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Food plant selection by stick insects (Phasmida) in a Bornean rain forest

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Abstract: Stick insects (Phasmida) are important herbivores in tropical ecosystems, but have been poorly investigated in their natural environment. We studied phasmids and their food plants in a tropical lowland rain forest in Borneo (Danum Valley, Sabah, Malaysia). Thirty species of phasmid were collected from 49 plant species during nocturnal surveys in the forest understorey. In most cases (35 plant species), experiments confirmed that these phasmids fed on those plant species from which they were collected. Partitioning of phasmid species among food plant species was highly significant. Two common species had a largely restricted diet: *Asceles margaritatus* occurred mainly on *Mallotus* spp. (Euphorbiaceae) and *Dinophasma ruficornis* on *Leea indica* (Leeaceae). Other phasmids fed on a broad spectrum of plant families and can be considered polyphagous (e.g. *Haaniella echinata*, *Lonchodes hosei herberti*). Feeding experiments were performed on captive phasmids using leaves from eight plant species. *Asceles margaritatus* showed a significantly higher consumption rate for *Mallotus miquelianus* leaves than for other plants, while *H. echinata* showed the opposite trend and the lowest consumption for *M. miquelianus*. However, *A. margaritatus* readily accepted foliage from several plant families, particularly when *Mallotus* was not offered at the same time. Therefore, studies on host specialisation by herbivores need to include their distribution in the natural vegetation.

Key Words: *Asceles margaritatus*, *Haaniella echinata*, herbivory, *Mallotus*, Phasmatodea, Phasmida, specialization, tropical rain forest

INTRODUCTION

Rates of herbivory in tropical forests are high, predominantly caused by insect herbivores (Coley & Barone 1996). Thus, patterns of their food plant specialisation strongly affect our understanding of insect biodiversity, community assemblages and conservation (Novotny *et al.* 2002a, b, 2004) as well as hypotheses about selection for plant defences, plant competition and insect–plant co-evolution (Bernays & Graham 1988, Coley & Barone 1996, Jaenike 1990). Phasmids are an important component of the herbivore fauna in tropical forests. The local density of these insects is often relatively low (Berger 2004), but since they are usually very large, they may contribute a great proportion of the animal biomass on, and damage to, the vegetation. In the crown of a large dipterocarp tree species at the study site, a small number of phasmid individuals (Ellwood *et al.* 2002) contributed an estimated 19% of the animal biomass (Ellwood & Foster 2004). Although phasmids have often been collected for taxonomic work or breeding purposes, they have been poorly studied in their natural environment. Notable exceptions include field studies on the neotropical *Lamponius portoricensis* (Sandlin & Willig 1993, Willig *et al.* 1993) and on some phasmid species in Panama (Berger 2004, Berger & Wirth 2004). In Borneo *c.* 300 species (10% of the global phasmid fauna) have been described (Bragg 2001, Redtenbacher 1906). Besides a short list of occasional food plants recorded by Bragg (2001), information on their feeding habits is restricted to non-native food plants (e.g. bramble, ivy) consumed by captive specimens. The goal of the present study was to survey the food plant range of phasmids in the understorey of a dipterocarp forest for the first time and to compare natural host range with selectivity in feeding experiments.

MATERIALS AND METHODS

Sampling methods and feeding experiments

The study was carried out in a mature lowland evergreen dipterocarp forest in the Danum Valley conservation

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area within a 2 km radius around the field centre (4° 58′N, 117° 48′E, 170 m asl). Mean annual rainfall is 2669 mm, mean temperature 26.7° C (Walsh & Newbery 1999). About 500 tree species have been recorded in two 4-ha plots, dominated by Euphorbiaceae and Dipterocarpaceae, particularly *Parashorea malaanonan* (Marsh & Greer 1992, Newbery *et al*. 1992, 1999).

Phasmids were collected at night (mostly 20h30–22h30) by surveying the entire understorey vegetation along trails in mature forest with a torch light during 11 nights in March 2004 and during a second visit in 12 nights in September and October 2004 (*c*. 200 man-hours). Occasional collections in secondary vegetation or forest margins were included. Presence or absence of leaf damage (irregular semicircular bitemarks along leaf margins, characteristic of orthopteroid herbivory) was recorded. Phasmids were individually collected in plastic bags including some foliage, and later transferred into plastic containers for feeding experiments (typically 30 × 15 × 15 cm, with a large opening in the lid covered by fine gaze). During the first night after capture, each phasmid was offered leaves from the plant from which it was collected in order to check whether this phasmid actually feeds on the observed 'host', since phasmids were rarely observed feeding during the survey when they usually stand in an upright position or flattened against the foliage. Note that this test may underestimate the number of food plants, since phasmids sometimes refrained from feeding during the first few nights after capture even if known food plants were offered (pers. obs.).

The following food choice experiments were carried out only for those phasmids collected in March. Two kinds of feeding experiments were performed on individual phasmids: (1) no-choice tests, where one leaf was offered to each phasmid for two nights (48 h), and (2) dual-choice tests, where leaves from two plants were offered simultaneously for one night (24 h). For no-choice tests, up to eight plant species were used that were either common phasmid hosts in the understorey (*Mallotus floribundus*, *M. miquelianus*, *Brownlowia peltata*, *Spatholobus* spp.), representative of the forest mid-stratum (*Macaranga hypoleuca*) or canopy (three dipterocarp tree species). Due to phasmid mortality and time constraints, most phasmid individuals only experienced a subset of experiments (in variable order); several phasmids died early although care was taken to maintain sufficient moisture and shade. In an attempt to minimize phasmid mortality by starvation, plants that were thought to be more likely consumed were offered first. Completely unfolded leaves were picked from intermediate positions on the twig; very young or old foliage was avoided. Leaves were maintained fresh during the experiment by small plastic vials with water and cotton wool surrounding the petiole. The amount of leaf area consumption was quantified by measuring the leaf area before and after the experiment and calculating biomass consumption. Initially, leaf area was measured by tracing the leaf on paper and weighing the paper cuttings on a microbalance, while for most tests a digital leaf area meter (CID Inc., CI-202) was used. Measurements of leaf area consumption did not differ significantly between methods and were therefore pooled in the analysis (Wilcoxon, $Z = 1.6$, $P = 0.11$, $n = 10$ leaves measured by both methods). Biomass consumption was calculated using mean specific dry weight data (mg cm^{-2}) for each plant species (leaf discs from ≥10 leaves per species, old and new leaves in same proportion, oven-dried at 60 ° C for over 2 d). In order to account for individual variation in the total consumption, pairwise comparisons in choice tests and no-choice tests were based on the proportions of each leaf consumed of the total biomass consumed from both leaves; these data were arcsine-square-root transformed. Multiple comparisons in no-choice tests were corrected for false discovery rate (Benjamini & Hochberg 1995).

For analysis of the distribution of phasmids on host plant species in the forest, only those cases were considered where feeding on the host was confirmed during the feeding experiment (cf. Novotny *et al.* 2002a). We analysed whether the phasmid × plant species associations were significantly more organized (compartmentalized) than random, indicating that phasmids differ in their host plant preferences. For the observed species association matrix a test statistic was obtained as

$$T_{\mathrm{obs}} = \sum (a_{rc} \cdot \log a_{rc})$$

where cell entries a_{rc} represent the number of cases a phasmid species r was found on a plant species c. T_{obs} was compared with the distribution of the T statistic from 10^5 randomly generated matrices (T_{ran}) using fixed row and column totals (Blüthgen *et al*. 2000; program available on http://itb.biologie.hu-berlin.de/∼nils/stat/). In order to avoid pseudoreplications of phasmid × plant interactions on the same or closely neighbouring plant individuals, only those replicates that were > 10 m apart from each other were considered in the analysis.

RESULTS

A total of 222 phasmids were collected, comprising at least 30 species and morphospecies that could be distinguished but not identified because of unresolved taxonomy (subfamily Necrosciinae) and/or immature stages. For 18 species collected in March, data from feeding experiments are summarized in Table 1. In most cases (62%), characteristic bitemarks were noted on the same leaf on which phasmids were encountered. For

Table 1. Phasmids collected in the forest around Danum Valley Field Centre, Sabah, Borneo in March 2004. Sex: f = female, m = male, j = juveniles. n = Number of individuals collected, Q = number of plant species accepted in at least one test : plant species rejected in all tests. Mean consumption (mg) in no-choice feeding tests shown for eight plant species.[1] Plants with shared superscript letters (A–C) are not significantly different in a paired t-test.[2] ° = rejected by at least half of the phasmids in no-choice tests, 0 = rejected in all no-choice tests,” = consumption (mg) in dual-choice tests shown for plants that were not offered in no-choice tests, – = not offered.

Subfamily/Species	Sex	n	*Mm*	*Mf*	*Mh*	*Bp*	*Sp*	*Pm*	*Hn*	*Dl*	Q
Aschiphasmatinae											
Dinophasma ruficornis (Redtenbacher)	f	2	0	0	–	–	0	0	–	0	2:5
Heteropteryginae											
Haaniella echinata (Redtenbacher)	j	31	61.3^{B}	81.3	162.7^{AB}	121.4^{A}	91.4	113.2^{AB}	98.5^{AB}	172.6^{A}	23:2
Lonchodinae											
Lonchodes hosei herberti Bragg	mfj	9	22.0	28.2	7.3	21.0	0	33.9	17.5	28.1	14:3
Lonchodes imitator (Brunner)	f	1	–	–	–	–	–	31.4	–	0	2:1
Lonchodes malleti Bragg	f	1	25.0	–	–	–	92.7	–	–	–	3:0
Lonchodes modestus (Brunner)	m	2	0	–	–	0	–	0	–	0	0:7
Lonchodes thami Bragg	m	1	0	–	9.3	–	27.0	0	0	0	3:4
Prisomera tuberculata (Kirby)		1	0	–	8.2”	–	–	0	13.8	12.3”	3:3
Necrosciinae											
Acacus sarawacus (Westwood)	mfj	7	0	–	0	–	0	0	–	0	1:10
Asceles margaritatus Redtenbacher	mfj	32	58.9^{A}	30.1^{AB}	19.8	21.3	$2.8^{\circ C}$	15.5^{B}	23.0^{B}	34.3^{B}	12:2
Asceles aff. *inquinatus*	mf	3	8.3"	2.4°	0	–	–	2.0°	–	0	3:4
Centrophasma longipennis (Günther)	mf	3	0	–	0	0	–	32.8°	–	0	3:6
Diardia diardi (de Haan)	mf	3	–	–	–	–	–	–	–	–	0:3
Necroscia prasina (Burmeister)	f	2	0”	0”	0”	–	–	–	–	0”	0:5
Marmessoidea rubescens (Saussure)		1	–	0	–	–	–	–	7.2	0”	2:2
Necrosciinae sp.1		1	–	–	0	–	–	6.7	–	120.4	3:1
Necrosciinae sp.2		1	–	0	0	–	–	2.1	–	13.6	2:3
Phasmatinae											
Prosentoria cf. *arrogans* Brunner	m	1	–	–	–	–	0	–	–	–	0:1

[1] Dipterocarpaceae: *Dl = Dryobalanops lanceolata, Hn = Hopea nervosa* King, *Pm = Parashorea malaanonan*; Euphorbiaceae: *Mh = Macaranga hypoleuca, Mf = Mallotus floribundus, Mm = M. miquelianus*; Fabaceae: *Sp = Spatholobus* spp.; Tiliaceae: *Bp = Brownlowia peltata.*

[2] Based on transformed proportional biomass consumption, corrected for false discovery rate; restricted to plants that were offered to ≥ 10 conspecific phasmids.

most phasmids (62% of n = 187 individuals), host plant feeding was confirmed experimentally. These experiments were relatively consistent: for plants with at least one positive feeding test, other tests with the same phasmid species were also positive in many cases (70% of n = 83). Confirmed host plants (total 35 species) and unconfirmed hosts with bitemarks (ten additional species) are shown in Appendix 1. Euphorbs were the most common hosts (48% of the confirmed cases), particularly *Mallotus floribundus* and *M. miquelianus*, two common understorey shrubs. Partitioning of phasmid species among confirmed host species was highly significant (R × C randomization test on spatially independent replicates, see Appendix 1; $T_{obs} = 205$, mean ± SD: $T_{ran} = 133 \pm 6.0$, $P < 0.0001$). Two phasmid species were relatively specialized: most *Asceles margaritatus* were found on *Mallotus* species, and most *Dinophasma ruficornis* occurred on *Leea indica*. When these two species were excluded from the analysis, the remaining phasmids showed a weaker, but significant non-random partitioning ($T_{obs} = 36.0$, mean ± SD: $T_{ran} = 25.9 \pm 3.4$, $P = 0.002$).

Phasmids also show highly variable consumption rates across eight plant species offered in feeding trials (Table 1). The three most common phasmid species usually accepted a wide spectrum of food plants and rejected only few species (see column ’Q’ in Table 1), e.g. *Spatholobus* was consistently rejected by *Lonchodes hosei*. In contrast, four phasmid species did not feed on any plant species during the tests. Note that the selected plants only included species on which phasmids were actually found or other species from the same families rather than a representative sample of the vegetation. For two phasmid species, *Asceles margaritatus* and *Haaniella echinata*, the number of individuals was sufficient for statistical comparisons of no-choice tests (Table 1). *Asceles margaritatus* showed significantly higher consumption of the euphorb *Mallotus miquelianus* than for three dipterocarp species and *Spatholobus*, while there was no significant discrimination between the two *Mallotus* species. *Haaniella echinata* showed a more even consumption across different plants, where *M. miquelianus* was among the least preferred plants. In dual-choice tests (Figure 1), *H. echinata* significantly preferred two dipterocarp species over *M. miquelianus*, while *A. margaritatus* showed the opposite trend (significant in the case of *Dryobalanops lanceolata*). *Asceles margaritatus* also significantly preferred *M. hypoleuca* over *D. lanceolata*, and both phasmid species significantly preferred *D. lanceolata*

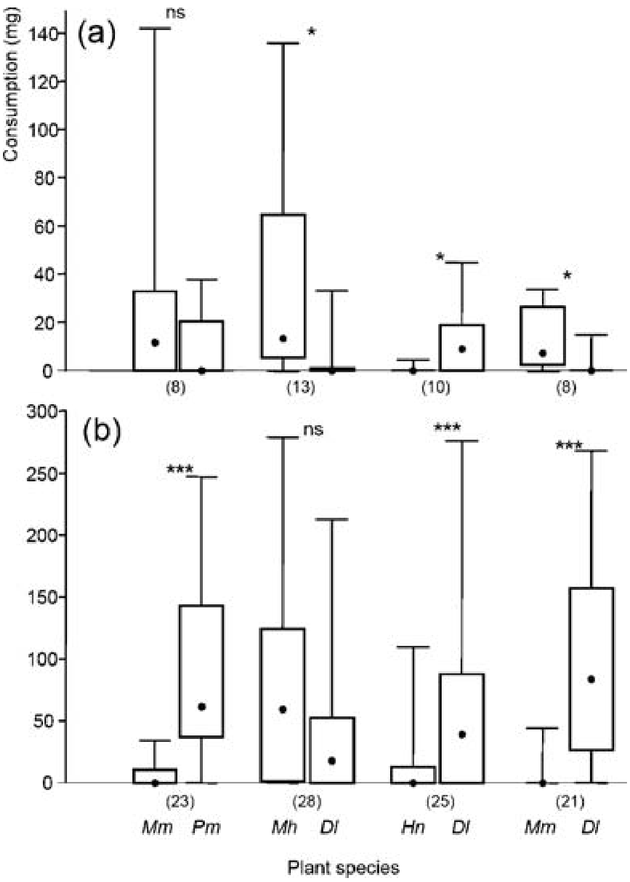

Figure 1. Plant preferences of the two most common phasmids, (a) *Asceles margaritatus* and (b) *Haaniella echinata*. Boxplots show consumption in dual-choice tests (median, quartiles, range), number of phasmid replicates in parentheses. Significance levels shown for paired *t*-tests on transformed proportions (ns: not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). For plant species abbreviations, see Table 1.

over *Hopea nervosa* (both Dipterocarpaceae), thus they discriminated between and within plant families.

DISCUSSION

Phasmids in the forest understorey are highly variable in their feeding preferences among rain forest plants. The most common species, *Asceles margaritatus*, was almost restricted to *Mallotus* hosts (Euphorbiaceae) in the examined forest and may be regarded as relatively specialized, although occasionally found on other plants and accepting a variety of plants in captivity. The same species also feeds regularly on a closely related plant genus, *Macaranga* (Euphorbiaceae), in other parts of Borneo (Bragg 2001, pers. obs.). Other *Asceles* species in Singapore and West Malaysia also typically feed on *Macaranga* (Seow-Choen 2000, Seow-Choen *et al.* 1994, Tay & Seow-Choen 1996). Another specialist is *Dinophasma ruficornis* that was most commonly found on *Leea* (Leeaceae) in our study. Congeneric species and related genera of the subfamily Aschiphasmatinae have been reported to be largely specialized on some Melastomataceae and *Leea indica* elsewhere (Bragg 2001, Seow-Choen 2000, Seow-Choen *et al.* 1994, Tay & Seow-Choen 1996). Perhaps not surprisingly, host plants of both specialized phasmids are highly common in the forest understorey at the study site (*Mallotus, Leea*) or adjacent secondary vegetation (*Macaranga*, some Melastomataceae) (pers. obs.).

In contrast, the common *Haaniella echinata* and *Lonchodes hosei* showed a more even distribution among host plant species from different families in the forest and can be considered highly polyphagous. This corresponds to the broad range of food plants recorded for other Heteropteryginae or *Lonchodes* species in West Malaysia (Tay & Seow-Choen 1996). Both species showed a greater feeding response for certain plants other than *Mallotus*. The three dipterocarp species offered in feeding experiments were often consumed as much or even more than euphorbs or other understorey plants, suggesting that phasmid herbivory on dipterocarp seedlings and saplings (or canopy trees, see Ellwood & Foster 2004) may be important. Among the phasmids that were collected once or only a few times, some species were similarly opportunistic in their food plant choices, while others may be regarded as more specialized – they rejected most or all plants offered including the ’hosts’ on which they were encountered. However, the low sample size in such species prevents any further statistical inference of specialization.

These results demonstrate that feeding experiments alone may not provide sufficient evidence for the degree of host specialization, and their distribution in the natural vegetation has to be taken into account. For instance, *Asceles margaritatus* was rarely found on different plants in the forest other than *Mallotus*, but readily accepted several plants from a variety of plant families in captivity, particularly when *Mallotus* leaves were not provided at the same time. *Asceles margaritatus* did show the greatest consumption for *Mallotus* leaves in experimental situations, but the effect was not always significant. A stronger discrimination between plants may have been obscured by unsuitable leaf stages chosen for the test: specialized phasmids strongly preferred young foliage of their respective host plant species over older foliage (unpublished data), while leaves of intermediate age were selected for this study. The ultimate reason for the selectivity (narrow realized niche) among a large spectrum of acceptable plants (broader fundamental niche) remains unknown. Phasmid performance, survival or reproductive success may be higher on those food plants selected in the wild, but the explanation awaits further investigations.

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Appendix 1. Host plants of phasmids collected between March and November 2004. Numbers following phasmid species abbreviations give spatially independent interactions (> 10 m apart) for all experimentally confirmed host plants (total number in parentheses if deviating from the former). Each '+' indicates one interaction where phasmids were captured on a plant showing characteristic bitemarks on the same leaf, but host consumption was not confirmed experimentally. Phasmid species: *Ai* = *Asceles* aff. *inquinatus, Am* = *Asceles margaritatus, As* = *Acacus sarawacus, Cl* = *Centrophasma longipennis, Di* = *Diardia diardi,, Dr* = *Dinophasma ruficornis, He* = *Haaniella echinata, Lh* = *Lonchodes hosei herberti, Li* = *L. imitator, Lma* = *L. malleti, Lmo* = *L. modestus, Lt* = *L. thami, Mr* = *Marmessoidea rubescens,* N = Necrosciinae (7 spp.), *Pa* = *Prosentoria* cf. *arrogans,* unid. = unidentified juveniles.

Actinidiaceae: *Saurauia ferox* Korth. – *He* 2, N 1

Annonaceae: *Fissistigma* sp. – *He* 1; *Goniothalamus* sp. – *Cl* 1; *Polyalthia insignis* (Hook. f.) Airy Shaw – *Am* +; *Popowia pisocarpa* Endl. – *He* 2, *Lh* 1, *Cl* 1

Cecropiaceae: *Poikilospermum* sp. – *Li* 1

Combretaceae: unidentified liana – *He* 3

Costaceae: *Costus* sp. – *He* 1

Dilleniaceae: *Tetracera indica* Merr. – *Dr* 1, *Am* +

Dipterocarpaceae: *Dryobalanops lanceolata* Burck – *He* 1; *Parashorea malaanonan* Merr. – *Lh* +, unid. +; *Parashorea tomentella* (Symington) Meijer – *As* +

Ebenaceae: *Diospyros* sp. – *He* +, *Lh* 1, *Am* 1

Euphorbiaceae: *Baccaurea stipulata* J. J. Sm. – *Lh* +; *Glochidion* sp. – *He* 2 (3); *Mallotus floribundus* Müll. Arg. – *He* 2, *Am* 22 (33), unid. 2; *Mallotus miquelianus* (Scheff.) Boerl. – *Am* 12 (15), unid. +; *Mallotus* sp. – *He* +, *Am* 2; *Mallotus wrayi* King ex Hook. f. – *He* 1, *Lh* 1 (2), *Am* 1, N 1

Fabaceae (= Leguminosae): *Bauhinia* sp. – *He* 1; *Spatholobus* spp. – *He* 4, *Pa* +; *Fordia* sp. – *He* 1

Flacourtiaceae: *Ryparosa hullettii* King – *He* 1, *Ai* ++

Lauraceae: unidentified trees – *Mr* 1

Leeaceae: *Leea* cf. *indica* Merr. – *Dr* 3 (5), *He* 3 (5), *Am* +, unid. +

Magnoliaceae: *Magnolia candollii* Link – unid. 1

Melastomataceae: *Clidemia hirta* D. Don. – N +

Meliaceae: *Aglaia* spp. – *He* 1, *As* 1, *Am* 3, N 1; *Chisocheton* sp. – *He* 1

Myrsinaceae: *Ardisia* sp. – *Lh* 1

Myristicaceae: *Knema* sp. – *He* +

Oleaceae: *Chionanthus pluriflorus* (Knobl.) R. Kiew – *Lh* 1

Passifloraceae: unidentified liana – *Lh* 1

Rubiaceae: *Uncaria* sp – *Lh* 1; *Urophyllum* sp. – *He* 2, *Lt* 1, unid. 1; unidentified lianas – *Lh* 1, unid. 1+

Sapindaceae: *Guioa pterorhachis* van Welzen – N +; *Paranephelium xestophyllum* Miq. – *Lh* 1

Selaginellaceae: *Selaginella* sp. – *He* 1

Sterculiaceae: *Pterospermum* sp. – *He* 2

Tiliaceae: *Brownlowia peltata* Benth. – *He* 3, *Lmo* +, *Am* 1

Verbenaceae: *Callicarpa longifolia* Lam. – *Li* 2

Vitaceae: *Tetrastigma* sp. – *He* 2, *Dd* +

Zingiberaceae: *Globba pendula* Roxb. – *He* 1; *Zingiber flagelliforme* J. Mood & I. Theilade – *Lma* 1