

# Can life-history and defence traits predict the population dynamics and natural enemy responses of insect herbivores?

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**Abstract.** 1. Life-history differences between herbivorous insects with eruptive and latent population dynamics are potentially useful for predicting population size variability. An association has also been demonstrated between herbivorous insect defence traits and the responses of various natural enemies.

2. Here predictions of population dynamics and natural enemy responses based on life-history and defence traits are tested using *Gonometa postica* Walker and *G. rufobrunnea* Aurivillius, two Southern Hemisphere Macrolepidoptera (Lasiocampidae) species. The temporal and spatial variation in pupal abundance and patterns of pupal parasitism and predation for both species are described and quantified for the first time.

3. Eleven sites were sampled over four generations across the region where both species have historically reached high population densities. Although there was evidence suggesting that population synchrony is driven by weather patterns, site-specific environmental differences contributed to the observed population variability. This study is the first to quantify the extent of population size variability of a species with an intermediate position on the eruptive–latent population dynamic gradient, where data on insect population dynamics is scarce.

4. Support for the life-history–population dynamic relationship was found, as intermediate population size variability for these species was observed. Larval and pupal defence traits, however, were poor and inconsistent predictors of mortality rate. Pupal cocoon structure differences, previously documented for these *Gonometa* species, may in fact explain the interspecific differences in natural enemy responses found.

5. Predicted population dynamics and natural enemy responses may, however, be overridden by ecological conditions. Nevertheless, life-history and defence traits provide a useful basis for predicting population dynamics of poorly studied species.

**Key words.** Bird predation, eruptive, *Gonometa*, latent, Macrolepidoptera, parasitism rate, pupa.

## Introduction

Understanding the population dynamics of insects and the responses of their natural enemies has been pivotal in ecological and applied entomological research (e.g. Nothnagle & Schultz, 1987; Cappuccino *et al.*, 1995; Berryman, 1996, 2003; Nylin,

2001). One such research focus is 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). By definition eruptive and latent species exhibit temporal population size fluctuations ranging from three to five and one to two orders of magnitude respectively (Price *et al.*, 1990). Eruptive species are thus more variable, fluctuating between a low (endemic) and high (epidemic) population densities phase, whereas latent species only have an endemic

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phase (Wallner, 1987; Price *et al.*, 1995; Leyva *et al.*, 2003). Another important focus in population ecology is the interaction between natural enemy responses and the dynamics of insect herbivore populations (e.g. Berryman, 1996, 2003; Muzika & Liebhold, 2000). These responses are defined as any relationship between the natural enemy and host (or prey) population size, such as attack rate or natural enemy assemblage size and composition (Gaston *et al.*, 1997; Frears *et al.*, 1999; Gentry & Dyer, 2002; Stireman & Singer, 2003). Finally, an association between natural enemy responses and herbivore defence traits has also been demonstrated (Bowers, 1993; Larsson *et al.*, 1993; Dyer & Gentry, 1999; Louda *et al.*, 2003), indicating a possible three-way interaction between population dynamics, life-history, and natural enemy responses.

Some support for the relationship between emergent population dynamics and species life-history traits (*sensu* Nylin, 2001) has been found. For example, the galling sawfly, *Euura lasiolepis* (Tenthredinidae) deposits eggs singly only in high-quality stems, 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 (wingless vs. winged), larval (gregarious vs. solitary), and over-wintering stage (larvae vs. pupae) traits have also been found to differ between eruptive and latent species of Northern Hemisphere 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 have a mixture of typical eruptive and latent 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 result in such dynamics (see Berryman, 2003). For example, although insects may have life-history traits typical of eruptive species, factors such as host plant distribution (Larsson *et al.*, 1993), predation, and parasitism (Brodmann *et al.*, 1997; Kouki *et al.*, 1998; Maron *et al.*, 2001; Tanhuanpää *et al.*, 2001; Raymond *et al.*, 2002), and abiotic factors (Azerefege *et al.*, 2001) can, either directly or indirectly, significantly alter the population dynamics observed (Björkman *et al.*, 2000; Steinbauer *et al.*, 2001). Nevertheless, the current evidence that different suites of life-history traits tend to be associated with species with eruptive compared with 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).

In contrast to the life-history trait–population dynamics association, the association between herbivorous insect defence traits and the responses of their various natural enemies (Bowers, 1993; Larsson *et al.*, 1993; Dyer & Gentry, 1999; Louda *et al.*, 2003) has been demonstrated, mainly, for Lepidoptera. Here, certain states of larval defence traits (physical defence, see Dyer & Gentry, 1999) are commonly associated with low natural enemy attack rates (or other responses, e.g. species richness) (Appendix 1). Owing to poor global coverage and taxonomic

representation, however, these patterns may not be widespread or consistent across taxa. Also, this limited data availability does not allow possible trade-offs between life-history and defence traits in the literature to be investigated.

Here the life-history trait–population dynamics association, and the host defence trait–natural enemy response relationship for *Gonometa postica* Walker and *G. rufobrunnea* Aurivillius (Lepidoptera; Lasiocampidae), two closely related, Southern Hemisphere Macrolepidoptera species was examined. Both these wild silk moth species are reported to reach eruptive proportions (Edwards, 1935; Zumpt, 1971; Hartland-Rowe, 1992) within central southern Africa, although no quantitative data are available on abundance fluctuations or their frequency. The pupal cocoons of both species are of economic value and are utilised by several small-scale wild silk industries that depend on harvesting natural populations (Veldtman *et al.*, 2002, 2007). The size of population fluctuations in these species, however, are unknown. In general there are limited data on the population dynamics of insects from southern Africa (McGeoch, 2002). This study describes and quantifies 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*. Next, the life-history traits of these *Gonometa* species were compared with those of eruptive and latent Northern Hemisphere Macrolepidoptera, and the comparison used to predict their likely position on the eruptive–latent population dynamics gradient. The extent of temporal and spatial variation in the population size of the two species were then quantified and used to evaluate the accuracy of population dynamics predictions based on life-history traits. Second, the relationship between *Gonometa* defence traits and natural enemy responses (i.e. Bowers, 1993; Larsson *et al.*, 1993; Dyer & Gentry, 1999; Louda *et al.*, 2003) were examined. Only larval defence traits of *G. postica* and *G. rufobrunnea* that are known to affect the responses (percentage induced mortality) of natural enemies to other Lepidoptera (Appendix 1) were considered. Because *G. postica* and *G. rufobrunnea* differ in certain defence traits, whether natural enemy-induced mortality differs between these species was also investigated.

## Methods

### *Life-history and defence traits*

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 defence traits of *Gonometa* species was also gathered from the literature and verified by personal observation.

*Gonometa postica* and *G. rufobrunnea* have pro-ovigenic (emerging adult female has a full complement of eggs available) females, lay eggs in clumps and show no oviposition preference, are bivoltine and over-winter in pupal diapause (Hartland-Rowe, 1992). Diapause is broken in early spring (September–October), and emerging moths mate and lay eggs to form the first generation. Eggs hatch within 2 weeks, and this generation develops for approximately 2 months before final instar larvae start to pupate (November–December). A varying proportion of these pupae undergo rapid development and emerge to give rise to the second generation in mid-summer (December–January), with pupation occurring in early autumn (March–April). The un-emerged first generation pupae and surviving second-generation pupae enter diapause, emerging only the following spring (see also Hartland-Rowe, 1992 for discussion of *G. rufobrunnea*).

*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 plants for *G. rufobrunnea* (Veldtman *et al.*, 2007). 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, pers. obs.). 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 3 m, as they frequently pupate on non-host species when host trees are smaller than 3 m (Veldtman *et al.*, 2007).

The effects of abundance and aggregation (defined as pupal abundance at the site scale and number of pupae per tree-branch respectively) 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. Consequently the strength of the relationship between parasitism and predation rate with pupal abundance or within-branch aggregation (predation only) of *G. postica* and *G. rufobrunnea* was identified. This allows the direction of potential significant responses

of larval parasitoids and pupal predators to *Gonometa* species pupal abundance and aggregation to be estimated.

#### Study sites

*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 utilised by *G. postica* was *A. erioloba* and *A. tortillis*, while *G. rufobrunnea* only utilises *Colophospermum mopane*.

The pupal stage summarises the ecological information of the larval stage (especially final instars) to a large extent. Because in the case of *Gonometa* species adults cannot feed, pupal size summarises the entire magnitude of resources gathered during these insects' lifetime. Consequently, the pupal stage was the only life stage surveyed in this study. Sampling was standardised 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.

Surveys of sites commenced in winter (June–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 (Fig. 1). 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 subsequent survey to determine if they had emerged successfully or showed evidence of natural enemy induced or other mortality. The resulting status of all live individuals in the final survey could consequently not be determined. Newly formed pupae counted in

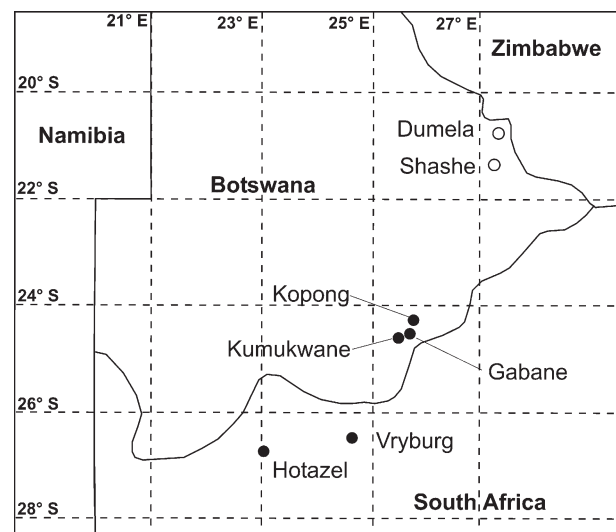


Fig. 1. Localities in South Africa and Botswana where *G. postica* (filled circles) and *G. rufobrunnea* (open circles) were sampled.

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. Cocoons were inspected to determine the status of the pupa: (i) parasitised; (ii) alive; (iii) predated by birds; (iv) dead as a result of unknown causes; or (v) successfully emerged. This was indicated respectively by the: (i) presence, or (ii) absence of small emergence hole(s); (iii) large irregularly shaped hole (>20% of cocoon wall) with no pupal remains, usually in the flank of the cocoon; (iv) light weight of the cocoon; or (v) a single large anterior emergence hole (pers. obs.). 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) (from here on *pupal parasitoids*). Because the number of pupae parasitised or predated can not be negatively related to the number of available pupae, percentage parasitism or predation was considered instead (Stireman & Singer, 2003). In addition, because site parasitism rates are highly variable in space and time, maximum attack rates may give more 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 9 pupae per site (preferred and minimum number respectively) (Stireman & Singer, 2002).

### 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 nine 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.

The significance of differences between *G. postica* and *G. rufobrunnea* in maximum parasitism and predation rates was determined by Likelihood Ratio  $\chi^2$  analyses for generations 1–3. Two-way (parasitised vs. not parasitised, and species) contingency table analyses of maximum parasitism frequencies were performed (Zar, 1984).  $\chi^2$  values were corrected for continuity using the Cochran correction (Zar, 1984). In this the importance of differences in parasitoid assemblages between generations was quantified.

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 (percentage pupae with neighbours) (because only birds attack the pupal stage), was determined by using generalised 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 when predation is more than 50%).

In all regressions, adjustments of  $\alpha$ -level significance for multiple testing was done using false discover rate correction (FDR) (García, 2004).

## 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 1). Both species have females with poor flying ability, weak oviposition site preference, and eggs are laid in clusters. Whereas *G. postica* life-history traits matched those of eruptive Northern Hemisphere Macrolepidoptera almost perfectly, however, host plant breadth, larval coloration, and aggregation behaviour in *G. rufobrunnea* were more similar to the characteristics of latent species (Table 1). Therefore, high temporal variability in the abundance of both *Gonometa* species was expected, with *G. postica* populations possibly exhibiting 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 (Fig. 2a–c). Within-site, across-generation population sizes fluctuations of both species typically ranged between two orders of magnitude (Fig. 2a–c). A comparison of between-generation correlations in pupal abundance

**Table 1.** 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	<i>G. postica</i>	<i>G. rufobrunnea</i>	Northern Hemisphere Macrolepidoptera	
			Eruptive	Non-eruptive
<b>Adults</b>				
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
<b>Larva</b>				
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
<b>Pupal cocoon</b>				
Coloration	Not-cryptic	Cryptic	—	—

\**G. postica* 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.

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,  $r^2 = 0.760$ ,  $P = 0.054$ ).

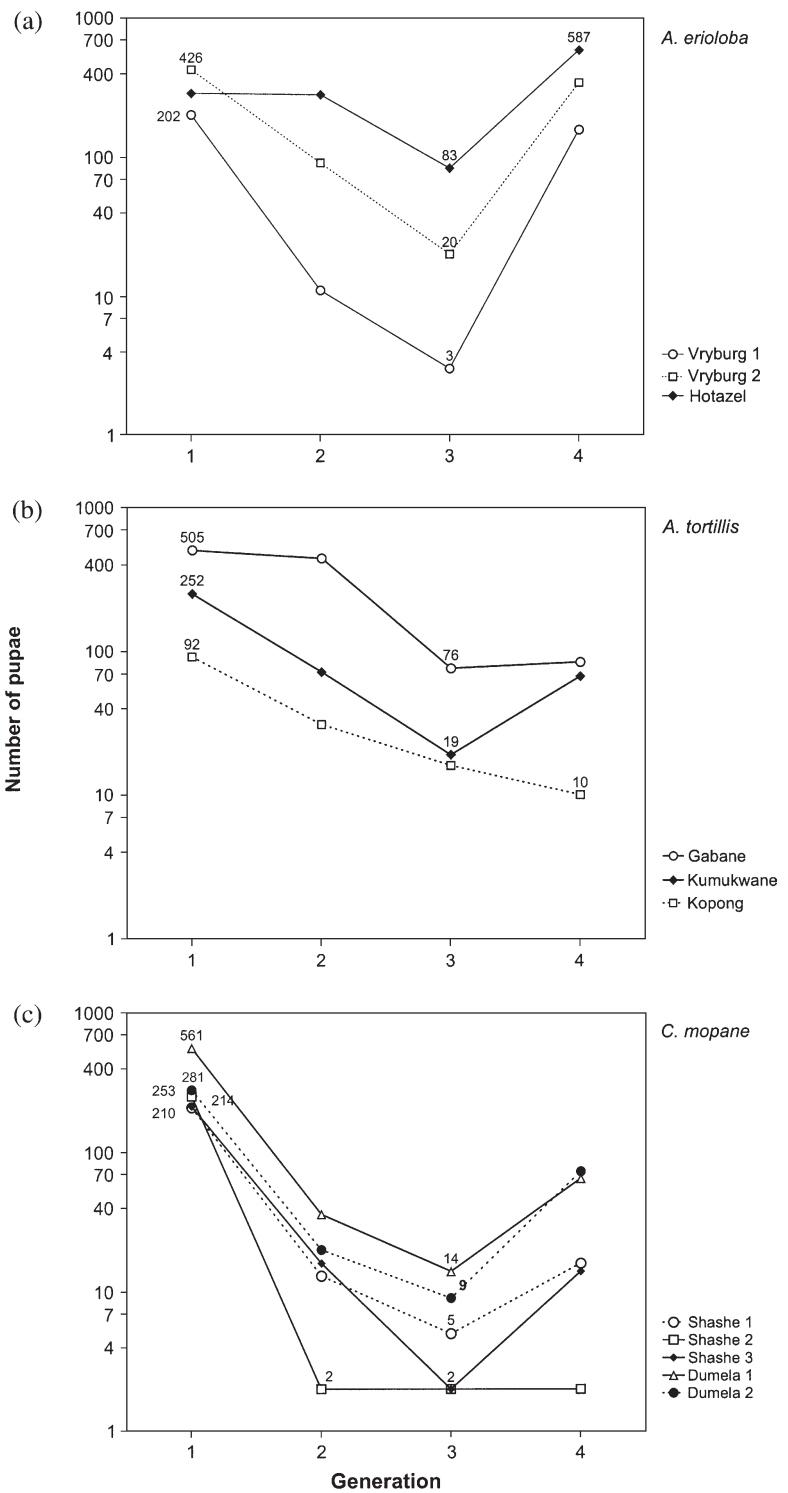
The temporal, within-site coefficient of variation of pupal abundance ranged between 67 and 109% (mean  $\pm$  SE:  $91 \pm 6$ ) for *G. postica* and between 132 and 194% ( $162 \pm 10$ ) for *G. rufobrunnea*. The spatial, within-generation coefficient of variation of pupal abundance ranged between 51 and 110% ( $90 \pm 13$ ) for *G. postica* and between 48 and 96% ( $74 \pm 10$ ) for *G. rufobrunnea*. 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-induced mortality rates.** 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. 3a). In contrast, average bird predation rate was 2% for *G. postica* vs. 40% for *G. rufobrunnea*. The percentage of *G. postica* pupae surviving was double that of *G. rufobrunnea* (Fig. 3a). 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. 3b–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 ( $Z = 0.212$ ,  $P = 0.832$ ).

Tachinidae parasitoid species associated with *G. postica* had significantly higher maximum parasitism rates (Table 2) 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 2). The remaining parasitoid species did not differ in maximum parasitism rate between the two host species. Thus *G. postica* and *G. rufobrunnea* differed 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 3). Response predictions based on appearance were incorrect for both host species considering any of the natural enemies (Table 3). Based on host 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*. Neither hymenopteran parasitoid nor bird predation rate, however, was correctly predicted based on host species aggregation behaviour (Table 3). Predicted and observed responses of natural enemies to *G. postica* and *G. rufobrunnea* defence traits thus did not show clear support for a defence trait–natural enemy response relationship.

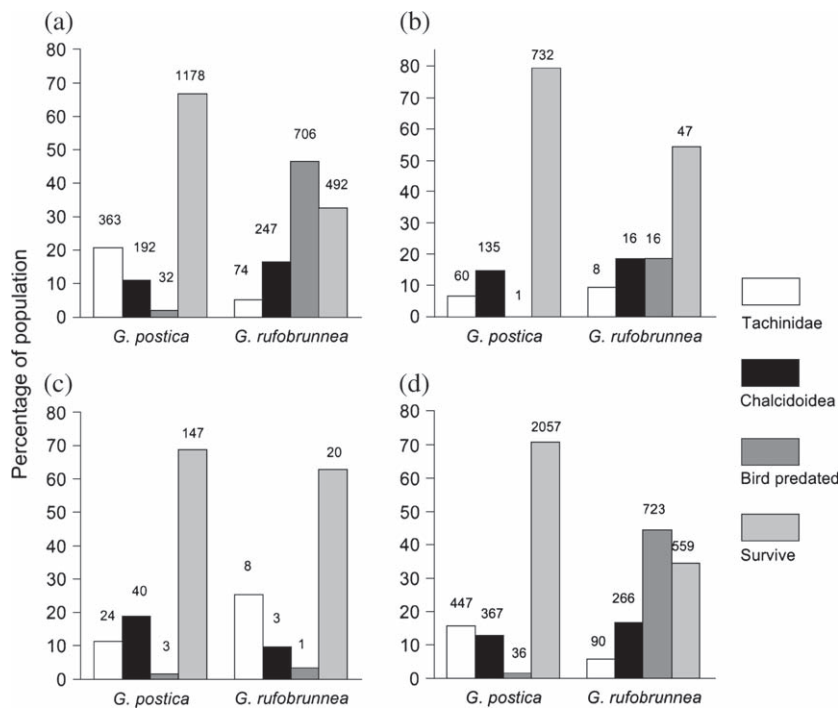
Pupal abundance and within-branch pupal aggregation were significantly positively related, with pupal abundance explaining at least 60% of the variation in within-branch pupal aggregation (Table 4). Percentage Tachinidae and Hymenoptera parasitism, and percentage predation recorded for *G. postica* pupae across the first three generations per site showed no significant relationship



**Fig. 2.** 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. 1, 2, 3, and 4 represent May 2000, January 2001, May 2001, and January 2002, respectively.

with pupal abundance (Table 4). Percentage predation was also not significantly explained by within-branch pupal aggregation (Table 4). For *G. rufobrunnea*, however, percentage parasitism by Tachinidae was significantly negatively related to pupal abundance, while percentage bird predation was significantly posi-

tively related to within-branch aggregation (Table 4). 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.



**Fig. 3.** 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 are 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.

## Discussion

### Life-history trait–population dynamics relationship

The 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. Although the limited duration of the study potentially caused larger fluctuations to go unobserved, this is unlikely, as across-site comparisons of sites selected over a wide geographic area,

**Table 2.** 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.

Parasitoid species or predator	Maximum percentage parasitism and predation						Likelihood ratio $\chi^2_c$		
	<i>G. postica</i>			<i>G. rufobrunnea</i>			Gen 1	Gen 2	Gen 3
	Gen 1	Gen 2	Gen 3 <sup>1</sup>	Gen 1	Gen 2 <sup>1</sup>	Gen 3 <sup>3</sup>			
<b>Tachinidae</b>									
<i>Pimelimyia semitestacea</i> (Villeneuve)	19.5	9.7	9.2 (20.0)	2.4	11.1	(14.3)	34.35***	0.11	0.94
? <i>Palexorista</i> sp.	59.9	2.8 (27.3)	1.2 (25.0)	1.4	(7.7)	(22.2)	167.18***	1.21	0.24
? <i>Tachinidae</i> sp.	11.5	1.4	1.3 (12.5)	4.2	(6.3)	0	7.38**	0.06	0.54
<b>Chalcididae</b>									
<i>Brachymeria</i> sp.	17.8	16.7	15.8 (21.1)	12.4	2.8 (18.8)	(11.1)	2.97	0.12	0.96
<i>Kriechbaumerella</i> sp.	3.1	5.0	2.6 (5.3)	14.3	(30.8)	0	26.41***	11.17***†	1.06
<b>Eurytomidae</b>									
<i>Eurytoma transvaalensis</i> (Cameron)	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 (8.3)	(7.1)	146.06***	9.57***‡	0.01

$\chi^2_c$  denote Cochran-corrected chi-square values. \*\* and \*\*\* denote  $P < 0.01$  and  $0.001$ .

Numbers in superscript indicate the number of sites sampled with less than nine pupae.

† Analyses with an expected value(s)  $< 1$ .

‡ Analyses with more than 20% of expected values  $< 5$ .

**Table 3.** Predicted responses of *G. postica* and *G. rufobrunnea* natural enemies based on selected Lepidopteran larval defence traits from the literature. Support for predictions based on defence traits as indicated by observed (Obs.) natural enemy responses (mortality rates) is indicated as 'yes' (Y) and 'no' (N).

Defence trait*	Character state	Parasitism rate				Predation rate	
		Tachinidae†		Hymenoptera‡		Bird§¶	
		Predicted	Obs.	Predicted	Obs.	Predicted	Obs.
<i>G. postica</i>							
Host plant breadth	Oligophagy	ne	—	ne	—	Low	Y
Physical defence	Urticating seta	High	Y	ne	—	Low	Y
Appearance	Not-cryptic††	Low	N	ne	—	High	N
Aggregation behaviour	Gregarious	High	Y	High	N	High	N
<i>G. rufobrunnea</i>							
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

'ne' indicates no effect was predicted from literature for the response of a particular natural enemy to a specific defence trait.

\*Defence traits defined according to Hunter *et al.* (1995).

Source of predictions on natural enemy responses: †Stireman and Singer (2003).

‡Gentry and Dyer (2002).

§Brower (1958). All *Gonometa* species life-history information is from Hartland-Rowe (1992).

¶Defence traits of pupal stage instead of the larval stage are considered.

††and palatable.

did not reveal population size fluctuations of 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. Only the pupal stages were considered in this analysis, however, and if one included variation in abundance from first-instar larvae (calculable from pupal surveys) to adults, this variability is likely to be higher. None the less, previous studies sampling the late larval instar

and pupal abundance have found variability of more than five orders of magnitude (see Varley *et al.*, 1973).

Nevertheless, results on the extent of temporal population variability in *Gonometa* species, as well as between-generation correlations, suggest that *G. rufobrunnea* is comparatively '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).

**Table 4.** 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 (generalised 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 deviance/d.f.	% DE	Slope	$\chi^2$	<i>P</i>
<i>G. postica</i> (15 d.f.)						
% 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
<i>G. rufobrunnea</i> (9 d.f.)						
% 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

% DE = percentage deviance explained.

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

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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 in population size (Lyytikäinen-Saarenmaa *et al.*, 1999). 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 not, however, be used to successfully predict more subtle between-species differences in the degree of eruptiveness (variability in abundance). This result suggests that eruptive–latent classifications are thus useful for predicting species population dynamics, provided that they fit one of these categories well, but less useful for species with intermediate degrees of population size variability (Leyva *et al.*, 2003; Ribeiro *et al.*, 2003).

Although not the objective of this study, the observed synchronous temporal changes in population abundance across all sampled sites (which ranged from 0.1 to 400 km) provides insight into the possible cause of population size fluctuations in *Gonometa* species, by suggesting broad-scale spatial synchrony. At a regional scale (100–300 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 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 are strongly correlated with 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 100 trees). These observations corresponded with reports of exceptional heavy summer rainfall in the area. The apparent synchrony observed in both *Gonometa* species populations may well be a consequence of regional climatic patterns.

#### *Relationship between defence traits and natural enemy responses*

In general, larval and pupal defence 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 defence traits, although similar traits have been shown to be important elsewhere (Brower, 1958; Dyer & Gentry, 1999; Gentry & Dyer, 2002; Stireman & Singer, 2003). Percentage parasitism and predation of *G. rufobrunnea* (Tachinidae), however, 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 (Guildford, 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 a consequence of differences in predation pressure between Mophane (*C. mopane* sites) and *Acacia* veld. The most likely predators of cocoons are rollers (*Coracias*) and hornbills (*Tockus*), (Hartland-Rowe, 1992; Gaston *et al.*, 1997), which are common across all sites in this study (Harrison *et al.*, 1997). Pupal cocoon structure differences documented for these two *Gonometa* species, however, may explain the interspecific differences in bird predation observed (Veldtman, 2004). Predators must be able to break open the cocoon to reach the pupae. The cocoons of *G. postica*, which are completely covered by calcium crystals, require a significantly greater force to break (Veldtman, 2004). This difference between the species was not simply an environmental effect as 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). Consequently, 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. Pupal cocoon structure differences may thus potentially affect natural enemy responses differently, as has been demonstrated for other species (Danks, 2002).

Between-species differences in bird predation may in turn explain the patterns of parasitism observed in this study. Tachinidae species richness has been shown to increase with the abundance of non-aposematic Lepidoptera, but is unaffected by the abundance of aposematic species (Stireman & Singer, 2003). Parasitoids use their host for a large portion of their life cycle and 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. This hypothesis is not supported, however, 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 (i.e. *Kriechbaumerella* sp.) may use different cues, for example attacking larvae at low within-branch aggregations, thereby avoiding risk from bird predation. Herz and Heitland (2003) showed that predators exploit all the diprionid sawfly cocoons in a sampled patch while Ichneumonidae parasitoids parasitise only a few. Therefore, although cocoon structure of *Gonometa* species potentially explain patterns of bird predation, alternative factors, such as parasitoid host-patch selection, need to be examined to explain the patterns in parasitism found. The observed response of natural enemies to their host's defence traits or abundance is thus complex, and may be due to interactions between different natural enemies depending on their foraging behaviour.

## Conclusions

This study shows 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 are phylogenetically closely related (i.e. similar except in a few life-history differences). The vast literature on outbreaks of forest insects (e.g. Royama, 1984; Teder *et al.*, 2000; Speer *et al.*, 2001; Peltonen *et al.*, 2002; Javois *et al.*, 2005) has highlighted the range of factors responsible for the observed population dynamics of these eruptive insects. These species, however, 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). To our knowledge, this study provides the first quantification of the extent of population size variability of a species with intermediate life-history traits on the eruptive–latent spectrum. Defence traits, on the other hand, clearly have more complex effects on natural enemy responses than has been found for some systems (Brower, 1958; Bowers, 1993; Larsson *et al.*, 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 differences in prey selection behaviour are likely to exist, the difficulty with predicting insect herbivore interactions with higher trophic levels is unsurprising. Even with more detailed study and greater taxonomic coverage of herbivore and natural enemies, accurate prediction may just not be possible. In addition, although life-history and defence characteristics are a valuable basis for predicting population dynamics and natural enemy responses, local ecological conditions can override the probability of these predicted dynamics and responses being realised. The progress that has already been made in linking life-history traits with eruptive or latent population dynamics, however, is promising. Additional case studies of species with an intermediate position on the population dynamic gradient are likely to provide further generality.

## Acknowledgements

We thank A. Botes (University of Stellenbosch) for assisting with fieldwork; F. and M. Taylor, (Development Consultancies) for making it possible to collect data in Botswana; farmers of the Northern Cape and North West Provinces for their hospitality and assistance, G. Pinsloo (Plant Protection Research Institute) for supplying information on parasitoid species, and S. Larsson, Ş. Procheş, A. Botes and two anonymous referees are thanked for making valuable comments on previous drafts of the manuscript. Liberty Life Trust and the National Research Foundation are thanked for funding the project. This material is based upon work supported by the National Research Foundation under Grant number GUN2053618 and GUN2053665. Any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and therefore the NRF does not accept any liability in regard thereto.

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Accepted 12 May 2007

**Appendix 1.** A comparison of selected Lepidopteran defence traits and their association with natural enemy responses; ‘no effect’ (NE) indicates no positive natural enemy response to different states of life-history characteristic. Defence trait state denoted in the body of table (i.e. specialist vs. generalist; hairy vs. smooth; aposematic vs. not cryptic and palatable vs. cryptic; solitary vs. gregarious) is associated with a positive natural enemy response.

Defence trait	Natural enemy response						
	Higher parasitism rates				Higher predation rates		Higher species richness
	Tachinidae*	Diptera†	Hymenoptera†	Parasitoids‡	Invertebrate‡	Bird§	Tachinidae*
Host plant breadth	NE	NE	NE	Specialist	Generalist	Specialist	Generalist
Physical defence	Hairy (ns)	NE	NE	NE	Smooth	Smooth	Hairy
Appearance	Cryptic	NE	NE	NE	Not-cryptic and palatable	Not-cryptic and palatable	NE¶
Aggregation behaviour	Gregarious	Gregarious	Gregarious	Solitary	—	Gregarious	NE

\*Stireman and Singer (2003) (only two larval appearance categories: aposematic vs. cryptic).

†Gentry and Dyer (2002).

‡Dyer and Gentry (1999), parasitoids comprise of 79 Ichneumonoidea, 5 Chalcidoidea and 13 Tachinidae species.

§Brower (1958).

¶Significant association between host being and cryptic species and Tachinidae species richness if interaction with host abundance considered.