CHAPTER 5

INTRASPECIFIC HOST PREFERENCES OF MOPANE MOTHS (*IMBRASIA BELINA*) IN MOPANE (*COLOPHOSPERMUM MOPANE*) WOODLAND

5.1 Introduction

Fundamental to the life cycle of most phytophagous insects is the finding of a suitable plant for oviposition, especially for species with relatively immobile larvae. 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 and offspring performance. However, while numerous studies do support this expectation (Rausher 1981; Denno *et al.* 1990; Dini & Owen-Smith 1995; Lower *et al*. 2003), a review of the literature has found that nearly half of studies found no such correlation (Mayhew 1997). Instead, oviposition may 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; Shiojiri *et al*. 2002; Nomikou *et al*. 2003); 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 may therefore be determined by trade-offs among multiple factors (Bernays & Graham 1988).

Until now, the focus of most host-preference studies has been to try and gain a better understanding of a species' host range, 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. Surprisingly, however, very little work has looked into this. In carrying out such a study, intraspecific variables (e.g. leaf size and shoot length) would require investigation so that preference may be detected at a finer scale of resolution, as variation within a trait is likely to be less within one species than across multiple species.

In mopane woodland, *Colophospermum mopane* trees (commonly known as 'mopane', see Chapter 2 for details) tend to dominate and generally comprise 90% of the total biomass (Guy 1981). Mopane is the main host species of the larvae of the mopane moth (*Imbrasia belina*, see Chapter 2 for details) and, where dominant, it may be fed on exclusively (Pinhey 1972; personal observation). Within mopane woodlands, outbreaks of mopane caterpillars are also common at certain times of the year (November/December and February/March), resulting in large stands of trees being completely defoliated (Ditlhogo 1996).

Although species diversity does not vary much within mopane woodland, a high degree of variability does exist in other ways, such as in the growth form and density of trees. While mopane usually ranges from about 10 m in height, with large areas of low scrub of 1-2 m, stands of trees up to 20 m high exist 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 variations in tree height has been identified to be variations in the soil, particularly depth and pH (O'Connor 1992). Variations in foliar chemical composition may therefore also be expected between habitat types. Furthermore, densities of mature mopane woodland vary greatly, ranging from a few trees per hectare in arid north-western Namibia (Viljoen 1989) to 481 trees ha^{-1} in south-eastern Zimbabwe (Kelly & Walker 1976) and 2,740 trees ha^{-1} in northern South Africa (this study). This high degree of variation within mopane woodlands thus results in very different habitat types which may, in turn, be expected to influence host preference by mopane moths at the habitat level.

Host preference at the tree level may 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 may be perceived as a single population with average or aggregate attributes, for example, while parasitic species (confined to one or a few trees) may see the vegetation as a collection of plants with individual traits (Edelstein-Keshet & Rausher 1989). The relative immobility of mopane caterpillars may therefore increase the moth's sensitivity of preference to the tree level. Additionally, selective oviposition may have evolved in mopane moths to reduce intraspecific competition for resources during outbreak sessions, as females could adjust the number of eggs laid according to the host quality and density of conspecifics (Tammaru *et al*. 1995). Therefore, unlike the majority of phytophagous species, where competition for food is considered unimportant (Jaenike & Holt 1991), outbreak species may have evolved the ability to select hosts based on resource quantity, rather than quality. However, a low degree of selectivity may also be expected for an outbreak species, as according to Price (1994), 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.

While looking at the effects of host preference (e.g. larval performance) is not in the scope of this project, investigating the degree of selectivity displayed by mopane moths and identifying what mopane tree characteristics determine this selectivity will help improve our understanding of the ecology of insect-plant relations, specifically for species achieving outbreak dynamics within monospecific tree stands. Additionally, understanding what factors influence the distribution and abundance of mopane caterpillars has socioecological value, as the edible caterpillar forms an important food source to rural communities and has become an important trading commodity (Munthali & Mughogho 1992).

The aim of this study was therefore to investigate intraspecific host preference by mopane moths within mopane woodland, by addressing the following three main questions: (1) Do ovipositing females display host preference at (a) the habitat level and (b) the individual tree level? (2) If so, which tree characteristics determine this preference? (3) Does resource quantity (tree size) influence host preference for oviposition in this outbreak species?

5.2 Methods

5.2.1 Study site

The study was carried out in the Venetia-Limpopo Nature Reserve (i.e. Venetia, see Chapter 2 for details). 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.

In late November to early December of 2002, just after the first batch of mopane moths had emerged and laid their eggs, 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.

5.2.2 Habitat description

The following information was recorded for each tree on each transect: 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 width dimensions. For each transect, mean tree height, mean stem diameter, mean stems per tree and total canopy volume/ha were then determined. Tree density/ha was also calculated, by counting the total number of trees within the transect area. Additionally, the mean nutritional value of foliage (protein, tannin and total polyphenolic content) in a transect area was determined by calculating the mean value from individual trees sampled in section 5.2.4.

5.2.3 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 2 out of 63 trees had a score of 3. However, in riverine areas, 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 by deviation from random behaviour, where a resource is utilised 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. Yet, due to the high probability of underestimated egg counts in riverine trees, this habitat could not be included in the test. Only woodland and scrub areas were therefore compared in this way. However, when looking at the habitat characteristics that may determine habitat selection, the 'percentage host trees' and the number of egg masses/ha were compared to (1) tree height, (2) tree density, (3) canopy volume/ha and (4) leaf nutritional value of all three habitat types, to look for similar or opposite trends.

5.2.4 Host preference – tree level

For each host 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-host trees were not necessarily within the transect area. Tree height, stem circumference and canopy width and height were recorded for all host and non-host trees.

For more detailed comparisons between host and non-host trees, additional data were collected from five tree pairs (host and non-host) per transect. Leaf size was measured for 15 mature, undamaged leaves, collected at random from all sides of the canopy. 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 50ºC) 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. Additionally, leaves were collected for chemical analysis, where the protein, tannin and total polyphenolic content was determined (see method details in Chapter 3).

To test the hypothesis that host selection by this outbreak moth species would be affected by resource quantity at the 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 for each habitat), and trees from like-habitat transects were grouped together.

The total number of egg masses found within each canopy class was then determined and 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, however, 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).

5.2.5 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 occured. 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-squared 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).

5.3 Results

5.3.1 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 consisted of 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 (Table 5.1). Tree density did not appear to differ between habitat types, however, when one riverine transect with an unusually high density (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. Foliar nutritional

Table 5.1 The mean ± SE values of variables describing the three mopane habitat types found in the Venetia-Limpopo Nature Reserve, namely: riverine, woodland and scrub mopane.

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
Alive stems/tree	2.37 ± 0.31	4.69 ± 0.47	4.06 ± 0.27
Trees/ha	1224 ± 389	2060 ± 340	2092 ± 111
Tannin:protein ratio	0.49 ± 0.05	0.74 ± 0.07	0.55 ± 0.09
Total polyphenols (mg/g)	56.0 ± 2.71	73.2 ± 4.63	60.5 ± 7.40
Utilization			
% host 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

value did not differ between habitat types, as there were no differences in the tannin:protein ratio or total polyphenolic content.

5.3.2 Host preference – habitat level

Riverine mopane had, on average, the highest percentage of host trees (38.9%), followed by woodland (10.6%) and lastly scrub mopane (0.5%), where only two trees with egg masses were found (Table 5.1). These differences were not quite significant ($P = 0.078$), yet this is most likely due to the high degree of variability within riverine (0-79 %) and woodland areas (0-29%). Both these habitats had two transects containing less than 5% host trees, indicating that *I. belina* may simply not occur in some areas. Excluding these unutilised 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 far greater number of egg masses/ha in riverine areas (which is likely to be underestimated) indicates that the greater percentage of host trees there is not simply due to an equal number of eggs being distributed among fewer trees. Looking specifically at habitat preference, woodlands were preferred over scrub areas ($\chi^2 = 58.5$, df = 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 host 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 5.2). The increase in the percentage of host trees with increasing mean tree height within a transect is clearly shown in Figure 5.1. Since both tree height and canopy volume/ha are indirect measures of foliage biomass, it

Table 5.2 Results from ANOVAS 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
% host tress	(riverine > woodland > scrub) §	0.078

Excluding one riverine transect with an unusually high tree density.

§ Relationship is shown, even though not significant (explanation given in text)

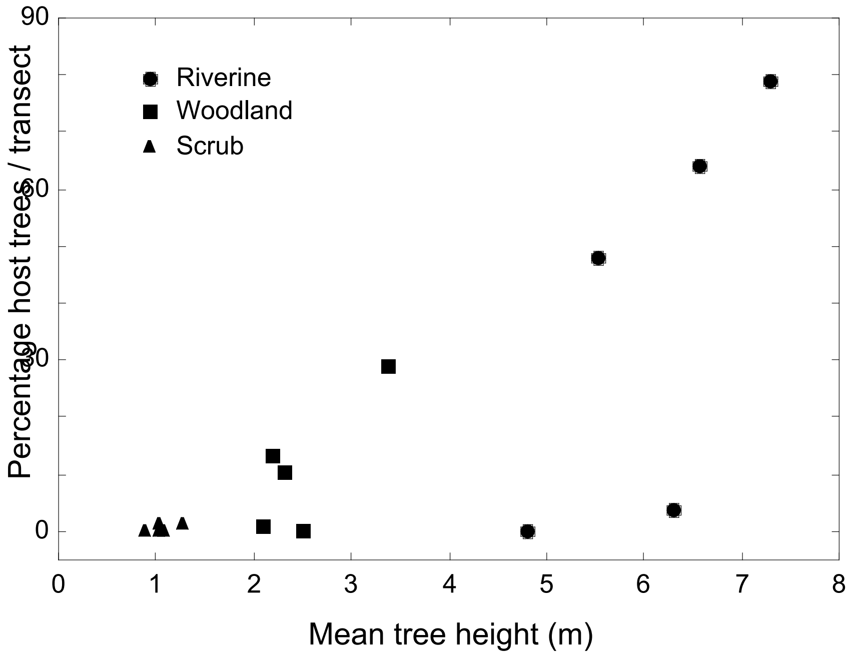

Figure 5.1 The percentage of host trees per transect versus the mean tree height of the corresponding transect.

appears that resources quantity, rather than quality, is the determinant of habitat preference by mopane moths.

5.3.3 Host selection – tree level

There were no differences in shoot length or leaf nutritional value between host and non-host trees. Individual host trees were, however, significantly taller with a larger shoot biomass than their neighbouring non-host tree in both riverine and woodland habitats (Table 5.3). In riverine areas, host trees also had significantly heavier shoots and larger leaves, yet this is most likely due to the corresponding greater leaf size and shoot length associated with larger trees (relationships with tree height: $F_{1,55} = 39.1$, $P < 0.01$, $R^2_{adj} = 0.40$ and $F_{1,54} = 27.6$, $P < 0.01$, $R^2_{adj} = 0.33$ for leaf size and shoot length respectively). Tree size therefore also seems to be the primary factor influencing oviposition at the tree level.

Confirming these results, the number of egg masses per tree was found to be significantly related to tree height ($F_{1,4} = 124$, $P < 0.01$, $R^2 = 0.961$; Fig. 5.2). Considering the habitat types separately, in riverine areas, which are dominated by tall trees, 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 (Fig. 5.3a). 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 (Fig. 5.3b). Here, an egg mass score of 3 was only found on the tallest trees, with a mean height of 4.2 m. Egg abundance per tree is therefore related to relative tree height in an area.

5.3.4 Host preference – canopy volume

Based on the number of trees available in each size class, trees from the smallest canopy volume class (0-50 m^3) were avoided, while those from the largest canopy class

Table 5.3 Results from Wilcoxon matched-pairs tests, comparing characteristics of host and non-host mopane trees in woodland and riverine habitats.

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

* Indicates significance at the 5% (*) or 1% (**) level

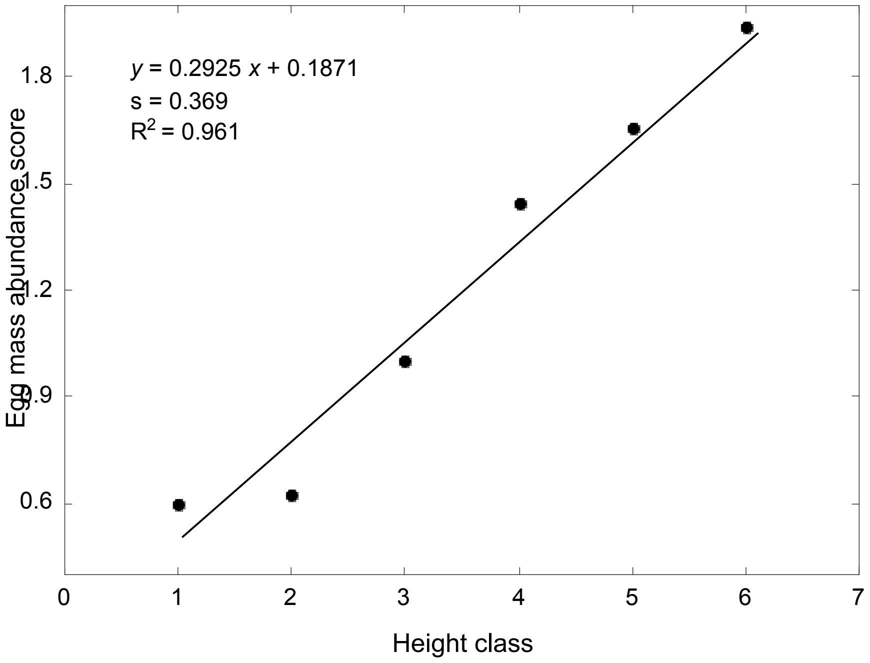

Figure 5.2 The relationship between the number of egg masses per tree (score 0-3) and tree height. Heights are grouped into the following classes: 1 = 0 - 1.5 m, 2 = 1.6 - 3 m, 3 = 3.1 - 4.5 m, 4 = 4.6 - 6 m, 5 = 6.1 - 7.5 m, 7 = > 7.5 m.

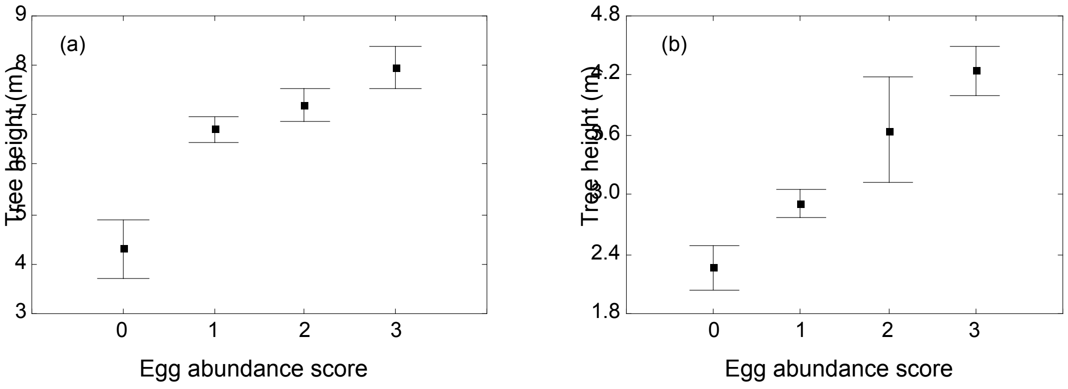

Figure 5.3 The mean (± SE) height of trees for each egg abundance score in mopane (a) riverine and (b) woodland habitats.

Table 5.4 The preference for different size 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 egg masses	Expected egg masses - trees/class (preference)#	Expected egg masses - total volume/class (preference)#
Riverine	0-50	17	34 (-)	Not applicable
	51-100	20	18 (0)	
	101-200	27	21 (0)	
	>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 Bonferroni confidence intervals.

(> 200 m^3) were preferred in riverine areas (Table 5.4). Similarly, in woodland areas, smallest canopy trees (0-10 m^3) were avoided and both the larger canopy classes were preferred (11-20 m^3 and > 20 m^3). However, when considering the actual resource availability in each class instead of tree number, no canopy size class was preferred or avoided. Instead, each was utilised as expected in relation to its availability, as can be seen in Table 5.4.

5.4 Discussion

Ovipositing mopane moths were found to display host selectivity at the habitat scale, as egg densities were highest in riverine areas and the scrub habitat was avoided compared to the woodland habitat. Tree size was determined as the primary factor influencing habitat preference, and individual host trees were also significantly taller than non-host trees. Additionally, the number of egg masses per tree increased with increasing tree size. Tree size therefore appears to be an important determining factor of oviposition by mopane moths. However, preference for larger canopied trees at the tree level was not found, as egg mass density was as expected according to available canopy volume within each canopy size class. The greater number of egg masses on taller trees within an area was therefore probably due to an increased chance of moths intercepting large trees, rather than actual preference.

It should be noted, however, that this direct relationship between egg mass density and available canopy volume may also be interpreted as a display of high selectivity. Studies have shown that oviposition behaviour by phytophagous insects is often modified by the presence of conspecific broods (eggs and larva), with females typically avoiding depositing eggs on previously exploited host resources (Nufio & Papaj 2001). Females may be able to distinguish between occupied and unoccupied hosts by various stimuli, such as the visual cue of an egg mass or a signal received through marking pheromones (Schoonhoven 1990). Such behaviour is thought to have evolved to reduce the competition for resources between their offspring (Prokopy 1981). For an outbreak species such as *Imbrasia belina*, that experiences resource limitation, moths could therefore have adopted this behaviour. Additionally, density-dependence can increase the preference for low ranking hosts if natural selection favours a broad oviposition strategy, where low-quality plants are accepted due to a reduced probability of offspring survival on densely populated higher quality plants (Mayhew 1997). Both these factors could therefore explain the apparent lack of preference for larger canopies on the tree level, and this would mean that mopane moths are not only selecting trees according to their initial resource availability (based on tree size), but also the relative availability through conspecific density.

According to Jaenike (1990), host plant abundance influences search time and specialisation. The high density of mopane trees would therefore allow for an unusually high degree of selectivity by mopane moths, despite their short adult life span, as search time for the correct species would be very low, thereby allowing more time for intraspecific specialisation. To test this, however, changes in oviposition behaviour with increasing egg mass densities should be investigated.

Apart from tree size, leaf size of host trees was also significantly larger than on non-host trees. While this would have had a positive affect on resource availability, the degree of influence on oviposition behaviour is questionable however, as such changes in total biomass per tree would be far more subtle and difficult to detect compared to changes in tree size. Additionally, preference based on tree size was not even found at the tree level, making preference based on a more detailed tree characteristic such as leaf size unlikely. A trait such as leaf size is, instead, expected to be more important for small immobile species, where individuals feed on only one or a few leaves. *Pemphigus* aphids, for example, were found to prefer large leaves on which the weight of stem mothers and their progeny was greater (Karban & Agrawal 2002). Mopane caterpillars, however, are relatively mobile in comparison and feed on a large number of leaves during their development. Additionally, the high degree of variability in leaf size on a single tree (Wiggins 1997; Chapter 7) would reduce the relevance of this trait.

With regards to leaf nutritional value and host preference, the lack of difference between leaf chemistry of individual host and non-host trees is not surprising, as very little variation was found between trees within the same habitat type. Foliar quality did, however, tend to differ between habitat types (although not significantly), yet habitat preference by mopane moths did not correspond to these differences. Woodlands, which had an intermediate level of preference, had a poorer foliar nutritional value than the unutilised scrub mopane. Assuming the measures of leaf chemistry measured here (tannin:protein ratio and total polyphenolics) are relevant to mopane caterpillar growth, it appears that host choice by mopane moths is therefore not determined by resource quality, but rather quantity.

An explanation for the apparent lack of importance of foliar quality could be that caterpillars have evolved various traits allowing them to handle the foliar chemical composition (Karban & Agrawal 2002). One such trait, for example, is that larvae may compensate for suboptimal foods by increasing their ingestion rate or duration of development (Schroeder 1986). Secondly, larvae could have various physiological and morphological traits enabling them to exploit their host plant, such as the production of enzymes (in the gut or saliva) that reduce the detrimental effects of potentially damaging plant compounds (Bernays & Chapman 2000). A third trait applicable to mopane caterpillars is their gregarious feeding behaviour when young, as this is known to enhance the ability of herbivores to exploit their host plants (Nahrung *et al*. 2001; Fordyce 2003). Denno and Benrey (1997), for example, found gregarious caterpillars to grow twice as fast in large groups (30 individuals) compared with smaller groups (1-10 individuals). 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). The adoption of such traits by mopane caterpillars is probable, as it would explain the species' ability to exploit a wide range of mopane trees and reach outbreak proportions.

While the key tree characteristic determining host preference by mopane moths has been identified as tree size in this study, it cannot be assumed that resource abundance alone is the only motivation behind this preference. The risk of predation, for example, identified as one of the most important influences on oviposition behaviour, could also play an important part (Lill *et al*. 2002). Mopane caterpillars are eaten by a wide range of species, including mammals (e.g. baboons, *Papio cynocephalus ursinus* and vervet monkeys, *Cercopithecus aethiops*), birds (34 species were documented by Styles 1995), and invertebrates (e.g. spiders, ants, and mantids; Styles & Skinner 1996). In a study by Kaitaniemi and Rouhomäki (2001), the disappearance of geometric moth larvae (*Epirrita autumnata*) in mountain birch (*Betula pubescens* spp. *czerepanovii*) was related to stem age (tree size). It was suggested it could be due to the smaller size and simple architecture of young stems, which may affect the probability of detection by predators. This too could then apply to mopane caterpillars on small mopane trees. Additionally, the greater resource availability per tree would prevent the need for larvae to migrate between trees, a time during which they are vulnerable to additional predators such as jackal (*Canis mesomelas*) and various ground birds.

Interestingly, in one of the few studies on intraspecific host preference, Björkman *et al*. (1997) also found a positive correlation between tree height and egg density for pine sawflies (*Neodiprion sertifer*) and their host species, Scots pine (*Pinus sylvestris*). They suggested that the preference for large trees could be due to microclimate. Within the range of mopane caterpillars, operative temperatures approaching the upper critical limit (43-48ºC) are common (Frears *et al*. 1997) and populations are known to die from desiccation (personal observation). Large canopied tress may therefore be preferred as they provide a larger amount of shade.

In conclusion, this study shows mopane moths to display a low degree of intraspecific host selectivity, as preference was only evident at the habitat scale. The apparent lack of host choice at the individual tree level; the lack of influence of resource quality on host choice; and the pattern of increasing egg mass density with increasing resource quantity (canopy volume) are all as one may expect for an outbreak species. Further work is, however, still needed to determine whether the direct relationship between tree size and egg density is driven by resource abundance, or other factors, such as predator avoidance. Similarly, the apparent lack of preference for large trees on the individual tree level is questionable, as it is possible that ovipositing females were actually avoiding conspecific egg masses to reduce intraspecific competition. Either way, identifying tree size as the primary determinant of oviposition not only helps in our understanding of the distribution and abundance of mopane moths within mopane woodland, but will also help in the future conservation of the species in localised areas, as management decisions can now be made accordingly to ensure suitable habitat is left intact.

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