *H. subagilis* were collected from leaf litter, this species must be classified as strictly related to the ground, most probably as other cryptically coloured members of the genus from the brown leech species complex (i.e. former subspecies of *H. zeylanica* Moquin-Tandon, 1827 and cognates; see Borda and Siddall 2010). Nevertheless, six individuals of *H. subagilis* (11%) were found on foliage. There are two possible explanations for this: (i) a small fraction of the population inhabits plants up to a height of 1 m; or (ii) the species comprises two or more cryptic taxa, which differ in their preferred microhabitat.

Intra- and interspecific competition between species of *Haemadipsa*

Southeast Asian dipterocarp forests are home to four terrestrial genera whose members very probably do not compete for food resources: many species of *Haemadipsa* suck blood of mammalians; those of *Tritetrabdella* that of amphibians (for the latest record see Nakano and Sung 2014); and members of *Phytobdella* Blanchard, 1894 that of reptiles (Moore 1938). The hosts of species of *Planobdella* Blanchard, 1894 remain unknown (see Blanchard 1849). The relationships between very closely related species, such as of *H. picta* and *H. subagilis*, were hitherto unravelled. Given that both species occur in lowland forests in very high numbers, one would ask how it is possible they co-exist without outcompeting each other.

Our survey suggests that *H. picta* reduces the level of interspecific competition by adopting a strategy of vertical distribution of individuals, thereby utilising a range of different host species. Further, modulation of intraspecific competition is achieved in two different ways: firstly as a consequence of the vertical distribution discussed above, we hypothesise that juveniles attach to smaller hosts (for example, rodents), and adults to larger hosts (pigs and primates); secondly through temporal separation of hunting periods between specimens of distinct sizes. Recently, Esser et al. (2016) showed that host body size is correlated with tick diversity, namely, the larger the host, the more diverse the ectoparasite fauna. It is therefore possible that host body size also determines the body size in land leeches.

Although we did not show how *H. subagilis* could affect the level of interspecific competition, and the sample size was definitely too low to draw any definite conclusions, over half of collected individuals came from riparian localities. This suggests that *H. subagilis* occupies a more specialised niche in comparison with *H. picta*, presumably due to being more sensitive to low humidity (the best evidence for this is the overall number of *H. subagilis* vs *H. picta* obtained during the dry season). Overall, our results are in agreement with the system described by Johnson and Herbers (2006): two sympatric parasite species inhabit the same environment because of very likely asymmetrical antagonism between them. This results in attenuation of negative effect of ectoparasites on mammals and prevents host population decline. In the case of *Haemadipsa* leeches, *H. picta* appears to be the stronger competitor, shaping the ecological relationship between species.

Foraging behaviour observations

The first precise description and classification of leech foraging behaviour was based on observations of the South American species *Haementeria ghilianii* de Filippi, 1849 (see Sawyer 1981). As *H. picta* and *H. subagilis* exhibit differential host search strategies, we report them as follows:

(1) *H. picta* shows resting posture (Fig. 5A) only when found on foliage. It exhibits both 'head movements' and

'body waving' exploratory behaviours (Fig. 5B), the first typically found in the larger individuals (adult), and the latter behaviour being typical of juveniles. *Haemadipsa picta* is generally more active and moves more rapidly than its smaller congener, and very often chases potential hosts. Similar behaviour was not observed in *H. subagilis*.

(2) *H. subagilis* attacks from ambush, i.e. it spends a considerable amount of time in a resting posture, and becomes active and attaches to a host when it comes very close. Immediately before the moment of attachment, an individual almost always performs head movements, but rarely demonstrates body waving.

(3) When *H. subagilis* attaches to the host's body, it almost never crawls on its host, instead it tries to penetrate the skin near the site of initial attachment.

(4) Differences between modes of movement were also detected during field observations. According to Sawyer (1981), there are two types of leech crawling styles: inchworm and vermiform, differentiated by the position of the body loop during movement, as exhibited by *H. ghilianii* and other leech species of considerable body size. In *H. picta* inchworm crawling of juveniles is replaced by vermiform crawling once an individual matures. *Haemadipsa subagilis*, although capable of moving in these ways, was observed to prefer vermiform crawling, irrespective of age.

The repertoire of foraging behaviours of other cryptically coloured species of *Haemadipsa* presumably resembles that of *H. subagilis*. Our observations illustrate the behavioural adaptations of both species to their co-occurrence in the uniform environment of the dipterocarp rainforest.

Conclusions and future directions

Haemadipsa picta aggregates along trails in order to increase its probability of finding a host, whereas such phenomenon was not confirmed for *H. subagilis*. Furthermore, ambush locality is size-dependent in *H. picta*, whereas in *H. subagilis*, which prefers ambush in the leaf litter, it appears to be a species-specific trait. Finally, *H. picta* affects the interspecific balance by vertical niche partitioning and very likely influences intraspecific competition by temporal separation of feeding in subadult and adult stages. Further studies are needed to discover habitat preferences of *H. subagilis*. Haemadipsid leeches inhabiting Bornean rainforest evolved different ways of attacking their hosts and, most probably, both species influence the balance between parasite and host populations system, making the coexistence of sympatric species possible. In our opinion, the collection of iDNA (for details see Schnell et al. 2015) from both species and individuals collected from various habitats and plant heights would allow for a more thorough examination of host preferences of leeches and individuals of particular dimensions. They would also deliver very desirable molecular data for a taxonomically challenging group – the brown leech species complex, which has inconsistent spatial dispersion (typically ground-living specimens vs a small fraction of population climbing on plants). Such premise might indicate the coexistence of cryptic species.

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