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Fine-scale abundance and distribution of wild silk moth pupae

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Abstract

Although several factors influence herbivore insect distributions at any particular scale, the most important determinants are likely to differ between species with different life histories. Identifying what these factors are and how they relate to life history forms an important component of understanding the population dynamics of species, and the habitat requirements necessary for their conservation. The pupal stage of two wild silk moth species, *Gonometa postica* Walker and *G. rufobrunnea* Aurivillius (Lepidoptera: Lasiocampidae), is the target of harvesting practices that are totally dependent on the availability of pupae from natural populations. Consequently, and partly due to poor knowledge of the species' biology, there is substantial interest in the distribution of pupae among and within trees for both these species. It was investigated whether between- and within-tree pupal distributions in these two species are non-random, and if so, whether there are relationships between pupation site use and tree characteristics such as tree size, available pupation space and branch position. Between-tree patterns in pupal abundance were random in terms of absolute spatial position, but markedly non-random with respect to tree characteristics. The apparent *G. postica* pupae were aggregated on large larval host plants, whereas the cryptic *G. rufobrunnea* pupae were aggregated on non-host plants. These patterns reflect the life history differences of the two species. In contrast, at the within-tree scale, branch position, aspect and tree shape influenced pupation site choice similarly for both species. These patterns might be related to microclimate. Documenting between-tree and within-tree patterns in *Gonometa* pupal distributions is the first step towards explaining pupation site selection, as well as identifying possible evolutionarily selective factors in the species, and generating testable hypotheses from these.

Keywords: between-tree, distribution, *Gonometa*, micro-climate, predation, pupa, SADIE, tree-size, within-tree

Introduction

The spatial distribution of herbivorous insects is in most instances non-random. A large body of literature has demonstrated, for example, that insect herbivores exhibit oviposition preferences, niche partitioning, and use of enemy-free space (e.g. Dethier, 1959; Strong *et al*., 1984; Casey, 1993; Bernays & Chapman, 1994; Price, 1997). Apart from such factors, species that differ in life-history strategy, defence characteristics, host plant specificity and microclimate preferences may be expected to have different distribution patterns (e.g. Strong *et al*., 1984; Wallner, 1987; Holmes & Schultz, 1988; Stork *et al*., 2001; Kessler & Baldwin, 2002; Ribeiro *et al*., 2003). Even within a species, different life stages are subject to different key factors influencing survival and the selection imposed is likely to result in a range of behaviours and microhabitat

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preferences (Price, 1997), and consequently, differences in distribution.

Generally, at the between-host plant scale, insect herbivore distributions may be influenced by host plant density (Williams *et al*., 2001), distance from the edge of a site (McGeoch & Gaston, 2000), habitat structure (Ellingson & Andersen, 2002), direct or plant-mediated interactions between herbivores (Riihimäki *et al*., 2003), avoidance of conspecifics (Stamp, 1980), spatial escape from natural enemies (Bernays, 1997; Williams *et al*., 2001), and species dispersal characteristics (McGeoch & Price, 2004). In addition, host plant selection may be based on host plant size or quality characteristics (Floater, 1997; Hodkinson *et al*., 2001), as well as previous levels of herbivory (Gilbert *et al*., 2001). Within plants, spatial distribution may be affected by heterogeneity in plant quality and defence (Orians & Jones, 2001; Kessler & Baldwin, 2002), niche partitioning (Dubbert *et al*., 1998), within- and between-species interactions (Cappuccino, 1988; Cappuccino *et al*., 1995; Faeth & Hammon, 1997), larval behaviour (Anstey *et al*., 2002), avoidance of natural enemies (Stamp & Wilkens, 1993; Wermelinger, 2002), or environmental thermal regimes (Stamp & Bowers, 1990; Klok & Chown, 1998, 1999). Therefore, identifying the specific factors responsible for the fine-scale abundance and distribution of insects is fundamental to explaining the patterns observed, understanding species population dynamics and, consequently, the habitat requirements necessary for their conservation and sustainable use (Ranius, 2001).

The spatial distributions of sessile life stages are often easily determined and thus useful for examining the mechanisms responsible for observed distribution patterns of species (e.g. Heads & Lawton, 1983; Hails & Crawley, 1992; Brewer & Gaston, 2002; Veldtman & McGeoch, 2004). In addition, the condition of individuals in the pupal stage is often largely a summary of the fate of previous or future life stages, e.g. larval performance, final instar parasitism and adult potential fecundity (Wickman & Karlsson, 1989; Veldtman *et al*., 2004). The pupal cocoons of two wild silk moth species native to southern Africa, *Gonometa postica* Walker and *Gonometa rufobrunnea* Aurivillius (Lepidoptera: Lasiocampidae) are economically valuable (Veldtman *et al*., 2002). Cocoons can be degummed to produce high quality silk, which rivals the silk produced from *Bombyx mori* (Linnaeus) (Lepidoptera: Bombycidae). Currently, the pupal stage is the target of harvesting practices that are totally dependent on the availability of pupae from natural populations (Veldtman *et al*., 2002). These pupae almost exclusively occur on the branches and stems of woody plant species (Hartland-Rowe, 1992). Because of the harvesting demand, and poor knowledge of the species biology, there is substantial interest in understanding factors influencing the distribution of pupae among and within trees for both *Gonometa* species. Apart from this applied value in predicting where individuals of these species occur, they provide an ideal study system to identify which factors determine the fine-scale abundance and distribution of the pupal stage of an insect herbivore. Furthermore, pupal information on *Gonometa* species will contribute to the development of an appropriate conservation strategy for these economically important species (McGeoch, 2002). Consequently, this study investigates if between and within-tree pupal distributions in *Gonometa postica* and *G. rufobrunnea* are non-random, and if so, if there are relationships between pupation site use and tree characteristics.

Materials and methods

Study area

Gonometa postica and *G. rufobrunnea* populations were examined at six and five sites respectively within the known (historic and recent records) eruptive range of these species (described fully in Veldtman *et al*., 2002). The dominant woody host species utilized by *G. postica* (at three sites each) was *Acacia erioloba* Meyer and *Acacia tortillis* Hayne (both Mimosaceae), while *G. rufobrunnea* only utilizes *Colophospermum mopane* Kirk ex Benth. (Caesalpiniaceae).

Sampling was standardized by delimiting an approximately rectangular area incorporating 100 trees at each site, to compensate for possible tree-density differences between host-plants and localities. An initial minimum of 40 first-generation cocoons per site was a prerequisite for selection, with at least three sites per host plant selected.

Life history

The females of both *Gonometa* species have limited flying ability and are short-lived (4–7 days). Within the study area, when diapause is broken in early spring (September to October), emerging moths mate and lay eggs to form the first generation. This generation develops for approximately two months before final instar larvae start to pupate (November to December). A varying proportion of these pupae undergo rapid development and emerge to give rise to the second generation in mid-summer (December to January), with pupation occurring in early autumn (March to April). The remaining first generation pupae and surviving second-generation pupae enter diapause, emerging only the following spring (Hartland-Rowe, 1992; R. Veldtman *et al*., unpublished). The cocoons of *G. rufobrunnea* are cryptically coloured (red) while those of *G. postica* are not (white) (Veldtman *et al*., 2002).

Cocoon sampling

Surveying of plots commenced in winter (June to July, 2000) and was repeated in mid summer (January, 2001). This sampling procedure was repeated the following year, all sites being surveyed four times by the end of January 2002. Newly formed pupae counted in the first, second, third and final survey are referred to from here on as generation one, two, three and four, respectively.

For each of the 100 trees per plot, the species, maximum height, number of branches and geographic spatial position were recorded. Tree species used for pupation were divided into three functional types namely, larval host plant (H); non-host plant (N); non-host plant with thorns (NT), as the use of each represents a different pupation strategy. Remaining on the host plant to pupate can guarantee that the correct host is oviposited on (Bernays & Chapman, 1994). On the other hand, using non-host plants can disrupt the search image of natural enemies (Guildford, 1992). Tree height was measured to the nearest 0.25 m and divided into three size categories: small (< 1.75 m), medium (1.75–3.00 m) and large (> 3.00 m). In addition, to standardize for three-dimensional size differences between trees, the number of branches per tree was estimated. At each site the smallest

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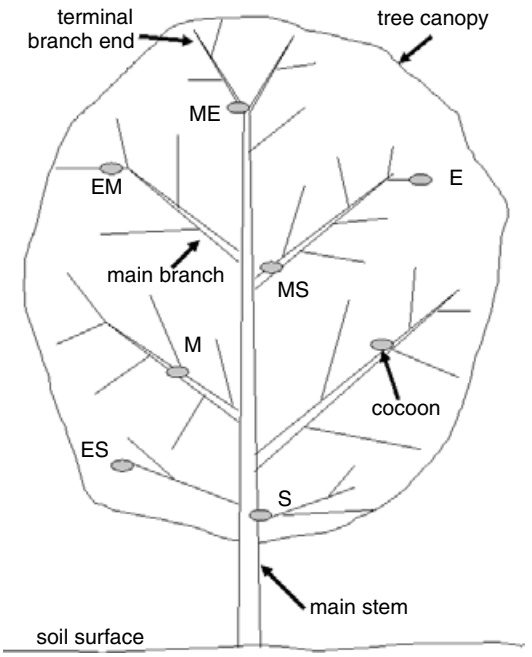

Fig. 1. Within-tree, branch position categories of *Gonometa* species pupae: edge (E, within 15 cm from terminal branch end); edge middle (EM, 15–30 cm from terminal branch end); edge stem (ES, terminal branch directly from main trunk); middle branch edge (ME, start of terminal branch 60 cm from edge); middle (M, middle branch); middle stem (MS, start of main branch); and stem (S) on tree trunk.

sampled tree (0.75 m tall) of the dominant woody host species present was taken to represent one branch, all other trees in the site were then expressed relative to this unit. The position of each tree within a site was measured at the main trunk of the tree with a hand-held Global Positioning System Receiver (GPS: Garmin Etrex, Garmin, International Inc., Kansas; ~3 m accuracy during measurement, see Veldtman, 2004 for further details).

Every tree was carefully searched and all pupae of the present generation (cocoons covered by setae) were counted (the time spent searching for pupae was proportional to number of branches per tree). For each pupa, its sex (see Veldtman *et al*., 2002), cocoon size, height in the tree (to the nearest 5 cm), distance from the main tree trunk (to the nearest 10 cm), branch position and aspect were recorded. Branch position was divided into seven categories: edge (E, within 15 cm from terminal branch end); edge middle (EM, 15–30 cm from terminal branch end); edge stem (ES, terminal branch directly from main trunk); middle branch edge (ME, start of terminal branch 60 cm from edge); middle (M, middle branch); middle stem (MS, start of main branch); and stem (S) on tree trunk (fig. 1). Aspect was determined with a compass, dividing measured directions into four sectors, each centred on a cardinal compass direction, i.e. north, east, south and west. At the start of the study, the number of pupae per aspect was not recorded directly in the first generation, but the number of first generation cocoons found in the second survey was counted instead. Consequently, the site sample sizes for which data on aspect use were available could be lower than for other variables, if some pupae became detached and were not resampled in the second survey.

Data analysis

Alpha level corrections for multiple testing were performed using the step-up false discovery rate (FDR) correction procedure, which has been shown to be the least over-corrective of current alpha-level correction methods (García, 2004).

Between-tree scale

At a between-tree scale, the objective was to determine if variation in pupal abundance could be explained by tree characteristics such as tree functional type, tree size, or by across-tree aggregation patterns. To determine if tree functional types (H, N, NT) or larval host plant size classes (small, medium, and large) had a greater or lower proportion of the pupae than expected from their recorded frequencies, Chi-square goodness of fit analyses were performed (Zar, 1984). Expected frequencies were calculated as the product of the proportion of trees of a category with the sites' total pupal abundance (expected pupal frequencies ≥ 5). For both groupings three categories were generally available for comparison. In cases where some groups did not have sufficient pupae to allow analysis (see Zar, 1984 for bias in Chi-square values), a two-category comparison was made.

Second, spatial analysis by distance indices (SADIE) methodology (Perry, 1995) was used to quantify the degree of departure from spatial randomness for the spatially-referenced (X,Y) recorded branch and pupal count data. Spatial non-randomness is based on the distance to regularity, which is the minimum cumulative distance to achieve a regular distribution of counts (Perry & Dixon, 2002). The index of aggregation (I_a) describes overall aggregation and values approximately ≤ 1.5 indicate significant aggregation (Perry, 1995; Perry *et al*., 1999).

The degree of clustering in number of pupae and branches was also quantified, using the index of clustering, v, that provides information on the degree of clustering for each spatially referenced point based on the magnitude of the count and its occurrence in relation to neighbouring counts (patches – counts greater than the sample mean, v_i and gaps – counts smaller than the sample mean, v_j; see Perry *et al*., 1999; Perry & Dixon, 2002). For each site–generation combination, I_a, mean v_i and mean v_j were calculated if pupae were found on more than 20% of the trees. At densities lower than this (e.g. mean count per tree < 0.2), it is not possible to quantify overall aggregation and spatial clustering (Korie *et al*., 2000; Winder *et al*., 2001).

Thereafter spatial matching between the spatial clustering in pupal abundance and number of branches was determined with spatial association statistics (see Winder *et al*., 2001; Perry & Dixon, 2002 for full description of method). All spatial non-randomness and association analyses were done using SADIEShell (v. 1.22 software, Kelvin F. Conrad and IACR-Rothamsted 2001).

Finally, to determine the amount of variability in pupal abundance explained by spatial and environmental variables (tree variables), trend surface analysis and stepwise model building approaches were applied (Legendre & Legendre, 1998). Trend surface analysis was first used to

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determine the best fit set of spatial variables (significant terms from the third order polynomial of GPS recorded latitude and longitude of each tree) that significantly contributed to explaining variation in pupal abundance (Legendre & Legendre, 1998). Thereafter, a stepwise model-building procedure (generalized linear model, Poisson distribution, log link function) was used to determine the additional variation explained by tree variables (number of branches, tree height and tree functional type) after spatial non-independence was accounted for. To prevent the sequence of additive model-building influencing which variables are included in the final model (Abraham *et al*., 1999; Randic, 2001), best subset analyses of only tree variables were done to rank them in order of the magnitude of variation explained. The tree variables were then sequentially added to the spatial model according to rank, until the percentage of deviance explained was not increased significantly, or all tree variables were included (see Legendre & Legendre, 1998).

Within-tree scale

At the within-tree scale, the objective was to quantify patterns in pupal abundance, and to determine how much of the within-tree distribution in pupal abundance is explained by pupal and tree variables. These included branch position, aspect, standardized cocoon height, cocoon height and distance from the tree trunk. First, the significance of differences in the numbers of pupae between different branch positions or aspects was determined by Chi-square goodness of fit (Zar, 1984). This was done for each site-generation combination separately, as well as for each *Gonometa* species in total. Expected frequencies were calculated as the expected proportion of pupae per category multiplied with a sites' total pupal abundance. For branch position, given the physical space constraints in the number of possible pupation sites in tree shape, all positions further than 30 cm from the tree's outer edge were lumped into one category, assuming that E, EM and all other categories combined would have equal frequencies of pupae by chance. For both branch position and aspect, the influence of sex was also taken into account (expecting equal numbers, see Veldtman *et al*., 2002) with Chi-square analysis of two-way contingency tables (Zar, 1984).

Second, the height frequency distribution of pupae for each primary host plant species was described after controlling for tree height differences between trees. To determine how pupae across sites were distributed in terms of relative tree height, the height recorded for each cocoon was divided by the height of the tree on which it was found. Thus, if pupae are found near the crown of trees, the standardized cocoon height value should be close to one. Distributions were determined for both species, and for *G. postica* populations on different dominant host-plant species separately. The hypothetical crown volume and distribution of each dominant host-plant species (i.e. *Acacia erioloba*, *A. tortillis* and *Colophospermum mopane*) were estimated from descriptions and drawings from Palgrave (1977), as well as from observations in the field.

Finally, potential factors responsible for within-tree pupal distribution patterns of *G. postica* and *G. rufobrunnea* were identified by determining how much of the variation in cocoon height and distance of the cocoon from the tree trunk could be explained by cocoon position attributes or tree characteristics. Functional type and height of tree, as well as branch position of the cocoon and sex were used as explanatory variables for cocoon height. Only tree functional type, tree height, and cocoon sex were used as explanatory variables for distance to trunk because branch position was logically correlated with distance to trunk. For the analysis of both continuous dependent variables, a generalized linear model assuming a normal distribution (log link function) was used (McCullagh & Nelder, 1989).

Results

Sites differed in the absolute and mean ($\pm$SE) number of branches, tree height, between sites, and spatial randomness, therefore offering a range of conditions to investigate pupal abundance patterns (appendix 1). In all but a few cases, counts of the number of branches per tree were randomly distributed within sites (appendix 1).

Between-tree variability

Significant patterns of non-randomness (both over- and under-utilization) were observed, after accounting for differences in the number of trees per site for each tree functional type (fig. 2a). For *G. postica*, the host plant was usually significantly over-utilized (ratio of observed to expected number of pupae greater than one) and only under-utilized (ratio smaller than one) in one case. In contrast, the host plant of *G. rufobrunnea* was under-utilized (fig. 2a). Both non-host tree functional types were significantly under-utilized by *G. postica* in most cases (only two cases of over-utilization). In contrast, either non-hosts with or without thorns were always significantly over-utilized by *G. rufobrunnea* (fig. 2a). Thus, *G. postica* pupated mostly on its primary host plant, while *G. rufobrunnea* tended to pupate on non-host plants in general. More *G. rufobrunnea* females were found on non-host plants and more males on the primary host plant relative to the opposite sex, and both sexes were significantly larger if occurring on non-host plant species (females: 40.02 ± 0.15 ($n = 353$) vs. 41.34 ± 0.18 mm ($n = 218$), t-value $= -5.49$, P-value < 0.001; and males: 32.46 ± 0.09 ($n = 719$) vs. 34.09 ± 0.17 mm ($n = 195$), t-value $= -8.17$, P-value < 0.001). *Gonometa postica* showed similar trends, but both sex ratio and female cocoon size were only significantly greater in non-hosts species where *A. tortillis* was the primary food plant (45.26 ± 0.14 ($n = 356$) vs. 46.13 ± 0.34 mm ($n = 55$), t-value $= -2.22$, P-value $= 0.027$).

Categorizing tree height of only host plant trees, marked differences in utilization were found between height classes, even after standardizing for frequency differences. In all cases large trees were over-utilized while small trees were consistently under-utilized. Where medium sized trees formed the largest category (Kopong), this size class was over-utilized (fig. 2b). Thus the largest of trees available within the site were over-utilized, independent of the actual size of the plant.

Among all trees, pupal abundances of both species were generally spatially random (table 1). Furthermore, in two out of three cases where aggregation was detected, other generations sampled at the same site were spatially random (table 1). However, despite spatial randomness in pupal abundance at the site scale, local clustering indices identified certain trees as contributing significantly to the formation

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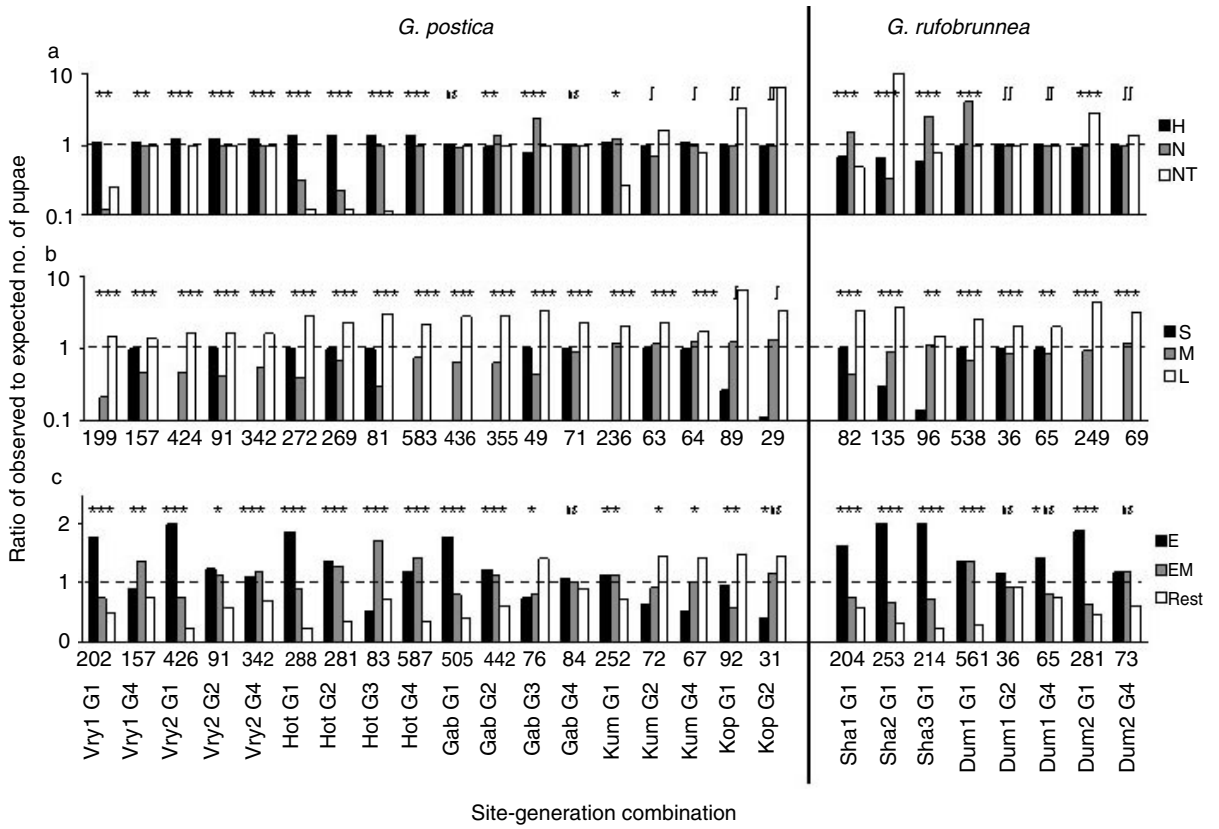

Fig. 2. Ratio of observed to expected number of *Gonometa postica* and *G. rufobrunnea* pupae for each site–generation combination (as in table 1) accounting for (a) tree functional type, (b) height differences between trees, and (c) branch position within trees. If bars are above one it indicates that a category is over-utilized (more individuals than expected), while when below one, under-utilization is indicated. The dotted line indicates when the observed and expected frequencies were equal. H, primary host plant; N, non-host plant without thorns; NT, non-host plant with thorns. Small (S), < 1.75 m; medium (M), 1.75–3.00 m; and large (L), > 3.00 m. (E), (EM) and (rest) denote edge, near edge, and all other branch positions. Sample sizes for b and c are indicated (a and c were similar). *, **, and *** indicate significance between categories at $P < 0.05$, 0.01, and 0.001. '∫' and '∫∫' indicate bias in chi square values when 20% of frequencies are below five, or if any frequency is below one respectively. ns, not significantly different; na, not applicable.

of patches of pupal abundance. Thus, pupae were aggregating on specific trees. Spatial association between number of pupae and number of branches was significant in almost all cases for *G. postica*, while few significant cases were found for *G. rufobrunnea* (table 1). Local spatial association values were usually significant for only a few single trees. Thus the number of pupae per tree was independent of tree spatial position within the site.

The total percentage deviance in pupal abundance explained for *G. postica* and *G. rufobrunnea* ranged between 15–69% and 19–75% (table 2). For both species the spatial component contributed little to explaining pupal abundance in most cases, explaining more than 20% of the deviance in only two out of 26 cases. In contrast, generally more than 30% of the deviance was explained by the pure environmental component (spatial non-independence taken into account) (table 2). Number of branches followed by tree height was the most important variable explaining the pupal abundance of *G. postica* between trees. For *G. rufobrunnea* this pattern was not as general, with tree functional type and height adding greater percentages of explained deviance in several data sets. For both species, number of branches and/or tree height was positively related to pupal abundance in all cases (table 2).

There was, however, a major difference between the species in the relationship between the tree functional type and pupal abundance. For *G. postica*, pupal abundance was significantly higher on its primary host plant than non-host plants in both *Acacia* veld types, whereas *G. rufobrunnea* pupal abundance was significantly lower on its host plant (table 2). Even though tree functional type added significantly to the percentage of explained deviance in 10 cases for *G. postica*, in half of these the regression coefficients were non-significant. In contrast, in four out of five cases tree functional type coefficients were significant for *G. rufobrunnea* (table 2). Thus, tree size seems to largely explain between-tree variation in pupal abundance for *G. postica*, while tree functional type was also important for *G. rufobrunnea*.

Within-tree variability

For each site–generation combination, the difference between expected and observed numbers of pupae per

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Table 1. Spatial clustering of *Gonometa* species pupae and association between number of pupae and number of branches of a sample tree.

Locality	Generation	*n*	Trees	I_a	v_i	v_j	*X*
G. postica							
Vryburg1	1	202	53	1.62**	1.71**	−1.67**	0.106
	4	157	44	1.00	0.69	−1.01	0.288**
Vryburg2	1	426	55	1.14	1.12	−1.20	0.519***
	2	91	33	0.84	0.83	−0.94	0.556***
	4	342	57	1.12	1.27	−1.31	0.197
Hotazel	1	288	42	1.06	1.17	−1.02	0.288**
	2	281	49	1.19	0.94	−1.17	0.334***
	3	83	23	1.00	0.90	−1.00	0.434***
	4	587	53	0.86	0.93	−0.88	0.396***
Gabane	1	505	60	1.13	1.06	−1.07	0.678***
	2	442	56	0.87	0.91	−0.89	0.492***
	3	76	29	1.06	1.12	−1.07	0.642***
	4	84	38	0.76	0.92	−0.77	0.512***
Kumukwane	1	252	51	0.91	0.69	−0.95	0.294***
	2	72	36	1.03	1.10	−1.08	0.573***
	4	67	36	1.27	1.27	−1.32	0.367***
Kopong	1	92	38	1.09	1.09	−1.17	0.303***
	2	31	27	0.97	0.85	−0.95	0.028
G. rufobrunnea							
Shashe1	1	204	46	1.24	1.15	−1.52*	0.236
Shashe2	1	253	59	1.58**	1.36	−1.54*	0.133
Shashe3	1	214	60	0.84	0.97	−0.88	0.178
Dumela1	1	561	81	0.91	0.94	−0.89	0.194
	2	36	25	0.91	0.89	−0.89	0.198
	4	65	45	1.77**	1.74**	−1.82**	0.206*
Dumela2	1	281	60	0.86	0.92	−0.88	0.390**
	4	73	36	0.96	0.98	−0.97	0.517***

Significant positive association (5% level, two tailed test) was determined using SADIE. I_a, v_i, v_j and *X* are the overall index of aggregation, mean clustering values of patches and gaps and overall association value respectively. *, **, and *** indicate significance at $P < 0.05$, 0.01, and 0.001. Underlined values were non-significant after column wide step-up false discovery rate (FDR) correction at the 0.05 level.

branch position was significant in most cases, with the edges of terminal branches and/or near edges of branches usually being over-utilized by pupae, while the pooled remaining branch positions were under-utilized (fig. 2c).

There were also significant differences between males and females in the frequencies of branch position occupied. For both species, males usually significantly over-utilized the edges of terminal branches, and in a few cases near edges of branches, while females mostly over-utilized the grouped remaining branch positions. Sex differences were significant for *G. postica* in nine cases (50%) (Vryburg2: generation (gen) 1, 2, and 4; Hotazel: gen 2, 4; Gabane: gen 1, 2; Kumukwane: gen 1, 4) and for *G. rufobrunnea* in three cases (38%) (Shashe1, Shashe3 and Dumela1: gen 1). The same utilization patterns for *G. postica* and *G. rufobrunnea* were evident when the total number of male and female cocoons per branch position was compared across the entire study. The percentage female cocoons in the 'rest' category was greater than that for males for both *G. postica* and *G. rufobrunnea* (fig. 3a).

The difference between expected and observed numbers of pupae between aspects was significant in most cases for *G. postica* (81%), but not *G. rufobrunnea* (25%). Where such differences were significant, northern and/or eastern aspects were over-utilized, while southern and/or western aspects were under-utilized (results not shown). Nonetheless, the same pattern was evident for both *G. postica* and *G. rufobrunnea* when the total number of male and female cocoons per aspect was considered across the entire study (fig. 3b). There were, however, no significant differ-ences in the frequencies of males and females with respect to aspect (results not shown).

The distribution of pupae in terms of standardized cocoon height showed marked differences between- and within-species (*G. postica*). For *G. postica* at sites with *Acacia erioloba*, cocoon height was normally distributed, with most cocoons just above mid-tree height (fig. 4a). At sites with *Acacia tortillis* cocoon height was also normally distributed, but in this case most cocoons were found just below mid-tree height (fig. 4b). In contrast, *G. rufobrunnea* had a left skewed distribution with most individuals at the two-thirds tree height mark (fig. 4c). However, in all cases most pupae were found below the height where the greatest available canopy volume of the primary host plant was expected to occur (fig. 4a–c).

In all cases the relationship between cocoon height and tree height was significantly positive (table 3). An analysis of cocoon height revealed that branch position, tree functional type and tree height, but not pupal sex, always contributed significantly to the percentage of deviance explained for *Gonometa* species (table 3). Cocoons with

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Table 2. Forward stepwise regression of pupal abundance used to determine the percentage of deviance explained (DE) by spatial and environmental (sample tree) variables.

Locality	Gen	d.f.	Scaled dev/d.f.	Percentage of explained deviance					Entry sequence of significant biological terms	Coefficients
				Total	Spatial	N_{BR}	H_T	FG_T		
G. postica										
Vryburg1	1	96	0.964	46.4	23.2	18.1	5.1	ns	N_{BR}; H_T	+; +
	4	95	0.833	43.1	9.3	33.8	ns	ns	N_{BR}	+
Vryburg2	1	95	0.909	59.5	8.9	44.0	4.6	2.0	N_{BR}; H_T; FT_T	+; +; ns
	2	96	0.880	56.7	2.5	52.2	2.0	ns	N_{BR}; H_T	+; +
	4	96	0.725	46.1	3.0	39.2	3.9	ns	N_{BR}; H_T	+; +
Hotazel	1	92	0.588	68.0	5.3	49.6	11.7	1.4	N_{BR}; H_T; FT_T	+; +; ns
	2	93	0.829	57.3	7.1	36.7	12.2	1.2	N_{BR}; H_T; FT_T	+; +; ns
	3	95	0.826	58.7	11.1	36.4	9.7	1.5	N_{BR}; H_T; FT_T	+; +; ns
	4	94	0.874	68.6	4.6	49.3	10.5	4.2	N_{BR}; H_T; FT_T	+; +; +(H)
Gabane	1	94	0.594	43.6	5.5	20.4	11.1	6.5	N_{BR}; H_T; FT_T	ns; +; +(H)
	2	92	0.773	38.9	4.3	21.9	8.5	4.2	N_{BR}; H_T; FT_T	ns; +; ns
	3	96	0.736	56.7	5.2	43.7	7.8	ns	N_{BR}; H_T	+; +
	4	95	0.867	30.9	2.1	ns	22.7	6.0	H_T; FT_T	+; −(N)
Kumukwane	1	93	0.795	48.2	4.6	25.7	ns	17.8	N_{BR}; FT_T	+; +(N)−(T)
	2	94	0.976	49.7	6.6	30.9	ns	12.2	N_{BR}; FT_T	+; +(N)−(T)
	4	95	0.867	38.2	6.3	18.8	ns	13.1	N_{BR}; FT_T	+; +(T)
Kopong	1	97	0.773	27.8	3.9	ns	23.9	ns	H_T	+
	2	98	0.861	15.2	ns	ns	15.2	ns	H_T	+
G. rufobrunnea										
Shashe1	1	93	0.905	52.3	5.9	16.3	1.6	28.4	N_{BR}; H_T; FT_T	ns; +; −(H)+(N)
Shashe2	1	94	1.001	74.9	31.0	2.8	11.9	29.2	FT_T; N_{BR}; H_T	−(H); +; +
Shashe3	1	93	0.752	24.0	3.9	16.3	2.2	1.5	N_{BR}; H_T; FT_T	+; ns; ns
Dumela1	1	95	1.036	51.7	9.1	ns	38.7	3.9	H_T; FT_T	+; −(H)
	2	98	0.930	19.2	ns	19.2	ns	ns	N_{BR}	+
	4	96	1.000	31.5	11.5	ns	20.0	ns	H_T	+
Dumela2	1	95	1.006	61.9	2.2	40.8	11.7	7.2	N_{BR}; H_T; FT_T	+; +; −(H)
	4	96	0.946	44.4	5.9	32.4	6.1	ns	N_{BR}; H_T	+; +

The total %DE by the spatial component (pure spatial and spatially structured environmental; see Legendre & Legendre 1998), as well as the increase %DE by sequentially added significant tree variables (additively the pure environmental component) is shown. The order of adding significant tree variables and their respective coefficients is also shown. N_{BR}, number of branches; H_T, tree height; FT_T, tree functional type (H, primary host; N, non-host; NT, non-host with thorns).
Number of pupae for each site–generation combination is as specified in table 1.

branch position category E, EM or ME were consistently found higher in the tree, while S category cocoons were found significantly lower. With respect to tree functional type, in all three regressions the cocoons on primary host trees were significantly higher than they were on non-hosts (table 3). For cocoons of *G. postica* on *A. tortillis* and *G. rufobrunnea*, cocoons on undefended non-host plants were significantly lower. This indicates that even when tree height is accounted for, tree functional type may still influence pupation height.

Finally, for both *Gonometa* species cocoon distance to the tree trunk always had a significant positive relationship with tree height (table 3). *Gonometa postica* cocoons were significantly further from the tree trunk if on a primary host plant, while *G. rufobrunnea* had a tendency to be closer if on a non-host without thorns, although tree functional type did not significantly explain this distance. *Gonometa postica* on *A. erioloba* and *G. rufobrunnea* were significantly closer to the trunk if cocoons were female, while for *G. postica* on *A. tortillis*, sex had no significant effect (table 3).

Discussion

By documenting between-tree and within-tree pupal distribution in *Gonometa* this study takes the first step to generating testable hypotheses to explain these patterns. The fine-scale pupal distributions of *G. postica* and *G. rufobrunnea* was markedly non-random (in a non-spatial context) at both scales considered and was significantly explained by tree characteristics. This suggests that there may be a selective advantage to the choice of oviposition and pupation sites in these species. However, at the between-plant scale different factors potentially determine the distributions of the two *Gonometa* species, while within plants similar factors may result in common pupal distributions.

Between-tree pupal patterns

At a between-tree scale, most *G. postica* pupae were found on large primary host trees, while *G. rufobrunnea* used large primary host trees as well as non-host trees (one-third

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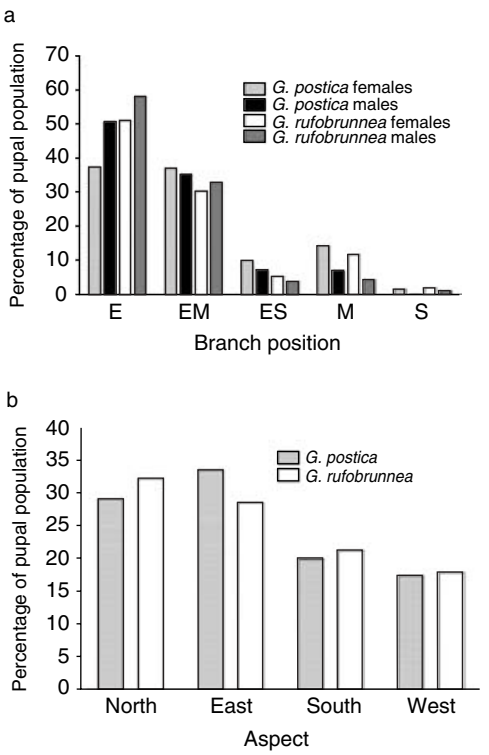

Fig. 3. Percentage of total pupal population categorized by (a) branch position and (b) aspect for *Gonometa postica* and *G. rufobrunnea*. E, EM, ES, M (including ME and MS), and S denote edge, near edge, stem edge, middle of branch and main stem respectively (see fig. 1).

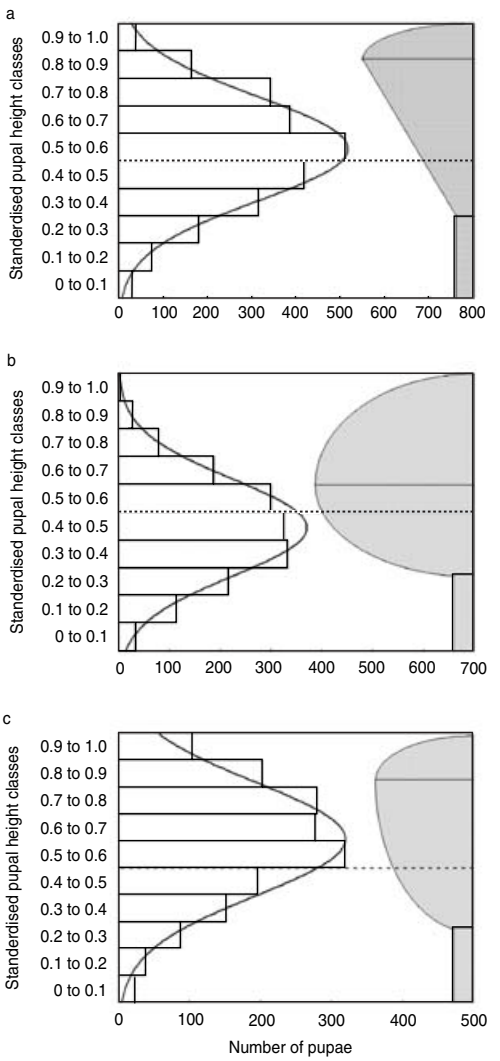

Fig. 4. Frequency distribution of standardized cocoon height of *Gonometa postica* pupae on *Acacia erioloba* (a) and on *A. tortillis* (b), as well as *G. rufobrunnea* on *Colophospermum mopane* (c). Shaded area next to distribution indicates hypothetical available pupation site volume. Dashed line indicates mid tree height.

of all pupae) irrespective of their size. Also, tree size explained more of the variation in *G. postica* pupal abundance, and had a stronger positive spatial relationship with abundance (i.e. areas with large numbers of branches had high pupal abundance) than *G. rufobrunnea*. Nonetheless, for both species pupal abundance patterns were not explained by the spatial position of trees, but rather specific properties of the tree (i.e. size and tree functional type). This suggests that trees used as pupation sites are individually selected by adults or larvae (evidence given below) irrespective of their position relative to other trees (see also Rodeghiero & Battisti, 2000). For example, if an unsuitable tree occurs immediately next to a highly suitable tree, pupae will only be found on the latter, and never, or rarely on the former. The strong trend in *G. rufobrunnea* towards more females, and larger pupae in general, on non-host plants is a curious result. It is possible that large larvae are more likely to disperse, or have greater dispersal distances, from the host plant before pupation (see also Gutierrez & Menendez, 1997; Etienne & Olff, 2004; Ness *et al*., 2004). As a result the pupae found on non-host plants will be larger and have a greater probability of being female (the larger sex in *Gonometa* species). Therefore, at the between-plant scale the two *Gonometa* species differed in the extent to which non-larval-host plants were used for pupation, as well as the importance of tree size in explaining pupal abundance.

Although several mechanisms can be used to explain why bigger trees have more pupae, two reasons suggest that oviposition behaviour of *Gonometa* adults is responsible for this pattern. First, host plant apparency is well known to affect the oviposition patterns of Lepidoptera (Courtney, 1982). For example, the oviposition pattern of *Imbrasia belina* (Westwood) (Saturniidae) (a species ecologically similar to *G. rufobrunnea*) is related to the apparency of the host plant, quantified as tree size and the proximity of neighbouring host plants (Wiggins, 1997). During oviposition site selection, location of host plants is partly visual in most butterflies, and if the host plant is conspicuous oviposition is usually limited to host plants (Wiklund, 1984). The primary hosts of both *Gonometa* species were highly apparent, generally the largest trees at the site, and most abundant. Large trees may thus be more apparent to ovipositing females and consequently receive more egg batches (Courtney, 1982; Batzer *et al*., 1995; Wiggins, 1997).

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Table 3. Generalized linear regression of the height and distance from the tree trunk where pupation occurred for *Gonometa postica* (for both host plants) and *G. rufobrunnea*.

Dependent variable	d.f.	Scaled dev/d.f.	Total % d.e.	Independent variables	Slope ± SE	Log likelihood	χ^2	*P*
G. postica on *A. erioloba*								
Cocoon height	2444	1.004	26.5	Branch position	+(E, EM, ME, M) −(S)	−13931	232.8	<0.001
				Tree functional type	+(*A.e.*)	−13826	24.04	<0.001
				Sex	ns	−13815	1.08	0.300
				Tree height	+	−14026	422.71	<0.001
Distance to trunk	2450	1.002	9.9	Tree functional type	+(*A.e.*)	−7843.3	37.70	<0.001
				Sex	−(F)	−7843.6	38.26	<0.001
				Tree height	+	−7896.4	143.93	<0.001
G. postica on *A. tortillis*								
Cocoon height	1609	1.007	45.5	Branch position	+(E, EM, ME)	−8826.3	103.29	<0.001
				Tree functional type	+(*A.t.*) −(N)	−8821.1	92.96	<0.001
				Sex	ns	−8775.1	0.84	0.657
				Tree height	+	−9131.6	713.78	<0.001
Distance to trunk	1613	1.004	34.0	Tree functional type	+(*A.t.*)	−5770.1	218.36	<0.001
				Sex	ns	−5674.6	27.32	<0.001
				Tree height	+	−5974.3	626.80	<0.001
G. rufobrunnea								
Cocoon height	1673	1.007	52.6	Branch position	+(E, EM, ME) −(S)	−9349.2	442.49	<0.001
				Tree functional type	+(*C.m.*) −(N)	−9181.4	106.98	<0.001
				Sex	ns	−9128.2	0.65	0.420
				Tree height	+	−9442.7	629.55	<0.001
Distance to trunk	1682	1.003	12.3	Tree functional type	−(N)	−4216.0	4.48	0.106
				Sex	−(F)	−4218.6	9.61	0.002
				Tree height	+	−4299.7	171.85	<0.001

The fit and percentage deviance explained (d.e.) by the total model as well as the significance of independent variables is shown. Branch position: E, EM, ES, ME, M, MS, and S; denote edge, near edge, stem edge, edge of branch, middle of branch, start of branch, and main stem respectively. Sex: female (F) and male (M); Tree functional type: primary host (*A.e.*, *Acacia erioloba*; *A.t.*, *A. tortillis*; *C.m.*, *Colophospermum mopane*), non-host no thorns (N) and non-host with thorns (NT).

Second, large host plants have a greater probability of sustaining higher numbers of final instars and larvae are thus more likely to remain and pupate on these plants (Batzer *et al*., 1995). Alternatively, larvae may die of starvation if the eggs they emerged from are located on small hosts (which are quickly defoliated, see Floater, 2001; Rhaindes *et al*., 2002) or co-occuring non-host plants (Dethier, 1959; Steinbauer *et al*., 2001; Hódar *et al*., 2002). The first instar larvae of Lepidoptera species that commonly oviposit on non-host plants (generally species that overwinter as eggs or small larvae) use silk threads to 'select' host plants (Bernays & Chapman, 1994). Consequently larvae will only survive if a suitable host plant is in close proximity (Leyva *et al*., 2003). The limited early instar dispersal ability of *Gonometa* suggests that if females oviposit on non-hosts, first instars may at best be able to disperse to suitable hosts directly next to the oviposited plant. Based on the large distances between the primary host plants of especially *G. postica*, early instar larvae are unlikely to successfully disperse to suitable hosts if oviposition occurs on unsuitable hosts. In general, oviposition on the host plant is typical of southern African Lasiocampidae (Scholtz & Holm, 1985). Pupal distributions may thus simply be a result of host plant size.

Conversely, pupation patterns of *Gonometa* species are unlikely to be the result of secondary larval host plant selection by later instars. Although Lepidoptera larvae are more likely to move to an object that is visually conspicuous (Bernays & Chapman, 1994), dispersal success to alternative hosts is usually low (Floater, 2001). The low number of pupae relative to available foliage on host plants suggests that defoliation by *Gonometa* is rare and remaining on the host plant will be less costly than moving to a secondary host plant of the same species (Batzer *et al*., 1995). There is thus little evidence to suggest that density dependent dispersal of larvae to secondary host plants occurs (see Rhaindes *et al*., 2002), and therefore adult oviposition patterns are the likely primary determinant of pupal distributions, at least for *G. postica*. However, the frequent use of non-host plants by *G. rufobrunnea* suggests that a secondary mechanism is required to explain the pupal distribution of this species. As an alternative, factors that influence pupal survival may influence the distribution of *G. rufobrunnea*. Pupal survival may be influenced by both abiotic (e.g. solar radiation) and biotic factors (e.g. natural enemy attack or avoidance) (Nowbahari & Thibout, 1990; Kukal, 1995; Lyon & Cartar, 1996; Hazel *et al*., 1998; Bennett *et al*., 2003). Non-host plants used by cryptic *G. rufobrunnea* pupae, which are vulnerable to bird predation (Veldtman, 2004), may serve as a form of enemy-free space. Predators, especially vertebrates, using visual cues may not only select high-density prey patches, but also form search images of prey against certain backgrounds (Guildford, 1992). Using non-host plants may thus be a method of escaping bird predation, by disrupting the search image of the predator (Brower, 1958; Hazel *et al*., 1998). Apparent *G. postica* pupae, which are virtually immune to predation (Veldtman, 2004), were seldom found on non-host plants, thereby supporting this hypothesis.

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Furthermore, when host plants have high larval densities, pupating on the same host plant will decrease the effectiveness of cocoon crypsis as an anti-predator defence (Brower, 1958).

Within-tree pupal patterns

At a within-tree scale *Gonometa* pupae of both species showed similar patterns of branch position and aspect use, as well as patterns of (non-standardized) cocoon height and distance from the trunk. It is thus unlikely that natural enemy avoidance played a role here. Rather, interspecific similarities in within-tree use suggest a common explanation (e.g. the influence of abiotic factors). Most pupae were found on the edge or near the edge of branches on the eastern and northern sectors of trees, on larger trees, and occurred higher and further away from the main stem. Although there are more pupation sites on terminal branches, within-tree pupation patterns were not simply a matter of space availability, as more exposed branch positions were used than would be expected. Instead, differences in solar radiation may explain these patterns. For pupae in trees there may be a trade-off between maximum rate of development and avoiding hot midday-temperatures that are potentially detrimental to their survival (Denlinger, 2002).

Branch positions near the trunk will receive the least solar radiation, while terminal branch positions will receive minimum shading (Kotzen, 2003). Therefore, it is possible that the cooler microclimates near the tree trunk (see Klok, 1998) are less favourable for pupal development, compared to those on the edge of branches that are most likely to receive oblique, early morning radiation (see Bryant *et al*., 2002). Differential aspect use within trees may also be explained by differences in thermal microclimate properties (Stork *et al*., 2001). In the Southern Hemisphere, northern and eastern aspects of trees will receive more solar radiation in the morning than southern and western aspects, while the reverse is the case in the afternoon (see Kotzen, 2003). Therefore, pupae positioned to receive maximum morning radiation may maximize developmental rates, without being exposed to detrimental afternoon radiation.

The difference in standardized cocoon height between *Gonometa* species (and between *G. postica* populations on different host plants) corresponded with differences in the shape of the primary host plants and provides further support for pupae avoiding direct solar radiation (i.e. high maximum temperatures). In all cases the maximum frequency height classes of both *Gonometa* species corresponded to regions below the maximum canopy volume of their host plants. Thus pupation site availability itself was not a major determinant of the position of pupae within trees, but rather, selection of pupation sites shaded at midday (see Kotzen, 2003). Therefore, within-trees, branch position, aspect and tree shape may influence pupation site choice by providing favourable microclimate conditions for pupae.

However, sex differences in pupation site use suggest an added unknown mechanism resulting in within-tree pupation patterns. Possibly, using terminal branch edges is advantageous for the rapid, post-eclosion daytime-dispersing males, while more sheltered branch positions allow cover until nightfall for females that have limited powers of dispersal (R. Veldtman, personal observation). Nonetheless, the stronger and more consistent patterns supporting the favourable microclimate hypothesis suggest that differences in received solar radiation is currently the most parsimonious explanation for within-tree pupal distributions.

Conclusions

It has been shown that pupae have distributions that maximize their survival, because selection for pupation sites by larvae largely determines pupal survival probability (Ruszczyk, 1996). However, when pupal survival is not affected by the distribution of the pupae, it appears that a herbivore insect will not modify its original spatial distribution in earlier life stages, and consequently similar patterns may still be visible in later life stages (see also Batzer *et al*., 1995). The marked differences between *Gonometa* species at a between-tree scale, but strong similarities at a within-tree scale, illustrate the scale dependence of factors influencing herbivorous insect distributions (see also Hamid *et al*., 1999). In the case of *Gonometa* species, the present study study describes the pupal distribution at two scales relevant to its commercial use and conservation. For example, when searching for pupae between trees, non-host plants can be largely ignored for *G. postica*, but may harbour many *G. rufobrunnea* pupae. In addition, seeding pupae within trees may be more successful when following observed natural pupation patterns.

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Appendix 1

Vegetation characteristics of sites (consisting of 100 trees each) where *Gonometa* species were sampled. The frequency of trees according to functional type (primary food plant (H); non-larval host plant (N); non-larval host plant with thorns (NT)) and primary host plants according to tree size (small <1.75 m; medium 1.75–3.00 m; large >3.00 m) is given. * and *** denote significant difference at $P<0.05$ and 0.001, while ** indicates $P>0.90$. I_a = Index of overall aggregation.

Species and Locality	Number of branches			Tree height	Tree functional type			Primary host size class		
	Total	Mean ± SE	I_a	mean ± SE	H	N	NT	Small	Medium	Large
G. postica										
Vryburg1	697	7.0 ± 0.6	1.03	3.50 ± 0.14	92	4	4	13	20	59
Vryburg2	888	8.9 ± 0.8	1.16	2.63 ± 0.13	82	18	0	15	25	42
Hotazel	342	3.4 ± 0.3	0.79	1.75 ± 0.12	71	8	21	15	36	20
Gabane	649	6.5 ± 0.9	1.10	2.25 ± 0.11	84	15	1	22	43	19
Kumukwane	572	5.7 ± 0.5	0.68*	2.25 ± 0.09	90	4	6	22	59	9
Kopong	321	3.2 ± 0.1	1.97***	2.00 ± 0.06	99	0	1	30	68	1
G. rufobrunnea										
Shashe1	1136	11.4 ± 1.3	1.12	1.75 ± 0.11	60	39	1	24	21	15
Shashe2	778	7.8 ± 0.4	1.03	2.00 ± 0.06	83	13	4	14	63	6
Shashe3	657	6.6 ± 0.3	1.10	2.38 ± 0.07	76	21	3	11	57	8
Dumela1	1110	11.1 ± 0.5	1.06	2.50 ± 0.08	99	1	0	5	77	17
Dumela2	1175	11.8 ± 0.7	1.52*	2.00 ± 0.08	96	0	4	28	60	8

Underlined values lost significance after column wide step-up false discovery rate (FDR) correction at the 0.05 level.

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