FEEDING PREFERENCES OF PHASMIDS (INSECTA: PHASMIDA) IN A BORNEAN DIPTEROCARP FOREST

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ABSTRACT. – Stick and leaf insects (Phasmida) representing 19 species (53 individuals) were collected in a lowland dipterocarp forest (Lambir Hills, Sarawak, Malaysia). Dual-choice tests were conducted to examine whether phasmids discriminate between young and old leaves of seven plant species. A second set of tests examined the preferences of phasmids for leaves from *Dryobalanops lanceolata* (Dipterocarpaceae) saplings versus leaves from the upper canopy of the same tree species. *Haaniella echinata* and other flightless species (Heteropterygidae and Lonchodinae) fed on nearly all plant species offered and showed significant preferences for old leaves in three plant species. In contrast, flying phasmids (Ashiphasmatinae and Necrosciinae) rejected leaves from most plants and did not show consistent leaf age choices. *H. echinata* and flightless phasmids preferred canopy leaves from *D. lanceolata* over leaves from saplings, regardless of leaf age. Our results are consistent with the hypothesis that young leaves of some plant species are better defended against generalist herbivores than old leaves and that saplings are better defended than adult trees. Since upper canopy leaves were highly palatable to understorey phasmids, factors other than chemical defences must contribute to the low abundance of phasmids in forest canopies.

KEY WORDS. – *Dryobalanops lanceolata*, forest canopy, *Haaniella echinata*, herbivory, leaf age, lowland rainforest.

INTRODUCTION

In virtually all ecosystems, herbivorous insects constitute a large proportion of the animal species and consume foliage, plant sap, or other plant parts from nearly the entire flora. The diversity of insect herbivores is highest in tropical rainforests (Novotny et al., 2004). Woody plants in tropical forests are more damaged by herbivores than those from temperate forests (Coley & Barone, 1996), but this increased damage is not necessarily accompanied by a higher density of herbivore individuals (Novotny et al., 2006). Comparative surveys on food plant selection of tropical herbivore communities have begun to unravel their actual host plant ranges and preferences (Basset, 1996; Barone, 1998; Basset, 1999; Novotny & Basset,

2005; Novotny et al., 2006). While many beetles and butterfly caterpillars are plant genus specialists, orthopteroids are often polyphagous (Novotny et al., 2002). However, for most species the natural host range is unknown. Few studies have compared the host plant selection of rainforest orthopteroid communities (e.g. grasshoppers, Rowell, 1978), including Phasmida (Tay & Seow-Choen, 1996; Novotny et al., 2002; Blüthgen et al., 2006). Phasmids and other orthopteroids such as katydids are usually less numerous than several other tropical insect taxa, particularly in comparison to the large holometabolous orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera). In canopy samples from Southeast Asian rainforests, orthopteroids typically contributed less than 3% of the arthropod individuals (Stork, 1987; Stork & Brendell,

1990; Floren & Linsenmair, 1997). Orthopteroids may be more abundant in lower forest strata, e.g. they contributed to 8.8% of the individual herbivores collected in New Guinea (Novotny et al., 2006). However, some species may represent an important part of the biomass of tropical insect herbivores due to their comparatively large body size (Bragg, 2001), which may lead to relatively high estimates of their biomass proportion of a canopy assemblage (Ellwood & Foster, 2004). Consequently, orthopteroids may significantly contribute to total herbivory in forest ecosystems.

The chiefly nocturnal feeding habit of phasmids may be one of the reasons why so few ecological investigations have been performed on this group so far. For most species, only one or few individuals can be found, and in our study only *Haaniella echinata* was sufficiently abundant to conduct statistical analyses at the species level. All other species were classified into two groups: phasmids that had functional wings and those that were unable to fly. This distinction was made based on the rule of thumb that phasmids with fully developed wings are more specialised, while flightless species are more generalised feeders (Bragg, 2001). Fully winged phasmids commonly deposit eggs on their specific host plants, while flightless species often scatter them on the forest floor, corresponding to the putative difference in host selectivity (Bragg, 2001). In tropical trees and shrubs, young leaves are particularly vulnerable to herbivore attack, partly because they cannot escape herbivores seasonally unlike many of their temperate counterparts that develop during early spring (Coley & Barone, 1996; Eichhorn et al., 2006). The herbivore density on rainforest trees is positively correlated with the temporal availability of young leaves (Basset, 1991; Basset, 1996). Young leaves generally contain more available nutrients, are usually softer, and have a higher water content (Slansky & Scriber, 1985; Coley & Aide, 1991).

Tree saplings or small understorey plants may have a lower tolerance for leaf losses and therefore should be less palatable than canopy trees. Censuses of herbivore damage have shown that exposed leaves in tree canopies were less frequently eaten than shade leaves and those from understorey plants (Lowman, 1985; Coley & Barone, 1996). Several factors may be associated with this stratification pattern, including microclimate variability, predation risks, and different levels of chemical defence (Lowman & Box, 1983; Lowman, 1985; Coley & Barone, 1996). Censuses of leaf damage alone are thus insufficient to unravel the underlying causes of different exposure to herbivores. In order to test whether leaves from saplings are better defended and less palatable than canopy leaves, and young leaves better defended than mature ones, actual feeding choices of herbivores need to be examined. However, at present only few experimental studies from tropical forests investigated such ontogenetic changes in leaf palatability to herbivores (e.g. Barone, 1998; Blüthgen & Metzner, 2007). Our study focuses on phasmids collected from a Bornean rainforest and their feeding choices among young and old leaves from seven common forest tree species. We included two Dipterocarpaceae species in our experiments, which usually dominate the upper canopy

and appear numerous as saplings on the floor of Southeast Asian rainforests. For one of the dipterocarps, *Dryobalanops lanceolata*, we compared the palatability of young and old leaves from saplings versus leaves from the crown of an emergent tree.

METHODS

The study was carried out in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20'N 113°50'E, 150–250 m a.s.l.). Lambir Hills receives an annual rainfall of 2,100 to 3,000 mm with a dryer period from January to March in some years (Sakai et al., 1999). With a total of 1,179 tree species recorded in a 52 ha (0.52 km^2) plot, this forest is one of the most diverse in the world (Condit et al., 2005). Phasmids were collected in March 2006 during 14 nights by inspecting understorey vegetation with electric torches along trails near the field station, including primary forest and forest edges. Phasmids were also searched for in the upper tree canopy, which was accessed with a canopy crane (2 days) and a canopy walkway (2 nights). From the crane, foliage of several tree crowns was beaten and falling insects caught in an upturned umbrella. Phasmids were individually kept in plastic containers ($25 \times 25 \times 10$ cm) with a large gauze window. These feeding chambers were placed in shade and moistened twice a day by spraying with water. Dual-choice tests were performed to compare each phasmid's preference for young or old leaves from one individual of seven tree species, which were selected because of their high abundance or their accessibility within the canopy (see Table 1 for a species list). Additional choice-tests were conducted on *Dryobalanops lanceolata*, comparing the consumption of leaves from two saplings (ca. 3 m tall) versus leaves of one old growth canopy tree (ca. 70 m tall) of the same species, which was the only conspecific tree accessible from the canopy walkway. Light green, apical leaves were regarded as young; older leaves were darker and grew near the base of the twigs. Very young, whitish and very old leaves with epiphylls were avoided. Leaf discs (4 cm in diameter) were punched from freshly harvested leaves. Depending on the size and previous consumption of the phasmid, 1–5 disc pairs were provided for each phasmid. For large *D. lanceolata* trees, leaves were too small for punching discs; hence entire leaves were used instead. A choice test with *Haaniella echinata* showed that they did not discriminate between entire margins and punched margins from the same leaf from a *D. lanceolata* sapling (Wilcoxon signed rank test, $p = 1.0$, $n = 10$ individuals). Equal amounts of leaf material from each treatment were offered to the phasmids. Leaves and discs were provided in an upright position in wet foam blocks to maintain their moisture during the trial. Each feeding trial was performed for 24 hours. After each trial, remaining leaf discs were scanned digitally and the resulting area was subtracted from the mean area of ten intact leaf disks to estimate the standard area of intact discs. Whole leaves of *D. lanceolata* were traced on paper prior to the test and scanned afterwards. Dry mass consumption was calculated using specific dry weight (mg cm^{-2}) for which one disc per leaf age and species was

oven-dried at 60°C for at least 2 days. Individuals that did not feed at all in an experiment were not considered in the statistical analysis of a choice test.

Consumed dry mass of young leaves was subtracted from consumed dry mass of old leaves to compute a leaf-age preference index, *d*. Prior to ANOVA, values of *d* were transformed in the following way to meet the conditions of normality and variance homogeneity: $d' = s - \sqrt{\log(|d| + 1)}$ where *s* maintains the original sign of *d*, thus $s = +1$ if $d \geq 0$ and $s = -1$ if $d < 0$. In the case of *D. lanceolata*, a two-way ANOVA was performed with stratum (canopy and understorey sapling) and phasmid groups (*H. echinata*, flightless and flying phasmids) as factors. The intercepts of the ANOVA indicate whether differences in consumption of young and old leaves (*d'*) differed from 0 for *H. echinata*, i.e. whether they preferred young or old leaves, respectively. Some species, especially the fully winged ones, suffered high mortality and sometimes died within a few days, and many phasmids were collected during the course of experiments. Therefore, comparisons of feeding patterns did not include all individuals and possible combinations of phasmid and plant species. However, most phasmids were included in several subsequent feeding trials with different plant species, but not exposed to replications of the same treatment. Leaves used in the feeding trials were usually collected from a single plant individual of each species) except for *D. lanceolata* (two saplings) and *Mallotus wrayi* (Euphorbiaceae) (five saplings) which were pooled for statistical analysis. No significant differences were found in leaf age choices across the five *M. wrayi* individuals (Kruskal-Wallis for each of the three phasmid groups, all $p \geq 0.19$).

RESULTS

Fifty-three individual phasmids from 19 species (five subfamilies) were found; most species were represented by a single individual (Table 1). Most individuals (49) were found in the understorey. Despite intensive searching in tree crowns, only three individuals (three species of Necrosciinae) were found in the canopy by beating foliage from the canopy crane; none were found during diurnal or nocturnal surveys on the canopy walkway. Furthermore, semicircular bite marks (typically for phasmids) were relatively common on plants in the understorey, but scarcely observed along the canopy walkway and on top of the two emergent dipterocarps *Dryobalanops lanceolata* and *Shorea smithiana*.

Haaniella echinata and some other flightless species fed on all plant species offered during feeding trials. *H. echinata* significantly preferred old leaves over young leaves in the canopy tree *Pseuduvaria nervosa*, the understory tree *Mallotus wrayi* and *D. lanceolata* saplings (Figs. 1, 2; Table 2). Preferences of the other flightless phasmids (individuals from several species pooled) were similar and significant for *P. nervosa* and *D. lanceolata*, but not for *M. wrayi* (Figs. 1, 2). For the remaining four plant species (three canopy trees and one myrmecophyte, *Macaranga beccariana*), no significant leaf age preferences were found (Table 1). Flying species (see Table 1) rejected some of the eight plant species tested or consumed much less leaf tissue (mean ± SE = 4.5 mg ± 1.7) than the flightless phasmids (28.2 mg ± 6.4; Table 1). For example, the winged phasmid *Orthomeria alexis* fed on *M. beccariana* on which the specimen was collected and on the closely related *Mallotus wrayi* (both Euphorbiaceae), but rejected leaves from both dipterocarps (Table 1). Winged phasmids did not discriminate consistently between young and old leaves (Fig. 1), except for *D. lanceolata* saplings.

Canopy leaves of *D. lanceolata* were generally preferred over leaves from saplings. This was true for any combination of young and old leaves and for *H. echinata* as well as the other flightless phasmids. Canopy preferences were significant in all cases (Fig. 2; Table 2). Phasmids from all groups did not differentiate significantly between young and old leaves from the canopy, in contrast to their preference for old leaves from saplings (Fig. 2; Table 2).

DISCUSSION

Phasmids differ substantially in their host plant specificity, ranging from highly specialised to broad generalists (Tay & Seow-Choen, 1996; Bragg, 2001; Blüthgen et al., 2006). Correspondingly, individual phasmids accepted the selected plant species to a different degree in our study. As expected (Bragg, 2001), their acceptance was largely predicted by their ability to fly: most fully winged species (which include all Ashiphasmatinae and most Necrosciinae) rejected most or all plants offered, while flightless species (all Heteropterygidae, all Lonchodinae and some Necrosciinae) usually consumed most plants. Few species deviated from this general pattern. Winged and wingless taxa occur convergently in several lineages within the order Phasmatodea (Whiting et al., 2003). For specialised herbivores, full-sized wings may be important to reach dispersed host plants and effectively distribute their offspring, while generalists often encounter potential hosts in close proximity. This suggests a coupling of two traits – host specialization and wings – in the evolution of phasmids.

The common generalist *Haaniella echinata* showed significant preferences for old leaves in three tree species (*Pseuduvaria nervosa*, *Mallotus wrayii* and saplings of *Dryobalanops lanceolata*). The other flightless species showed the same preference (albeit not significant in freeding trials with *M. wrayii*). This suggests that young leaves in these plant species are less palatable to generalist herbivores than old leaves which may correspond with higher levels of secondary metabolites in young leaves – a pattern found in numerous tropical plant species (Coley & Aide, 1991; Turner, 1995; Coley & Barone, 1996). Leaf age choices of four phasmid species from another Bornean rainforest correspond to these findings: two specialised, winged species were found to prefer young foliage of their host plants, while two generalists (including *H. echinata*) preferred old leaves of two *Mallotus* species that represent the common hosts of one of the specialists (Blüthgen & Metzner, 2007). These choices were consistent with results from experiments using leaf extracts

from young leaves applied to discs from old leaves and *vice versa,* suggesting that variation in leaf chemistry is crucial in the discrimination of leaf age by phasmids (Blüthgen & Metzner, 2007).

Haaniella echinata and the other generalist phasmids also showed a significant preference for exposed leaves from the crown of the emergent *D. lanceolata* over leaves from the saplings of this species. This was true for any combination of young and old leaves from the canopy versus saplings, hence even young canopy leaves were more palatable than old leaves from saplings. No difference was found between young and old canopy leaves of *D. lanceolata*. In three of the four remaining canopy tree species studied, phasmids did not discriminate leaves of different ages either. Like *D. lanceolata* saplings, young leaves of another understorey
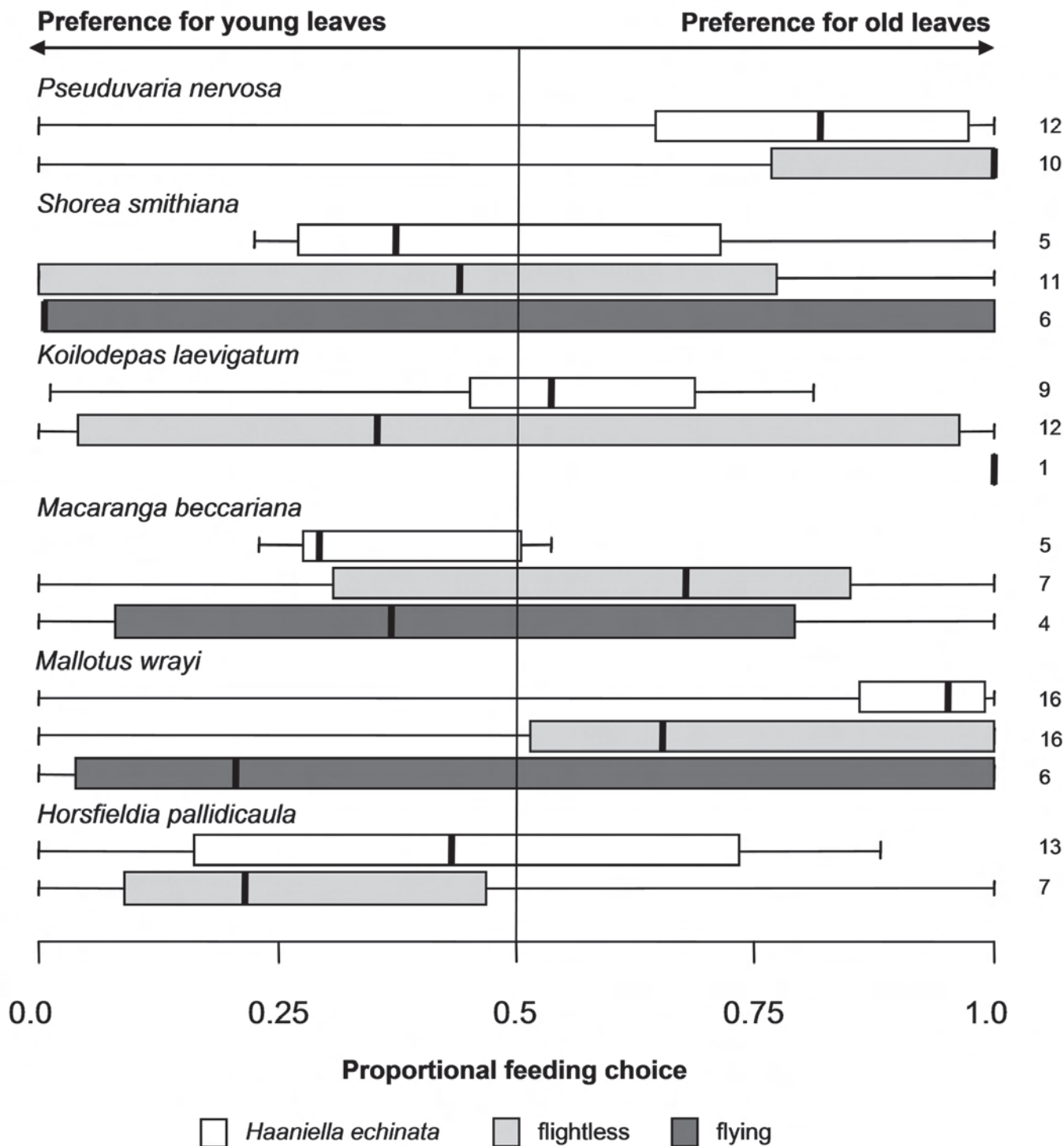

Fig. 1. Dietary preferences of *Haaniella echinata*, other flightless species (pooled) and flying phasmid species (pooled) for different leaf age of six species of trees. Boxplots show the proportion of dry mass consumed from old leaves in relation to total consumption (consumption of old leaves / consumption both young and old leaves) in dual-choice tests (median, quantile, range). Values above 0.5 indicate preference for old leaves. The number of phasmid individuals is provided to the right of each bar.

Table 1. Phasmids collected in Lambir Hills. Plant stratum and phasmid origin are given as: c = canopy, u = understorey. Phasmid sex is given as f = female, m = male and j =juveniles. Flight: ✓ = fully winged species, × = flightless species. n = number of individuals collected. Values show mean consumption of leaves [mg dry weight] across seven plant species (leaf ages and strata pooled) [1,2]. – = trial not attempted.

Family or subfamily / species	Origin	Sex	Flight	n	Pn	Dl	Ss	Kl	Mb	Mw	Hp
Aschiphasmatinae											
Eurybistus fallax Bragg	u	m	✓	1	0.00	0.00	–	0.00	–	0.00	0.00
Kerabistus klantei Bragg	u	fm	✓	2	0.00	0.00	–	0.00	0.00	0.00	–
Orthomeria alexis (Westwood)	u	fm	✓	4	–	0.00	0.00	–	6.83	1.95	–
Heteropterygidae											
Dares validispinus Stål	u	fm	×	4	13.26	19.59	25.93	1.20	3.01	6.81	1.40
Haaniella echinata (Redtenbacher)	u	fmj	×	17	71.91	139.27	122.86	109.50	111.67	16.44	43.33
Hoploclonia cuspidata Redtenbacher	u	f	×	1	0.00	43.39	–	–	–	0.00	0.00
Lonchodinae											
Lonchodes hosei hosei (Kirby)	u	fmj	×	6	2.55	15.72	22.42	7.38	4.29	0.88	121.68
Lonchodes jejunus (Brunner)	u	fmj	×	6	17.39	10.51	0.00	4.32	7.42	3.08	0.00
Lonchodes sp.	u	j	×	1	2.01	9.89	–	0.00	–	1.38	0.00
Necrosciinae											
Acacus vulgaris [new species]	u	f	×	1	47.70	24.81	144.91	4.12	11.41	1.10	44.44
Asceles moricula (Redtenbacher)	u	f	✓	1	–	27.87	0.00	0.35	11.41	8.07	–
Necrosciinae sp. 1	c	j	✓	1	0.00	16.96	26.57	0.00	0.00	0.00	–
Necrosciinae sp. 2	c	j	✓	1	–	15.40	71.69	0.00	0.00	0.00	–
Necrosciinae sp. 3	c	j	✓	1	0.00	11.19	4.36	0.00	0.00	0.00	–
Necrosciinae sp. 4	u	m	✓	1	0.00	0.11	–	0.00	–	0.00	0.00
Necroscia sp.	u	f	✓	1	–	4.71	7.25	–	–	–	–
Orthonecroscia deflorata (Redtenbacher)	u	fm	✓	2	0.00	0.00	–	0.00	0.00	1.45	–
Paraloxopsis korystes Günther	u	j	✓	1	–	–	–	–	–	–	–
Phyllidae											
Phyllium siccifolium (Linnaeus)	c	j	(✓×)[3]	1	–	0.00	–	0.00	0.00	0.87	–

[1] Annonaceae: Pn = Pseuduvaria nervosa J.Sincl. (c); Dipterocarpaceae: Dl =Dryobalanops lanceolata Burck (cu), Ss = Shorea smithiana Symington (c); Euphorbiaceae: Kl = Koilodepas laevigatum Airy Shaw (c), Mb = Macaranga beccariana Merrill (u), Mw = Mallotus wrayi King ex Hook.f. (u); Myristicaceae: Hp = Horsfieldia pallidicaula W.J.de Wilde (c).

[2] Comparisons of consumption across plant species should be interpreted with caution, since different plants were used in subsequent trials, not simultaneously. Some plants were not offered to all individual phasmids.

[3] Males winged, but females flightless (species not included in analysis)

plant *Mallotus wrayi*, were significantly less consumed by *H. echinata* than old ones, which was not the case in the ant-defended *Macaranga beccariana*.

This pattern suggests that *D. lanceolata* saplings are better defended chemically or mechanically against generalist herbivores than adult trees, although only one individual canopy tree of this species could be included in the study. For saplings, leaf protection may be more crucial than for canopy trees. Canopy leaves are more numerous, and large trees may better tolerate loss of leaf tissue to herbivores. At least for this common dipterocarp tree, the high palatability of canopy leaves highlights the need for an alternative explanation as to why phasmids and other herbivores are uncommon in the
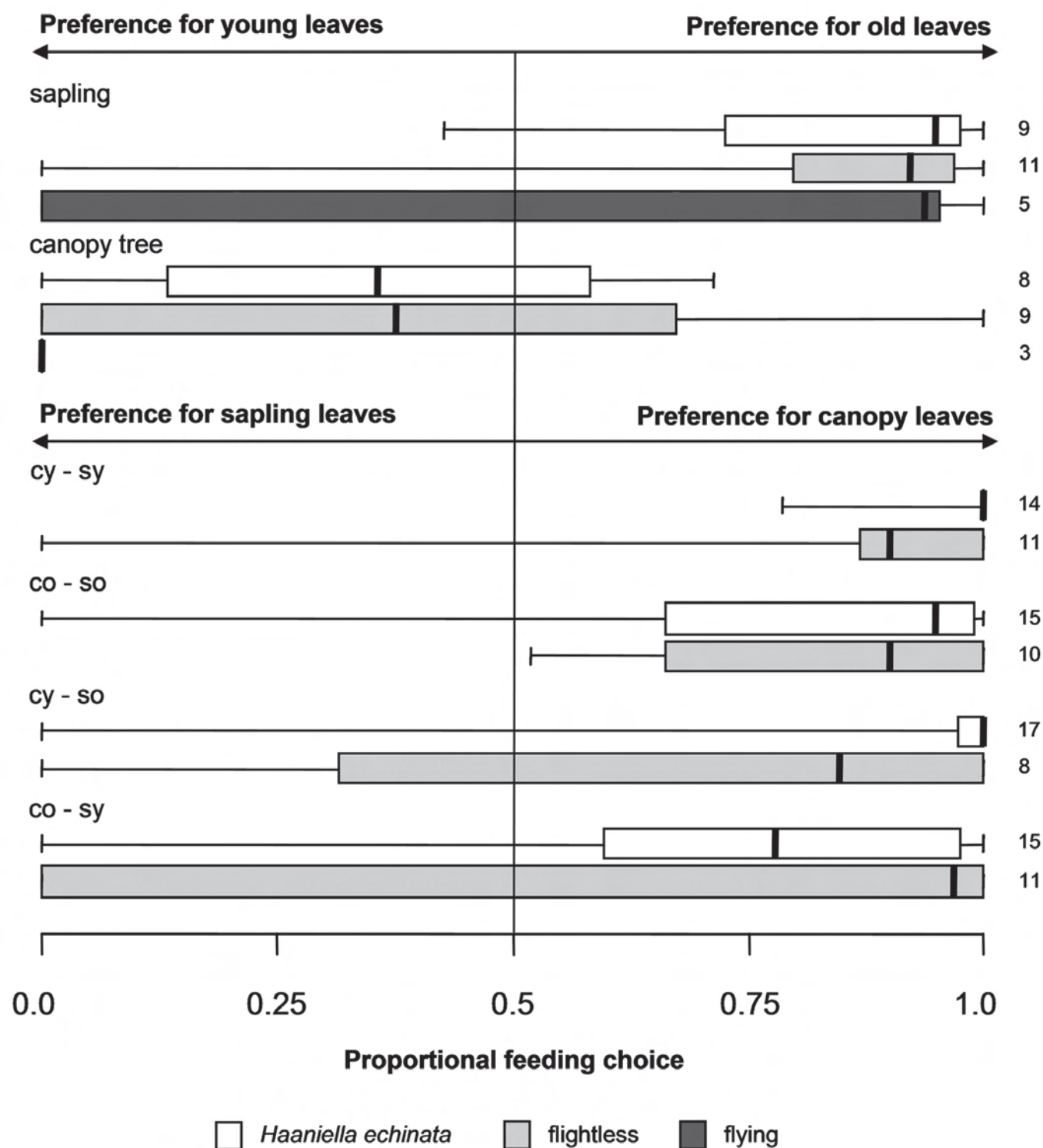

Fig. 2. Leaf age preferences between saplings and an old growth canopy tree of the dipterocarp *Dryobalanops lanceolata* (c = canopy, s =sapling, y = young, o = old). Proportions of consumption of old leaves and canopy leaves were calculated in relation to total consumption. Values above 0.5 indicate preference for old or canopy leaves, respectively. The number of phasmid individuals is provided to the right of each bar.

Table 2. ANOVA results for feeding trials (see Figs. 1 and 2). Intercept shows deviation from an equal consumption of young and old leaves ($d = 0$) for *Haaniella echinata*. Significance levels are indicated by asterisks as ** $p < 0.01$, *** $p < 0.001$.

	ANOVA	Intercept
Plant species (Fig. 1)		
Pseuduvaria nervosa	$F_{1,20} = 0.90$	$t = 3.26$ **
Shorea smithiana	$F_{2,17} = 0.16$	$t = 1.30$
Koilodepas laevigatum	$F_{2,19} = 0.35$	$t = 1.07$
Macaranga beccariana	$F_{2,13} = 0.61$	$t = 0.96$
Mallotus wrayi	$F_{2,35} = 17.08$ ***	$t = 8.39$ ***
Horsfieldia pallidicaula	$F_{1,18} = 0.01$	$t = 1.35$
Dryobalonops lanceolata (Fig. 2)		
Two-way ANOVA: Phasmid + Stratum	$F_{3,41} = 6.95$ ***	$t = 0.7$
Stratum	$F_{1,43} = 14.49$ ***	$t = 1.69$
Phasmid	$F_{2,42} = 1.49$	$t = 1.58$
Canopy young – sapling young	$F_{1,23} = 15.10$ ***	$t = 11.80$ ***
Canopy old – sapling old	$F_{1,21} = 0.01$	$t = 3.87$ ***
Canopy young – sapling old	$F_{1,21} = 1.50$	$t = 4.71$ ***
Canopy old – sapling young	$F_{1,23} = 0.90$	$t = 3.87$ ***

canopy. During our survey we found very few phasmids and observed very little leaf damage in the canopy. Other studies have also shown a much lower overall level of herbivory in the canopy compared to the understorey (Lowman, 1985; Coley & Barone, 1996).

Three nonexclusive hypotheses are suggested to potentially explain the apparent higher density of phasmids in the understorey: (1) It seems likely that abiotic factors are unfavourable in the canopy. For instance, the microclimate in the upper canopy becomes extremely hot and dry during the daytime (Sakai et al. 1999, measured at the same *D. lanceolata* tree sampled in this study), where the phasmids would run the risk of desiccation; (2) Understorey plants of different species occur in close proximity, making it easy for generalists to choose from different food plant species. A mixed diet may benefit generalists by providing complementary nutrition and/or reducing the accumulation of specific toxic compounds (Bernays et al., 1994). Host plant switches in the canopy would require much more effort for flightless phasmids; (3) Apart from feeding, other factors of the life history may require proximity to the ground. For instance, female *H. echinata* bury their eggs in leaf litter (Bragg, 2001). These hypotheses merit more detailed investigation in the future.

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