Intraspecific host preferences of mopane moths (*Imbrasia belina*) in mopane (*Colophospermum mopane*) woodland

Halszka Hrabar[1*], Dawood Hattas[2] & Johan T. du Toit[1‡]

[1]*Mammal Research Institute, Department of Zoology and Entomology,*
University of Pretoria, Pretoria, 0002 South Africa

[2]*Department of Botany, University of Cape Town, Rondebosch, Cape Town, 7700 South Africa*

Colophospermum mopane trees are a common larval food plant of the mopane moth (*Imbrasia belina*), which commonly reaches outbreak proportions. Our study investigated factors determining host tree choice by ovipositing mopane moths within a single host species (*C. mopane*). Tree size was the primary determinant of oviposition at both the habitat (tall riverine-, medium height woodland- and short-shrub mopane) and individual tree scale, with an increase in the number of egg masses with increasing tree size (estimated by height and canopy volume). Preference for larger trees was only evident at the habitat scale, however, as individual trees were utilized as expected according to the availability of their canopy size class. More detailed tree characteristics, such as leaf size, shoot size, stem number and even leaf chemistry (protein:tannin ratio and total polyphenols) had no influence on host choice. Host choice was based on the most obvious measure of resource abundance, namely tree size, as expected for an outbreak species, since resource availability rather than nutritional quality is likely to be the primary determinant of larval survival.

Key words: host choice, resource abundance, tree size, outbreak, oviposition.

INTRODUCTION

Fundamental to the life cycle of phytophagous insects is the location of a suitable plant for oviposition, especially for species with relatively immobile larvae, or monophagous species. Frequently, it is assumed that females select host plants that provide qualitatively and quantitatively the best food for their larvae, as natural selection should favour a positive relationship between adult oviposition preference and offspring performance. However, while numerous studies do support this expectation (e.g. Denno *et al.* 1990; Lower *et al.* 2003; Agrell *et al.* 2006), nearly half of studies have found no such correlation (see review by Mayhew 1997). Instead, oviposition can be influenced by other factors, such as predator avoidance for offspring (Denno *et al.* 1990; Mappes & Kaitala 1995; Björkman *et al.*1997; Mira & Bernays 2002); leaf biomechanical properties (Peeters *et al.* 2006); adult survival and performance (Mayhew 2001; Scheirs 2002); host distribution (Ballabeni *et al.* 2001), host patch size or density and plant architecture (Marquis *et al.*

2002). Preferences might therefore be determined by trade-offs among multiple factors (Bernays & Graham 1988).

Until now, most host-preference studies have focused on understanding the host range of a species, and have therefore looked at interspecific preferences (Wehling & Thompson 1997; Carrière 1998). In a habitat where the preferred host species dominates, however, interspecific host choices are largely irrelevant and instead, intraspecific preference is expected to be of greater importance (e.g. Björkman *et al.* 1997; Leimu *et al.* 2005). Surprisingly, little work has focused on this aspect.

In mopane woodland, *Colophospermum mopane* Kirk ex J. Léonard, trees (commonly known as 'mopane') tend to dominate and generally comprise 90% of the total woody plant biomass (Guy 1981). This deciduous, xeric savanna woodland species is well-known for its suite of chemical defences (Ferreira *et al.* 2003), yet it is the main host species for the larvae of the mopane moth (*Imbrasia belina* Westwood, 1849; Alloy *et al.* 1996) and, where dominant, it represents the single host species for mopane caterpillars (Pinhey 1972; Hrabar 2005). Outbreaks of mopane caterpillars are common at certain times of the year (November/December

*Author for correspondence. E-mail: hhrabar@zoology.up.ac.za
‡Present address: Department of Wildland Resources, Utah State University, Logan, UT, U.S.A.

and February/March), resulting in the complete defoliation of large stands of mopane trees (Ditlhogo 1996).

Although tree species diversity is low within mopane woodland, there is high variability in the growth form and density of mopane trees within this habitat. While mopane trees typically grow to approximately 10 m in height, or else occur as low scrub of 1–2 m high, stands of trees up to 20 m high exist (on deep, nutrient-rich alluvial soil) and are termed 'cathedral mopane' (Van Wyk 1993). Associated with these height differences is a difference in plant architecture, as shrubs are usually multi-stemmed, while taller trees tend to be single-stemmed (Fraser *et al.* 1987). The principle cause of these differences in tree height has been identified as variation in the soil composition, particularly depth and pH (O'Connor 1992) and moisture stress (Hempson *et al.* 2007). Variable foliar chemical composition is therefore also expected between habitat types (Kraus *et al.* 2004). Furthermore, densities of mature mopane in woodland vary greatly, ranging from <10 trees/ha in arid north-western Namibia (Viljoen 1989) to 481 trees/ha in southeastern Zimbabwe (Kelly & Walker 1976) and 2740 trees/ha in northern South Africa (this study). This high degree of variability within mopane woodlands thus results in very different habitat types for mopane moth larvae, which may in turn influence host preference by ovipositing female mopane moths at the habitat level.

Host preference at the individual tree level might also be important for mopane moths, as the mobility of larvae affects the way in which adults perceive the vegetation. For species that move readily between plants while feeding, the vegetation could be perceived as a single continuous food source, with average or aggregate attributes. By contrast, species confined to one or a few trees might perceive the vegetation as an array of food sources, each with individual traits (Edelstein-Keshet & Rausher 1989). The relative immobility of mopane caterpillars (they tend to only move to a new host tree once leaves on the initial host are depleted) might, therefore, require host plant selection by adults at the individual tree scale. However, eruptive population dynamics of phytophagous insects could be due to a lack of selectivity by ovipositing females, as there is no within-generation feedback between deteriorating food resources and natality (Price 1994).

Our study aimed to investigate intraspecific host choice by mopane moths within mopane wood-land by determining if ovipositing moths display host preference at (a) the habitat level and/or (b) the individual tree level, and if so, identifying which tree characteristics determine this preference.

METHODS

Study site

The study was carried out in the Venetia-Limpopo Nature Reserve, situated in the Limpopo Province of South Africa (22°08'27'S and 29°13' 28'E). The study site is fenced, 34 500 ha in extent, and the vegetation of the region is classified as 'Mopane Veld' (Acocks 1953). The area has flat topography with sandstone underlying deep (>2 m) colluvial soils.

The study area is characterized by wet, hot summers (monthly mean maximum 32°C from October to December) and dry, mild winters (monthly mean maximum 24.7°C in June). The mean annual rainfall for Pontdrift, about 15 km from the reserve, is 366 mm (1967–1997) with a 36% coefficient of variation. Rainfall usually occurs between October and March with a peak in January (Smit & Rethman 1998).

While there is no 'cathedral' mopane within Venetia, the mopane community may still be divided into three different habitat types, namely: short scrub, medium height woodland and tall riverine habitats, with mean heights of 1.1 m, 2.5 m, and 5.6 m, respectively.

Habitat description

In late November to early December of 2002, just after the first batch of mopane moths had emerged and laid their eggs (which are laid in clusters of 35–335 eggs, on mopane leaves, twigs or branches; Ditlhogo 1996), five representative areas for each of the three habitat types (scrub, woodland and riverine) were identified and a transect set out within each (i.e. 15 transects). All transects were 5 m wide and either 100, 50 or 25 m in length, depending on tree density (longer transects were required in low density areas in order to include enough trees) and habitat patch size (some riverine areas were particularly small).

To quantitatively describe each area, detailed information was recorded for the first 25–35 trees along each transect, depending on tree density. For one riverine transect, only 19 trees were sampled due to the very low tree density.

The following was recorded: live tree height (m), basal stem diameter (cm), number of live stems, canopy width at the widest point (m) and canopy

height (m). A rough estimate of canopy volume was calculated for each tree as the volume of a cylinder with canopy height and radius dimensions. For each transect, mean tree height, mean stem diameter, mean stems per tree and total canopy volume/ha were determined. Tree density/ha was also calculated, by counting the total number of trees within the transect area. Mean protein, tannin and total polyphenolic content of the foliage in a transect area was determined (as indicators of the nutritional value) by calculating the mean value from individual trees sampled (see details under 'foliar chemical analysis' section).

Host preference – habitat level

Within each transect, all trees with mopane caterpillar egg masses from the current season were identified as host trees and tagged. Egg mass abundance per tree was recorded on a scale of 0–3, where 0 = 0 egg masses, 1 = 1 egg mass, 2 = 2 egg masses and 3 = 3 or more egg masses. The percentage of host trees was calculated for each transect, together with the total number of egg masses/ha. Estimates of egg mass densities were likely to be accurate in scrub and woodland areas, as trees were small enough to search thoroughly and the exact number was deducible from most egg mass scores. In woodlands, for example, only two out of 63 trees had a score of 3. In riverine areas, however, large tree size and the high number of '3' scores (which could mean more than three egg masses) prevented accurate density calculations. The degree of error also presumably increased with increasing tree size.

The term 'preference' is defined as a deviation from random behaviour, where a resource is utilized significantly more than expected in relation to its availability (Singer 1986). To specifically test the prediction that mopane moths would prefer a certain habitat type, the relationship between egg mass number/ha and available canopy volume/ha was investigated. However, due to the high probability of underestimated egg counts in riverine trees, this habitat could not be included in the test, i.e. only woodland and scrub areas were compared in this way. To determine the habitat characteristics influencing habitat selection, however, the relationships between 'percentage utilized trees' or number of egg masses/ha and (1) tree height, (2) tree density, (3) canopy volume/ha and (4) leaf nutritional value were investigated for all three habitat types.

Host preference – individual tree level

For each utilized tree, the nearest conspecific neighbour without egg masses was identified and tagged. This enabled a comparison between trees used as oviposition sites by moths, compared to those that were also present in the area, but not used. Non-utilized trees were not necessarily within the transect area. Tree height, stem circumference and canopy width and height were recorded for all utilized and non-utilized trees.

For more detailed comparisons, additional data were collected from five tree pair contrasts (utilized and non-utilized) per transect. Leaf length was measured for 15 mature, undamaged leaves, collected at random from all sides of the canopy, where the length of the right leaflet was measured in millimetres from the growth point to the leaf apex. The length of the current year's shoot growth (which was easily identifiable from the apparent growth point) was measured for 15 shoots per tree to the nearest centimetre. To estimate shoot biomass, 15 shoots were clipped and subsequently weighed after oven drying (at 50°C) to a constant mass. The number of shoots on the entire tree was then estimated by counting the exact number within a volume of canopy, and multiplying this by the estimated proportion of the canopy the sample volume represented. Total shoot mass was then calculated accordingly. Shoot density was measured as the number of shoots on the terminal 50 cm of a branch, for five branches per tree.

Foliar chemical composition was determined for each tree, from mature leaves collected randomly from around the canopy. The random collection of leaves represents leaf consumption by mopane caterpillars, as they do not discriminate between young and old leaves – all leaves on a branch (or an area of a branch) or tree are consumed (pers. obs.).

Foliar chemical analysis

Leaves were first air-dried in brown paper bags and later oven-dried at 50°C for at least four days. Samples were then milled through a 1 mm screen. Crude protein content was determined according to the Dumas method (AOAC 2000). Total phenols and condensed tannins were analysed in accordance with Hagerman (1995). Total phenols were quantified using the Prussian blue assay for total phenols and condensed tannins were assayed using the acid butanol method for proanthocyanidins. Dried leaf material (~0.05 g per sample) was

extracted with 3 ml of 70% aqueous acetone by sonicating in an ice-water bath for 30 min and centrifuging at 2000 g for 10 min. A 0.1 ml aliquot of the supernatant was used in both assays. *Sorghum* tannin that was previously extracted and purified as described in Hagerman (1995) was used as the condensed tannin standard while Gallic acid was used to standardize total phenols. Total phenols and condensed tannin quantities were calculated as mg/g DW (dry weight), while protein was calculated as the percentage of DW.

A detailed chemical analysis of secondary metabolites was not within the scope of this project, especially since mopane is well-known for its complex chemical make-up (Ferreira *et al.* 2003). Secondary metabolites such as tannin, that accumulate in high concentrations and are often stable end products, are most likely to be directly correlated with total allocation to secondary metabolites (Herms & Mattson 1992). Additionally, carbon-based secondary compounds (CBSCs) such as phenols and tannins, have been considered as one of the most general chemical barriers of woody plants against herbivores (Feeny 1970). Total polyphenolic and condensed tannin content were therefore determined, together with the protein (N) content.

To test the hypothesis that host selection by this outbreak species would be affected by resource quantity at the individual tree level, trees within riverine and woodland transects were divided into four and three 'canopy volume' classes, respectively. Riverine classes included: (1) 0–50, (2) 51–100, (3) 101–200 and (4) >200 m^3, while woodland classes included: (1) 1–10, (2) 11–20 and (3) >20 m^3. Only transects with 75% host trees were considered (i.e. three woodland and three riverine), and trees from like-habitat transects were grouped together.

The total number of egg masses found within each canopy class was then compared to the number expected. For woodlands, the expected number was first calculated according to the number of trees within each class and secondly, according to the total canopy volume available within each class. Utilization of different size trees in relation to the number available could therefore be determined, together with preference based on actual resource availability. Once again, this was only possible for woodland areas. For riverine areas, the expected number of egg masses was only calculated according to tree number (due to inaccurate egg density estimations).

Statistical analyses

Variation across habitat types in each variable (shoot length, leaf length etc.) was analysed using a single factor ANOVA. When significant variation was found, post hoc Tukey tests were carried out to determine between which habitats significant differences occurred. Data were log-transformed when not normally distributed.

Most data describing individual trees were not normally distributed. For each descriptive variable, Wilcoxon matched-pairs tests were therefore used to test for differences between host and non-host trees.

Chi-square goodness-of-fit analyses were used to determine whether certain canopy volume classes were used disproportionately to their availability, both in terms of tree number and total canopy volume (Zar 1999). Where significant variation was found, Bonferroni confidence intervals were used to determine which classes were preferred or avoided (Miller 1966; Neu *et al.* 1974; Byers & Steinhorst 1984).

RESULTS

Habitat description

The three mopane habitat types differed significantly in mean tree height, canopy volume/ha and the number of live stems/tree. Riverine areas contained significantly taller trees with fewer stems and a greater canopy volume/ha than woodland or scrub areas, while woodland areas consisted of taller trees with a greater canopy volume/ha than scrub areas (Tables 1 & 2). Tree density did not appear to differ between habitat types. However, when one riverine transect (which was not representative of the rest of the population, and had unusually high density of 2720 trees/ha compared to a mean of 850 trees/ha) was excluded from the analysis, tree density in riverine areas was significantly less than in woodland and scrub areas (Table 2). The tannin:protein ratio and total polyphenolic content were highest in the woodland habitat and lowest in riverine areas, but these differences between habitat types were not significant.

Host preference – habitat level

Riverine mopane had, on average, the highest percentage of utilized trees (38.9%), followed by woodland (10.6%) and scrub mopane (0.5%), where only two trees with egg masses were found (Table 1). These differences were not quite signifi-

Table 1. Means (±S.E.) of variables describing the three mopane habitat types found in the Venetia-Limpopo Nature Reserve, namely: riverine, woodland and scrub mopane (gdw–dry weight).

Variable	Riverine	Woodland	Scrub
Habitat description			
Tree height (m)	6.11 ± 0.43	2.50 ± 0.23	1.07 ± 0.06
Canopy volume/ha (m^3)	1898 ± 433	280 ± 60	56 ± 7
Live stems/tree	2.37 ± 0.31	4.69 ± 0.47	4.06 ± 0.27
Trees/ha	1224 ± 389	2060 ± 340	2092 ± 111
Tannin:proteinratio	0.49 ± 0.05	0.74 ± 0.07	0.55 ± 0.09
Total polyphenols (mg/gdw)	56.0 ± 2.71	73.2 ± 4.63	60.5 ± 7.40
Utilization			
% utilized trees	38.9 ± 15.9	10.6 ± 5.23	0.44 ± 0.27
Egg masses/ha	632 ± 306	224 ± 87.7	8.00 ± 4.90

cant ($P = 0.078$), yet this is most likely due to the high degree of variability within riverine (0–79%, S.D. = 35.7) and woodland areas (0–29%, S.D. = 11.7). Both these habitats had two transects containing less than 5% utilized trees, indicating that *I. belina* may simply not occur in some areas some years. Excluding these non-utilized areas, the percentage of host trees rose to 17% in the woodland and 64% in the riverine areas. Similarly, the number of egg masses/ha rose from 224 and 632 to 366 and 1040 in woodland and riverine areas, respectively. The higher egg mass density in riverine versus woodland habitats does not appear to be an effect of reduced tree density in the former habitat. Looking specifically at habitat preference, woodlands were preferred over scrub areas ($\chi^2 = 58.5$, d.f. = 1, $P < 0.01$; riverine habitat not included in analysis). Mopane moths do therefore appear to display host preference at the habitat scale**.**

The pattern of utilized tree abundance and egg mass density decreasing from riverine to woodland to scrub mopane matches that of tree height and canopy volume/ha, but none of the other descriptive variables (Table 2). With the increase in the percentage of utilized trees with increasing mean tree height within a transect (Fig. 1.), and since both tree height and canopy volume/ha are indirect measures of foliage biomass, this suggests that resources quantity, rather than quality, appears to be the primary determinant of habitat preference by mopane moths.

Host selection – individual tree level

Shoot length and leaf chemistry did not differ between utilized and non-utilized trees. Individual utilized trees were, however, significantly taller, with a larger shoot biomass, than proximate non-utilized trees in both riverine and woodland habitats (Table 3). In riverine areas, shoot weight and leaf size were significantly greater on utilized trees, yet this is most likely due to the corresponding greater leaf size and shoot length associated with larger trees (Hrabar 2005). Tree size, therefore, seems to be the primary factor influencing oviposition at the individual tree level.

Table 2. Results from ANOVA and Tukey tests for variables describing differences between riverine, woodland and scrub mopane habitat types.

Variable	Habitat comparison	*P*-value
Tree height	riverine > woodland > scrub	<0.001
Canopy volume/ha	riverine > woodland > scrub	<0.001
Tree density[#]	woodland > scrub = riverine	0.006
Stems/tree	woodland = scrub > riverine	0.002
Tannin:protein ratio	woodland = scrub = riverine	0.072
Total polyphenolics	woodland = scrub = riverine	0.096
% utilized trees	(riverine > woodland > scrub)[†]	0.078

[#]Excluding one riverine transect with a high tree density.
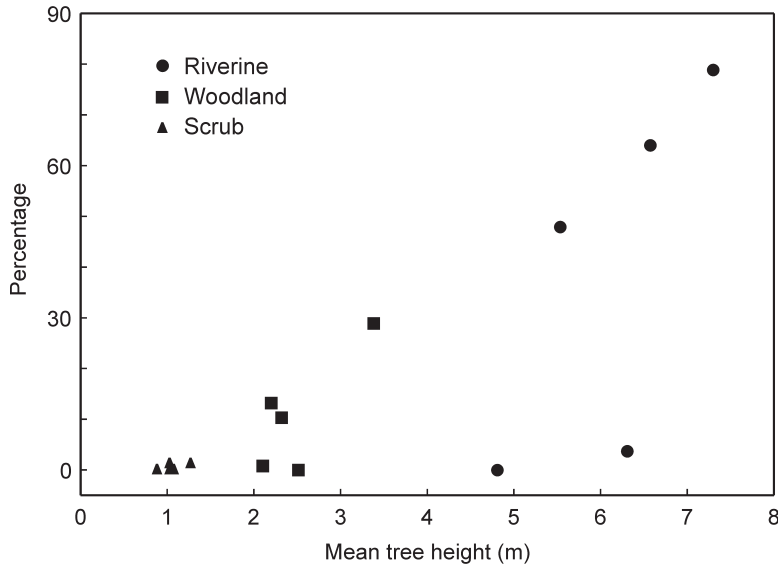[†]Relationship is shown, even though not significant (explanation given in text).

Fig. 1. The percentage of host trees per transect *versus* the mean tree height of the corresponding transect.

In accordance with this result, the number of egg masses per tree was significantly related to tree height ($F_{1,4} = 124$, $P < 0.01$, $R^2 = 0.961$; Fig. 2). In riverine areas, where tall trees dominated, trees as tall as 4–5 m were hardly utilized. Most host trees were >6 m in height, on which egg mass abundance only increased slightly with increasing tree height. In woodland areas, however, where the mean tree height was only around 2.5 m, the increase in egg mass number with increasing tree height was far more apparent. Here, an egg mass score of 3 was only found on the tallest trees, with a mean height

of 4.2 m. Egg mass abundance per tree is therefore also related to the relative tree height in an area.

Host preference – canopy volume

Based on the number of trees available in each size class, trees from the smallest canopy volume class (0–50 m³) were avoided, while those from the largest canopy class (>200 m³) were preferred in riverine areas (Table 4). Similarly, in woodland areas, smallest canopy trees (0–10 m³) were avoided and both the larger canopy classes were preferred (11–20 m³ and > 20 m³). However, when consider-

Table 3. Results from Wilcoxon matched-pairs tests, comparing characteristics of utilized and non-utilized mopane trees in woodland and riverine habitats.

Variable	Habitat type	Utilized *vs* non-utilized trees	P-value[†]
Tree height	riverine	utilized > non-utilized	<0.01**
	woodland	utilized > non-utilized	<0.05*
Total shoot biomass	riverine	utilized > non-utilized	<0.01**
	woodland	utilized > non-utilized	<0.05*
Shoot weight	riverine	utilized > non-utilized	<0.05*
	woodland	utilized = non-utilized	1.00
Shoot length	riverine	utilized = non-utilized	0.14
	woodland	utilized = non-utilized	0.16
Leaf length	riverine	utilized > non-utilized	<0.01**
	woodland	utilized = non-utilized	0.78
Tannin: protein ratio	riverine	utilized = non-utilized	0.57
	woodland	utilized = non-utilized	0.53
Total polyphenolics	riverine	utilized = non-utilized	0.36
	woodland	utilized = non-utilized	0.10

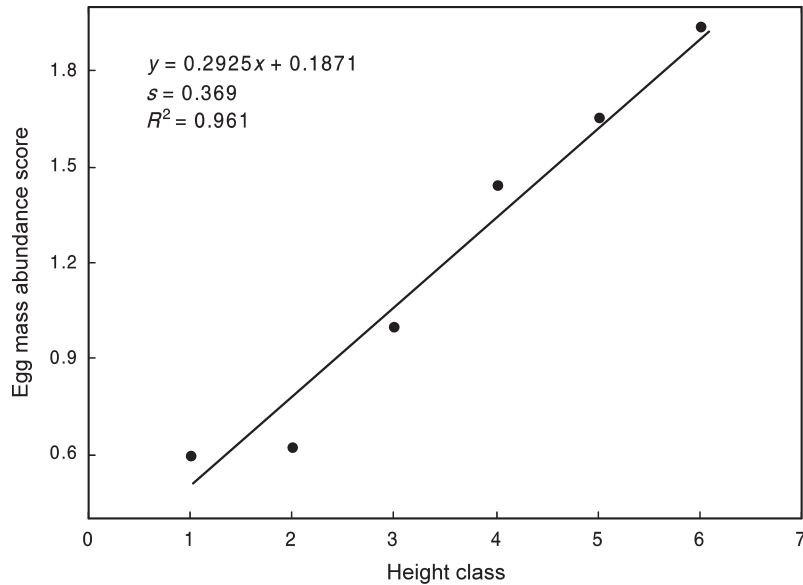[†]Significance at the 5% (*) or 1% (**) level.

Fig. 2. The relationship between the number of egg masses per tree (mean determined from scores of 0–3) and tree height. Heights are grouped into the following classes: 1 = 0–1.5 m, 2 = 1.6–3 m, 3 = 3.1–4.5 m, 4 = 4.6–6 m, 5 = 6.1–7.5 m, 7 = >7.5 m.

ing the actual resource availability in each class (i.e. total canopy volume available) instead of tree number, no canopy size class was preferred or avoided. Instead, each was utilized as expected in relation to its availability (Table 4).

DISCUSSION

Ovipositing mopane moths displayed host selectivity at the habitat scale, as egg densities were highest in riverine areas, while woodland areas were preferred over scrub areas. Tree size (height and canopy volume) was determined as the primary factor influencing which trees were utilized, and

egg mass number per tree was also positively correlated to individual tree size. Unlike host choice by numerous other phytophagous species (see reviews by Jaenike 1990; West & Cunningham 2002), no relationship between oviposition by females and leaf nutritional value was found. This lack of influence of leaf chemistry on oviposition site may be due to the lack of variability in leaf chemistry found in this study. Hrabar (2005), however, found that even when the foliar nutritional value of mopane was significantly improved after elephant browsing, there was no positive influence on *I. belina* egg mass density. Our indicators of leaf

Table 4. Use of different sized mopane tree canopies by ovipositing mopane moths, firstly based on the number of trees within a canopy volume class and secondly, on the total canopy volume within a class.

Habitat	Canopy volume (m^3)	Observed trees with egg masses	Expected trees with egg masses (preference)[#]	Frequency of egg masses expected from canopy volume (preference)[#]
Riverine	0–50	17	34 (−)	
	51–100	20	18 (0)	
	101–200	27	21 (0)	Not applicable
	>200	20	11 (+)	
Woodland	0–10	5	16 (−)	6 (0)
	11–20	8	6 (+)	7 (0)
	>20	14	5 (+)	14 (0)

[#]Symbols indicate classes used significantly more (+), less than (−), or equal to their availability (0), determined by 95% Bonferroni confidence intervals.

chemistry (tannin:protein ratio and total polyphenol concentration) that might be relevant to mopane caterpillar growth (Coley *et al.* 2006) did not influence egg mass density. It thus appears that host choice by mopane moths was not determined by resource quality, but rather quantity.

The lack of a relationship between host choice and foliage nutritional value could be due to the caterpillars of this specialist species having evolved various traits allowing them to handle the foliar chemical composition of their main host species (Karban & Agrawal 2002). Examples of such traits include compensation for suboptimal food by increasing ingestion rate (Schroeder 1986) and employment of various physiological and morphological traits (e.g. the production of enzymes in the gut or saliva, that reduce the detrimental effects of potentially damaging plant compounds such as tannins). The gregarious feeding behaviour of young mopane caterpillars may also enhance their ability to exploit their host plant (Fordyce 2003). Large groups are thought to either cause nutrient sinks or prevent induced defences in intact plants compared with smaller groups of caterpillars (Karban & Agrawal 2002).

Apart from tree size, other tree characteristics associated with positive host choice included leaf size and shoot weight, which were significantly greater on riverine host trees. The degree to which these variables influenced oviposition behaviour is questionable, however, as moths also laid their eggs on trees with no leaves at all in late-flushing woodland areas. Additionally, in woodland areas where leaf and shoot size is more relevant to biomass availability than in riverine areas (due to the smaller tree size), leaf and shoot size were no greater on utilized trees. The larger size of these variables on riverine utilized trees is, instead, most likely due to their positive relationship with tree size i.e. leaf and shoot size increase with tree height (Hrabar 2005).

Despite the positive relationship between tree size and egg mass number, the degree to which ovipositing females actually select host trees in relation to resource availability is not clear. Preference for tall, treed areas was found at the habitat scale, yet at the individual tree level egg mass density was, as expected, according to available canopy volume within each canopy size class. One interpretation here is that the greater number of egg masses on taller trees, within an area, is due to an increased chance of moths intercepting large trees, rather than an actual behavioural prefer-

ence. On the other hand, oviposition behaviour by phytophagous insects is often modified by the presence of conspecific broods (eggs and larva), with females typically avoiding previously exploited host resources (Schoonhoven 1990; Nufio & Papaj 2001), presumably to reduce the competition for resources between their offspring (Prokopy 1981; Tammaru *et al.* 1995).

Additional factors (besides resource availability) driving the relationship between tree size and egg mass number also need to be considered. Predation risk (Lill *et al.* 2002) and microclimate could play an important role in influencing oviposition behaviour. Interestingly, the abundance of geometric moth larvae (*Epirrita autumnata*) in mountain birch (*Betula pubescens* ssp. c*zerepanovii*; Kaitaniemi & Rouhomäki 2001), as well as egg density of pine sawflies (*Neodiprion sertifer*) on Scots pine (*Pinus sylvestris*; Björkman *et al.* 1997) were both found to be positively correlated to stem age (tree size). In both studies this relationship was interpreted as a higher degree of predation on smaller trees, due to a higher probability of detection by predators. This could also apply to the vulnerability of *I. belina* on small mopane trees, as this host plant is eaten by a wide range of species, from mammals to invertebrates (Styles & Skinner 1996). Furthermore, it has been suggested that the preference for large-canopied trees might be related to the larger amount of shade provided (*viz.* microclimate requirements; Björkman *et al.* 1997). Indeed operative temperatures commonly approach the upper critical thermal limit (43–48°C) (Frears *et al.* 1997) and caterpillars do die from desiccation. Further investigation into the effects of predation and microclimate on larval survival with increasing tree size is therefore needed.

In conclusion, mopane moths displayed intraspecific host preference at the habitat level, based on tree size rather than the variables of leaf chemistry measured here (protein:tannin ratio and total polyphenols). The degree of host selection at the individual tree level is unclear, however, as the direct relationship between egg mass number and canopy volume could be due to the increased chance of moths intercepting large trees; or due to moths avoiding conspecific competition for resources. Further work is needed to answer this question, yet our study has identified resource abundance rather than nutritional value of mopane foliage as the primary determinant of oviposition by mopane moths. This is in accordance with what is expected for an outbreak species, where resource

availability is likely to be the limiting factor for larval performance.

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