CHAPTER 1

Predicting population dynamics and natural enemy responses from herbivore life history and defensive traits

INTRODUCTION

Understanding the population dynamics of insects has long been of interest as a result of both its economic and ecological significance (Nothnagle & Shultz 1987; Wallner 1987; Cappuccino *et al.* 1995; Nylin 2001). One research focus has been the identification of life history differences between herbivorous insects with eruptive and latent population dynamics (e.g. Dodge & Price 1991; Thompson & Pellmyr 1991; Larsson *et al*. 1993; Miller 1996; Ribeiro *et al*. 2003). Typically, eruptive species exhibit temporal population size fluctuations ranging from three to five orders of magnitude, whereas latent species fluctuate between only one to two orders of magnitude (Price *et al.* 1990). Eruptive species therefore fluctuate between low (the endemic phase) and high population densities (the epidemic phase), whereas, by definition latent species have only an endemic phase (Price *et al.* 1990). In general therefore, population size variability in eruptive species is considered to be far higher than that in latent species (Wallner 1987; Price *et al.* 1990; Price *et al*. 1995; Leyva *et al*. 2003). A further important focus in population ecology has been the interaction between natural enemy responses and the dynamics of insect herbivore populations (Wallner 1987; Price *et al.* 1990; Berryman 1996; Muzika & Liebhold 2000). These responses are defined as any relationship between the natural enemy and host (or prey) population size, e.g. attack rate or natural enemy assemblage size and composition (Gaston *et al*. 1997; Frears *et al*. 1999; Gentry & Dyer 2002; Stireman & Singer 2003). An association between natural enemy responses and herbivore defensive traits has also been demonstrated (Larsson *et al*. 1993; Bowers 1993; Dyer & Gentry 1999; Louda *et al*. 2003).

Because generality in the relationship between life history traits and population dynamics has potential application in both conservation and pest management (Nothnagle & Shultz

1987), by facilitating predictions of population size variability, it has been explored fairly extensively (e.g. Price *et al.* 1990; Larsson *et al*. 1993; Hunter 1995; Miller 1996). Some support for the relationship between emergent population dynamics and species life history traits (i.e. those traits that are not readily classified as morphological, physiological or behavioural; Nylin 2001) has been found. For example, the galling sawfly, *Euura lasiolepis* (Tenthredinidae) deposits eggs singly on high quality foliage contributing to latent population dynamics (Price *et al*. 1990). In contrast, the spruce budworm, *Choristoneura fumiferana* (Tortricidae), deposits eggs in masses on low quality foliage, contributing to observed eruptive dynamics (Price *et al*. 1990). Adult female, larval and overwintering stage traits have also been found to differ between eruptive and latent species of Northern Hemisphere (NH) Macrolepidoptera (Hunter 1995). There are, however, at least two problems with such generalities. First, eruptive and latent species are extremes on a gradient of population size variability, and species with moderate population size fluctuations may not have readily predictable life history traits (Price *et al.* 1990; Nylin 2001; Steinbauer *et al*. 2001). Second, even if different life history traits are associated with eruptive versus latent population dynamics, it does not necessarily follow that they are the cause of such dynamics. For example, although insects may have life history traits typical of eruptive species, factors such as host plant distribution, predation pressure and abiotic factors can, either directly or indirectly, significantly alter the population dynamics observed (Larsson *et al*. 1993; Björkman *et al*. 2000; Azerefegne *et al*. 2001; Steinbauer *et al*. 2001). For example, insect herbivore populations have been shown to be kept below epidemic levels by both predation and parasitism of larval and pupal herbivore life stages (e.g. Kouki *et al*. 1998; Tanhuanpää *et al*. 2001; Raymond *et al*. 2002). Consequently, species with eruptive dynamics may switch between endemic and epidemic phases when escaping from their natural enemies in either space (Brodmann *et al*. 1997; Maron *et al*. 2001; Raymond *et al*. 2002) or time (Berryman 1996). Consideration of species interactions with their biotic (e.g. natural enemies) and abiotic environments (e.g. climate), in addition to life history traits, is thus clearly important (Nylin 2001; Steinbauer *et al*. 2001). Nevertheless, the current evidence that different suites of life history traits tend to be associated with species with eruptive compared to latent population dynamics (e.g. Hunter 1995), makes the dichotomy a potentially useful starting point for understanding the population dynamics of poorly known species. In addition, further

comparative studies are needed to strengthen our understanding of this association (Price *et al.* 1990).

Considering the biotic interactions affecting the life history - population dynamics relationship, an association has been demonstrated between herbivorous insect defensive traits and the responses of various natural enemies (Larsson *et al*. 1993; Bowers 1993; Dyer & Gentry 1999; Louda *et al*. 2003). Although demonstrated largely for Lepidoptera, certain states of larval defensive traits (*sensu* Dyer & Gentry 1999) are commonly associated with low attack rates (or other responses, e.g. species richness) by natural enemies (Table 1). First, generalist herbivore species tend to suffer greater predation by invertebrate predators than specialists, whereas specialists suffer higher levels of vertebrate predation than generalists (Table 1). By contrast, host-plant breadth has little clear effect on parasitoids (but see Dyer & Gentry 1999). Morphological defensive structures (e.g. urticating setae) in turn, are an apparently effective deterrent of invertebrate predators, but not of parasitoids (Table 1). Setae may even increase vulnerability of herbivores to some parasitoid families (i.e. Tachinidae) (Stireman & Singer 2003). The effect of larval appearance is less clear because an increase in apparency may increase the level of natural enemy attack for a palatable species, but not a toxic species (Lindström *et al*. 2001; Gentry & Dyer 2002). Generally, however, non-aposematic Lepidoptera life stages are considered to be more vulnerable to predators than aposematic life stages (Table 1). Finally, gregarious larvae tend to be more susceptible to parasitism than solitary larvae (Table 1) (but see Dyer & Gentry 1999; Floater 2001), although gregarious sawfly species may be better protected from predators as a result of increased effectiveness of their acid-based defences (Larsson *et al*. 1993). However, these patterns of natural enemy responses have only been documented by a few studies, global coverage and taxonomic representation is poor, and patterns observed may not be widespread or consistent across taxa.

Here we test predictions of population dynamics and natural enemy responses based on life history and defensive traits using two closely-related, Southern Hemisphere Macrolepidoptera species. *Gonometa postica* Walker and *G. rufobrunnea* Aurivillius (Lepidoptera; Lasiocampidae) are wild silk moth species that are reported to reach eruptive proportions (Edwards 1935; Zumpt 1971; Hartland-Rowe 1992) within central southern Africa, and on which several small-scale wild silk industries depend (Veldtman *et al*. 2002). The pupal cocoons of both species are constructed from high quality silk and their cocoons are considered

Table 1. A comparison of selected Lepidopteran defensive traits and their association with natural enemy responses. Defensive trait state is denoted in the body of the table (i.e. specialist vs. generalist; hairy vs. smooth; aposematic vs. not cryptic and palatable vs. cryptic; solitary vs. gregarious), and is associated with a positive natural enemy response. 'no effect' (ne) indicates no positive natural enemy response to different states of life history characteristic.

Defensive trait	Natural enemy response						
	Higher parasitism rates				Higher predation rates		Higher species richness
	Tachinidae[1]	Diptera[2]	Hymenoptera[2]	Parasitoids[3]	Invertebrate[3]	Bird[4]	Tachinidae[1]
Host plant breadth	ne	ne	ne	specialist	generalist	specialist	generalist
Physical defence	hairs (ns)	ne	ne	ne	smooth	smooth	hairs
Appearance	cryptic	ne	ne	ne	not-cryptic & palatable	not-cryptic & palatable	ne*
Aggregation behaviour	gregarious	gregarious	gregarious	solitary	-	gregarious	ne

[1] Stireman & Singer 2003 (only two larval appearance categories: aposematic vs. cryptic); [2] Gentry & Dyer 2002; [3] Dyer & Gentry 1999, parasitoids comprise of 79 Ichneumonoidea, 5 Chalcidoidea and 13 Tachinidae species; [4] Brower 1958. *Significant association between host being and cryptic species and Tachinidae species richness if interaction with host abundance considered.

an economically valuable natural resource. At present the supply of cocoons to small-scale silk industries in the region is dependent on harvesting of natural populations (Veldtman *et al*. 2002). Unfavourable weather conditions (rainfall dislodging early instar larvae), timing of moth emergence with host phenology (first instar food availability) and a reduction in natural enemy attack rates have all been proposed to result in the marked population fluctuations observed (Hartland-Rowe 1992). Population size fluctuations for these species have never been quantified. Here we describe and quantify for the first time the temporal and spatial variation in pupal abundance and patterns of pupal parasitism and predation for both *G. postica* and *G. rufobrunnea*.

We also examine the extent to which 1) the life history trait - population dynamics association, and 2) the host defensive trait - natural enemy response relationship, of these two phylogenetically closely related species agree with those found for other Lepidoptera in the literature to date. To address the first objective we compare the life history traits of these two *Gonometa* species with that of available data on eruptive and latent Macrolepidoptera. From this we predict where these species are likely to occur on the eruptive-latent population dynamics gradient. We then quantify the extent of temporal and spatial variation in the population size of the two species, comparing within-generation pupal abundances across sites, and across-generation abundances within sites. These data are then used to evaluate the accuracy of population dynamics predictions based on life history traits. With the second objective, we examine the relationship between *Gonometa* defensive traits and natural enemy responses. We consider larval defensive traits of *G. postica* and *G. rufobrunnea* that are known to affect the responses (percentage induced mortality) of natural enemies to other Lepidoptera (Table 1). Because *G. postica* and *G. rufobrunnea* differ in certain defensive traits, we investigate whether natural enemy-induced mortality and assemblage structure differ between these species. To explain the natural enemy response - defensive trait results that we find, we examine two additional properties of these *Gonometa* species, namely pupal abundance and cocoon structure.

METHODS

Life history and defensive traits

Gonometa postica and *G. rufobrunnea* have pro-ovigenic females, are bivoltine and overwinter in pupal diapause. 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 un-emerged first generation pupae and surviving second-generation pupae enter diapause, emerging only the following spring.

Information on the life history traits of *Gonometa* species was gathered from the literature and personal observations. Information on female flying ability was obtained from personal observations, while oviposition preference and larval aggregation behaviour was partly from personal observation and the findings of Hartland-Rowe (1992). Egg clutch size, larval coloration (Hartland-Rowe 1992), host breadth, physical defence structures (Scholtz & Holm 1985; Hartland-Rowe 1992) and pupal coloration (Veldtman *et al*. 2002) are from the literature. Life history information on eruptive and latent Northern Hemisphere Macrolepidoptera was extracted from Hunter (1995).

Information on the defensive traits of *Gonometa* species was also gathered from the literature and verified by personal observation. *G. postica* is moderately polyphagous (see Hunter 1995) because it feeds only on the leaves of two angiosperm families (Mimosaceae: *Acacia erioloba* Meyer, *A. tortillis* Hayne, *A. mellifera* Benth., and the alien, *Prosopis glandulosa* Torrey; Caesalpiniaceae: *Brachystegia* spp., *Burkea africana* Hook.), while *G. rufobrunnea* is a monophage, on *Colophospermum mopane* Kirk ex Benth. (Caesalpiniaceae) (Scholtz & Holm 1985; Hartland-Rowe 1992). The larvae of both *Gonometa* species have urticating setae, which are later incorporated into the pupal cocoon wall (Scholtz & Holm 1985; Hartland-Rowe 1992). The final instar larval coloration of *G. rufobrunnea* is highly cryptic, while in *G. postica* its contrasting white, brown and black coloration renders it highly visible against the host plant background (Hartland-Rowe 1992). Similarly, the cocoons of *G. rufobrunnea* are cryptically coloured while those of *G. postica* are not (Veldtman *et al*. 2002).

Both species pupate on branches of woody plants, usually, being larval host trees for *G. postica* and non-hosts for *G. rufobrunnea*. The late instars of *G. postica* may be solitary or gregarious, depending on the number of larvae per tree, and are highly visible (Hartland-Rowe 1992). In contrast, *G. rufobrunnea* is solitary (Hartland-Rowe 1992), although up to 30 final instar larvae have been observed on the branch of a mopane tree (J. Klok, personal observation). Aggregations of final instar larvae of *G. postica* are assumed to become aggregations of pupae, at least at the tree level, because larvae are unlikely to leave their food-plant to pupate. The same will hold for *G. rufobrunnea* when found on trees higher than three metres, as they frequently pupate on non-host species (Hartland-Rowe 1992) when host trees are smaller than three metres.

The effects of abundance and aggregation (defined as pupal abundance at the site scale and number of pupae per tree-branch) are well known in the field of insect herbivore population dynamics (Crawford & Jennings 1989; Cappuccino *et al*. 1995; Bouaïchi & Simpson 2003; Stireman & Singer 2003; Aukema & Raffa 2004). Therefore the effect of *Gonometa* pupal abundance and within-branch aggregation on natural enemy induced mortality was also investigated. We identify the strength of the relationships between parasitism and predation rate with pupal abundance or within-branch aggregation (predation only) of *G. postica* and *G. rufobrunnea*. This allows the direction of potential significant responses of larval parasitoids and pupal predators to *Gonometa* species pupal abundance and aggregation to be estimated.

One additional defensive trait of these species, pupal cocoon structure, was also investigated. Emerging parasitoids must break through the cocoon wall and predators must be able to break open the cocoon to reach the pupae. Therefore, pupal structure may potentially affect natural enemy responses, as has been shown for other species (Danks 2002). We investigated the cocoon properties of these *Gonometa* species in an attempt to explain potential differences found. The properties (surface structure and surface chemical composition) of *Gonometa* species cocoons were examined by scanning electron microscopy (SEM) while cocoon mechanical strength was determined by impact tests. Differences in the surface structure of *G. postica* and *G. rufobrunnea* cocoons were examined after gold plating of the sample (Goodhew 1975) (Accelerating voltage: 20 kV; working distance: 6.0 mm; spot-size: 192; probe current: 19 pA). The chemical composition of structures on the cocoon surface was

determined by energy dispersive system (EDS) analysis of X-rays (Accelerating voltage: 20 kV; working distance: 13.0 mm; spot-size: 473; probe current: 1.5 nA). Depending on the energy dispersed from the sample, the elements on the surface of the sample can be identified (keeping in mind that traces of gold are found due to the gold plating of the sample) (Goodhew 1975).

Finally, differences in the force required to break the cocoons of *G. postica* and *G. rufobrunnea* were determined with an Izod Impact Tester (manufacturer: Ceast, type no. 6546). Cut sections of the cocoon flank were used. Readings (to the nearest 0.05 J) were taken after releasing a 15-Joule swing arm from rest, at 90º (cocoon sections) from the point of impact. Cocoon sections were clamped in such a way that they would be hit perpendicular to the length of the cocoon that the section was taken from. Cocoon sections provided readings independent of cocoon shape and length (between 32-38mm for males and 40-50mm for females, Veldtman *et al*. 2002) and were used to test for possible differences between species and sexes. Between eight and ten individuals of each species-sex combination were used in the trial.

Study Sites

Gonometa postica and *G. rufobrunnea* populations were examined at six and five sites respectively within the known (historic and recent records) distribution range of these species, spanning a distance of 400 km between the two furthest localities for *G. postica*, and 60 km for *G. rufobrunnea* (General introduction, Fig. 5). The localities were Vryburg and Hotazel in North-central South Africa and Gabane, Kumukwane, and Kopong in South-Eastern Botswana for *G. postica* and Shashe and Dumela in North-Eastern Botswana for *G. rufobrunnea* (see Veldtman *et al*. 2002 for further site details). The dominant woody host species utilized by *G. postica* at the first two localities was *Acacia erioloba* and at the final three, *A. tortillis*.

Between one and three sites were selected at each locality, with two at Vryburg (~ 1.5 km apart), three at Shashe (~ 0.1 km apart) and two at Dumela (~ 2.5 km apart). No cocoon harvesting took place within a 1 km radius of these sites prior to and for the duration of the study. Sampling was standardized by delimiting an approximately rectangular area incorporating 100 trees per 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 site selection, with at least three sites per host plant selected.

Surveys of sites commenced in winter (June to July, 2000) and were 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. During each survey the number and fate of newly formed pupae were recorded. In addition, pupae that were found to be alive were re-inspected in a following survey to determine if they had emerged successfully or showed evidence of natural enemy induced mortality. The resulting status of all live individuals in the final survey could consequently not be determined. Newly formed pupae counted in the first, second, third and final survey are referred to as generation one, two, three and four respectively from here on.

Cocoon surveys

Within each site every tree was carefully searched for cocoons. The percentage of pupae with at least one neighbour within a radius of 60 cm was taken as a measure of within-branch pupal aggregation. All cocoons were inspected to determine if the pupa inside the cocoon was i) parasitised, ii) predated by birds, iii) alive, iv) dead as a result of unknown causes or v) had successfully emerged. This was indicated (respectively) by the i) presence of small emergence hole(s), ii) large irregularly shaped hole (>20% of cocoon wall) with no pupal remains, usually in the flank of the cocoon, iii) no holes present and cocoon heavy, iv) no holes present and cocoon light in weight or v) a single large anterior pipe-shaped emergence hole (see Veldtman *et al.* 2004). Generations are readily distinguishable based on cocoon appearance. New cocoons have a dense setal cover and their colour contrasts sharply with older, more faded cocoons. Although cocoons can persist on trees for far longer, cocoons older than the previous generation cannot be accurately assigned to a specific generation and were not considered.

Six koinobiont parasitoid species (parasitoids that emerge after the host has pupated, see Hawkins *et al*. 1992; also known as larval-pupal parasitoid species, Peigler 1994) could be identified from the shape and size of emergence holes left in the cocoon wall of a parasitised pupa (Veldtman *et al.* 2004) (are from here on referred to as pupal parasitoids). Because the number of pupae parasitised or predated is necessarily positively related to the number of available pupae, percentage parasitism or predation was considered (Stireman & Singer 2003). When site parasitism rates are highly variable in space and time, a comparison of maximum attack rates may give valuable insights into the vulnerability of a host species to specific

parasitoid species (Stireman & Singer 2003). Comparing the maximum attack rates of different parasitoid species permits the ecological risk of a host species to each parasitoid species to be determined using an inverse measure of its refuge size from parasitism (e.g. the maximum proportion of individuals failing to escape parasitism) (Stireman & Singer 2003). Maximum parasitism rates for each parasitoid species were taken as the highest rate observed across all sites in each generation with more than 25 or nine pupae (preferred and minimum number respectively) available. For sites with less than nine pupae, maximum parasitism rates were not calculated (Stireman & Singer 2002). Total percentage parasitism across all sites as well as mean (± S.E.) parasitism rate per site for each generation were determined for *G. postica* and *G. rufobrunnea* parasitised by tachinid and hymenopteran parasitoids.

One idiobiont parasitoid species (larval growth/development is arrested after parasitism; Hawkins *et al*. 1992) was recorded by counting the number of 'dwarf' sized cocoons per site (Veldtman *et al*. 2002; Veldtman *et al*. 2004). These cocoons were formed by mid-instar larvae parasitised by ?*Disophrys* sp. (Braconidae). The parasitism of early (second and/or third) instar larvae by ?*Disophrys* sp. is described in detail elsewhere (Veldtman *et al*. 2004). The number of early instar larvae parasitised by ?*Disophrys* sp. (from here on termed a larval parasitoid) was taken to be independent of pupal abundance, as considerably more individuals may have been be available for attack or were killed by other mortality sources (e.g. abiotic), than the number of pupae counted suggest. Consequently, number of pupae attacked and not percentage attacked was used for this parasitoid species.

Statistical analysis

General temporal (within-site, across generations) and spatial variability (within-generation, across sites) in pupal abundance for *G. postica* and *G. rufobrunnea* were expressed as the standard error of the mean and the coefficient of variation (%). Spearman's correlation coefficients were used to test the strength and significance of correlations of pupal abundance between successive generations for both *Gonometa* species. Squared correlation coefficients were also determined to allow direct comparison with the findings of Price *et al*. (1995).

In all analyses involving percentage pupal parasitism and predation, only the first three sampled generations were included because the fourth generation was not re-inspected in a following survey. Furthermore, only those sites with at least 9 pupae per generation were used

in these analyses, because fewer individuals would not permit meaningful calculation of parasitism or predation rates (see Stireman & Singer 2003).

A comparison of percentage parasitism, predation and total mortality between *G. postica* and *G. rufobrunnea* were done with Mann-Whitney U tests (data was not normally distributed). Differences in the number of larvae parasitised by ?*Disophrys* sp. per site and sampled generation (across all generations between *G. postica* with different host plants, and *G. rufobrunnea*) were determined using Kruskal-Wallis ANOVA.

The significance of differences between *G. postica* and *G. rufobrunnea* in maximum parasitism and predation rates was determined by Likelihood Ratio X^2 analyses for generation one to three. Two-way (parasitised vs. not parasitised, and species) contingency table analyses of maximum parasitism frequencies were performed (Zar 1984). Chi-square values were corrected for continuity using the Cochran-correction (Zar 1984). In this the importance of differences in parasitoid assemblages between generations was quantified.

Differences in pupal parasitoid 'assemblages' (parasitism rates and species composition) associated with *G. postica* on different host plants, and *G. rufobrunnea* were quantified using cluster analysis of group averages determined by the Bray Curtis similarity index (PRIMER v. 5.0, Clarke & Warwick 1994; Clarke & Gorley 2001). Because the number of parasitised pupae cannot have a negative relationship with host abundance, the number of parasitised pupae observed for a specific parasitoid species at each site was standardised by dividing it by recorded site host abundance, to give parasitism rate. Because the parasitoid assemblage was dependent on parasitoid species composition (presence-absence) and parasitism rate ('abundance') the contribution of parasitoid species with high parasitism rates were weighted equally with those with low parasitism rates by applying a fourth root transformation to the data (Clarke & Warwick 1994). Analysis of Similarities (ANOSIM) was first used to determine if significant differences between generations in parasitoid assemblages existed for each *Gonometa* species. Thereafter, between species differences in parasitoid assemblage structure were analysed separately for each generation (Clarke & Warwick 1994).

Generalised linear models assuming a Poisson error structure were used to determine the percentage of deviance explained in Tachinidae, Hymenoptera and total parasitoid species richness by pupal abundance for both *G. postica* and *G. rufobrunnea* (Dobson 2002). The significance of differences between slopes estimates for the two species were determined using

the Tukey-Kramer method, where the critical value ($Q_{\alpha[k,v]}$) is from the studentized (q) distribution (see *p*.508 in Sokal & Rohlf 1981).

The relationship between *G. postica* and *G. rufobrunnea* percentage pupal parasitism and bird predation with host abundance, and *G. rufobrunnea* percentage bird predation with within-branch aggregation (% pupae with neighbours) (because only birds attack the pupal stage), was determined by using generalized linear models (binomial distribution, logit link function) (Collett 1991; Hails & Crawley 1992). The relationship between *G. rufobrunnea* percentage parasitism and percentage bird predation was also determined because birds may eat pupae that are parasitised (e.g. especially Dumela sites in the first generation with more than 70% predation).

The significance of possible differences between species and sexes (nested within species) in the impact force required to break cocoon sections were determined using ANOVA. The sections of at least eight individuals per sex of each species were used in the cocoon section trial.

RESULTS

Spatial and temporal variation in abundance

Both *Gonometa postica* and *G. rufobrunnea* have life history traits more typical of eruptive than latent Macrolepidoptera (Table 2). Both species have females with poor flying ability, weak oviposition site preference, and eggs are laid in clusters. However, whereas *G. postica* life history traits matched those of eruptive NH Macrolepidoptera almost perfectly, host plant breadth, larval colouration and aggregation behaviour in *G. rufobrunnea* were more similar to latent species characteristics (Table 2). Therefore, high temporal variability in the abundance of both *Gonometa* species was expected, with *G. postica* populations with possibly higher temporal variability than *G. rufobrunnea*.

Pupal abundance at all sites decreased between the first and third generations sampled irrespective of species or host plant utilised. Between the third to the fourth generation, pupal abundance increased at most sites (Figs. 1a-c). Within-site, across-generation population sizes fluctuations of both species typically ranged between two orders of magnitude (Figs. 1a-c).

Table 2. A comparison of adult and larval life history traits of *Gonometa postica* and *G. rufobrunnea* (this study) with eruptive and non-eruptive Macrolepidoptera of the Northern Hemisphere (see Hunter 1995).

Life history trait	*G. postica*	*G. rufobrunnea*	Northern Hemisphere Macrolepidoptera	
			Eruptive	Non-eruptive
Adults				
Female flying ability	Poor, females larger than males	Poor, females larger than males	Poor, wings reduced or non-functional	Wings fully functional, no sexual dimorphism
Oviposition preference	None	None	None	Yes
Egg clutch size	Clusters	Clusters	Masses or clusters	Single
Larva				
Host breadth	Polyphagous*	Monophagous	Polyphagous	Monophagous or few
Physical defence[#]	Urticating setae	Urticating setae	Spines, urticating setae, etc.	None
Coloration	Not cryptic and palatable	Cryptic	Aposematic	Cryptic
Aggregation behaviour				
(early instars)	Gregarious	Gregarious	Gregarious	Solitary
(late instars)	Solitary or gregarious	Solitary	Solitary or gregarious	Solitary
Pupal cocoon				
Coloration	Not-cryptic	Cryptic	-	-

**G. postica* is feeds on four plant genera in two families and is thus only moderately polyphagous (see text). [#] The cocoons of both *Gonometa* species are also covered by these urticating setae.

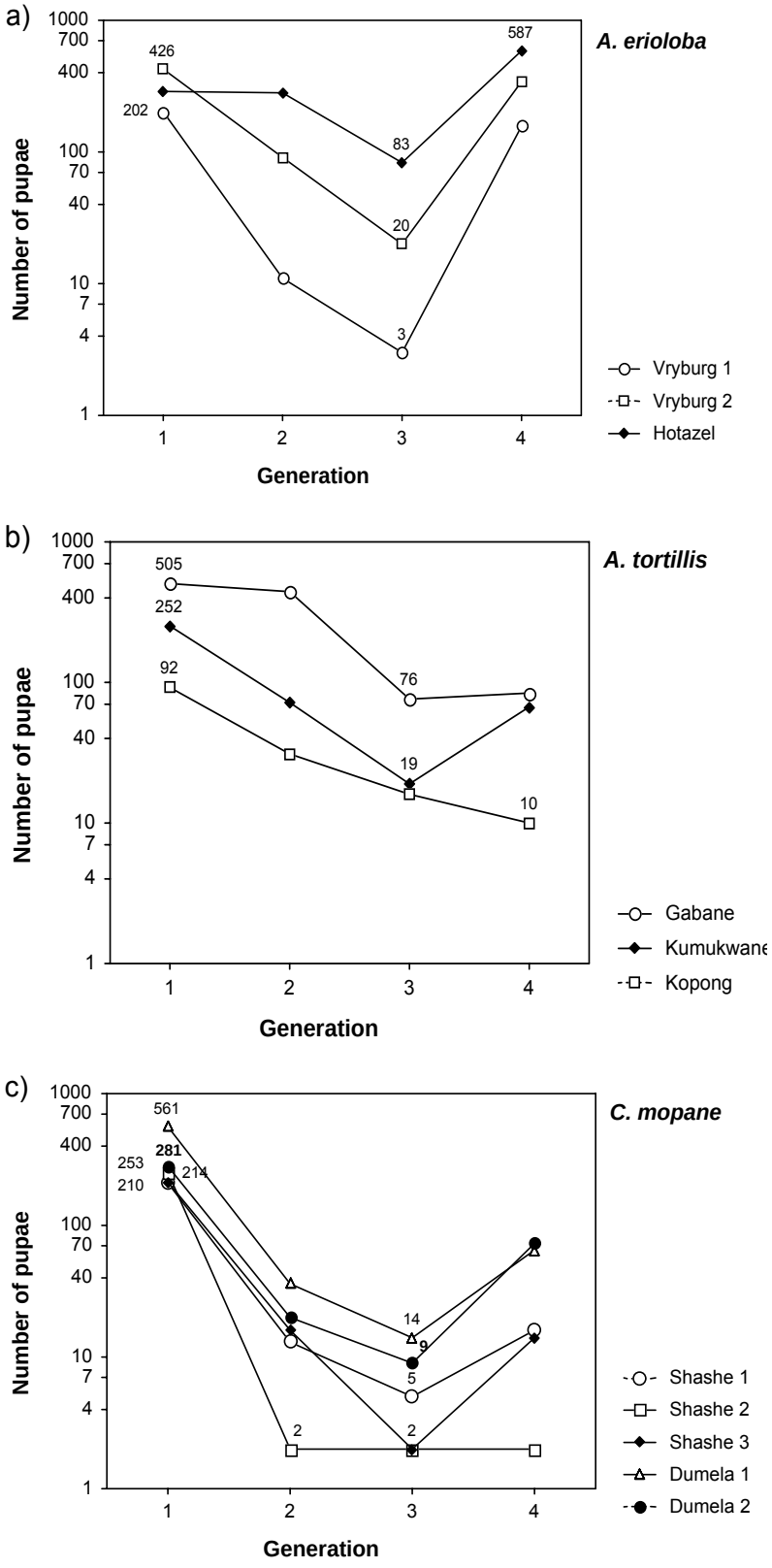

Figure 1. Temporal variation in cocoon abundance for sites: *G. postica* on a) *Acacia erioloba* or b) *A. tortillis* and c) *G. rufobrunnea* on *Colophospermum mopane*. The minimum and maximum number of pupae for each site over the four sampled generations is given.

A comparison of between-generation correlations in pupal abundance revealed *G. postica* abundances to be better correlated between successive generations than *G. rufobrunnea*. *G. postica* (six sites) had two significant correlations (generation 1 vs. 2, $r^2 = 0.785$, $P = 0.019$; generation 2 vs. 3, $r^2 = 0.889$, $P = 0.005$; generation 3 vs. 4, $r^2 = 0.294$, $P = 0.266$) while *G. rufobrunnea* (five sites) had none (generation 1 vs. 2, $r^2 = 0.490$, $P = 0.188$; generation 2 vs. 3, $r^2 = 0.674$, $P = 0.089$; generation 3 vs. 4, $r^2 = 0.760$, $P = 0.054$).

The temporal, within-site coefficient of variation of pupal abundance ranged between 67-109% for *G. postica* and between 132-194% for *G. rufobrunnea* (Table 3). The spatial, within-generation coefficient of variation of pupal abundance ranged between 51-110% for *G. postica* and between 48-96% for *G. rufobrunnea* (Table 3). The within-species comparison for *G. postica*, revealed that sites with different host plants had similar spatial and temporal ranges of variability. *G. rufobrunnea* thus exhibited higher temporal variation in pupal abundance than *G. postica*, whereas both species had similar levels of spatial variability.

Differences in parasitoid mortality rates and assemblage structure

Summing the natural enemy induced mortality of *Gonometa* species pupae across the first three generations indicated that *G. postica* was parasitised twice as frequently by Tachinidae parasitoids than *G. rufobrunnea* (Fig. 2a). In contrast, bird predation rate was 2% for *G. postica* but 40% for *G. rufobrunnea*. The percentage *G. postica* pupae surviving was double that of *G. rufobrunnea* (Fig. 2a). Looking at the three generations separately, this same pattern was evident for the first generation, but became progressively more different in the second and third generation (Fig. 2b-d). Across the first three generations *G. rufobrunnea* had significantly higher percentage bird predation ($Z = -3.755$, $P < 0.001$) and percentage total mortality ($Z = -2.281$, $P = 0.023$) than *G. postica*, although percentage parasitism did not differ ($Z = 0.212$, $P = 0.832$). Across all four generations, *G. postica* at sites with *A. erioloba* as host plant suffered higher mortality from the larval parasitoid species, ?*Disophrys* sp., than either *G. postica* on *A. tortillis* or *G. rufobrunnea* ($H = 15.885$, $P < 0.001$). Imposed mortality on *G. postica* on *A. tortillis* and *G. rufobrunnea* did not differ significantly from each other.

Table 3. Temporal, within-site variability (n = number of sites per species or host plant) and spatial, within-generation variability (n = number of sampled generations) in pupal abundance for *G. postica* and *G. rufobrunnea*. %CV = coefficient of variation.

Species	Temporal variability (within site, across generations)		Spatial variability (within generation, across sites)							
Site	Gen 1-4		Gen 1		Gen 2		Gen 3		Gen 4	
	mean ± SE	%CV	mean ± SE	%CV	mean ± SE	%CV	mean ± SE	%CV	mean ± SE	%CV
G. postica										
Vryburg 1	93.3 ± 50.7	108.7								
Vryburg 2	219.8 ± 97.5	88.7								
Hotazel	309.8 ± 103.9	67.1								
Gabane	276.8 ± 114.3	82.6								
Kumukwane	102.5 ± 51.2	100.0								
Kopong	37.3 ± 18.8	100.8								
Across sites			294.2 ± 61.4	51.1	154.7 ± 69.6	110.2	36.2 ± 14.0	94.5	207.8 ± 89.2	105.1
G. rufobrunnea										
Shashe 1	61.0 ± 49.7	163.0								
Shashe 2	64.8 ± 62.8	193.8								
Shashe 3	61.5 ± 50.9	165.6								
Dumela 1	169.0 ± 131.1	155.1								
Dumela 2	95.8 ± 63.3	132.2								
Across sites			303.8 ± 65.6	48.3	17.4 ± 5.5	71.0	6.4 ± 2.3	80.1	34.0 ± 14.5	95.6

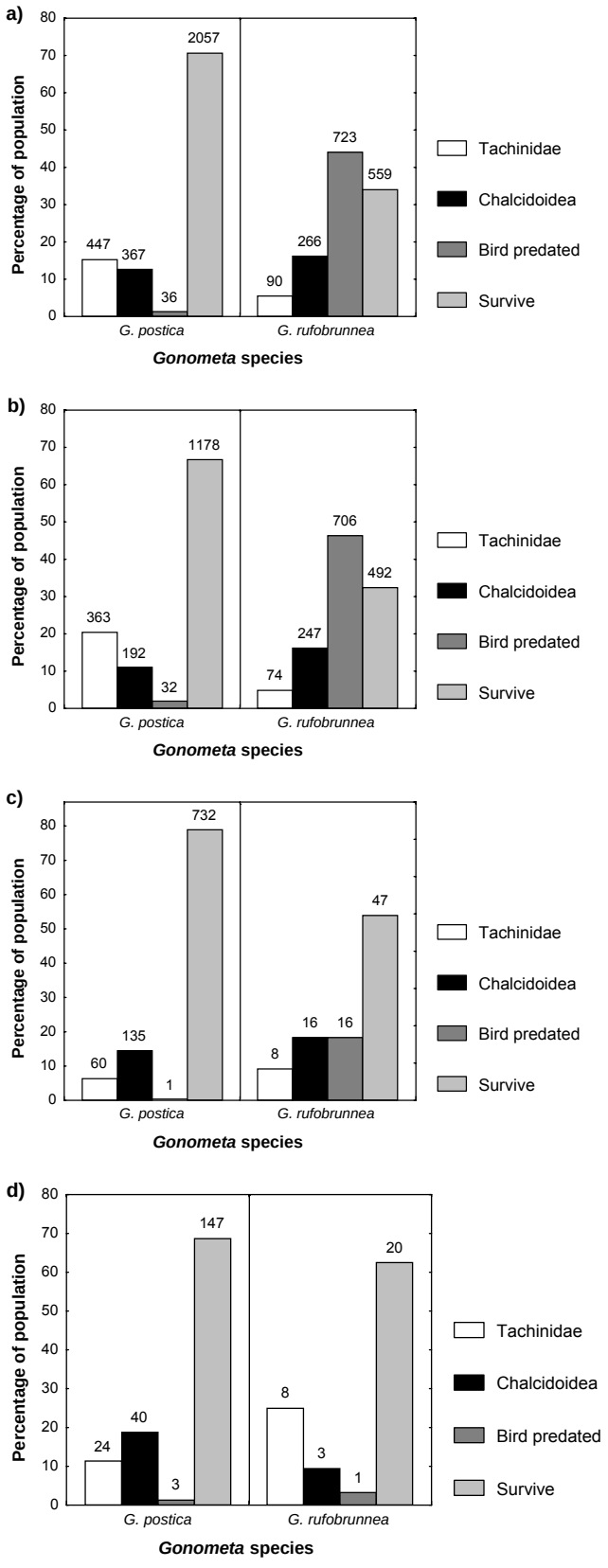

Figure 2. Percentage *G. postica* and *G. rufobrunnea* pupae parasitised by Tachinidae and Chalcidoidea parasitoid species, percentage predated by birds, as well as the percentage surviving. Data is presented for a) all three generations combined, as well as for the b) first, c) second and d) third generations. Number above bar indicates number of pupae.

Differences in mean Tachinidae and Hymenoptera parasitism rates were not significant for *G. postica* in generation one (Z = 1.524, P = 0.128), two (Z = -0.241, P = 0.810) or three (Z = -0.626, P = 0.530). For *G. rufobrunnea*, however, hymenopteran parasitism rate was significantly higher than that of Tachinidae species in generation one (Z = -2.611, P = 0.009), although not in generations two (Z = 0.145, P = 0.885) or three (Z = 0.408, P = 0.683). However, Tachinidae parasitoid species associated with *G. postica* had significantly higher maximum parasitism rates (Table 4) than *G. rufobrunnea*. For the hymenopteran parasitoid, *Kriechbaumerella* sp., and bird predation, the pattern was reversed with significantly greater maximum mortality rates observed for *G. rufobrunnea*. Tachinidae species maximum parasitism rates were higher only for the first sampled generation, but *Kriechbaumerella* sp. parasitism and bird predation were also significantly different (although with bias) in the second generation (Table 4). The remaining parasitoid species did not differ in maximum parasitism rate between the two host species. Thus *G. postica* and *G. rufobrunnea* differed only in ecological risk with respect to bird predation, and Tachinidae and *Kriechbaumerella* sp. parasitism.

Despite *G. postica* and *G. rufobrunnea* larvae and pupae both having urticating seta, the response of Tachinidae parasitoids and bird predation was only correctly predicted for *G. postica* (Table 5). Response predictions based on appearance were incorrect for both host species considering any of the natural enemies considered (Table 5). Based on species aggregation behaviour, the response of tachinid parasitoids was correctly predicted, with low rates of parasitism for the solitary *G. rufobrunnea*, and high rates for the gregarious *G. postica*. However, neither hymenopteran parasitoid nor bird predation rate was correctly predicted based on species aggregation behaviour (Table 5). Predicted and observed responses of natural enemies to *G. postica* and *G. rufobrunnea* defensive traits thus did not show clear support for a defensive trait – natural enemy response relationship.

Table 4. Maximum percentage parasitism and predation of pupae (> 25 pupae present per site; > 9 are shown in brackets) for *G. postica* (six sites) and *G. rufobrunnea* (five sites) in four successive generations (e.g. Gen 1). Significant differences in maximum attack rates between *G. postica* and *G. rufobrunnea* are shown. $X^2_{c'}$ denote Cochran-corrected chi-square values. ** and *** denote p < 0.01 and 0.001.

Parasitoid species or Predator	Maximum percentage parasitism and predation								
	G. postica			*G. rufobrunnea*			Likelihood Ratio $X^2_{c'}$		
	Gen 1	Gen 2	Gen 3[1]	Gen 1	Gen 2[1]	Gen 3[3]	Gen 1	Gen 2	Gen 3
Tachinidae									
Pimelimyia semitestacea	19.5	9.7	9.2 (20.0)	2.4	11.1	(14.3)	34.35***	0.11	0.94
?*Palexorista sp.*	59.9	2.8	1.2 (25.0)	1.4	(7.7)	(22.2)	167.18***	1.21	0.24
?*Tachinidae sp.*	11.5	1.4	1.3 (12.5)	4.2	(6.3)	0	7.38**	0.06	0.54
Chalcididae									
Brachymeria sp.	17.8	16.7	15.8 (21.1)	12.4	2.8	(11.1)	2.97	0.12	0.96
Kriechbaumerella sp.	3.1	5.0	2.6 (5.3)	14.3	(30.8)	0	26.41***	11.17***†	1.06
Eurytomidae									
Eurytoma transvaalensis	1.6	2.9	3.6 (15.8)	1.4	0	(11.1)	0.13	1.14	0.33
Bird predation	7.6	3.2	2.4	79.0	43.8	(7.1)	146.06***	9.57**††	0.01

† Analyses with an expected value(s) < 1; †† analyses with more than 20% of expected values < 5. All X^2 analyses except those underlined remained significant after sequential Bonferroni correction. Numbers in superscript indicate the number of sites sampled with less than nine pupae.

Table 5. Predicted responses of *G. postica* and *G. rufobrunnea* natural enemies based on selected Lepidopteran larval defensive traits from the literature. Support for predictions based on defensive traits as indicated by observed (Obs.) natural enemy responses (mortality rates) is indicated as 'yes' (Y) and 'no' (N). 'ne' indicates no effect was predicted from literature for the response of a particular natural enemy to a specific defensive trait.

Defensive trait	Character state	Parasitism rate				Predation rate	
		Tachinidae[1]		Hymenoptera[2]		Bird[3]*	
		Predicted	Obs.	Predicted	Obs.	Predicted	Obs.
G. postica							
Host plant breadth	Oligophagy	ne	-	ne	-	low	Y
Physical defence	Urticating seta	high	Y	ne	-	low	Y
Appearance	Not-cryptic (and palatable)	low	N	ne	-	high	N
Aggregation behaviour	Gregarious	high	Y	high	N	high	N
G. rufobrunnea							
Host plant breadth	Monophagy	ne	-	ne	-	high	Y
Physical defence	Urticating seta	high	N	ne	-	low	N
Appearance	Cryptic	high	N	ne	-	low	N
Aggregation behaviour	Solitary	low	Y	low	N	low	N

Source of predictions on natural enemy responses: [1] Stireman & Singer 2003; [2] Gentry & Dyer 2002; [3] Brower 1958. All *Gonometa* species life history information is from Hartland-Rowe 1992. *Defensive traits of pupal stage instead of the larval stage are considered.

The parasitoid assemblage of *G. rufobrunnea*, but not *G. postica*, was significantly different between generations (Table 6). Separate analysis of the pupal parasitoid assemblages of *G. postica* and *G. rufobrunnea* in generation one, as well as two and three, indicated significant differences between species and host plant groupings (Table 6). No significant between-host plant difference in the parasitoid assemblage was found for *G. postica* (Table 6). Pupal abundance explained more variation in hymenopteran and total parasitoid species richness for *G. rufobrunnea* than for *G. postica*, with all relationships being positive (Table 7). A relationship between Tachinidae species richness and pupal abundance was significant for *G. rufobrunnea* only. *Gonometa rufobrunnea*'s Tachinidae and Hymenoptera parasitoid species richness was 40 % and 23 % better explained by pupal abundance than for *G. postica* (Table 7). Thus, generally parasitoid species richness was better explained by pupal abundance for *G. rufobrunnea* than *G. postica*, although the regression slopes were not significantly different between the two species.

Pupal abundance and within-branch pupal aggregation were significantly positively related, with pupal abundance explaining at least 60 % of the variation in within-branch pupal aggregation (Table 8). Percentage Tachinidae and Hymenoptera parasitism, and percentage predation recorded for *G. postica* pupae across the first three generations per site showed no significant relationship with pupal abundance (Table 8). Percentage predation was also not significantly explained by within-branch pupal aggregation (Table 8). For *G. rufobrunnea*, however, percentage parasitism by Tachinidae was significantly negatively related to pupal abundance, while percentage bird predation was significantly positively related to within-branch aggregation (Table 8). Percentage parasitism by Tachinidae and percentage pupal predation were also negatively related. Thus, percentage natural enemy-induced mortality of *G. rufobrunnea*, but not *G. postica*, was related to pupal abundance and within-branch pupal aggregation.

Table 6. Differences in the parasitoid assemblages of *Gonometa postica* and *G. rufobrunnea* using ANOSIM (analysis of similarities). Global R-values approaching one indicate strong dissimilarity.

Category Group	Comparison	Global R	P -value
Generation			
G. postica	-	0.038	0.283
G. rufobrunnea	-	0.480	0.001
	Gen 1 vs. Gen2	0.375	0.008
	Gen 1 vs. Gen3	1.000	0.048
	Gen 2 vs. Gen3	0.321	0.200
Species			
Generation 1	*G. postica vs. G. rufobrunnea*	0.184	0.074
Generation 2 & 3	*G. postica vs. G. rufobrunnea*	0.240	0.031
Host plant			
Generation 1	-	0.474	0.005
	A. erioloba vs. *A. tortillis*	0.296	0.100
	A. erioloba vs. *C. mopane*	0.456	0.036
	A. tortillis vs. *C. mopane*	0.549	0.018
Generation 2 & 3	-	-0.070	0.765

Table 7. Relationships between parasitoid species richness and pupal abundance for both *G. postica* and *G. rufobrunnea* sampled in the first to third generation (generalised linear models, Poisson distribution). The percentage deviance explained (%DE) and slope of the coefficient is shown. *, ** and *** denote significance at $P < 0.05$, 0.01 and 0.001 respectively. Significant regression slopes were not significant between the two host species ($\alpha = 0.05$).

Type of parasitoid species richness	*G. postica* (n = 17; df = 15)			*G. rufobrunnea* (n = 11, df = 9)		
	%DE	X^2	Slope (± SE)	%DE	X^2	Slope (± SE)
Tachinidae	13.4	2.48	0.0008 ± 0.0005	53.3	9.58**	0.0018 ± 0.0006
Hymenoptera	24.2	4.97*	0.0012 ± 0.0005	47.1	8.42**	0.0015 ± 0.0005
All	40.8	10.69**	0.0010 ± 0.0003	64.6	16.55***	0.0016 ± 0.0004

All significant regressions, except those underlined, remained significant after column wide false discovery rate correction (García 2004).

The surface of *G. postica* cocoons was found to be almost uniformly covered with crystals (Figs 3a & b). In contrast, the crystal coverage of *G. rufobrunnea* was limited to the areas between surface fibres, appearing as small patches of crystals (Figs 4a & b) (results similar across six cocoons examined per species). The crystals were consequently responsible for the white colour of a *G. postica* cocoon, and the white speckles on a *G. rufobrunnea* cocoon. EDS-analysis of X-rays indicated that the crystals of both species consisted predominantly of calcium (possibly calcium oxalate, see Macnish *et al*. 2003) (Fig. 5). A highly significant difference in impact strength necessary to break the cocoon surface was found between the species (*G. postica* greater than *G. rufobrunnea*), and to a lesser extent between the sexes of each (females greater than males) (Species: $F_{(1,34)} = 33.03$, $P < 0.001$; Sex: $F_{(2,34)} = 7.20$, $P = 0.002$) (Fig. 6).

Table 8. The relationship between *G. postica* and *G. rufobrunnea* pupal abundance and percentage pupal parasitism and bird predation, as well as *G. rufobrunnea* within-branch aggregation (% pupae with neighbours) with percentage bird predation is shown (generalized linear models, binomial distribution). The relationship between *G. rufobrunnea* percentage parasitism and bird predation, as well as between within-branch aggregation and pupal abundance is also shown.

Dependent variable	Independent variable	Scaled dev/d.f.	% DE	Slope	χ^2	P
G. postica (15 df)						
% pupae with neighbours	$\log_{10}$(pupal abundance)	1.114	63.1	+	28.55	<0.001
% Tachinidae parasitism	$\log_{10}$(pupal abundance)	0.877	3.8	ns	0.51	0.474
% Hymenoptera parasitism	$\log_{10}$(pupal abundance)	0.922	2.6	ns	0.37	0.545
% Predation	$\log_{10}$(pupal abundance)	0.809	1.8	ns	0.22	0.636
	% pupae with neighbours	0.883	12.7	ns	1.92	0.166
G. rufobrunnea (9 df)						
% pupae with neighbours	$\log_{10}$(pupal abundance)	1.097	76.4	+	32.01	<0.001
% Tachinidae parasitism	$\log_{10}$(pupal abundance)	1.032	49.0	-	8.92	0.003
	% Predation	1.040	32.3	-	4.47	0.034
% Hymenoptera parasitism	$\log_{10}$(pupal abundance)	1.086	5.6	ns	0.58	0.444
	% Predation	1.014	0.2	ns	0.01	0.906
% Predation	$\log_{10}$(pupal abundance)	1.034	26.3	ns(+)	3.32	0.068
	% pupae with neighbours	1.087	45.9	+	8.30	0.004

All significant regressions, except those underlined, remained significant after column wide false discovery rate correction (García 2004).

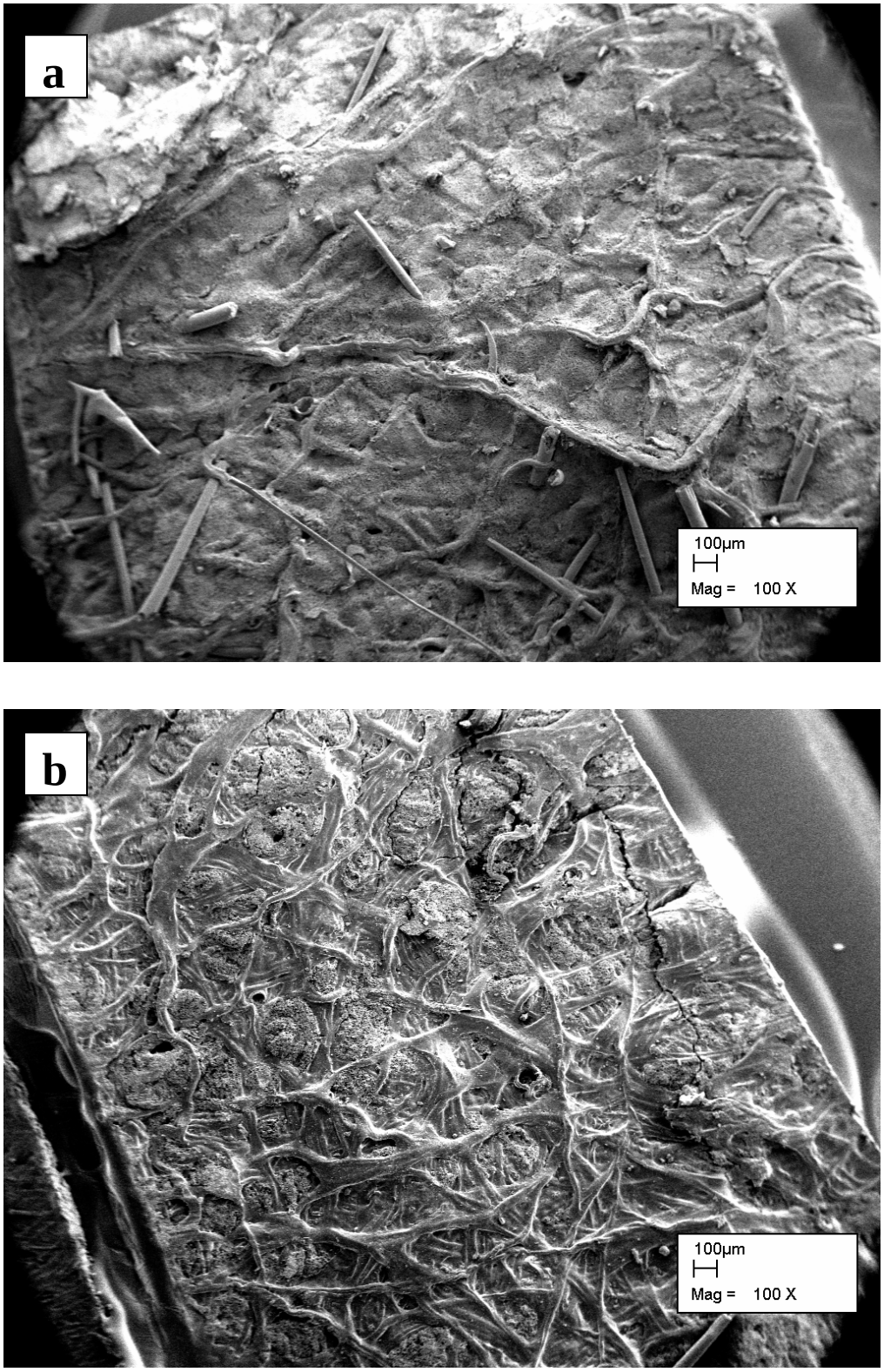

Figure 3. Outer cocoon surface of representative *G. postica* (a) and *G. rufobrunnea* (b) cocoons at low magnification.

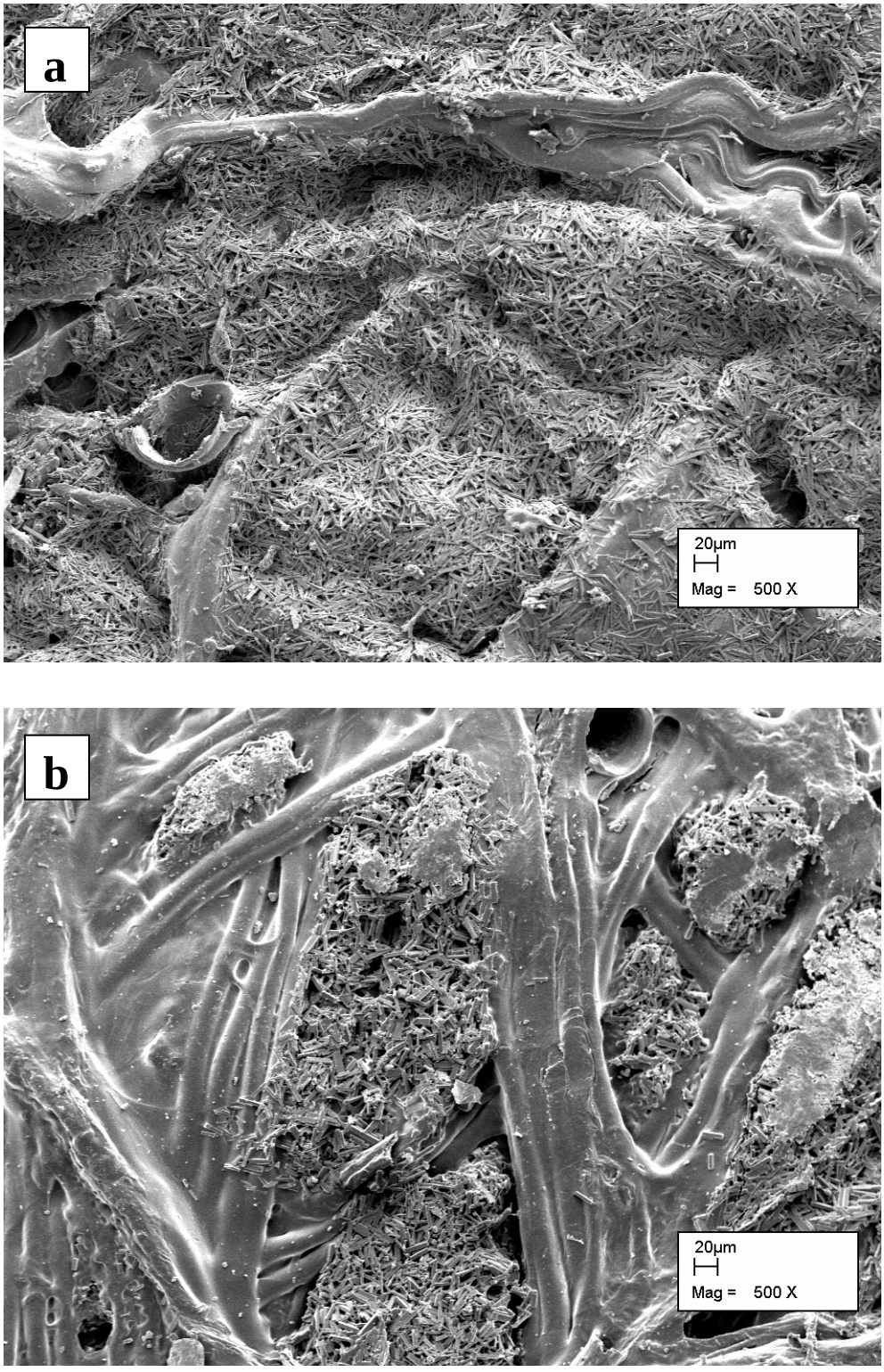

Figure 4. Outer cocoon surface of representative *G. postica* (a) and *G. rufobrunnea* (b) cocoons at high magnification.

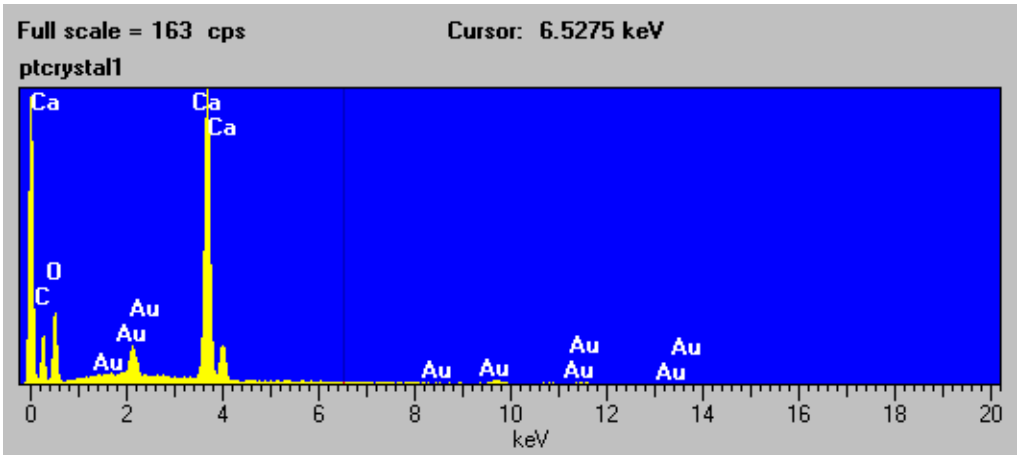

Figure 5. Example output of EDS X-ray analysis of crystals (possibly calcium oxalate – CaC_2O_4) observed on the cocoon surface of *G. postica* and *G. rufobrunnea*. Ca = calcium, C = carbon, O =oxygen, and Au = gold.

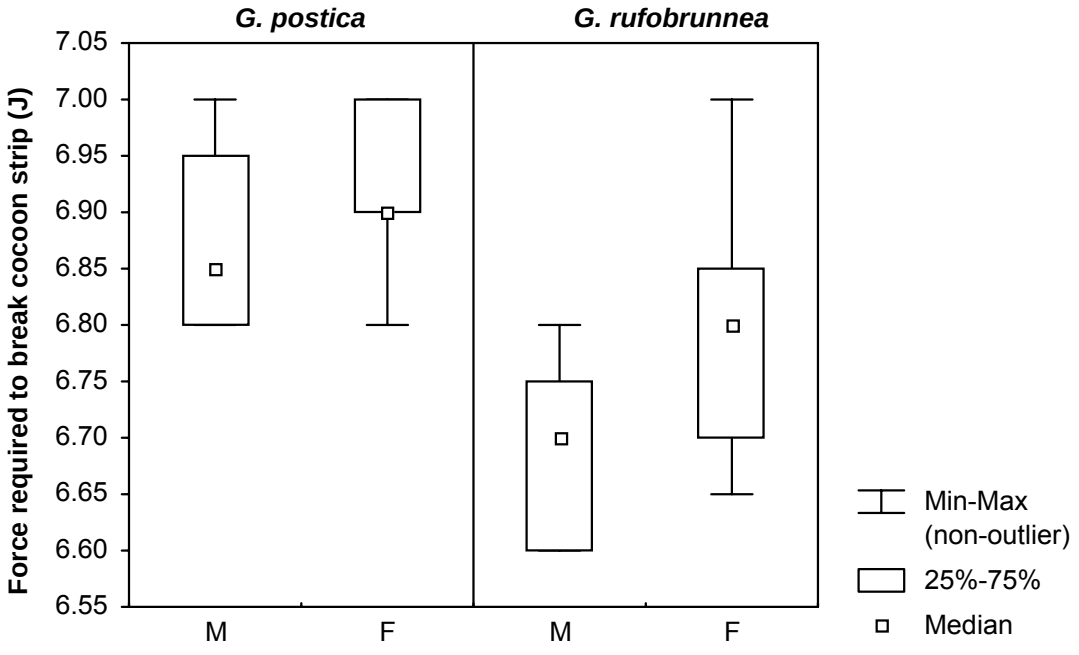

Figure 6. The effect of species and sex (M, F) (nested within species) on the force required to break a section of the cocoon wall of *G. postica* and *G. rufobrunnea* (n = 8 or more per species sex grouping).

DISCUSSION

Life history trait – population dynamics relationship

Pupal abundance of both *Gonometa* species in this study ranged between two orders of magnitude across the four surveyed generations at a total of 11 sites. This is lower than the three to five orders of magnitude change in population size reported for eruptive Macrolepidoptera (Price *et al*. 1990). Based on the population size variability quantified in this study both *Gonometa* species would thus be classified as latent species. However, due to the limited duration of the study potentially larger fluctuations may not have been observed. If this were indeed the case, both *Gonometa* species may have been in an endemic phase for the duration of this study. Nonetheless, although these sites were not randomly selected, they covered a wide geographic area, and even across site comparisons revealed population size fluctuations of no more than two orders of magnitude. This suggests that if *Gonometa* species are indeed eruptive, these eruptions are infrequent, occurring at a minimum frequency of five generations. Longer-term population monitoring of these species is therefore necessary to confirm their type of population dynamics.

Nonetheless, results on the extent of temporal population variability in *Gonometa* species as well as between-generation correlations suggest that *G. rufobrunnea* is somewhat more eruptive than *G. postica*. This is despite *G. rufobrunnea* having two traits (host breadth and larval coloration) more typical of latent Macrolepidoptera than *G. postica* (Hunter 1995). However, between-generation correlations for both species were substantially weaker (in the order of 50-80 % r^2) than those documented for a classic latent species, *Euura lasiolepis*, with squared correlation coefficients of 90% or more (Price *et al*. 1995). In contrast, the eruptive European pine sawfly (*Neodiprion sertifer*), which fluctuates between three to four orders of magnitude, between endemic to epidemic phases, shows only infrequent significant between-generation correlations (Lyytikäinen-Saarenmaa *et al*. 1999). Of the three between-generation comparisons made per species, correlations were significant in two cases for *G. postica* and near significant in two cases for *G. rufobrunnea*. Therefore, this suggests that *Gonometa* species fit somewhere in between the two extremes of the population dynamics gradient. The life history trait differences between these species could, however, not be used to successfully predict more subtle between-species differences in the degree of eruptiveness (variability).

Eruptive-latent classifications are thus useful for predicting species population dynamics, provided that they fit one of these categories well, but for intermediate species predictions are difficult (Leyva *et al*. 2003; Ribeiro *et al*. 2003).

The apparent spatial synchrony observed in the temporal changes in population abundance across all sampled sites provides some insight into the possible cause of population size fluctuations in these *Gonometa* species. In this study all populations, independent of the distance between them (which ranged from 0.1 km to 400 km), showed a similar decline from the first to the third generation, and most populations showed an increase from the third to fourth generation. Spatial synchrony in population dynamics has been shown to decline with distance (Buonaccorsi *et al*. 2001; Peltonen *et al*. 2002). The population dynamics observed in this study therefore suggest broad-scale spatial synchrony. Mechanisms underlying spatial synchrony include dispersal patterns, tropic interactions (natural enemy induced mortality) and the influence of environmental variables (the so-called Moran effect) (Peltonen *et al*. 2002; Jones *et al*. 2003). Research on the mitochondrial-DNA variation of *G. postica* reveals little genetic structuring of populations, and therefore apparently fairly frequent dispersal of individuals between them (Delport *et al*. 2003). However, evidence for the ability of dispersal to synchronise population dynamics in butterflies has so far been found to operate only at local scales of a few kilometres (Sutcliffe *et al*. 1996). Natural enemy induced mortality was highly variable in space and time and is therefore unlikely to be responsible for population synchronicity. At a regional scale (100 to 300 km) populations may show broad patterns of synchrony due to spatial correlation in climate (Sutcliffe *et al*. 1996; Koenig 2002; Jones *et al*. 2003). For eruptive forest Lepidoptera and other insects it has been shown that population synchrony at a regional scale is well explained by spatial correlation in climatic variables (Peltonen *et al*. 2002). Predictions of locust outbreaks across southern Africa have shown strong correlations between the previous year's rainfall and the population size of locusts in the following year (Todd *et al*. 2002). In *Gonometa* species large-scale population decline may be caused by heavy rainfall that results in high early instar mortality (see Hartland-Rowe 1992). During population surveys in the winter of 2000 (observing number of pupae per site every 20 km along major roads) a large region in the north of Northern Cape Province had very low population sizes (one pupa per site). These observations corresponded with reports of

exceptional heavy summer rainfall in the area. Therefore, the apparent synchrony observed in both *Gonometa* species populations is most likely a consequence of regional climatic patterns.

Although there was evidence for broad scale spatial synchrony in pupal abundance in *Gonometa* species, pupal abundances at adjacent sites (within two kilometres of each other) were often an order of magnitude different. This demonstrates the highly patchy distribution of these species and population asynchrony at a local scale. Population asynchrony can reduce temporal variation in population size at a local scale, when increasing and declining populations cancel each other out (Ranius 2001). Such asynchrony between neighbouring populations may be due to dispersal (Sutcliffe *et al*. 1996) or natural enemy induced mortality (Berryman 1996; Maron *et al*. 2001; Jones *et al*. 2003).

Relationship between defensive traits and natural enemy responses

In general, defensive traits were found to be poor and inconsistent predictors of mortality rate in *Gonometa* species. In addition, although there were interspecific differences in natural enemy responses (e.g. bird predation), responses could not be explained by differences in these species defensive traits, although similar traits have been shown to be important elsewhere (Brower 1958; Dyer & Gentry 1999; Gentry & Dyer 2002; Stireman & Singer 2003). However, *G. rufobrunnea* percentage parasitism (Tachinidae) and predation were related to pupal abundance and within-tree aggregation respectively. This suggests that cocoon crypsis in *G. rufobrunnea* may be effective at limiting the risk to visually-based bird predation as long as cocoons occur at low branch densities (Guilford 1992). *G. postica* pupae, however, were not predated by birds, irrespective of their abundance or level of aggregation. This is contrary to expectations as palatable, non-cryptic species are often heavily impacted by predators (Brower 1958, Dyer & Gentry 1999). Differences in predation between these *Gonometa* species are unlikely to be due to more predatory birds species in Mophane veld (*C. mopane* sites) compared to *Acacia* veld. Roller (*Coracias*) and hornbill (*Tockus*) species, which are the likely predators of cocoons (Hartland-Rowe 1992), generally occur at all sites of this study (Harrison *et al*. 1997). However, the pupal cocoon structure differences documented for these two *Gonometa* species may explain the interspecific differences in natural enemy responses found. The calcium layer on the outer cocoon wall was found to be related to the force required to break the cocoon surface. The cocoons of *G. postica*, which are completely covered by calcium

crystals, require a significantly greater force to break. Therefore, birds may be able to penetrate the cocoons of *G. rufobrunnea* more readily than those of *G. postica*, making *G. rufobrunnea* pupae a more viable food resource for birds. This was not simply an environmental effect because the interspecific crystal coverage difference is visible with the naked eye, and explains the documented cocoon colour difference between these *Gonometa* species (Veldtman *et al*. 2002).

Between-species differences in bird predation may also explain the patterns of parasitism observed in this study. Tachinidae species richness has been shown to increase with the abundance of non-aposematic but not aposematic Lepidoptera (Stireman & Singer 2003). Parasitoids use their host for a large portion of their life cycle, there is therefore a selective advantage to using a host species that has a lower probability of predator attack – so called "enemy free space" (Jeffries & Lawton 1984; see Berdegue *et al*. 1996 for hypotheses that require testing). Therefore, a host protected from bird predation (i.e. aposematic hosts) may represent enemy free space for Tachinidae (Stireman & Singer 2003). Similarly, therefore, the relative resistance of *G. postica* pupae to bird predation may result in greater total and maximum Tachinidae species parasitism rates in *G. postica* than in *G. rufobrunnea* populations. However, this hypothesis is not supported by the observed increase in *G. rufobrunnea*'s tachinid parasitism rates when pupal predation was low, which indicates that *G. rufobrunnea* is also utilised by tachinids. Furthermore, *G. postica* and *G. rufobrunnea* cocoons collected from areas close to Gabane and Dumela during the fourth generation survey, both had very high *Pimelimyia semitestacea* (Tachinidae) parasitism rates (59 % (n = 94) and 53 % (n = 123)). Therefore, an alternative explanation for greater parasitism of *G. postica* by tachinids is that parasitoid species use both species opportunistically, but that tachinids are more severely affected by bird predation than hymenopteran parasitoids. Tachinids and birds both use visual cues for location of their host (Brower 1958; Stireman & Singer 2003), if both prefer to attack larvae or pupae at high densities, cocoons containing tachinid parasitoids may suffer greater bird predation. Hymenopteran parasitoids may use different cues (e.g. they may attack larvae at low within branch aggregations) and consequently are not negatively affected by parasitising hosts at high within-branch aggregations that are greatly at risk from bird predation (i.e. *Kriechbaumerella* sp.). It has been shown that predators exploit all diprionid sawfly cocoons in a patch while Ichneumonidae parasitoids parasitise only a few (Herz & Heitland 2003).

Therefore, although cocoon structure of *Gonometa* species potentially explain patterns of bird predation, alternative factors such as host-patch selection need to be determined to explain the patterns in parasitism found. The observed response of natural enemies to their host's defensive traits or abundance is thus complex, and may be due to interactions between different natural enemies depending on their characteristics (i.e. behaviour).

The dominant enemies for these *Gonometa* species, as well as the level of parasitism and predation have been quantitatively determined for the first time. However, a caveat in all recorded natural enemy responses in this study is that the effects of temporal variation and *Gonometa* species abundance on natural enemy responses cannot be separated. Whether natural enemies would respond in a similar way in a following generation of high pupal abundance is not known. However, because both *Gonometa* species showed similar population decline from generation one to three, interspecific comparisons of natural enemy responses are valid. The consistent differences between *G. postica* and *G. rufobrunnea* natural enemy induced mortality rates, parasitoid species richness, assemblage structure, mortality as a function of abundance and aggregation, make it unlikely that observed natural enemy responses were simply due to chance. Furthermore, the spatial and temporal scale of pupal surveys (2907 *G. postica* cocoons, and 1627 *G. rufobrunnea* cocoons) in this study (Fig 2 a-c) and pupal collections (1177 *G. postica* cocoons, and 542 *G. rufobrunnea* cocoons) from these and additional areas (over five generations in total from four additional regions to those surveyed) make the discovery of other common or moderately common parasitoid species unlikely. If rare parasitoid species were missed, they would have very low attack rates and therefore unlikely to have a significant influence on the mortality rates reported here. Therefore, although the temporal duration of this study was short and the responses of natural enemies highly variable, the effects of *Gonometa* species defensive traits on their enemies' responses could be evaluated.

Accurately predicting an unstudied insect herbivore's population dynamics and the responses of its natural enemies remains a difficult goal. This study has thus confirmed that although life history traits may be a useful starting point for interpreting population dynamics or predicting population size ranges (Nylin 2001; Steinbauer *et al*. 2001), these traits cannot be used to predict with certainty that one species is more eruptive than another, even if the species

show phylogenetic dependence. The vast literature on outbreaks of forest insects (e.g. Royama 1984; Teder *et al*. 2000; Speer *et al*. 2001; Peltonen *et al*. 2002) has highlighted the range of factors responsible for the observed population dynamics of these eruptive insects. However, these species are in the minority of herbivore insects (Hunter 1995) and a more in-depth understanding of this relationship may be achieved by investigating less dramatically eruptive species in other systems (see also Price *et al*. 1990; Ribeiro *et al*. 2003). Defensive traits, on the other hand, clearly have more complex effects on natural enemy responses than has been found for some systems (Brower 1958; Larsson *et al*. 1993; Bowers 1993; Dyer & Gentry 1999), especially when several types and taxa of natural enemies (e.g. tachinid and hymenopteran parasitoids, and birds) are involved. Given that between natural enemy interactions and difference in prey selection behaviour may exist, the difficulty in predicting insect herbivores interactions with higher tropic levels is unsurprising. Even with more detailed study and greater taxonomic coverage of herbivore and natural enemies, accurate prediction may just not be possible. This warns against predicting the responses of unstudied insect herbivores natural enemies. However, the progress that has already been made in linking life history traits with eruptive or latent population dynamics is promising. Further study of species with an intermediate position on the population dynamic gradient is likely to provide the generality required.

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