The ecology of southern African wild silk moths (*Gonometa* species, Lepidoptera: Lasiocampidae): consequences for their sustainable use

by

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The ecology of southern African wild silk moths (*Gonometa* species, Lepidoptera: Lasiocampidae): consequences for their sustainable use

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ABSTRACT

The pupal cocoons of two southern African wild silkmoth species, *Gonometa postica* and *G. rufobrunnea* (Lepidoptera: Lasiocampidae), are composed of high quality silk and have potential as a commercially viable resource. However, limited ecological research has been done on these species, and their population dynamics is especially poorly known. A steady and predictable supply of cocoons is paramount to the economic sustainability of a wild silk industry. There is thus an urgent need for documenting and understanding the population dynamics of southern Africa's *Gonometa* species. Here, the temporal and spatial variation of pupal (and thus cocoon) abundance, as well as associated natural enemies, are described for both *Gonometa* species for the first time. The larval parasitoid species emerging from parasitised pupae were quantitatively associated with species-specific emergence holes, making field-identification of these species possible. Eleven sites in total were sampled, over four generations, across the region where both species have historically reached high population densities. Apparent spatial synchrony in pupal abundance found between sites suggests that climate is responsible for observed population size fluctuations. As predicted from their life history traits, temporal variability was lower than expected for classically eruptive species. *Gonometa* species thus have an intermediate position on the population dynamics gradient. In turn, the responses of natural enemies were not predictable from *Gonometa* species defensive traits, but appear to be mediated

by between-species cocoon strength differences. Using data on the number of *G. postica* pupae per tree and associated parasitism at several sites, the importance of the degree of spatial explicitness in the quantification of aggregation and the detection of density dependence was illustrated. The spatially explicit method gave different results and more information regarding the spatial pattern of pupal abundance and parasitism than non- and semi-explicit methods. Similarly, the detection of density dependence in parasitism rates was affected by the use of spatially explicit data, with the spatial explicit approach giving different and more biologically informative results than traditional, non-spatially explicit methods. This has marked implications for previous insect-host - parasitoid studies aimed at detecting density dependence. The variability in cocoon size, a surrogate for larval performance, adult fecundity and silk yield, revealed that gender, followed by species, contributed most to observed size differences, with no clear differences between generations or localities. Finally, the between-host plant and within-host plant distribution of *G. postica* and *G. rufobrunnea* pupae was quantified, chiefly investigating the deterministic nature of the choice of pupation site. The distribution of both species at these scales was found to be markedly non-random, with pupae generally preferring specific tree characteristics and micro-sites. These results now provide the basis for recommending an appropriate utilisation strategy for southern Africa's wild silk moths. Based on the spatial and temporal variability in pupal abundance observed, a constant and predictable cocoon supply for natural harvesting is unlikely. Long-term, broad-scale documentation of *Gonometa* species population cycles may make it possible to predict cocoon availability in the future. Until such research is done, it is recommended that the current practise of only collecting cocoons from which moths have emerged be continued. Simultaneously, artificial rearing and seeding as alternative utilisation strategies should be experimentally explored based on the information gathered and patterns identified here.

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GENERAL INTRODUCTION

"Spatial aggregation, or non-random search, by natural enemies, both predators and parasitoids, in response to patchy distributions of prey or hosts has a profound effect upon the population dynamics of victim and hunter populations."

Heads & Lawton 1983

"Claiming that an activity is sustainable requires us to predict the future. Reliable prediction of the future requires an especially profound understanding of the past and present. No qualifications are required in order to argue in favour of sustainability. But achieving sustainability will require the advances made by ecologists in years to come."

Begon *et al*. 1996

Population dynamics have formed a central part in the scientific field of ecology around which many theories and assumptions are based (Haukioja 1993; Cappuccino 1995; Price 1997). On the centre stage of population dynamics is population regulation, i.e. how and when is regulation achieved. It is currently generally accepted that natural insects populations (and other animals) that fluctuate, do not fluctuate randomly but are bounded by an upper and lower long-term stationary probability limits (Turchin 1995, Price 1997). In contrast, the means by which a population is regulated under natural conditions has been much disputed. The Nicholson-Bailey school advocates that population regulation is accomplished by density dependent factors, while the Davidson, Andrewartha and Birch school states that these factors are not important for population regulation (Turchin 1995; Price 1997). Despite a proposal that population regulation could be achieved by density independent factors alone (Andrewartha & Birch 1954; Den Boer 1968), it is now generally accepted that regulation cannot occur without density dependence (Hanski 1990; Godfray & Hassell 1992; Turchin 1995). Also, it has been repeatedly demonstrated that the probability of detecting density dependence in natural populations increases with the length of the time series data for the specific population (Hassell *et al*. 1989; Godfray & Hassell 1992; Woiwod & Hanski 1992; Turchin 1995). Whether

density dependence exists is no longer the only major question in population ecology, however, the mechanisms by which regulation is achieved and their general importance (relative frequency of occurrence or interactions) remains to be answered (Turchin 1995).

Two contrasting mechanisms (of many, i.e. metapopulation dynamics, competition etc.) responsible for population regulation are so called 'Top down' and 'Bottom up' forces, with host plants and natural enemies respectively, determining herbivore population dynamics (Turchin 1995, Price 1997). In general, because the fitness of herbivorous insects is dependent on food quantity and quality (Stamp 1993), bottom up effects are likely to be important to the population dynamics of these insects (White 1978, 1984). Galling-sawflies have been found to be principally governed by bottom-up forces due to the high host and organ specificity between the insect and its host and strong oviposition preference resulting in stable population dynamics (Price *et al*. 1995; Price 1997). In the case of leaf-miners, bottom up forces seem to be of overriding importance, with both the latent and eruptive states of species not exhibiting density dependence with natural enemy caused mortality (Auerbach *et al*. 1995). The variation in quality and availability of leaves seem to drive the population dynamics of leaf-miners (Auerbach *et al*. 1995).

The effects of natural enemies on other herbivorous insects have, however, revealed conflicting results. For example, parasitoids have been shown to be the main factor regulating the population dynamics of certain forest Lepidoptera (Berryman 1996). Many studies on Lepidoptera larvae have implied that their natural enemies have shaped their behaviour and morphology (colour and defence structures) (Heinrich 1993; Montlor & Bernays 1993; Weseloh 1993, Gentry & Dyer 2002). Also, biological control has illustrated how important natural enemies are for regulation, with alien herbivore pests being controlled by their natural enemies and the predators of natural enemies preventing effective regulation (Price 1997).

An alternative mechanism of population regulation can operate through endogenous (all density dependent) factors such as competition and dispersal, where the specific population is not regulated by other trophic levels (Price 1997). For example, larval survival could be determined by competition for high quality food or when dispersal from defoliated hosts increase mortality (e.g. the processionary caterpillar, Floater 1997).

Effects of food availability and/or quality can interact with the effects of natural enemy attack to produce complex population dynamic patterns (Price 1987; Haukioja 1993; Turchin

1995, Price 1997). Insect herbivores can occur for long periods at low densities through regulation by their natural enemies, but due to changes in some exogenous factor (e.g. climate, Janzen 1993; or only temperature, Stamp 1993) the population increases to a level where food may become limiting (Turchin 1995, Price 1997). It is thus likely that both bottom up and top down factors influence herbivore population dynamics through density dependence under natural variable abiotic (density independent) conditions (Price 1997; Lundberg *et al*. 2000). However, the individual importance of these factors for different insect species is unknown.

For *Gonometa postica* and *G. rufobrunnea*, that have historically exhibited eruptive population dynamics in only part of their distribution range (Hartland-Rowe 1992; Veldtman *et al*. 2002), complex interactions such as those described above are likely. Insect populations experiencing rapid increase in abundance after removing the effects of one or more regulating factors undergo population release (Price 1997). Studying populations experiencing such population release can thus be very helpful in determining the key regulating factors. Alternatively, comparing the population dynamics of *Gonometa postica* and *G. rufobrunnea* is one method of identifying which factors are possibly responsible for population regulation (Cappuccino 1995; Hunter 1995; Price 1997).

Why the pupal stage?

Gonometa species have a relatively long history of exploitation in southern Africa. Traditionally, the pupal cocoons of *Gonometa* species were used by the Bushmen of southern Africa to make ankle rattles (Peigler 1993). In the early eighties Geoff Bailey experimented with degumming *G. rufobrunnea* cocoons from Shashe in Botswana. These trials proved successful and the degummed silk he produced sparked interest in the potential for commercial utilisation of this species (G. Bailey, pers. comm.). After a crash in *G. rufobrunnea* populations in the late eighties, commercial utilisation ceased. A few years later technology was developed to degum and process empty *G. postica* cocoons (from which moths have emerged). The utilisation of this species has subsequently increased and currently the demand for *G. postica* cocoons greatly exceeds the amount available from natural harvesting.

This study only surveyed the numbers of pupae of *G. postica* and *G. rufobrunnea* at various sites where both species commonly reach high abundances. Studying only the pupal stage of *G. postica* and *G. rufobrunnea*, as opposed to other life stages or the complete life

cycle, was done for the following reasons. First, as with any scientific study logistical constraints have to be considered when designing a sampling program. Due to the difficulties associated with detailed replicated life table studies encompassing the whole life cycle, a trade off between number of sites and time spent at a site needs to be optimised. As the focus of this research was the general ecology of *Gonometa* species and its implications for its sustainable utilisation, an approach of concentrating on the pupal stage at several localities was favoured above the traditional life table approach where more detailed information is gathered for fewer localities (see Carey 2001 for review). Second, the information content of the pupal stage is high compared to, and largely a summary of the fate of, other stages, e.g. larval performance, potential fecundity of adults, final instar parasitism. Third the pupal stage of *Gonometa* species is the stage of longest duration. This facilitated a temporal survey program of populations over an extensive area during the over-wintering stage. The pupal stage is also suited to abundance surveys because individuals are highly apparent and sessile. As one of the main foci of this study was the description of local scale pattern in abundance, both of these characteristics were a prerequisite. The study of sessile life stages is common in insect herbivore ecology and has led to significant advances in the understanding of population dynamics (Heads & Lawton 1983; Hails & Crawley 1992; Brewer & Gaston 2002). Finally, because the pupal stage is the target stage of sustainable utilisation activities, it is most important to study this stage. No research to date has addressed the question of population size variability or extent of natural enemy induced mortality of these two economically important species.

Wild silk as a sustainable resource

The global increasing human population of developing countries and the increasing consumerism and exploitation of developed and developing countries are placing more and more pressure on their natural resources (Begon *et al*. 1996). Now and in the future, sustainable resource utilisation will become increasingly important. It is therefore necessary to know exactly what managing a resource in a sustainable manner entails. Environmental sustainability, according to Goodland (1995), is the maintenance of natural capital ("the stock of environmentally provided assets"). This is important because natural capital is limited (non-renewable) (Hilborn *et al*. 1995). Natural resource overexploitation should not be seen as a true source of income but as 'liquidation' (Goodland 1995). Overexploitation may only be

discovered after a resource has been critically damaged, because present constant yield does not guarantee that a resource will be sustainable in the future. To meet the criteria of sustainability, natural capital should therefore not be used, only the income from it (i.e. renewable resources). This will prevent the degradation of the future value of natural capital (Goodland 1995). In the case of *Gonometa* species, natural populations can be seen as 'natural capital' and overexploitation could result in extinctions of local populations.

There are three methods of utilising southern Africa's wild silk species namely, *i*) harvesting of natural populations, *ii*) artificial rearing of fertilised eggs to the pupal stage, and *iii*) seeding (mass release) of individuals in unoccupied natural areas. Harvesting cocoons from wild populations has several advantages over establishing an artificial rearing industry. No host plant plantations have to be established and eggs and larvae do not have to be intensively cared for (see Snyman 1993). Unfortunately there are also disadvantages with the utilisation of wild silk. Natural populations have to attain high densities before harvesting becomes economically viable and annual population sizes are unpredictable and may fluctuate widely from year to year and between localities. If the factors (biotic or abiotic) that cause eruptions of *Gonometa* species can be identified, it may be possible to predict when and where outbreaks will occur. Harvesting cocoons from outbreak areas would ensure that the density is economically viable. Simultaneously, the ecological sustainability of harvesting should be taken in to account. The potential extinction of *Imbrasia belina* (Lepidoptera: Saturniidae) populations from South Africa is a warning to the over exploitation of commercially valuable insects (see McGeoch 2000).

Between 1986 and 1987, *G. rufobrunnea* pupae from natural populations were harvested only at sites where cocoons (Fig. 1a, b) were abundant, as it was not profitable to do so when there were fewer than two cocoons per square meter (Hartland-Rowe, unpublished). People in rural areas used a "five minute count" method to determine cocoon abundance (Hartland-Rowe 1992). Harvesting commenced when 120 cocoons could be counted in the allotted time (C.H. Scholtz, pers. comm.). The following year cocoon densities were no longer economically viable, and the industry collapsed. It is not known whether this was caused by overexploitation or if it was a natural population fluctuation (McGeoch 2000). A lack of knowledge on the biology of this silk moth (*G. rufobrunnea*) possibly led to the overexploitation of this natural resource (Hartland-Rowe 1992). The effects of harvesting areas of high abundance on future

yields were not known or even considered. One possible solution for preventing overexploitation of a fluctuating natural resource is to use an optimal threshold strategy (Hilborn *et al*. 1995). Cocoons can be stored indefinitely, without deterioration in quality (Hartland-Rowe 1992). Thus in times when cocoons are under the threshold density, surplus stock from stores from previous years may be processed. It is, however, unlikely that an estimated threshold will be correct without information on the natural densities and survival of *Gonometa* species. To date no such information has been published.

An alternative option to using an optimal threshold strategy may be to only collect cocoons from which moths have emerged. TEXTEC, the textile technology division of the CSIR South Africa, has found that empty cocoons can still be used for silk production (S. Worth, pers. comm.). TEXTEC developed the technology to process silk from empty cocoons. Although *Gonometa* populations may be unaffected by the harvesting of empty cocoons, their availability still needs to be determined to ensure long-term economic sustainability. Also, as previously mentioned, the quality of silk extracted from emerged cocoons is lower compared to occupied ones. There is thus still a demand for cocoons occupied by live pupae, although only old cocoons are utilised at present. Current harvesting enterprises have stated that harvesting of occupied cocoons does not take place (Liberty Life Trust Wild Silk Workshop, 5 November 2002).

With *Bombyx mori* (Lepidoptera: Bombycidae), although artificial rearing has high implementation costs and is labour intensive, a successful industry can produce sustained yields and production can become profitable (see Snyman 1993). The major constraint in rearing *Gonometa* species artificially is the lack of detailed knowledge on the ecology of the species, such as larval growth in response to host quality. Wild silk moths in general are difficult to rear with few exceptions (Scoble 1995). Preliminary trials by Hartland-Rowe (1992) to rear life stages of *G. rufobrunnea* using the same methods as used with *B. mori* were largely unsuccessful. Trials indicated that larvae did not accept cut mopane (host plant) as food and consequently all larvae died of starvation. From 30 000 eggs only a single cocoon was produced (Hartland-Rowe 1992). However, exploratory rearing trials of *G. postica* on potted *Acacia erioloba* and *A. tortillis*, and *G. rufobrunnea* on *Colophospermum mopane*, have indicated that larval rearing is possible (pers. obs.). Larvae (Fig. 2a, b) readily accept potted

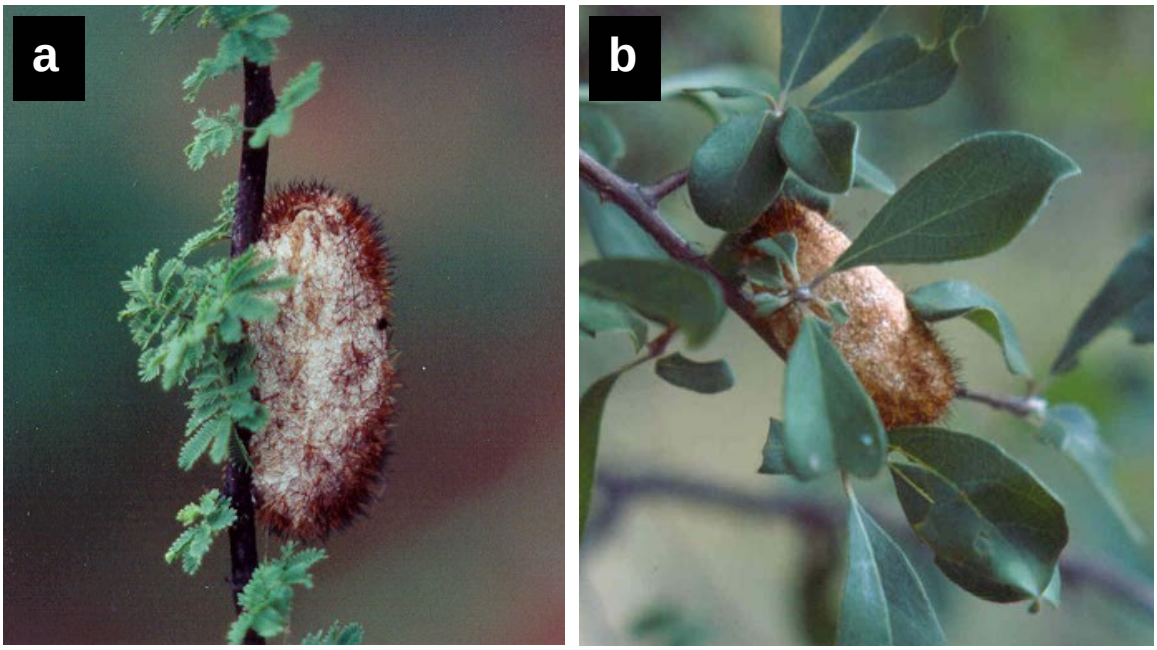

Figure 1. Occupied pupal cocoons of a) *G. postica* and b) *G. rufobrunnea*.

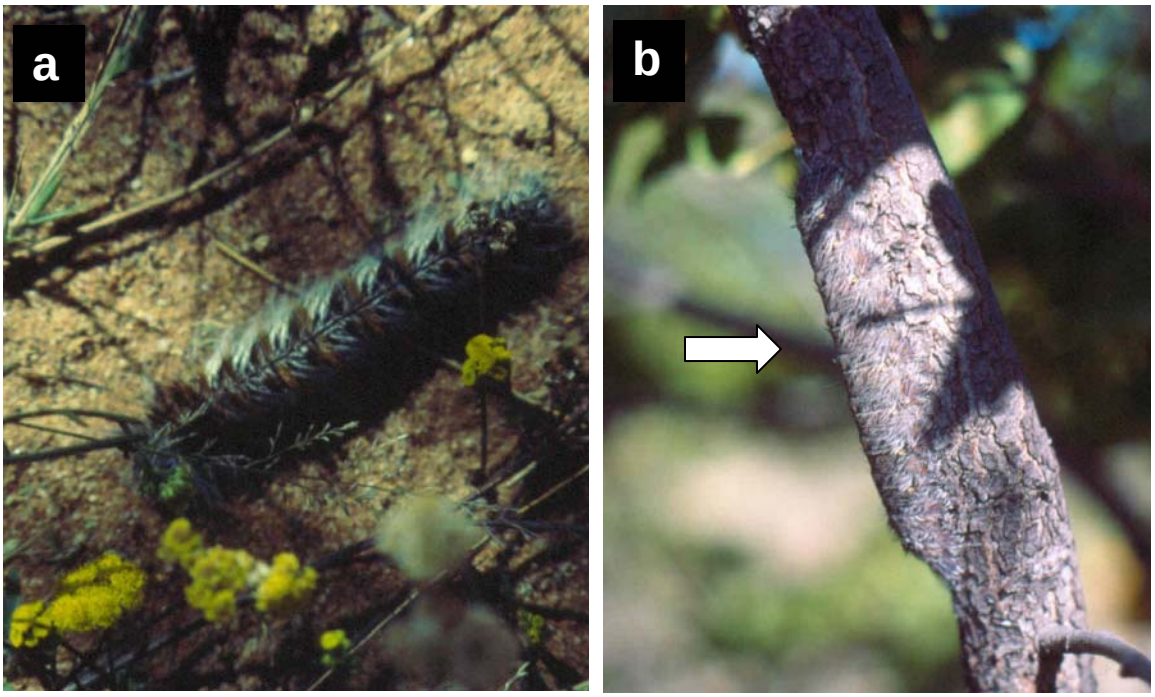

Figure 2. Final instar larvae of a) *G. postica* and b) *G. rufobrunnea*.

food plants as hosts. Furthermore, synchronising mass moth emergence was found to be a major constraint in artificial rearing. The stochastic difficulties commonly associated with small population sizes apply here. Pairing one male per female is possibly insufficient to guarantee fertilisation. It also seems that males need to fly some distance before mating with females (pers. obs., and has also been documented for *Gonometa podocarpi*, see Okelo 1972). The documentation of the mating behaviour of *Gonometa* species is the crucial first step in making artificial rearing a viable utilisation strategy. This utilisation method thus requires more detailed experimentation to enable recommendations for implementation.

Seeding can be seen as a hybrid method between natural harvesting and artificial rearing where a life stage, e.g. pupa, is collected and released in suitable habitat elsewhere (Hartland-Rowe 1992). As this option utilises natural host plants reducing costs of rearing larvae, while simultaneously, improving survival and thereby increasing the number of individuals that can be harvested. In theory, seeding could establish new natural populations that could be harvested. Hartland-Rowe (1992) reported that preliminary seeding trials for *G. rufobrunnea* had varying degrees of success. Cocoons, adults and eggs were used to seed natural habitats were *Gonometa* populations were absent or present in low densities (Hartland-Rowe 1992). Collected occupied cocoons were glued to the host plant, from which male and female moths (Figs 3 & 4) emerged and mated to form a new generation. Cocoon seeding was reasonably successful with new populations being established in 50% of the cases (Hartland-Rowe 1992). In contrast, adult-seeding trials proved to be ineffective. Seeding was found to be most successful when occupied cocoons were glued to the host plants (low bushes) and were covered by shade netting. The shade netting was removed only after larvae reached the mobile late instars. Measured field egg mortality of 50% caused by parasitoids and a 70% loss of small larvae due to insect predation was reduced to less than 3% overall mortality when this method was used (Hartland-Rowe 1992). In spite of this success, mortality of late-instar larvae due to predators and parasitoids still posed a problem. Another method of seeding involved placing successfully fertilised eggs in an open envelope and stapling it to the host plant. Of these eggs, 50 % survived and larvae became very abundant on the host. The first few instars did however suffer 70% mortality from invertebrate predators (assassin bugs and spiders) (Hartland-Rowe 1992). Previous seeding trial results thus show great potential and illustrate that populations can be established more or less at will (Hartland-Rowe 1992).

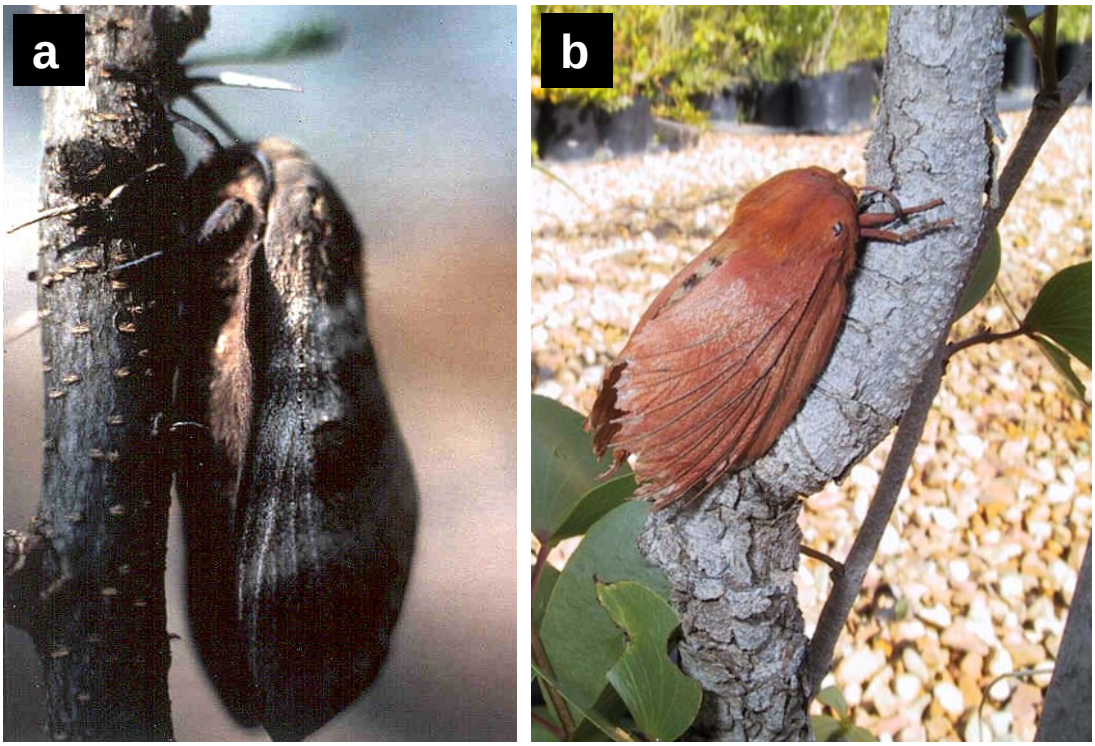

Figure 3. Adult female moths of a) *G. postica* and b) *G. rufobrunnea*

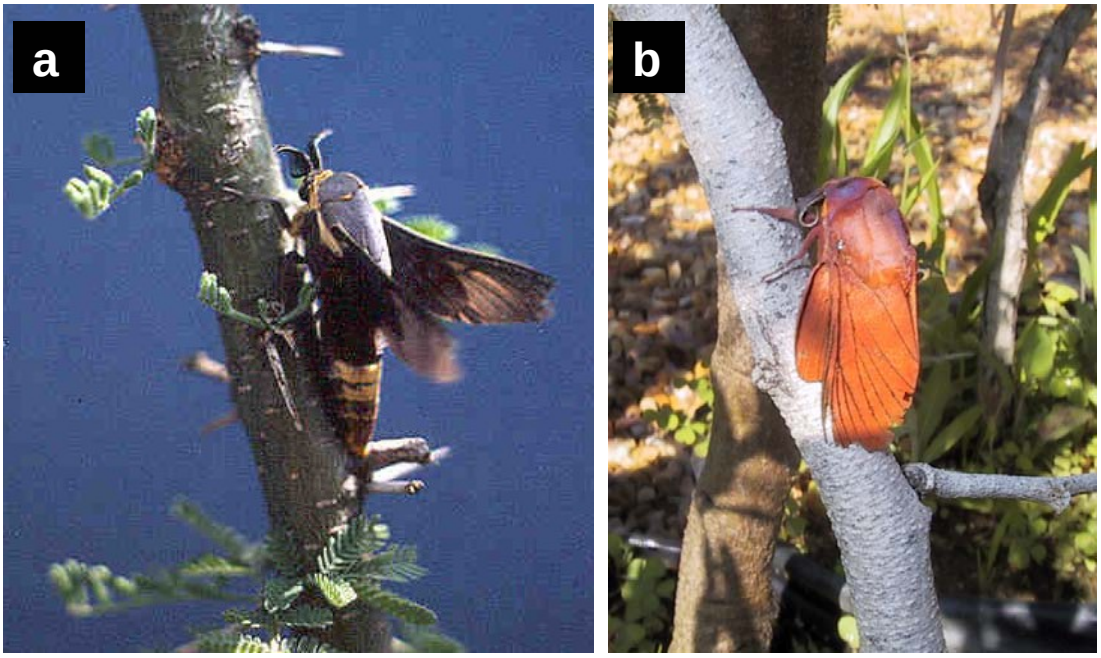

Figure 4. Adult male moths of a) *G. postica* and b) *G. rufobrunnea*

It is, however, important to consider that wild silk moths are not seen by all as a valuable resource. Many cattle and game farmers regard these species to be a serious pest. Cocoons of both *Gonometa postica* and *G. rufobrunnea* have been reported to cause rumen impaction and death of cattle (Edwards 1935; Zumpt 1971). In dry years when cocoons were especially abundant many animal deaths were reported. When animals ingest the cocoons they become untangled in the rumen by the action of stomach-acids, causing rumen material to become entangled in the loosening silk strands (fibres). This leads to rumen impaction and ultimately the death of the animal (Edwards 1935; Zumpt 1971). In 1995 farmers in Namibia threatened to use chemical control to eradicate *Gonometa postica* (C.H. Scholtz, pers. comm.). Recently, however, conflict between wild silk harvesters and live stock farmers has disappeared in previous conflict hot spots in Namibia (I. Cummings, pers. comm.).

Study area

Gonometa postica and *G. rufobrunnea* populations were examined at six and five sites respectively within the known (historic and recent records) eruptive range of these species, spanning a distance of 400km between the two furthest localities for *G. postica*, and 60km for *G. rufobrunnea* (Fig. 5). The localities were Vryburg and Hotazel in North-central South Africa (Fig. 6) and Gabane, Kumukwane, and Kopong in South-Eastern Botswana (Fig. 7) for *G. postica* and Shashe and Dumela in North-Eastern Botswana (Fig. 8) for *G. rufobrunnea* (see Veldtman *et al*. 2002 (Chapter 5) for further site details). The dominant woody host species utilized by *G. postica* at the first two localities was *Acacia erioloba* Meyer and at the final three, *Acacia tortillis* Hayne (both Mimosaceae), while *G. rufobrunnea* is monophagous on *Colophospermum mopane* Kirk ex Benth. (Caesalpiniaceae).

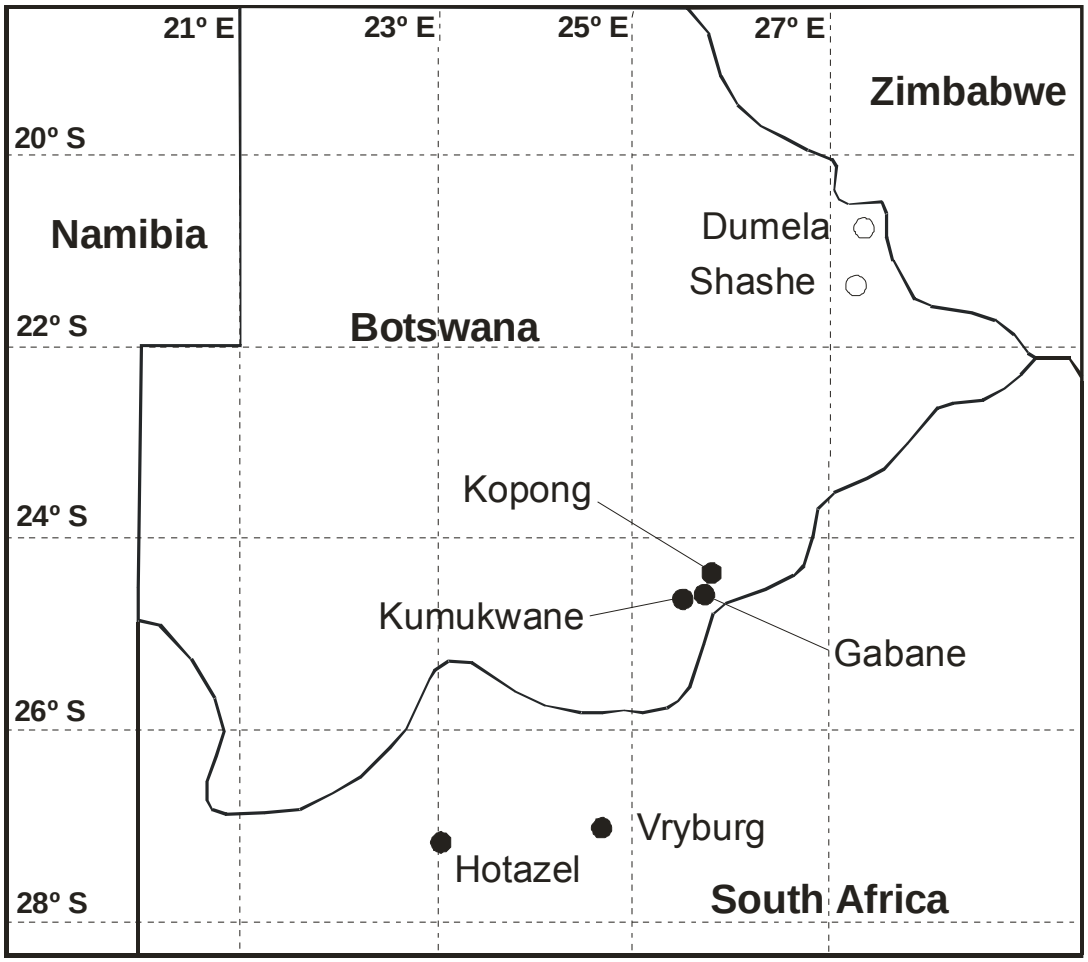

Figure 5. Localities in South Africa and Botswana where *G. postica* (filled circles) and *G. rufobrunnea* (open circles) were sampled.

Figure 6. *Acacia erioloba* veld characteristic of Vryburg and Hotazel where *G. postica* was sampled.

Figure 7. *Acacia tortillis* veld, characteristic of Gabane, Kumukwane, Kopong and Mogoditshane (see Chapter 5) where *G. postica* was sampled.

Figure 8. *Colophospermum mopane* veld, characteristic of Shashe and Dumela where *G. rufobrunnea* was sampled.

The selection of sites was extremely difficult. First, because *Gonometa* spp. population size fluctuates widely from year to year, only sites with a high probability of having cocoons in at least one of the repeated surveys was worthwhile to sample. At the start of this study there was no way of knowing *a priori* that an unoccupied site would be colonised by a following generation. Second, although there is sufficient time for the sampling of *Gonometa* species populations during winter, there is approximately only one month between the pupation of the first and second generations during early summer. Consequently, this limits the spatial extent and number of sites that could be sampled during this study. Third, all individuals were surveyed to allow site-specific absolute population fluctuations to be determined, at the expense of more, but less detailed, surveyed sites. As a consequence of these constraints, sites were not equally spaced from one another. Most sites were sufficiently spaced to be considered independent, only the three Shashe sites were less than 1,5 km apart. The last mentioned problem of spatial independence was due to the lack of suitable sites for sampling *G. rufobrunnea* during the first pupal surveys (sites unsuitable due to either obvious human disturbance or inaccessibility). As this study aimed to quantify both large and small scale

patterns in the ecology of *Gonometa* species, the survey layout was considered acceptable for this broad aim.

Thesis objectives and structure

The first aim of the proposed PhD study was to contribute to the understanding of insect population dynamics. This was done by studying two species that are taxonomically closely related, but differ in evolved life history traits and ecological characteristics. The second aim is to make recommendations regarding the sustainable use of *Gonometa postica and G. rufobrunnea* pupal cocoons based on the findings of the first aim.

Each chapter is presented as a research paper and consequently some of the methods and references overlap. Chapter one deals with the general ecology of *Gonometa postica* and *G. rufobrunnea* species, comparing their population dynamics and the dominant natural enemies associated with the pupal stage. Chapter two (published as Veldtman *et al.* 2004, *African Entomology*) links parasitoid species responsible for larval parasitism with species-specific emergence holes left in the pupal cocoon upon parasitoid emergence. This allows parasitoid identification based on emergence hole characteristics in the field. Chapter three considers the specific meaning of aggregation in ecology, by describing the within-site pupal abundance of *G. postica*, and emphasises the importance of including spatial position when describing spatial pattern in insect abundance. Chapter four builds on the latter and applies a similar rationale to another fundamental concept in ecology, namely density dependence. Using spatially explicit method of quantifying in aggregation, the relationship between parasitism rate and host abundance may be better defined. Chapter five (published as Veldtman *et al.* 2002, *African Entomology*) quantifies the size variability of the pupal cocoons of both species over the geographic range of this study and discusses ecological and economic implications. Chapter six deals with the fine scale variability in pupal abundance and possible factors that explains it. These results are of direct importance for sustainable harvesting of pupae, identifying favoured pupation sites and general spatial patterns in pupal distribution. The general conclusion synthesises the results and conclusions of all chapters, provides a standardised survey method to allow long-term, broad-scale documentation of *Gonometa* species population cycles, as well as making recommendations on the sustainable utilisation of southern African wild silk moth species based on the findings of this study.

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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.

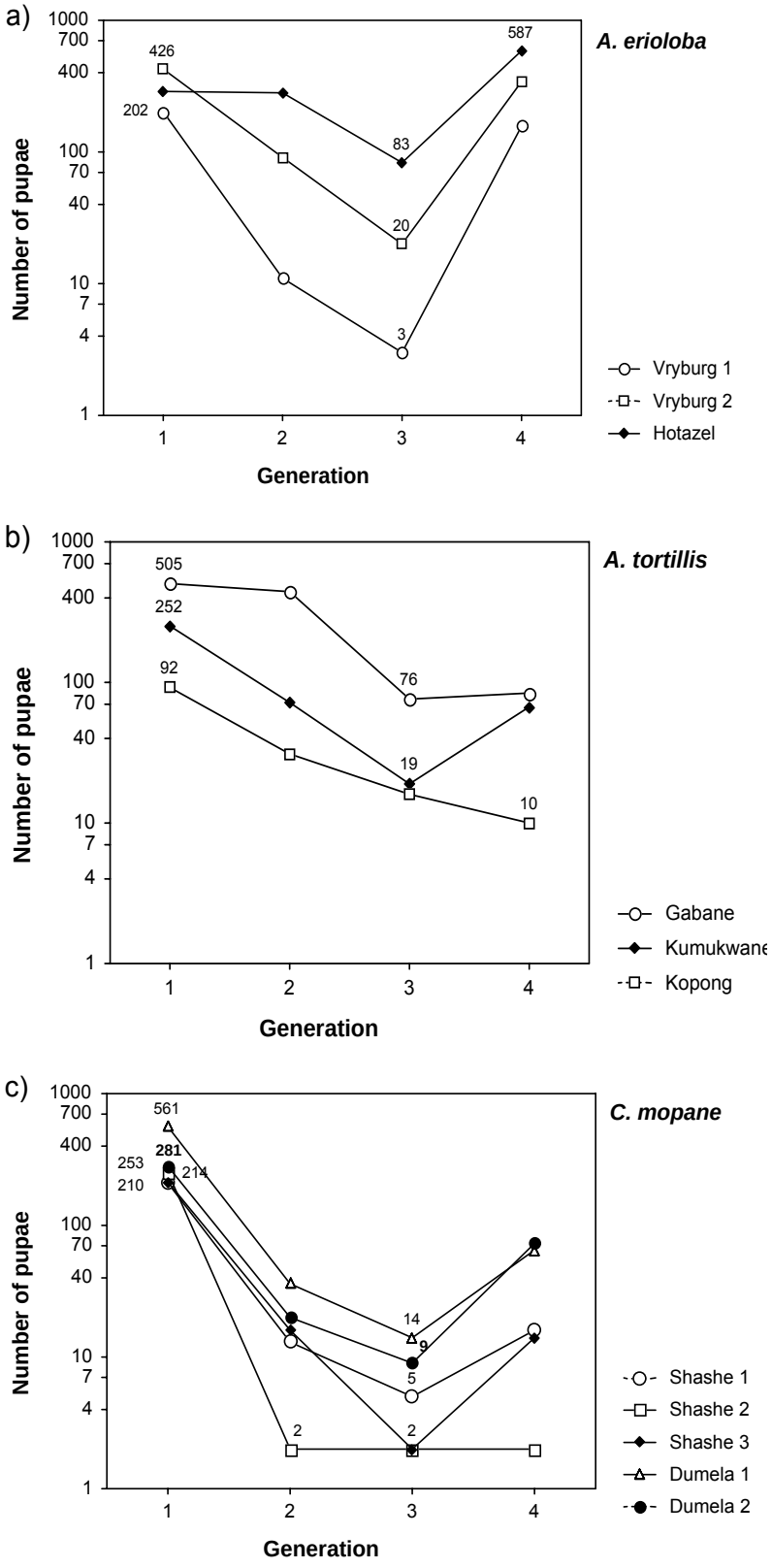

Figure 1. Temporal variation in cocoon abundance for sites: *G. postica* on a) *Acacia erioloba* or b) *A. tortillis* and c) *G. rufobrunnea* on *Colophospermum mopane*. The minimum and maximum number of pupae for each site over the four sampled generations is given.

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

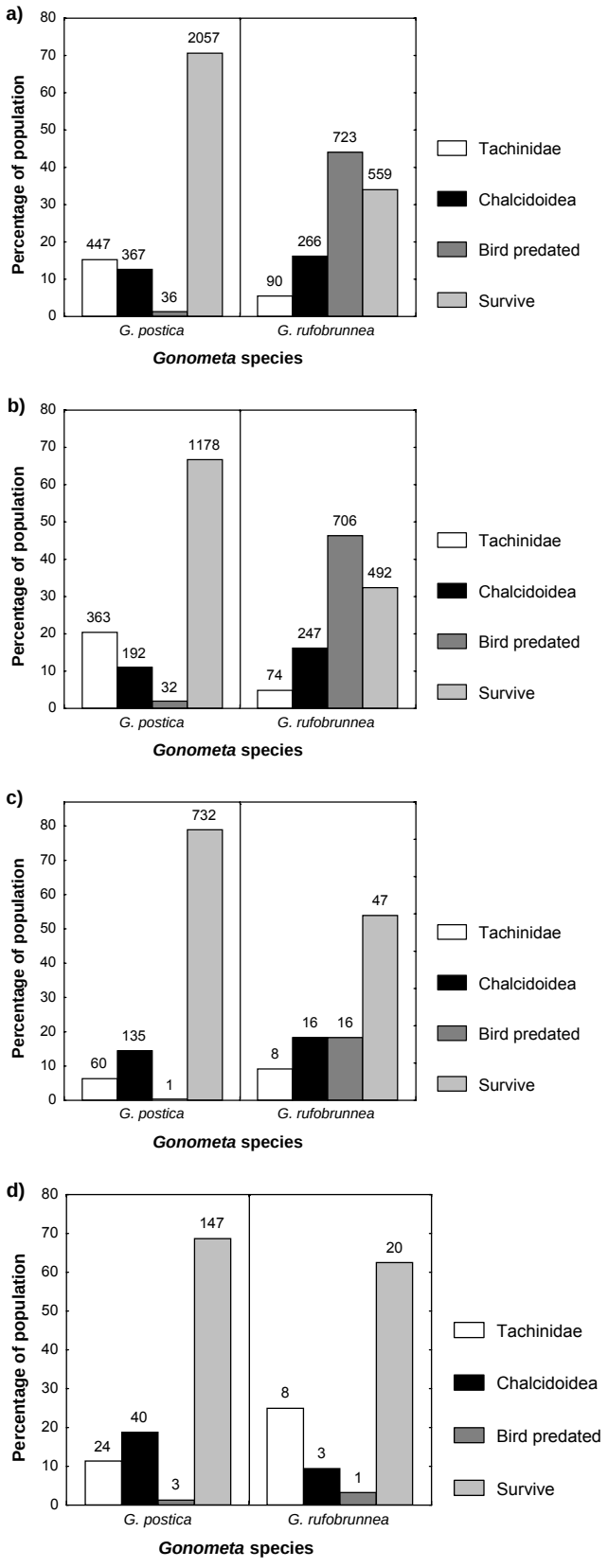

Figure 2. Percentage *G. postica* and *G. rufobrunnea* pupae parasitised by Tachinidae and Chalcidoidea parasitoid species, percentage predated by birds, as well as the percentage surviving. Data is presented for a) all three generations combined, as well as for the b) first, c) second and d) third generations.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

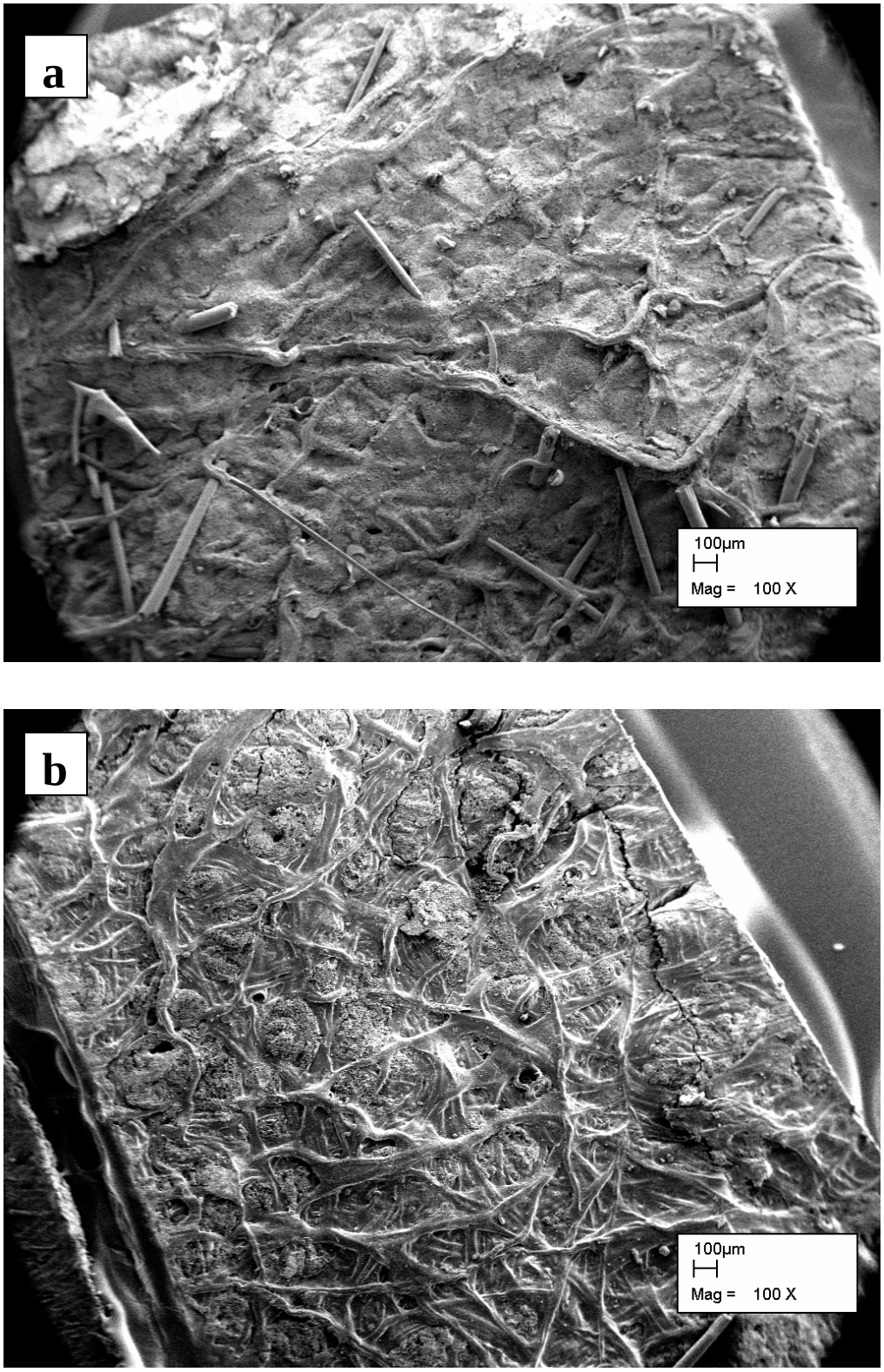

Figure 3. Outer cocoon surface of representative *G. postica* (a) and *G. rufobrunnea* (b) cocoons at low magnification.

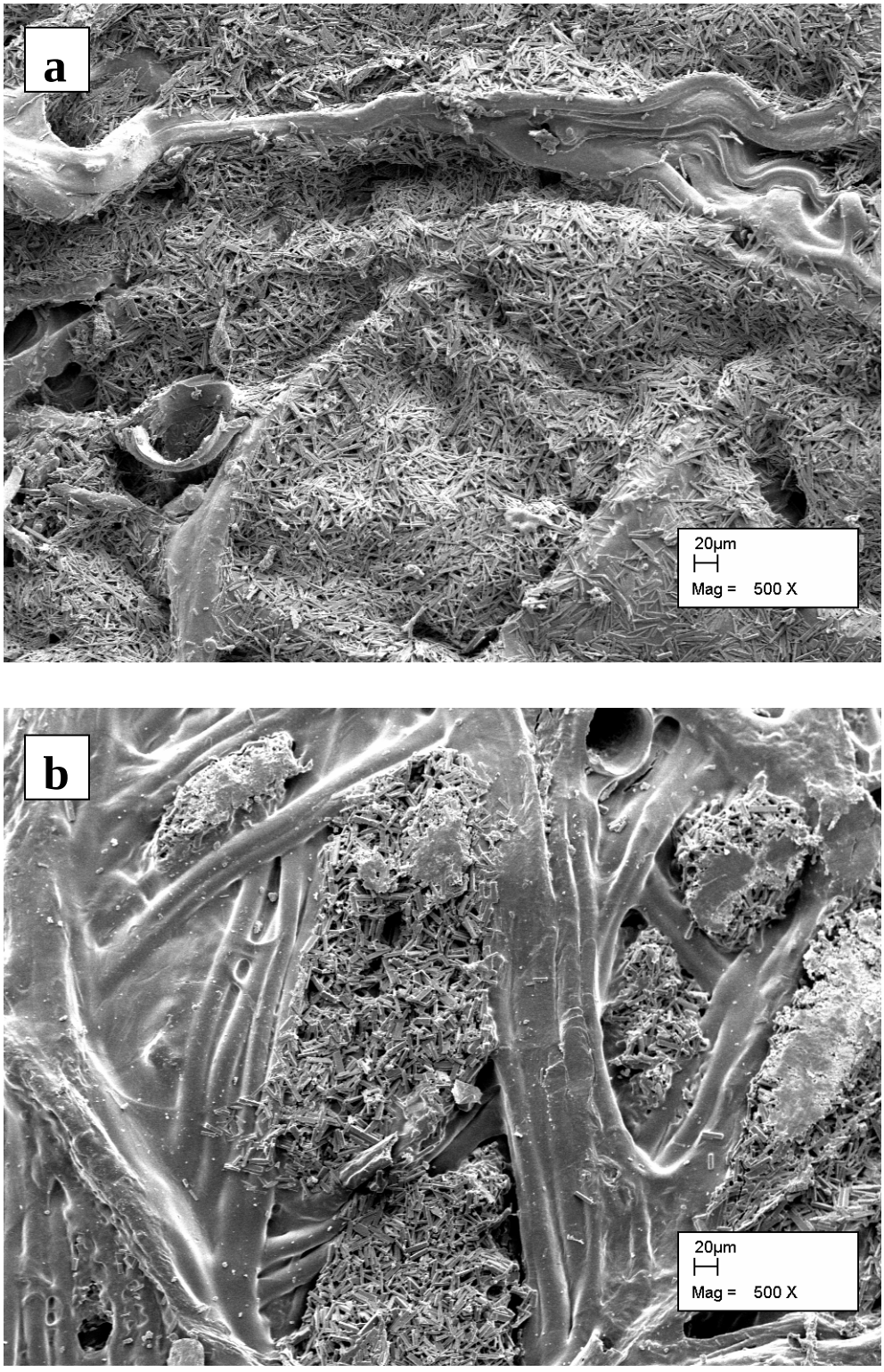

Figure 4. Outer cocoon surface of representative *G. postica* (a) and *G. rufobrunnea* (b) cocoons at high magnification.

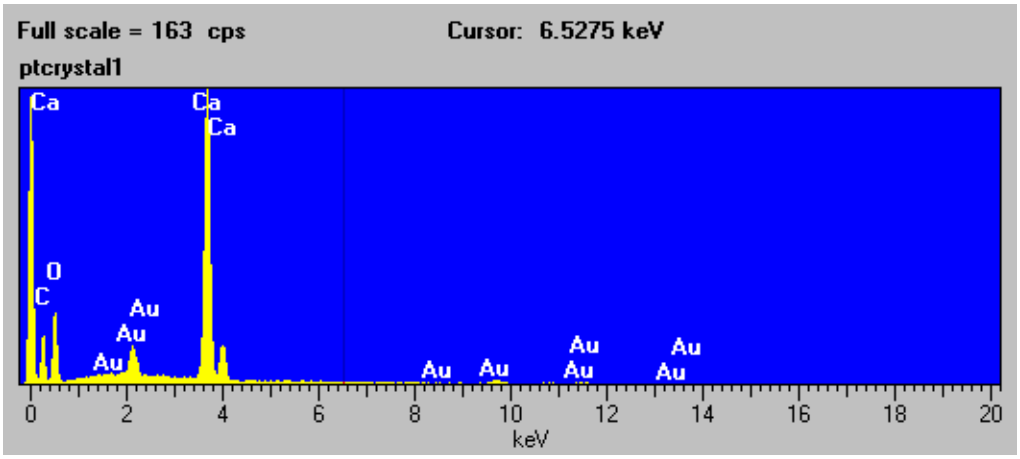

Figure 5. Example output of EDS X-ray analysis of crystals (possibly calcium oxalate – CaC_2O_4) observed on the cocoon surface of *G. postica* and *G. rufobrunnea*. Ca = calcium, C = carbon, O =oxygen, and Au = gold.

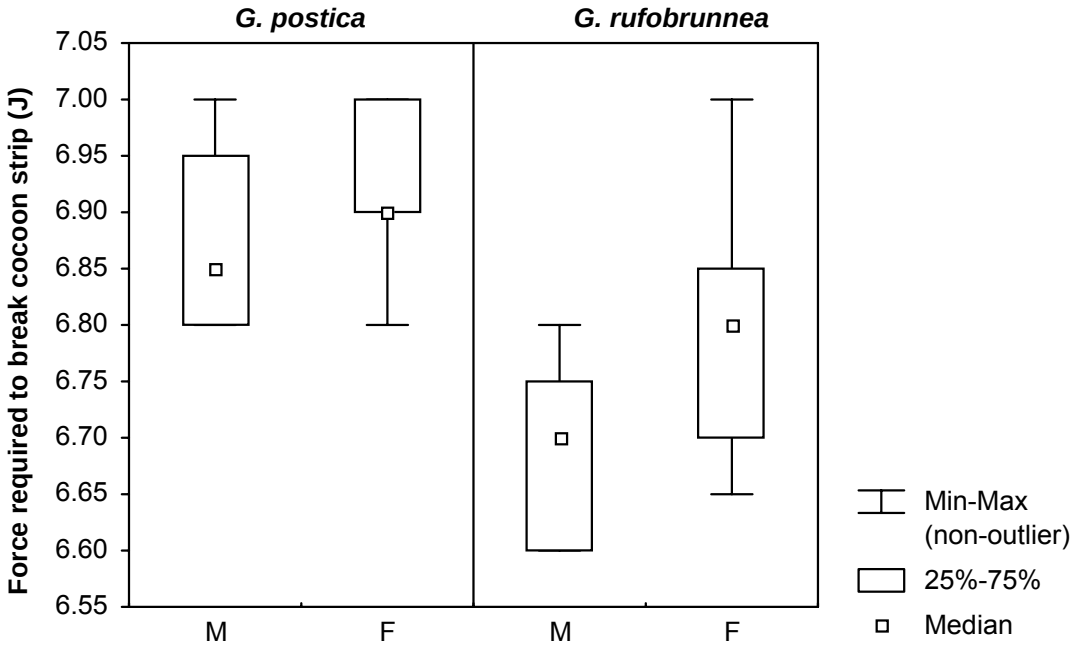

Figure 6. The effect of species and sex (M, F) (nested within species) on the force required to break a section of the cocoon wall of *G. postica* and *G. rufobrunnea* (n = 8 or more per species sex grouping).

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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CHAPTER 2

The parasitoids of southern African wild silkmoths (Lepidoptera)

Gonometa postica Walker and *Gonometa rufobrunnea* Aurivillius (Lasiocampidae) are the only two indigenous moth species in southern Africa that are currently used in silk production. *Argema mimosae* de Boisduval (Saturniidae) is, however, another species that has been considered for silk production. The pupal cocoons of *Gonometa* species can be degummed to produce silk of high quality, and presently, the wild silk industry is limited by the supply of naturally harvested cocoons (Veldtman *et al*. 2002). Although aspects of the biology (food plants, distribution etc.) of the two *Gonometa* species and *A. mimosae* are known (Pinhey 1975; Scholtz & Holm 1985; Oberprieler 1995), their population dynamics have not been studied. This has significant implications for silk yields and sustainable harvesting. One component likely to play an important role in the population dynamics of these herbivorous insects is natural enemy-induced mortality, including parasitoids (Walde & Murdoch 1988; Marron & Harrison 1997, Hassell 2000). The research findings of Hartland-Rowe (1992) are currently the only quantitative description (however, without measures of variability) of the importance of parasitism for a southern African *Gonometa* species. His work on *G. rufobrunnea* revealed that three species of egg parasitoids (Table 1) cause 50 % mortality of the eggs, and larval parasitoids 30 % of mortality in late larval instars (Hartland-Rowe 1992).

The first step in establishing the impact of parasitoids on their hosts is to identify the species involved and, if possible, establish a guide to their identification in the field. The use of natural-enemy-specific markings on herbivore insect galls, mines or pupal cases (including emergence hole characteristics) to identify mortality induced by a particular species greatly facilitates estimation of species-specific mortality levels (see for example, Heads & Lawton 1983; Brewer & Gaston 2003). Studying parasitoid attack on the pupal stage of *Gonometa* species is possible in the field because predators (birds and rodents) do not remove the cocoon

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Table 1. List of known parasitoid species of *Gonometa* spp. from southern Africa (*Gonometa postica* (Walker), *Gonometa rufobrunnea* (Aurivillius)), East Africa (*Gonometa podocarpi* (Aurivillius), *Gonometa fasciata* (unknown)), as well as other Lasiocampidae (*Eutricha capensis* (Linnaeus), *Eutricha truncata* (Walker), *Streblote concolor* (Walker), *Bombycomorpha pallida* (Walker) and *Bombycomorpha bifascia* (Distant)) and Saturniidae species (*Argema mimosae* (de Boisduval), *Imbrasia belina* (Westwood), *Imbrasia cytherea* (Fabricius), *Imbrasia bubo* (Bouvier)) known to be parasitised by the same species. Species names of hosts are according to most recent classification (Vári *et al.* 2002).

Order Family	Species[1]	Life stage attacked	Host species
Diptera			
Tachinidae	***Pimelimyia semitestacea*** (Villeneuve) (syn. *Sturmia semitestacea* Vill.)	larva [2]	*G. postica* [7, 9, 8], *G. rufobrunnea* [2, 8], *B. fasciata* [9], *B. pallida* [9]
	Tachina convergens [9] (Wiedemann) (syn. *Sturmia convergens* Wiedemann & *Sturmia dilabida* Villeneuve (Curran))	?	*G. postica* [9]; *E. capensis* [9], *E. truncata* [9]; *S. concolor* [9]
	Carcelia evolans [9] (Wiedemann) (syn. *Zenillia evolans* Wiedemann)	?	*Gonometa* sp.[9] (either *G. postica* or *G. rufobrunnea*); *I. belina* [8]; *I. cytherea* [10]
	Palexorista gilvoides (Curran) [3] (syn. *Sturmia gilvoides*_Curran [4])	larva [3,4]	*G. podocarpi* [3,4]
	Palexorista sp. 1* [2]	larva [2]	*G. rufobrunnea* [2]
	?*Palexorista* sp.*	larva	*G. postica, G. rufobrunnea*
	?Tachinidae sp.[5]	?	*G. postica, Gonometa* sp. [5]
Hymenoptera			
Braconidae	**?*Disophrys* sp.**	larva	*G. postica, G. rufobrunnea*
	Meteorus trilineatus (Cameron) [4]	larva [4]	*G. podocarpi*
Ichneumonidae	*Pimpla mahalensis* (Gribodo) [4]	larva [4]	*G. podocarpi*
Chalcididae	***Brachymeria* sp. 1****	larva	*G. postica, G. rufobrunnea*
	Brachymeria sp. 2** [2]	larva [2]	*G. rufobrunnea* [2]
	***Kriechbaumerella* sp.**	larva	*G. postica, G. rufobrunnea*

Table 1. continued

Order Family	Species[1]	Life stage attacked	Host species
	Hockeria crassa (Bouček)		*I. cytherea* [10]
	Hockeria nudaureliae (Bouček)		*I. cytherea* [10]
	***Hockeria* sp. 1**	larva	*A. mimosae*
	Hockeria sp. 2 [2]	larva [2]	*G. rufobrunnea* [2]
	Hockeria sp. 3 [10]		*I. belina* [10]
Eurytomidae	***Eurytoma transvaalensis*** (Cameron) [2]	larva; hyper pars.	*G. postica, G. rufobrunnea* ?*Disophrys*
Perilampidae	***Perilampus* sp.**	hyper pars.	*P. semitestacea*
Eulophidae	*Pediobius anastati* (Crawford) [2, 5]	egg [2]	*G. postica*[11], *G. rufobrunnea* [2], *Gonometa* sp.[5]
	Pediobius sp.	egg [8]	*I. belina* [8]; *I. cytherea* [10]; *I. bubo* [8]
Eupelmidae	*Anastatus bifasciatus* (Fonscolombe) [2]	egg [2]	*G. fasciata* [2]
	Anastatus sp. 1 [2]	egg [2]	*G. rufobrunnea* [2]
	Anastatus sp. 2 [8]		*I. belina* [6], *I. cytherea* [10]
	Anastatus sp. 3 [3, 4]	egg [3, 4, 6]	*G. podocarpi* [3, 4]
	Mesocomys pulcriceps (Cameron) [2]	egg [6]	*G. postica* [11], *G. rufobrunnea* [2], *Gonometa* sp.[5], *A. mimosae* [8]; *I. belina* [6], *I. cytherea* [10], *I. bubo* [10]
	Tineobius gonometae (Ferrière) [2]	larva [2]	*G. postica* [11], *G. rufobrunnea* [2]

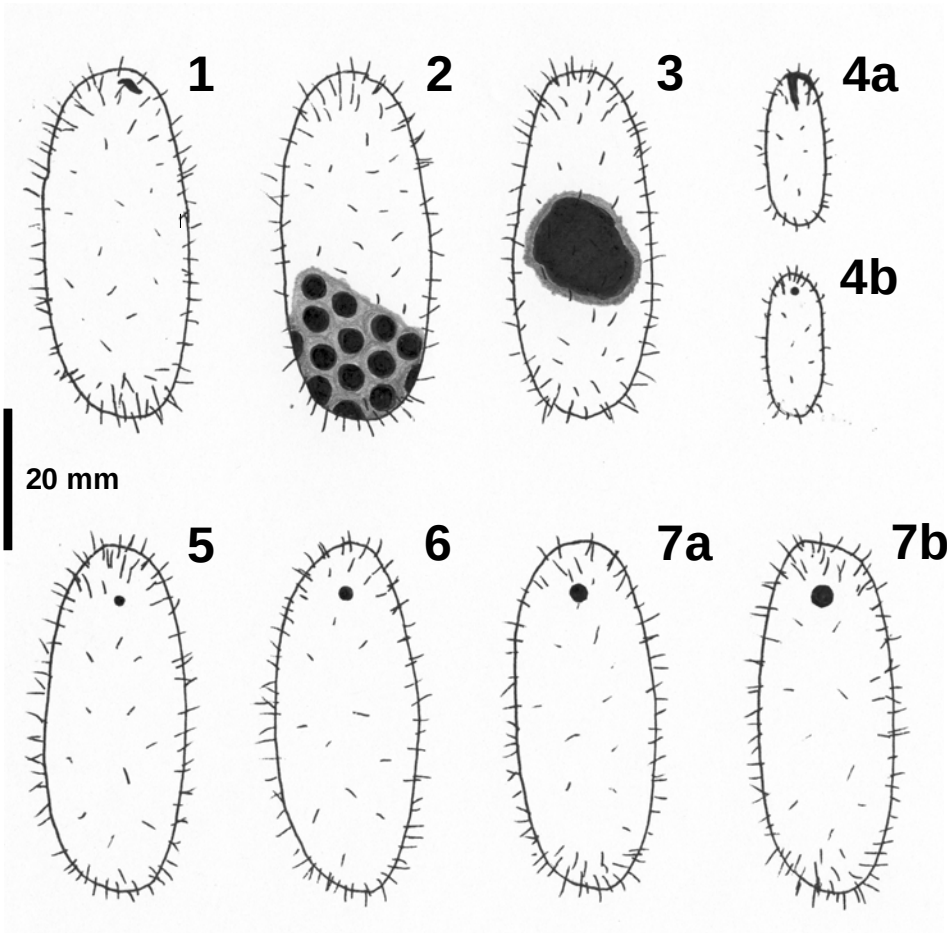
(1) Boldface denotes species recorded in this study. Number 2-11 denote other information sources: (2) Hartland-Rowe 1992, (3) Austara 1971, (4) Okelo 1972, or (5) Esther Kioko (unpublished), (6) Scholtz & Holm 1985, (7) Crosskey 1984, (8) Peigler 1994, (9) Cuthbertson & Munro 1941, (10) Geertsema 1975, (11) Records from the Biosystematics division of the Plant Protection Research Institute, Agricultural Research Council, South Africa. Similar numbers of asterisks indicate that unidentified species are of the same genus, region and have the same host species and may be thus the same species; hyper pars. = hyperparasitoid.

casing during predation, and parasitoids leave species-specific, characteristic emergence holes (Hartland-Rowe 1992). Here, we provide a list of the egg and larval parasitoid species of these southern African wild silk moths, with information on the life stage and host species attacked. The characteristics of emergence holes formed by each larval parasitoid species on the *Gonometa* cocoon is also described.

Information on previously identified parasitoid species of southern African *Gonometa* species was compiled from a few key references (Table 1). However, the results presented are based mostly on collections and surveys made by us in regions where host species are known to reach high abundances (Veldtman *et al*. 2002). Occupied cocoons were collected from localities within the known (historic and recent records) outbreak range of both species (*Gonometa postica* from Vryburg, Hotazel (North-central South Africa), Gabane, Kumukwane, Mogoditshane and Kopong (South-Eastern Botswana) and *G. rufobrunnea* from Shashe and Dumela (North-Eastern Botswana), see Veldtman *et al*. 2002 for co-ordinates). Pupal collections were made during the overwintering and first generation stages of both species (July 2000 and January 2001). Cocoons of *A. mimosae* were also collected in Gabane in July 2000. Collectively, the larval parasitoids of *G. postica* and *G. rufobrunnea* resulted in a median parasitism rate of approximately 30% at sampled localities (Veldtman *et al.* in prep.).

All parasitoids emerging from the collected pupae were recorded, as were the size and shape of their emergence hole(s). The sizes of emergence hole of some species' were also measured. Laboratory-emerged parasitoid species could consequently be linked to characteristic emergence holes (Fig 1-7). Parasitoid species (Hymenoptera and Diptera) were identified by taxonomists at the Biosystematics Division, Plant Protection Research Institute, Agricultural Research Council, Pretoria. Voucher specimens are to be placed in the National Collection of Insects, Plant Protection Research Institute, Pretoria.

The parasitoids of East African *Gonometa* species are also listed (Table 1) to highlight possible patterns in genera responsible for parasitism. Similarly, other Lasiocampidae and Saturniidae species parasitised by the same parasitoid species or genus in southern Africa are also provided (Table 1). Below is an outline of the parasitoid species associated with *G. postica* and *G. rufobrunnea* (as well as one species parasitising *A. mimosae*) and descriptions of their emergence hole characteristics.



Figures 1-7. Characteristic emergence hole(s) left by parasitoid species emerging from *Gonometa postica* and *G. rufobrunnea* pupal cocoons. (1) *Pimelimyia semitestacea*, (2) ?*Palexorista* sp., (3) ?Tachinidae sp., (4) dwarf *Gonometa* species cocoons formed after parasitism by a ?*Disophrys* sp. showing characteristic emergence holes a) after successful emergence of parasitoid (cracked open) and b) after hyperparasitism by *Eurytoma transvaalensis*, 5) *Eurytoma transvaalensis* emerging as primary parasite, (6) *Brachymeria* sp. 1, (7) *Kriechbaumerella* sp. a) male and b) female.

Parasitoid species and their emergence holes

Diptera

Pimelimyia semitestacea Villeneuve (Tachinidae) (Table 1) is probably the best-known larval parasitoid of southern African *Gonometa* species, and is described in several key references (Cuthbertson & Munro 1941; Crosskey 1984; Hartland-Rowe 1992). This species differs from others in that it emerges from the host cocoon in the larval stage, pupating in the soil. Upon emergence larvae force themselves through a single, small, irregular, tear-shaped emergence hole of 1-3 mm in diameter at the anterior of the cocoon (Fig. 1). The edge of this hole is usually brittle and may possibly be a result of larvae (which do not have biting mouthparts) forming the emergence hole by enzymatic breakdown of the silk. Larvae have been observed to sequentially force themselves through the same tiny emergence hole, ballooning outwards. Larvae are negatively phototropic and readily tunnel into wood shavings or fine sand to pupate. Up to 16 larvae have been found to emerge from a single female host, but between one and three for male cocoons and five and nine for the larger females are more usual.

?*Palexorista* sp. (Table 1) form multiple emergence holes (usually between 3-15, 3-4 mm in diameter), each of which is covered by an operculum prior to fly emergence (Fig. 2). The puparia are not separated into compartments inside the cocoon. Although no adults emerged in the laboratory, puparia of all parasitised cocoons showed characters similar to those of the genus *Palexorista. Palexorista* species have a puparium with each of the paired posterior spiracles in the form of prominent trifid "boss", with simple slits (D. Barraclough pers. comm.). Several cases of cocoon deformation were observed in the field when the emergence holes of this species were present. This may also indicate enzymatic breakdown of the posterior end of the cocoon for larvae to embed themselves in the cocoon wall upon pupation. Hartland-Rowe (1992) mentioned a *Palexorista* sp. as an important larval parasitoid of *G. rufobrunnea*, at Shashe (near Francistown), Botswana. As material collected during this study is also from this area, the species found in this study is likely to be that species (Table 1).

An unknown parasitoid species (Table 1) that leaves a characteristic, large, irregularly shaped, dark brown edged, exit hole in the flank of the cocoon (Fig. 3), has only been observed in the field with no individuals emerging from collected material. The emergence hole of this species can be distinguished from those that would result from bird predation (Hartland-Rowe

1992) because pupal remains are present and bird predation typically results in larger holes. This species may also be of the Tachinidae, as an unidentified Tachinidae species from East Africa evidently leaves a similar-shaped emergence hole (E. Kioko pers. comm.).

Hymenoptera

The 'dwarfism' phenomenon observed in *G. postica* cocoons (see Veldtman *et al*. 2002) is caused by a primary parasitoid, possibly a species of *Disophrys* (Braconidae), that parasitises the early larval instars of *G. postica* and *G. rufobrunnea.* ?*Disophrys* sp. was found to be hyperparasitised by *Eurytoma transvaalensis* (Cameron) (Eurytomidae). Successful emergence by ?*Disophrys* sp. is characterised by a dwarf cocoon with a small crack at the anterior end (Fig. 4a), while *E. transvaalensis* leaves a small (usually single) circular emergence hole (Fig 4b). Upon dissection, most dwarf cocoons were found to contain a ?*Disophrys* sp. pupal cocoon (consisting of white silk), as well as the larval head and other remains of the parasitised host. In some dwarf cocoons only the larval remains were found with no emergence holes, possibly indicating unsuccessful primary parasitism. Evidence of hyperparsitism is clear from the similarly sized emergence holes in both the host's and primary parasitoid's cocoons, indicating that *E. transvaalensis* emerged from the braconid's cocoon first. *Eurytoma transvaalensis* also emerged from normal sized cocoons of both *Gonometa* species. However, no Braconidae cocoon or any primary parasitoid remains were found, suggesting that this species is a facultative hyperparasitoid. Hartland-Rowe (1992) described *Eurytoma transvaalensis* as the most abundant Hymenopteran larval parasitoid of *G. rufobrunnea*.

In addition to *E. transvaalensis*, two other parasitoid species (*Brachymeria* sp. 1 and *Kriechbaumerella* sp., both Chalcididae) form smooth (regular), circular emergence holes (Figs. 4b, 5, 6, 7a, 7b). These Chalcidoidea parasitoids escape from cocoons using strong mouthparts to chew a circular smooth hole, with larger individuals forming larger holes. The average emergence hole size and observed variability are provided for each of these species from material that emerged in the laboratory (Fig. 8). Although the shape of the emergence hole of all three species do not differ, the diameter of the holes do (Fig. 8), and it is possible to distinguish them in the field.

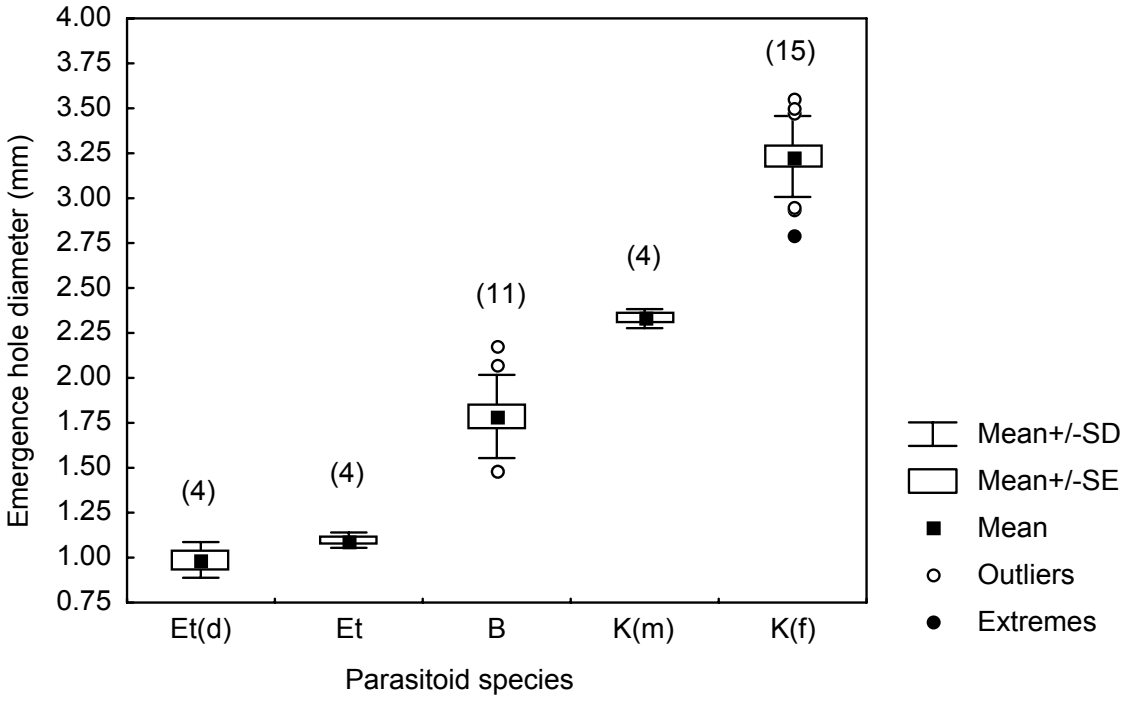


Figure 8. Variability in parasitoid cocoon emergence hole diameter for parasitoid species leaving a circular emergence hole: Et(d) = *Eurytoma transvaalensis* emerging from dwarf cocoons; Et = *Eurytoma transvaalensis*; B = *Brachymeria* sp. 1; K(m) = *Kriechbaumerella* sp. (male); K(m) = *Kriechbaumerella* sp. (female). Numbers in brackets are sample sizes.

Eurytoma transvaalensis emerging from dwarf or normal sized cocoons leaves a hole between 1.0-1.1 mm in diameter, while *Brachymeria* sp. 1, which shows marked intraspecific variability in body length (range in emergence hole diameter represents 33% of the mean), forms emergence holes 1.5-2.1 mm in diameter. The *Brachymeria* species recorded as parasitising both *G. postica* and *G. rufobrunnea* is thought to be the same species previously found to parasitise *G. rufobrunnea* (Table 1). If this species and the *Palexorista* species mentioned earlier are indeed the same species as previously described (Hartland-Rowe 1992), the larval parasitoids recorded to date are shared by all southern African *Gonometa* species.

The emergence holes formed by *Kriechbaumerella* sp. show marked sexual size dimorphism (Fig. 8). Males are smaller and form smaller holes, 2.3-2.4 mm in diameter, while

adult females are larger with emergence holes ranging from 2.9-3.5 mm in diameter. Although sample size was small, species that form circular smooth emergence holes showed no cases of overlap in emergence hole diameter (Fig. 8). Emergence hole diameter is thus an adequate measure for species identification.

Hockeria sp. 1 (Chalcididae) was the only parasitoid (n = 2) to emerge from 31 viable *A. mimosae* cocoons collected. This species forms an emergence hole (diameter approximately 3 mm) just below the ring of mimetic parasitoid emergence holes of the cocoon (see Oberprieler 1995 for host cocoon characteristics). Hartland-Rowe (1992) recorded another unidentified species of this genus emerging from *G. rufobrunnea*. It is not possible to determine if these two species are the same.

Despite Hartland-Rowe (1992) mentioning the value of noting the emergence hole characteristics of *G. rufobrunnea* larval parasitoids for species identification, this is the first time that these characteristics are described and quantified for both *Gonometa* species in southern Africa. The information provided here makes it possible to determine the parasitoid species responsible for parasitism of field parasitised pupa. Future collections of pupae will greatly aid in confirming the identity of the unidentified taxa listed in this study. Most importantly, future research on field parasitism rates of *Gonometa* populations, requiring the identification of parasitoid species, will benefit from the species list, descriptions and figures provided.

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CHAPTER 3

Dimensions of spatial heterogeneity: a classification of non-, semi- and explicit spatial heterogeneity

INTRODUCTION

Understanding the causes of spatial heterogeneity in the abundance of organisms is central to ecology. The quantification of spatial pattern in biotic and abiotic variables, and how such pattern may influence species interactions and their responses to resources, is an ongoing research focus (Ives & Klopfer 1997; Stewart *et al*. 2000; Wiens 2000; Liebhold & Gurevitch 2002). Typically, species occurrences are aggregated and numbers of individuals are unevenly distributed across sites (Cole 1946; Perry *et. al*. 2002). Although aggregation is an inherent species property (a function of species dispersal and behavioural patterns), the occurrence of individuals at different densities across space may also reflect a response to biotic and abiotic environmental conditions (e.g. resource quality and availability) (Taylor 1984; Wiens 2000). The study of the aggregation of individuals is almost as old as ecology itself (Raunkiaer 1934; Cole 1946). That it remains a focus in ecology today (Perry *et al*. 2002) is testimony to its significance as an emergent property of responses of species to their environment, and its importance in interactions within and across trophic levels (Hassell & Pacala 1990; Sevenster 1996; Murrell *et al*. 2001; Plotkin *et al*. 2002; Porter & Hawkins 2003; Warren *et al*. 2003).

One of the consequences of the widespread significance of aggregation is the extensive array of methods that have and continue to be developed for its measurement (Dale *et al*. 2002; Perry *et al*. 2002). However, these methods differ in their information content, biological relevance, and conclusions regarding the form of spatial heterogeneity (e.g. clumped or random) that they identify (Perry 1998; Wiens 2000; Tenhumberg *et al*. 2001). Moreover, a distinction has recently been made between measures of spatial heterogeneity (*sensu* Wiens 2000) that do and do not incorporate spatial information, and the degree to which these methods provide solutions that are spatially explicit (Wiens 2000; Perry *et al*. 2002). In this

study we highlight the spatial reference-related (spatial co-ordinates, e.g. latitude and longitude) differences between methods in terms of both the data used and pattern identified (synthesizing the approaches of Wiens (2000) and Perry *et al*. (2002)).

We distinguish three major groups of methods, i.e. those that are spatially non-explicit, semi-explicit and explicit, and discuss their application to abundance and occurrence data. Distinguishing between these approaches has become particularly important with the continued proliferation of analytical methods (and associated terminology, see Dutilleul & Legendre (1993)) (e.g. Plotkin *et al*. 2002; Perry & Dixon 2002), and the absence of comprehensive empirical comparisons between them (see Dale *et al*. 2002 for theoretical relationships). We propose a classification scheme for various measures of spatial heterogeneity for both occurrence and abundance data, based on the degree to which the described pattern is spatially explicit. The framework provided allows measures and their strengths to be compared, highlights the most commonly used examples of these measures, and proposes a hierarchy of information content and biological relevance. We emphasize opportunities that exist for empirical comparisons of spatially explicit and non-explicit approaches to the measurement of spatial heterogeneity, and the potential value of spatially explicit approaches for the re-evaluation of theory developed using more traditional methods. The potential problems with quantifying different dimensions (i.e. the same entity with increasing amounts of available spatial information) of spatial heterogeneity but using them interchangeably, are illustrated using field-collected abundance data on an insect-herbivore, and the number of individuals parasitised and the imposed parasitism rate. Using these data we test whether the form of spatial heterogeneity found, for abundance data only, depends on the degree to which the method used to describe it is spatially explicit. We thus test if there is a difference between spatially non-explicit, semi-explicit and explicit methods in the form of spatial heterogeneity identified, and thus the conclusions drawn about aggregation.

Dimensions of spatial heterogeneity

Although the aggregation of individuals has been a recurring theme in ecology for many decades (Raunkiaer 1934; Cole 1946, Taylor 1984, Perry *et al*. 2002), until recently the lack of adequate spatial analytical methods has limited the examination of spatially explicit phenomena (Liebhold *et al*. 1993; Perry *et al*. 2002). The wide array of possible approaches to

the measurement and interpretation of aggregation that are now available were recently reassessed in light of current analytical developments (Coomes *et al*. 1999, Dale *et al*. 2002, Perry & Dixon 2002). However, these reviews do not consider the quantification of aggregation *per se* but rather any spatial pattern described in ecology. We use the term 'spatial heterogeneity', *sensu* Wiens (2000), to broadly encompass the array of spatial patterns (aggregation being only one of these) that can be described (Table 1, Fig. 1). Spatial heterogeneity can formally be defined as "discontinuities in space" (Wiens 2000), or pattern in spatial data (Liebhold & Gurevitch 2002), and may be quantified for either abundance (count), or occurrence (presence-absence) data. Although, spatially-referenced occurrence data can be transformed (with a loss of fine scale spatial information) to abundance per unit area (Perry & Dixon 2002; Perry *et al*. 2002), the use of untransformed occurrence data is common in ecology (Coomes *et al*. 1999; Plotkin *et al*. 2002 Wiegand & Moloney 2004). Therefore, defining terminology for spatial heterogeneity in both abundance and occurrence data will further contribute to unambiguous definitions in spatial ecology. Nonetheless, potential differences between the forms of spatial heterogeneity describe are likely to be greater for abundance than occurrence data, because spatial references are accompanied by recorded variable. Consequently, we focus on the differences between different degrees of spatial explicitness using abundance data (see Coomes *et al*. 1999; Plotkin *et al*. 2002; Wiegand & Moloney 2004 for detailed coverage of measures used to describe occurrence data).

The term ‘aggregation’ has commonly been used to denote the grouping of elements or a contagious condition of spatial heterogeneity. However, this term does not distinguish between the dimension (thus the level of spatial explicitness) used to quantify this form of spatial heterogeneity (i.e. the method used) (Wiens 2000). Because the form of spatial heterogeneity that is identified (e.g. overdispersed versus underdispersed, or regular versus aggregated, Table 1) may differ depending on the measure used to identify it (Perry 1998), the term 'aggregation' has become potentially misleading. Therefore, to allow unambiguous reporting of results, a need for formalised terminology to describe different forms of spatial heterogeneity has arisen. Here we use ‘aggregation’ as a loose, generic term for any grouping of elements (which is one form of spatial heterogeneity), and use the terminology outlined in Table 1 for reference to specific dimensions, measures and forms of spatial heterogeneity. The terms provided are

Table 1. Classification of spatial heterogeneity in abundance and occurrence data based on the degree of spatial explicitness (spatially non-explicit, semi-, and explicit). For each category an example of a measure used to determine the form of spatial heterogeneity is given. With each the measure terms and definitions used as well as synonyms (chronological order of use) and spatial applications or statistics used to quantify it are presented. Numbers in superscript denote source of terminology or example of recent use. For abundance data different measures to quantify correlation (A* vs. A^, with different symbols representing different data sets) are given. (Z), (D) and (X,Y) denote measured attribute, measured distance and spatial co-ordinates (e.g. latitude and longitude) respectively.

Measure *Form*	Definition	Synonyms	Spatial applications	Example statistics
		1. Spatially non-explicit heterogeneity		
A) Statistical heterogeneity [1] (Z)	Skewness in the frequency distribution of counts; usually the relationship between the mean and variance [1]	Spatial distribution [2, 3]; Parametric intensity [4]; Density aggregation [5];	No spatial pattern applications [1, 4, 6, 7]; Spatially non-explicit modelling of species area relationships [3]	Poisson index of dispersion [8, 9]; Moore's index [10] Morista's index [10, 11]
Over dispersed [4, 10]	Variance greater than the mean – Negative binomial or geometric distribution [8, 12]	Aggregation [3, 9, 13]; Aggregated [14]		
Under dispersed [4, 10]	Variance smaller than the mean – Binomial distribution [12]	Uniform [12]; Regularity [9]; Regular [8]		
Dispersed [4]	Variance approaches the mean – Poisson distribution [8, 12]	Randomness [9]; Random [10]		
A* vs. A^) Correlation [15]	Magnitude of one variable measured at a sampling point changes as that of another changes [15]		Spatially non-explicit matching of variables	Spearman R [15]
B) Nearest neighbour distance [11] (D)	Distance between spatially referenced point and its nearest neighbour/s	Spatial distribution [16]	Test for spatial randomness with no spatial reference [11]	NN; kNN [10]

Table 1. continued

Measure *Form*	Definition	Synonyms	Spatial applications	Example statistics
		2. Spatially semi-explicit heterogeneity		
A) Spatial structure [17] [(Z, X, Y), local pattern not incorporated [11]]	Values measured for points in space are similar, dissimilar or not related to neighbouring points	Surface pattern spatial heterogeneity [18]; Spatial abundance structure [19]	Allowance for spatial dependence in quantification of biological responses[7, 20]	Moran's *I* [17]; Trend surface analysis [17];
Spatial dependence [17]	Spatial structure in response variable due to spatial structuring in explanatory variables [20]		Sampling design [17]; Variance partitioning [17]	
Spatial autocorrelation [17]	Degree of dependence in error components of data due to neighbouring sites having an influence on the measured value [20]	Spatial clustering [21]	Identification of patch size [17]; Measuring correlation between neighbouring points [17]	
Positive autocorrelation [17]	Points close in space are more similar than expected by chance [17]			
Negative autocorrelation [17]	Points close in space are more dissimilar than expected by chance [17]			
No significant autocorrelation	Points close in space are spatially independent			
A* vs. A^) Cross-correlation [22]	Determine to which degree two data sets exhibit concordant periodic variations[17]		Describes relationship between co-occurring species [22]	Mantel statistic [17]

Table 1. continued

Measure *Form*	Definition	Synonyms	Spatial applications	Example statistics
B) Spatial distribution [15, 23] (X, Y)	Physical position (distribution) of sample points in two-dimensional space [23]; Location of clusters of points in study arena [24]	Point pattern spatial heterogeneity [18]; Spatial aggregation [5]; Spatial clustering [24]	Presence-absence data [18]	Index of aggregation (SADIE-map) [6,23]
	3. Spatially explicit heterogeneity			
A) Spatial non-randomness [1] (Z, X, Y), local pattern incorporated[11]	Difference between physical arrangement of the counts and randomisations of these counts [1]	Spatial arrangement [4, 25]; Spatial distribution [6, 26]	Determination of overall pattern [1]	Index of aggregation (SADIE regular) [1, 10];
Regular [1, 4]	Sample counts are equally spread among sampling points			
Random [1, 4]	The spatial arrangement of counts is no different from that expected by chance			
Aggregated [1, 4]	Arrangement of counts are non-random [27]	Spatial aggregation [25]		
Spatial clustering [28]	Counts are clustered into patches (groups of high counts) and gaps (groups of low counts)	Spatial patchiness [6]	Identifying the location of patches and gaps [1]	Mean and local clustering values (SADIE red/blue) [6]
Local indices of spatial autocorrelation [29]	Describes spatial autocorrelation for each sampled data point [29]	Local spatial autocorrelation indices [30]	Determining local indicators of non-stationarity [29]; Detect outliers of the global spatial autocorrelation value[29]	LISA statistic[29]

Table 1. continued

Measure *Form*	Definition	Synonyms	Spatial applications	Example statistics
A* vs. A^) Spatial Association [27, 31]	Degree of matching between two sets of spatially referenced counts [27, 31]		Method for detecting correlation between two sets of spatially referenced data [31, 32, 33]	Mean and local association values (SADIE Association test) [27]
Significant association [27, 31]	Spatial matching of clusters of two sets of data [27, 31]			
Significant dissociation [27, 31]	Spatial mismatching of clusters of two sets of data [27, 31]			
Non-significant association	Degree of spatial matching or mismatching is not significantly different from expected by chance			
B) Point-cluster analysis [24] (X, Y)	Number of sampling points connected to at least one neighbour within a minimum specified distance [24]	Spatial clumping [24]	To determine size and position of clusters of sampling points [24]	No statistic as yet, but rather descriptive, i.e. distance moved [24]

(1) Perry 1998; (2) He & Legendre 2002; (3) He & Gaston 2003; (4) Bohan *et al.* 2000a; (5) Tenhumberg *et al*. 2001; (6) Perry *et al*. 1999; (7) Jumars *et al*. 1977; (8) Bliss & Fisher 1953; (9) Perry & Hewitt 1991; (10) Dale *et al.* 2002; (11) Perry *et al*. 2002 (12) Iwasa *et al*. 1981; (13) Gross & Ives 1999; (14) Rosewell *et al*. 1990; (15) Zar 1984; (16) Williams *et al.* 2001; (17) Legendre & Legendre 1998; (18) Dutilleul & Legendre 1993; (19) Brewer & Gaston 2002; (20) Legendre *et al*. 2002; (21) Ni *et al*. 2003; (22) Rossi *et al*. 1992; (23) Perry 1995a; (24) Plotkin *et al*. 2002; (25) Perry 1995b; (26) Ferguson *et al*. 2000; (27) Perry & Dixon 2002; (28) Wiens 2000; (29) Anselin 1995, (30) Sawada 1999; (31) Winder *et al.* 2001; (32) Korie *et al*. 2000; (33) Thomas *et al*. 2001;.

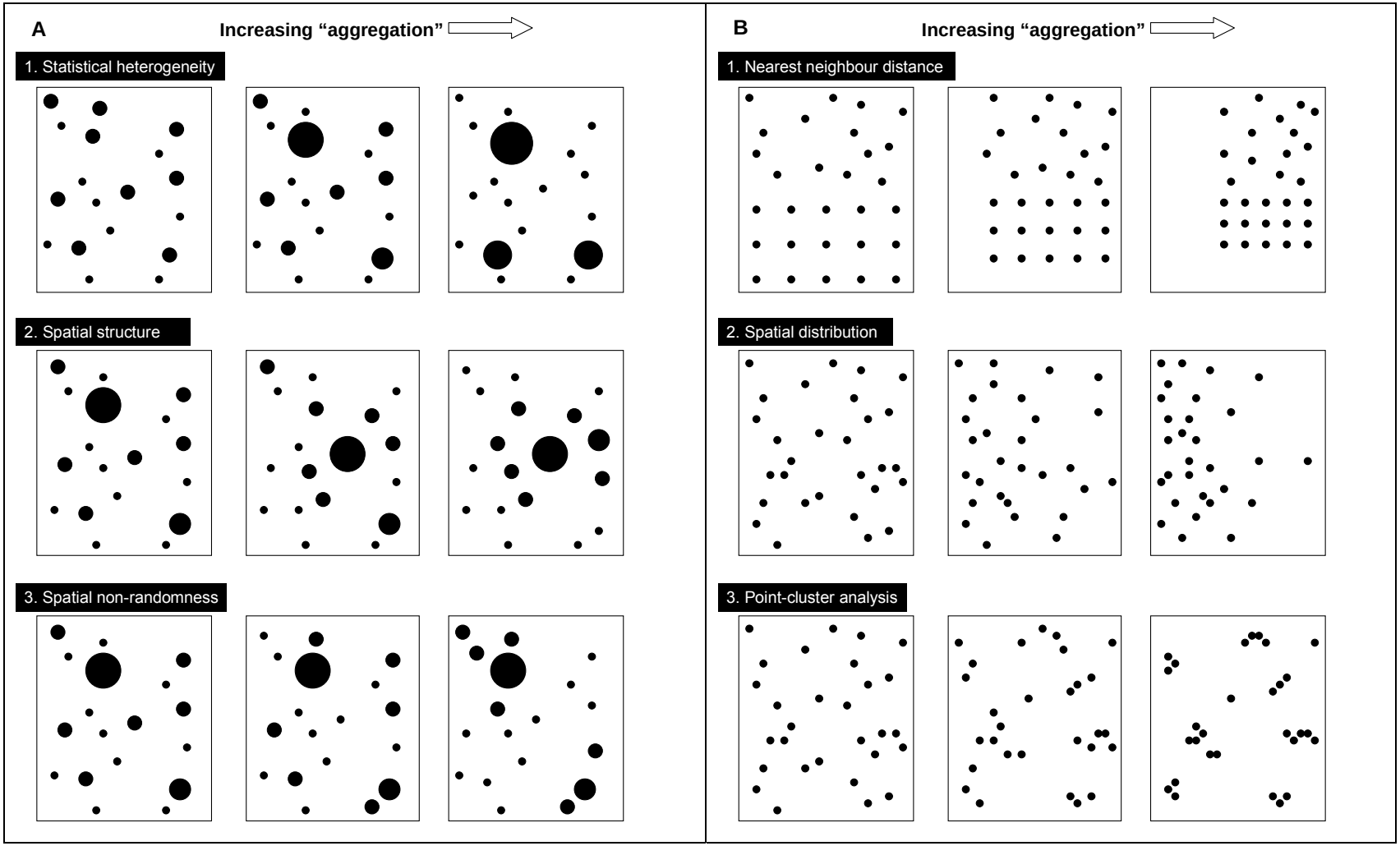

Figure 1. Different measures of spatial heterogeneity in abundance (A) and occurrence (B) data in ecology, with 'aggregation' increasing from left to right. Measures numbered 1, 2 and 3 represent spatially non-explicit, semi-explicit and explicit spatial heterogeneity respectively. In A. all sampling points within a study area/block have the same spatial references, with the size of a circle denoting the magnitude of a count at that sampling point. In B. each circle denotes the presence of an individual.

largely a synthesis of those in the literature, and their distinction here is intended to avoid confusion between the data type, category and form of spatial heterogeneity described by different measures of spatial heterogeneity (Table 1). In the following paragraphs I outline the three categories that vary in the degree to which they are spatially explicit, each generally represented by a single commonly used measure of spatial heterogeneity in abundance and occurrence data. The three dimensions are spatially non-explicit, spatially semi-explicit and spatially explicit heterogeneity (Table 1). In addition, for abundance data we list a method for each dimension of spatial heterogeneity used to correlate the spatial heterogeneity in two data sets.

Statistical heterogeneity and nearest neighbour distance (quantified for abundance and occurrence data respectively) can be considered measures of spatially non-explicit heterogeneity, because records are taken across a series of sampling points in a site, which are not spatially referenced (e.g. Williams *et al*. 2001) (Table 1, Fig. 1). In fact statistical heterogeneity can be said to be totally independent of spatial pattern. Nonetheless, not using spatial information (spatially non-explicit heterogeneity) can be seen as the preceding step of using spatial information (spatially semi- and explicit heterogeneity, Table 1) in a classification of spatial data use. Spatial structure (abundance data) (Legendre & Legendre 1998) and spatial distribution (occurrence data) (Perry 1995a), are measures of spatially semi-explicit heterogeneity, because although spatial dependencies or patterns can be accounted for (Perry *et al*. 2002), the heterogeneity described is not explicitly related to any particular location within the study site (i.e. the exact pattern of specific locations or areas within a site are unknown) (Wiens 2000). Spatial non-randomness and point-spatial clustering are measures of spatially explicit heterogeneity (Table 1, Fig. 1). These measures are spatially explicit because spatial heterogeneity may be related to particular sample points or areas within the study arena (Wiens 2000). For example, with spatial non-randomness the position of areas of comparatively high counts can be described, while point-spatial clustering describes the position and size (number of individuals) of groups of individuals (Plotkin *et al*. 2002).

The traditional, spatially non-explicit approach to the measurement of heterogeneity, statistical heterogeneity (Table 1), is merely the relationship between the variance and the mean of the frequency distribution of counts and can be quantified by the Poisson index of dispersion (Perry 1998) (Table 1, Fig. 1). Animal abundance, usually with many zero and few

large counts, is also considered overdispersed when fit by the negative binomial distribution (NBD) (Bliss & Fisher 1953; Williams *et al.* 2001). In such cases the index of aggregation of the NBD, *k*, is less than unity (Bliss & Fisher 1953). However, the ability of *k* to describe ecologically relevant spatial pattern has long been contested (Taylor *et al*. 1979). For example, the inverse of k behaves inconsistently over ranges of over dispersion even when the NBD fits the data, indicating the inadequacy of *k* to describe statistical heterogeneity (Taylor *et al*. 1979). Also, the NBD is not suitable for quantifying aggregation in patches of variable size (Sevenster 1996), or predicting abundance from occupancy in some cases (Warren *et al*. 2003). Furthermore, Perry & Hewitt (1991) and Perry (1995b) consider overdispersion to be of limited interest when investigating the spatial heterogeneity of individuals, because overdispersion in biological data is virtually universal (Taylor *et al*. 1978). The relationship between two variables described by statistical heterogeneity can only be determined by correlation (Table 1). Although the two data sets may share spatial references, spatial references are not included in the quantification of the relationship. Any correlation detected will therefore be spatially non-explicit.

The quantification of spatial structure, a semi-explicit approach, has also been used to measure spatial heterogeneity (Jumars *et al*. 1977; Dessaint *et al*. 1991; Loch & Zalucki 1998; Brewer & Gaston 2002) (Table 1, Fig. 1). If the values of any point-referenced, continuous variable are spatially dependent or spatially autocorrelated, then the data are spatially heterogeneous (Legendre & Legendre 1998; Wiens 2000; Perry *et al*. 2002) (Table 1). Positive autocorrelation, for example, indicates that adjacent values of a variable are more similar to each other than expected by chance (Sokal & Oden 1978; Koenig 1999). Determining this area of comparative homogeneity, or 'patch size' of biotic and abiotic variables is of particular interest in spatial ecology (Legendre & Fortin 1989; Koenig & Knops 1998; Koenig & Haydock 1999; Manson 2000). However, although spatial structure is quantified from spatially-referenced data, it does not incorporate information on patterns associated with physical positions (local pattern) (Perry *et al*. 2002), i.e. the value of an autocorrelation function is not influenced by the exact position of two sampling points in the study arena, only by their relative positions measured by the distance between them (Legendre & Legendre 1998). The spatial structure of two variables may be compared by cross–correlation methods (Table 1, see also Rossi *et al.* 1992). Although this allows the spatial references of each

variable to be considered, it is not possible to determine if the quantified spatial patterns match in a particular direction. Any relationship between the two variables will thus be spatially semi-explicit.

The more recent, spatially explicit approach to describing heterogeneity in spatially referenced count (abundance) data, involves the measure of spatial non-randomness (Perry 1998) (Table 1, Fig. 1). The quantification of this measure is based on the Spatial Analysis by Distance IndicEs (SADIE) method, which measures how much an observed arrangement of counts differs from a completely regular arrangement of the same counts (Perry 1995a). Using this method, spatial heterogeneity is quantified by an overall measure of non-randomness, as well as the degree to which individual sample counts contribute to overall clustering into patches (areas of high abundance counts) and gaps (areas of low abundance counts). The contribution of an individual sample to a local patch or gap is defined by a local clustering index (Perry *et al*. 1999; Perry & Dixon 2002). Consequently, local spatial pattern is dependent on the size of the count and its spatial position relative to neighbours (Perry *et al*. 2002). This is currently the most widely-used spatially explicit method that quantifies spatial heterogeneity from count data and simultaneously permits hypothesis testing (Bohan *et al*. 2000b; Ferguson *et al*. 2000; Korie *et al*. 2000; Thomas *et al*. 2001; Winder *et al*. 2001, Perry *et al*. 2002). Spatial association (Table 1) is a method that is able to determine overall and local (spatially explicit) matching in spatial heterogeneity based on spatial non-randomness (Perry & Dixon 2002). Because spatial association compares the spatial pattern of two variables instead of only counts, this method has greater power to detect significant relationships between them (Winder *et al*. 2001).

Developing largely as a separate field, geostatistics has also made attempts to describe spatially explicit heterogeneity (Anselin 1995; Sawada 1999). Local indices of spatial autocorrelation (LISAs) provide spatial information that is spatially explicit in much the same way that spatial non-randomness does (Table 1). With this measure the semi-explicit spatial autocorrelation index, which summarises largely all local autocorrelation indices, can be further scrutinised to detect areas of non-stationarity and to detect outliers of the global spatial autocorrelation value (Anselin 1995). Since this measure is very similar in conception to spatial non-randomness, LISA's were not calculated for this data set.

Although these three approaches have all been used, some extensively, to quantify spatial heterogeneity, few comprehensive comparisons have been made between them (although see Dale *et al*. 2002, Perry *et al*. 2002). However, the results of statistical heterogeneity analyses have been found to be unrelated to those of spatial structure (Dessaint *et al*. 1991) and spatial non-randomness (e.g. Perry 1995b; Perry 1998; Bohan *et al.* 2000a), although the latter relationship has not been fully explored. Furthermore, although *k* of the NBD is still regularly used to describe spatial heterogeneity (e.g. He & Gaston 2000; Tenhumberg *et al.* 2001; Williams *et al*. 2001), the conclusions reached using this measure have also not been quantitatively compared with the results of spatial structure and spatial non-randomness. Consequently, whether the degree of spatial explicitness of the measure used to describe spatial heterogeneity, i.e. statistical heterogeneity, spatial structure and spatial non-randomness, determines the form of spatial heterogeneity identified, has not been shown. Here, I thus test if these measures are interchangeable in the light of their current use, i.e. does the degree of spatial explicitness incorporated in a measure of spatial heterogeneity matter?

METHODS

Study Area

Gonometa postica populations were examined at five localities within the known (historic and recent records) outbreak range of this species, spanning a distance of 400km between the two furthest localities. The localities were Vryburg (26°59'S, 24°40'E) and Hotazel (27°15'S, 23°03'E) in North-central South Africa and Gabane (24°37'S, 25°46'E), Kumukwane (24°38'S, 25°40'E), and Kopong (24°31'S, 25°48'E) in South-Eastern Botswana. The dominant woody host species utilized by *G. postica* at the first two localities was *Acacia erioloba* Meyer and at the remainder, *Acacia tortillis* Hayne (both Mimosaceae) (Veldtman *et al*. 2002).

One site was selected at each locality, except at Vryburg where two sites (approximately 1.5 km apart) were selected. Sampling was standardized by delimiting an approximately rectangular area (plot) 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 plot was a prerequisite for site selection.

Surveys of plots commenced in winter (June to July, 2000) and were repeated in mid summer (January, 2001). During the first survey, the number and fate of overwintering pupae were recorded. With the second survey, the resulting fate of those individuals that were alive in the first survey as well as the number of new first generation pupae were recorded. Similarly, the fate of these first generation pupae were followed (two subsequent surveys repeated at same periods as above) until mid-summer of the following year (January 2002).

Cocoon sampling

Within each plot every tree was carefully searched for cocoons. Cocoons were inspected to determine the fate of the pupa inside the cocoon, i.e. i) parasitised, ii) alive, iii) dead as a result of unknown causes, or iv) successfully emerged. This was indicated respectively by the i) presence or ii) absence of small emergence hole(s), iii) light weight of the cocoon or iv) a single large anterior emergence hole (pers. obs.). Parasitoid species responsible for parasitism may be identified from the shape and size of emergence holes left in the cocoon wall of a parasitised pupa (Veldtman *et. al* 2004). The number of pupae and parasitised pupae per tree were counted.

The position of each tree within a plot was measured at the main trunk of the tree with a hand held Global Positioning System (GPS). For trees in close proximity to each other the direction and distance between the two trees were noted and assigned to one of three categories (half, quarter and a tenth of the third (last) decimals of a minute) based on hand drawn maps which specifically documented this fine scale distribution of trees. These spatial co-ordinates were used in all spatial analyses.

For the investigation of the spatial pattern of parasitism, only sampling points (trees) with at least one pupa were included in analyses, as parasitism events can logically not be observed if there are no pupae. All counts of pupae or parasitised pupae were thus made per tree. At each site, pupae parasitised by different species of parasitoid were either analysed individually, or collectively ('all species') as a measure of total parasitoid mortality (see also Heads & Lawton 1983; Williams *et al*. 2001). Additionally we also considered the proportion of parasitised

pupae (parasitism rate from here on), which was transformed into integers by multiplying by ten and rounding off.

Quantification of spatial heterogeneity in abundance: what do the data say?

Spatial heterogeneity in three types of site recorded abundance data, namely number of pupae, number of parasitised pupae and parasitism rate (all per tree) were quantified using three measures, i.e. statistical heterogeneity (Table 1, A1), spatial structure (Table 1, A2) and spatial non-randomness (Table 1, A3), representing an increase in the degree of spatial explicitness with which the pattern was quantified (Table 1, Fig. 1A). This permitted direct comparison between the results of the three approaches in the conclusion reached regarding the form of spatial heterogeneity in the data.

Statistical heterogeneity

Statistical heterogeneity was quantified by determining the relationship between the mean and the variance of the frequency distribution for count data (Perry & Hewitt 1991) (Table 1). The Poisson index of dispersion (s^2/m) was calculated by dividing the sample variance by the sample mean (Perry & Hewitt 1991). If this index is close to unity the data have a Poisson distribution. When this index is smaller or greater than one it indicates that the distribution is under- and over dispersed and the data are best fit by a binomial or negative binomial distribution (or another over-dispersed distribution, e.g. gamma distribution) respectively (Table 1). Significant departures from randomness were determined by calculating $(n-1)*(s^2/m)$ and comparing it to the X^2_{n-1} distribution (Perry & Hewitt 1991).

Another measure of statistical heterogeneity, namely the index of aggregation, *k*, was also used to describe statistical heterogeneity. When the negative binomial distribution fits the data and the value of *k* is greater than unity (Bliss & Fisher 1953), count data are considered to be aggregated (Tenhumberg *et al.* 2001; Williams *et al*. 2001). The index *k* ranges from zero to infinity (∞) and the larger the value of *k* the greater the degree of aggregation (Bliss & Fisher 1953; Williams *et al*. 2001). The fit of the data to the negative binomial distribution (NBD) was tested using the method of Bliss and Fisher (1953), where *k* is first determined by a maximum likelihood solution and then used in the formula

$$U = s^2 - (\bar{x} + \bar{x}^2/\hat{k}_2) \quad (1)$$

to calculate the difference between observed and expected second moments. Adequate fit by the NBD is indicated if *U* falls within the range of its standard deviation (Bliss & Fisher 1953).

Spatial structure

Spatial structure was quantified using spatial autocorrelation (SAAP v 4.3 and Moran's *I*) (Wartenberg 1989), because there was no *a priori* evidence for spatial dependence in any of the biotic variables due to physical variables of the study sites (Legendre *et al*. 2002) (Table 1). The optimal number of equal-length distance classes was determined using Sturge's rule (Legendre & Legendre 1998). Overall correlogram significance (determined by comparing each distance class to a Bonferroni corrected α-level) was a prerequisite for the indication of spatial structure (Legendre & Legendre 1998). The size and significance of Moran's *I* values in distance classes with sufficient sample size were then examined. Often, when analysing biological data, the greatest Moran's *I* values are expected for the first distance class (Legendre & Legendre 1998).

Spatial non-randomness

SADIE methodology was used to quantify the degree of departure from spatial randomness for the spatially referenced (X,Y) count data in this study (Table 1). Spatial non-randomness is based on the distance to regularity (minimum cumulative distance to achieve a regular distribution of counts, thus when all sample counts are equal to the mean) that can be quantified for the data set as a whole (overall aggregation) or indicate the contribution of each sample point (degree of clustering) to local departures from randomness within the data set (Perry *et al*. 1999). The significance of overall aggregation was tested by dividing the actual distance to regularity by the average distances of randomisations of the sample counts, to give the index of aggregation (I_a) (Perry 1995a). This index summarises the spatial arrangement of the counts relative to one another (Perry *et al*. 1999; Perry & Dixon 2002). Although significance is actually tested, values of I_a of approximately 1.5 and greater indicate significant aggregation (Perry *et al*. 1999)

Whether or not there is evidence of overall aggregation, the degree of clustering in count data can be quantified (Perry & Dixon 2002). The index of clustering, *v*, provides information on the degree of clustering for each spatially referenced point based on the magnitude of the

count and its occurrence in relation to neighbouring counts. Clustering occurs in two forms, namely patches (counts greater than the sample mean, v_i) and gaps (counts smaller than the sample mean, v_j). For random arrangements of counts, v_i and v_j have expected values of 1 and -1. Values greater than these expected values indicate membership by the count of a patch ($v_i > 1.5$) or gap ($v_j < -1.5$) (Perry *et al*. 1999). Non-randomness is formally tested by comparing mean v_i and mean v_j values with their expected values of 1 and -1 for random arrangements (Perry *et al*. 1999). If mean v_i and mean v_j are not significant, the lack of overall, strong clustering into patches and gaps is indicated (Perry *et al*. 1999; Perry & Dixon 2002).

Within each plot, I_a, mean v_i and mean v_j was calculated for every parasitoid species that attacked pupae on more than 20% of the trees occupied by pupae. At densities lower than this (e.g. mean count per tree < 0.2), it is not possible to quantify overall aggregation and spatial clustering (Winder *et al*. 2001). The maximum ratio of non-zero values to total number of measured values that still allows the detection of significant spatial clustering (sufficient power) has been shown to be 4: 25 (Korie *et al*. 2000). In this study the lowest ratio was 9 to 38; within the specified limit. All non-randomness statistics were calculated with SADIEShell v. 1.21, red-blue analysis.

RESULTS

The number of pupae, number of parasitised pupae and parasitism rate varied greatly between sites (see Appendix). On average (± SE) there were 319 (± 66) pupae per plot occupying 52 (± 3) trees. Single parasitoid species parasitised an average of 50 (± 10) pupae on 22 (± 3) trees, while all parasitoids together parasitised 111 (± 25) pupae on 34 (± 4) trees per plot. There were thus marked differences in host abundance at the between sample (tree) scale in this study.

Quantification of spatial heterogeneity in abundance

In the following paragraphs the results of the three measures used to quantify spatial heterogeneity in *Gonometa postica*'s pupal and parasitised pupal abundance, as well as the parasitism rate of its parasitoids are reported.

Statistical heterogeneity

The number of pupae was over-dispersed in the majority of cases, but did not fit the NBD in any case (Table 2). Number of parasitised pupae was over-dispersed in two thirds of the cases and the NBD provided a significant fit in most cases. Parasitism rate was always over-dispersed but did not follow the NBD in a third of all cases. The discrepancy between presence of over-dispersion and adequate fit by the NBD was a result of more extreme over-dispersion than allowed for by this distribution (Bliss & Fisher 1953), evident from the large variance to mean ratios in these instances (Table 2, see also Warren *et al*. 2003). The index of aggregation of the NBD, *k*, was usually below 1.0 when the index of dispersion indicated significant over-dispersion, and greater than 1.0 or approached infinity when the data were not over-dispersed. Thus in terms of statistical heterogeneity the form of spatial heterogeneity identified was predominantly aggregated (Table 2, see Fig. 2a, c).

Table 2. Spatial heterogeneity (statistical heterogeneity, spatial structure and spatial non-randomness) for number of *Gonometa postica* pupae, parasitised pupae and parasitism rate (individual or all parasitoid species) per tree for each site. Statistical heterogeneity: s^2/m = the Poisson index of dispersion; fit by the negative binomial (NB) distribution: yes (Y) and no (N); k = the index of aggregation. Spatial structure: P(I) = overall Moran's I correlogram significance. Spatial non-randomness: I_a, overall index of aggregation. Form of spatial heterogeneity (FSH) quantified is indicated as being aggregated (A), random (R) or regular (E), or present (yes (Y)) and absent (no (N)). *, ** and *** denote significance at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ level respectively. - indicates value unavailable

Site	**Statistical heterogeneity**								**Spatial structure**				**Spatial non-randomness**			
Species or Category	Number of pupae				Parasitism rate				Number of pupae		Parasitism rate		Number of pupae		Parasitism rate	
	s^2/m	NB	k	FSH	s^2/m	NB	k	FSH	P(I)	FSH	P(I)	FSH	I_a	FSH	I_a	FSH
Vryburg1																
Pupae	4.39***	N	-	A					0.218	N			1.34*	A		
?*Palexorista* sp.	3.87***	N	-	A	2.79***	N	-	A	0.210	N	0.383	N	1.37*	A	0.85	R
All species	4.45***	N	-	A	1.73**	Y	∞	A	0.114	N	0.791	N	1.46*	A	1.13	R
Vryburg2																
Pupae	6.69***	N	-	A					0.281	N			0.92	R		
Brachymeria sp.	2.87***	Y	0.427	A	2.73***	Y	0.441	A	0.096	N	0.411	N	0.76	R	0.86	R
P. semitestacea	2.43***	Y	1.004	A	3.32***	Y	0.804	A	0.535	N	1.000	N	1.01	R	0.98	R
All species	3.95***	Y	0.972	A	2.37***	N	-	A	0.505	N	0.519	N	0.85	R	0.89	R
Gabane generation 1																
Pupae	11.12***	N	-	A					0.834	N			1.19	R		
Brachymeria sp.	3.80***	Y	0.279	A	3.84***	Y	0.225	A	0.891	N	0.001	Y	1.16	R	1.10	R
P. semitestacea	2.42***	Y	0.381	A	2.21***	Y	0.396	A	0.795	N	0.499	N	0.99	R	1.14	R
All species	5.85***	N	0.608	A	2.33***	N	-	A	0.637	N	0.043	Y	1.09	R	1.13	R

Table 2. continued.

Site	**Statistical heterogeneity**								**Spatial structure**				**Spatial non-randomness**			
Species or Category	Number of pupae				Parasitism rate				Number of pupae		Number of pupae		Parasitism rate		Number of pupae	
	s^2/m	NB	k	FSH	s^2/m	NB	k	FSH	P(I)	FSH	P(I)	FSH	I_a	FSH	I_a	FSH
Gabane generation 2																
Pupae	10.01***	N	-	A					1.000	N			0.90	R		
Brachymeria sp.	2.97***	Y	0.491	A	2.16***	Y	0.586	A	1.000	N	0.922	N	0.63**	E	0.75	R
P. semitestacea	2.29***	Y	0.317	A	4.07***	N	0.296	A	1.000	N	1.000	N	0.73*	E	0.90	R
All species	5.61***	Y	0.476	A	2.93***	N	-	A	0.659	N	0.621	N	0.74*	E	0.86	R
Kumukwane																
Pupae	3.82***	N	-	A					0.125	N			1.12	R		
?Tachinidae sp.	1.18	Y	2.391	R	5.19***	Y	0.219	A	0.654	N	0.825	N	0.86	R	0.75	R
P. semitestacea	1.31	Y	1.407	R	5.21***	Y	0.234	A	0.128	N	0.522	N	1.24	R	0.99	R
All species	1.56**	Y	2.319	A	3.79***	N	-	A	0.162	N	0.462	N	1.19	R	1.11	R
Kopong																
Pupae	1.26	N	-	R					0.508	N			0.94	R		
P. semitestacea	0.96	Y	∞	R	5.89***	Y	0.129	A	0.530	N	0.088	N	1.16	R	1.16	R
All species	0.90	Y	∞	R	4.19***	Y	0.428	A	0.324	N	0.898	N	0.96	R	1.09	R

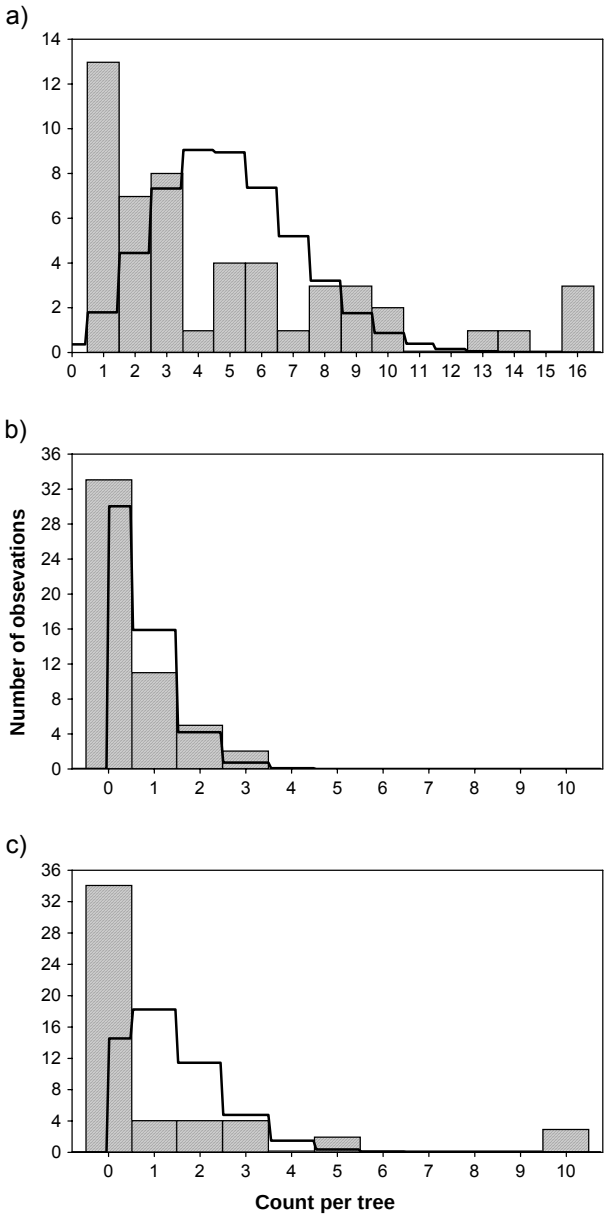

Figure 2. Statistical heterogeneity described by the frequency distribution of a) number of pupae, b) number of parasitised pupae and resulting c) parasitism rate of *P. semitestacea* at Kumukwane. Fitted line denotes an expected Poisson frequency distribution for the data. See Table 2 for specific statistics.

Spatial structure

No significant spatial structure (positive autocorrelation) was detected for number of pupae or number of parasitised pupae per tree (Table 2). No correlograms met the criteria of overall significance, and Moran's *I* was significant for the first distance class in only one case (number of pupae at Kopong) Other distance classes had significant Moran's *I* values but were characterised by small Moran's *I* values ($I < 0.2$), with only one or two isolated significant distance class per correlogram (e.g. Fig 3a-c). For parasitism rate there were two cases of overall correlogram significance (i.e. Gabane first generation pupae parasitised by *Brachymeria* sp. and all species, Table 2), but in both cases the first distance class was not significant, and only the second, and third and six distance class respectively was significant. For all three sets of abundance data, individual Moran's *I* values were small and significant for only one or two scattered distance classes, with no appreciable pattern overall (i.e. Moran's *I* values close to zero) (e.g. Fig. 3a, b, c).

Spatial non-randomness

Spatial heterogeneity in the counts of samples (Table 2), and their clustering into gaps and patches (Table 3), were generally not significant for either number of pupae or parasitised pupae and in no cases for parasitism rate. The pattern identified using this measure was thus mostly random (Fig. 4a, b, c). Exceptions that were significantly aggregated, were pupae and number of parasitised pupae at Vryburg1, (Table 2) with significant clustering into gaps and patches (Table 3). Another exception showing significant regularity was the number of parasitised pupae at Gabane (Table 2), with a significantly smaller degree of patchiness or gappiness than expected my chance (Table 3).

At Kumukwane, representative of other sites, although abundance data was mostly overdispersed (spatially non-explicit heterogeneity, Fig. 2), there was no significant spatial structure (semi-explicit heterogeneity, Fig 3.), or overall aggregation into gaps and patches, although certain sample points represented single sample point patches and gaps (spatially explicit heterogeneity, Fig 4).

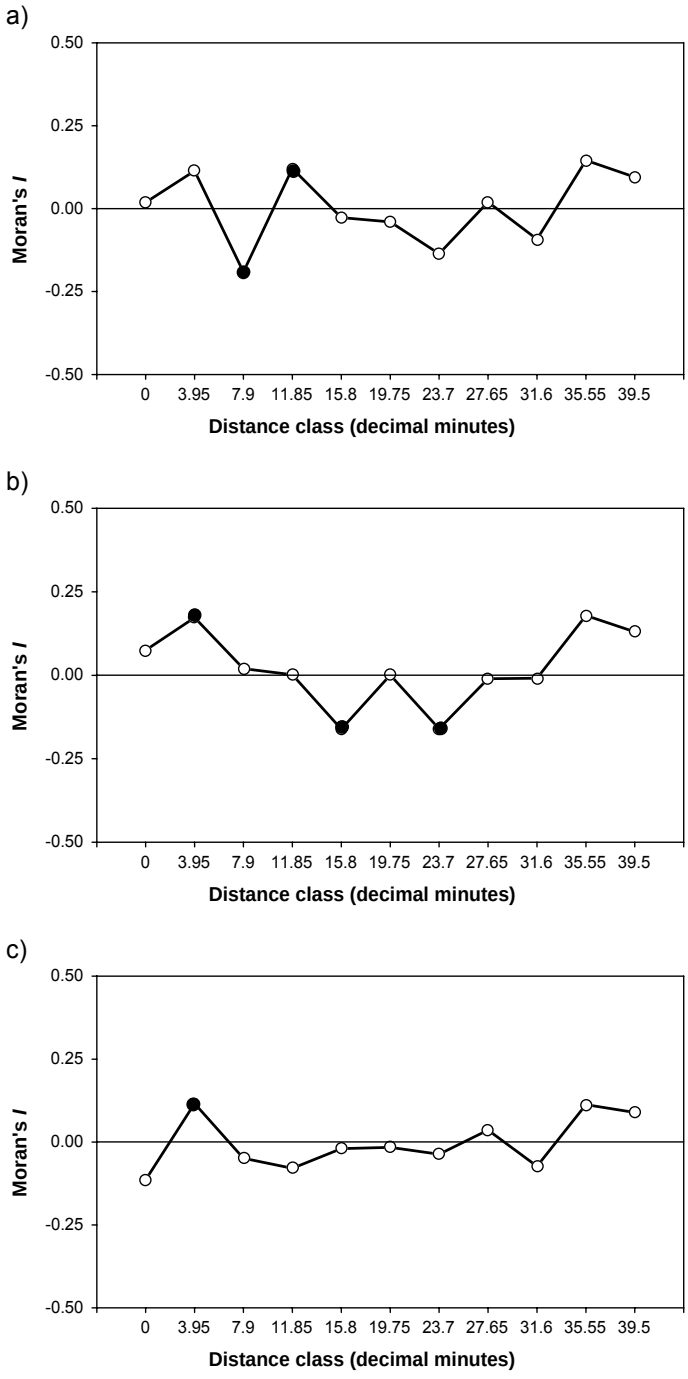

Figure 3. Spatial structure indicated by correlograms of Moran's *I* for a) number of pupae and b) number of parasitised pupae and resulting c) parasitism rate of *P. semitestacea* at Kumukwane. Significant distance classes are indicated with filled circles. See Table 2 for overall Moran's *I* correlogram significance. Number of point pairs per distance class: (1) 52; (2) 114; (3) 147; (4) 190; (5) 194; (6) 196; (7) 152; (8) 126; (9) 76; (10) 21; and (11) 10.

Table 3. Spatial non-randomness in terms of overall aggregation (also in Table 2) and local clustering of the number of *Gonometa postica* pupae and parasitised pupae, and resulting parasitism rate. n = number of non zero sampling points (maximum 100); I_a, overall index of aggregation; mean v_i and mean v_j, indices of clustering of patches and gaps respectively. * and ** denote significance at the $p < 0.05$ and $p < 0.01$.

Site	n	Number of pupae or parasitised pupae			Parasitism rate		
Species or Category		I_a	mean v_i	mean v_j	I_a	mean v_i	mean v_j
Vryburg1							
Pupae	53	1.34*	1.17	-1.48*			
?*Palexorista* sp.	40	1.37*	1.42*	-1.45*	0.85	0.97	-0.95
All species	46	1.46*	1.37	-1.55*	1.13	1.15	-1.24
Vryburg2							
Pupae	55	0.92	1.03	-0.96			
Brachymeria sp.	23	0.76	0.76	-0.76	0.86	0.89	-0.90
P. semitestacea	34	1.01	0.98	-0.93	0.98	1.00	-0.99
All species	42	0.85	1.03	-0.86	0.89	0.83	-0.83
Gabane (generation 1)							
Pupae	60	1.19	0.99	-1.22			
Brachymeria sp.	17	1.16	0.95	-1.20	1.10	1.06	-1.08
P. semitestacea	18	0.99	0.70	-1.01	1.14	1.34	-1.19
All species	35	1.09	0.86	-1.12	1.13	1.25	-1.16
Gabane (generation 2)							
Pupae	56	0.90	0.94	-0.84			
Brachymeria sp.	25	0.63**	0.71	-0.65**	0.75	0.74	-0.89
P. semitestacea	15	0.73*	0.75	-0.71*	0.90	0.55	-0.93
All species	32	0.74*	0.73	-0.74	0.86	0.81	-0.91
Kumukwane							
Pupae	51	1.12	0.76	-1.07			
?Tachinidae sp.	18	0.86	0.79	-0.86	0.75	1.02	-0.73*
P. semitestacea	17	1.24	1.07	-1.2	0.99	1.20	-0.94
All species	34	1.19	0.93	-1.00	1.11	1.30	-1.03
Kopong							
Pupae	38	0.94	0.87	-0.94			
P. semitestacea	9	1.16	1.10	-1.23	1.16	1.07	-1.18
All species	16	0.96	0.92	-1.03	1.09	1.13	-1.15

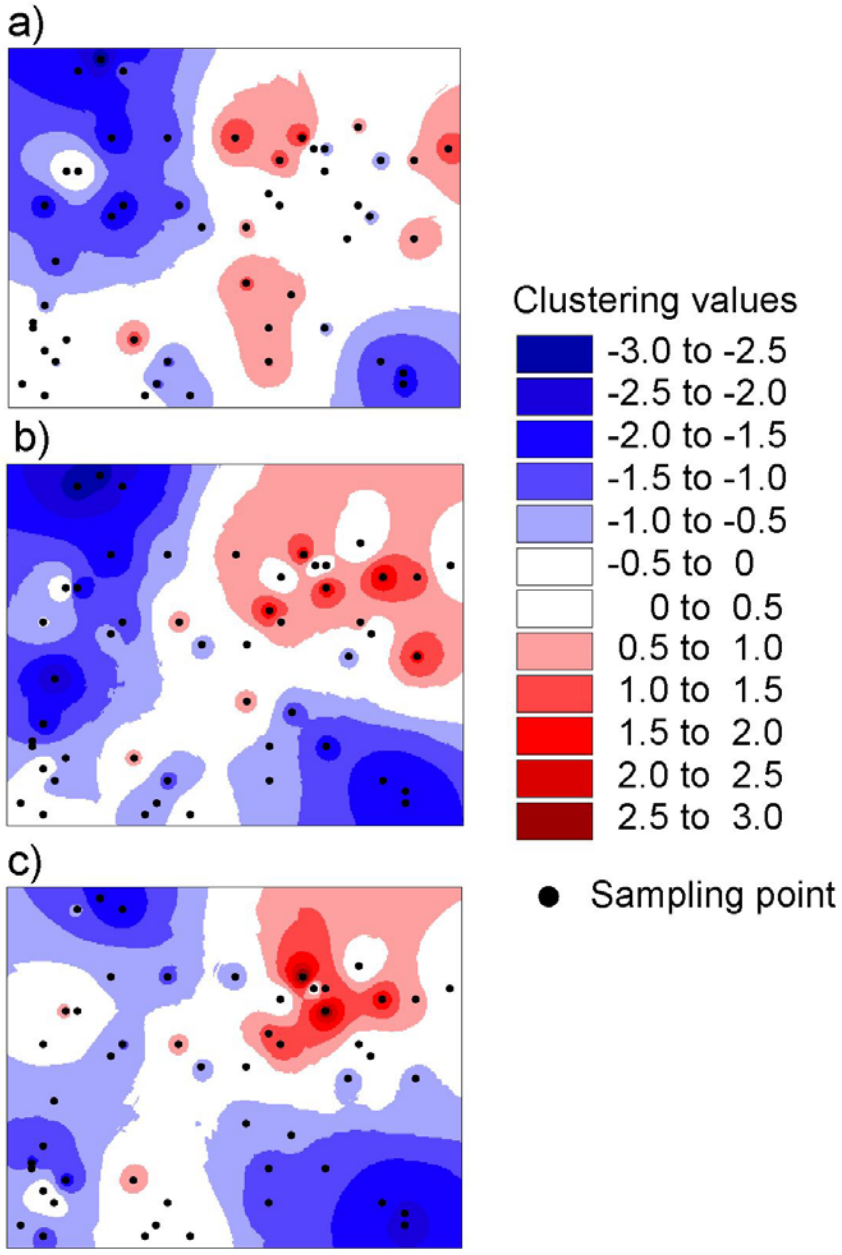

Figure 4. Spatial non-randomness indicated by least distance weighted interpolation of clustering indices of a) number of pupae, b) number of parasitised pupae and resulting c) parasitism rate of *P. semitestacea* at Kumukwane. Areas coded > 1.5 denote areas of significant positive (v_i), and < -1.5 areas of significant negative (v_j), clustering (Perry *et al*. 1999). See Table 2 for statistics.

DISCUSSION

The form of spatial heterogeneity detected for pupal abundance, parasitised pupae or parasitism rate at any particular site was inconsistent across the three methods used, and the methods were thus not interchangeable with respect to the form of spatial heterogeneity described. Data were in some cases over-dispersed (statistical heterogeneity), but spatially random (spatial structure and spatial non-randomness). Also, significant spatial non-randomness was present in the absence of spatial structure in some cases (e.g. Vryburg1, Gabane (second generation)). Thus, the spatially non-explicit approach demonstrated almost exclusively that the data were aggregated, while according to the semi-explicit approach the data were random in all cases. The spatially explicit approach also mostly indicated randomness, but did detect three cases of aggregation and regularity each. Therefore, using spatially referenced counts changed the conclusions reached regarding the form of spatial heterogeneity (from aggregated to random). Further, using a method that describes spatial heterogeneity at different locations within a site (thus spatially explicit), increased the ability to detect non-random spatial heterogeneity. This was also graphically visible from the three sets of data that these three measures were quantified for Kumukwane (Figs 2, 3, 4) (representative of the majority of localities).

Although spatial heterogeneity quantified in data is also a function of the scale of investigation (Wiens 2000), our study only compares different measures at the same scale, thereby controlling for scale. However, this study was limited in the sense that the data did not encompass the full range of possible patterns that are described by spatial non-randomness. For example in most cases there was no significant clustering into patches and gaps. Therefore it was unlikely that spatially semi-explicit heterogeneity would be identified with measures of spatial structure. It is suspected that if there were multi-sample point patches and gaps, that spatial structure would reveal stronger and significant patterns. Nonetheless, were this the case where these patches were, would not be known when quantifying spatial structure. In this study which compares the three dimensions of spatial heterogeneity, a measure of spatially explicit heterogeneity in abundance data provided the most detailed spatial information at the between-plant scale.

The problem with describing different forms of spatial heterogeneity correctly is partly a theoretical and partly a methodological problem. When the objective is to quantify spatially explicit heterogeneity, but a semi-explicit method is used, then the problem is methodological. On the other hand, when quantifying non-explicit spatial heterogeneity but interpreting it as equivalent to explicit spatial heterogeneity, then the problem is theoretical because the spatial heterogeneity described is not of a similar dimension. The diverse array of methods available to quantify spatial heterogeneity is partly due to the dimensionality of spatial heterogeneity (Wiens 2000). Methods cannot simply be selected based on data type or objective, but a relevant dimension also has to be considered. In some instances systems may be simple enough to be described by spatially non-explicit measures of spatial heterogeneity. If the objective is to simply know what the variation in count size between sample points are, then a frequency distribution will adequately describe the statistical properties of the data (Dutilleul & Legendre 1993). However, when values are autocorrelated, the form of spatial heterogeneity indicated by statistical heterogeneity will not differ from a scenario where no autocorrelation is present (Wiens 2000). As a consequence, potentially important information is lost. Repeating spatial patterns (i.e. multiple peaks of variability, see Legendre & Legendre 1998) may be more accurately described by semi-explicit measures, because differences between locations within data sets will be non-significant or weak. The presence of spatial autocorrelation indicates the size of an area that have sample points with counts more similar to each other, than samples further away (Legendre & Legendre 1998). However, although samples may have autocorrelated values, the position and number of areas with significantly higher or lower values compared to the entire data set is unknown. Also, when describing the average spatial heterogeneity of samples, local pattern is averaged out. In a similar manner that statistical heterogeneity cannot describe all the possible permutations identifiable with spatial structure, spatial structure cannot encompass all possible dataset pattern variations distinguished by spatial non-randomness. In this case aggregation, regularity and randomness (Table 1) refers to the spatial non-randomness of measured or recorded quantities for every spatially referenced sample point (Perry 1995; Perry 1998). Complex spatial mosaics may best be described by spatially explicit measures of spatial heterogeneity, which can allow for sample point differences in heterogeneity (see also Wiens 2000).

In population count data, there are two added complications with using spatial structure to describe spatial heterogeneity. First, spatial autocorrelation and other geostatistical methods assume stable covariance structure (Legendre & Legendre 1998; Perry 1998; Perry *et al*. 2002), which may not be the case for rapidly dispersing organisms with highly patchy occurrence in a study arena (Perry 1998). Second, Moran's *I* is sensitive to asymmetry as it increases the kurtosis and variance of the data that makes it harder for the correlogram to reach significance (Legendre & Legendre 1998). To counter this problem the data is usually normalized before computing correlograms to ensure that a single autocorrelation function can describe the area of study. However, counts comprising large numbers of zero values and high counts in close proximity may not fulfil the assumption of stable covariance structure or asymmetry (normality) (Perry 1998). This study shows that when sample points are spatially independent, but differ widely in abundance, local patterns are not detected by spatial structure. In some cases, although no significant spatial structure was detected, spatial non-randomness did indicate certain sampling points forming significant patches and gaps.

Therefore, a major difference between spatial structure and spatial non-randomness is the ability of spatial non-randomness to describe local (within-site) spatial heterogeneity. The value of an autocorrelation function is not influenced by position of two sampling points in a site, only by the distance between them (Legendre & Legendre 1998). When a measured variable is accompanied by a spatial reference at each sampling point, trend surface analysis and spatial autocorrelation can be used to describe spatial non-independence (Dutilleul & Legendre 1993; Legendre & Legendre 1998). However, these two methods cannot be used to make biological inferences regarding sample point specific local pattern (Perry *et al*. 2002), limiting the biological relevance of spatial structure for analysis of population count data (Perry 1998). Spatial non-randomness, based on both abundance and spatial position data, is currently the only option for describing spatial heterogeneity in abundance where local pattern is important (Perry & Dixon 2002; Perry *et al*. 2002).

The possible implications of not specifying the dimension of spatial heterogeneity when quantifying it, where aggregation in one dimension does not translate to aggregation in higher dimensions, may be severe. For example, in the host parasitoid literature heterogeneity in host parasitism risk (of which abundance is the most obvious, Hassell 2000) has been said to result in stable host-parasitoid populations cycles, if this risk is sufficiently aggregated (variance of

the hosts frequency distribution a certain times greater than the mean) (Hassell 2000). In the field of plant ecology, aggregation has been proposed to facilitate species coexistence (Murrell *et al*. 2001). In the following paragraphs the implications of the dimension of spatial heterogeneity affecting the form of spatial heterogeneity detected, are discussed. Both examples also illustrate the importance of using specific terminology to describe spatial heterogeneity in ecology.

Implications of quantifying spatially explicit heterogeneity

Studies concerning host-parasitoid interactions almost universally assume that the host species have heterogeneous abundance patterns (Godfray *et al*. 2000). However, current descriptions of aggregation in host abundance are still almost exclusively quantified by spatial heterogeneity (Hassell 2000). In fact the CV^2-rule, which specifies that the aggregation of hosts that lead to density dependent heterogeneity in attack rates, is described by a negative binomial frequency distribution of the data (Hassell 2000). The results presented here however suggest that semi-and spatially explicit dimensions of heterogeneity will not identify the same form of spatial heterogeneity as this spatially non-explicit dimension. In some laboratory or artificial field conditions the frequency distribution may adequately describe the effect of host abundance on parasitism, but more complex mosaics and patterns of spatial non-independencies may not. Therefore relevant (explicit) spatial pattern in host abundance may have been undescribed in previous studies, although being important in determining interactions between parasitoid and host.

The recent use of the experimental findings (Stoll and Prati 2001) to discuss the influence of aggregation on species coexistence (Murrell *et al*. 2001) highlights potential problems with using unspecific terminology for different measures of spatial heterogeneity (thus non-explicit, semi-explicit, and spatially explicit heterogeneity). In Stoll and Prati's (2001) study, the 'random' treatment consisted of point occurrences of plant seedling species mixes while the 'aggregated' treatment consisted of mono-specific area occurrences species mixes. This is consistent with the increase in aggregation specified for point-cluster analysis (Fig 1, B3). However, Murrell *et al*. (2001) illustrate an aggregated condition as the spatial distributions (Fig 1 B2) of two species not over lapping, and a random condition when species overlap occurrence and this overlap occurs at random. They thus imply that the spatially explicit result

of Stoll and Prati's (2001) experiment is similar to their theoretical, untested, illustration of the effect of semi-explicit occurrence of potentially competing species. Furthermore, the varied terminology used to describe spatial heterogeneity by Murrell *et al*. (2001) "…aggregation, segregation (overdispersion), and the spatial randomness..." is unspecific and confuses not only the category of spatial heterogeneity, but also the form described. By stating that 'aggregation' promotes species coexistence (e.g. Murrell *et al*. 2001; Stoll & Prati 2001) authors imply by default that spatial heterogeneity described by spatially non-explicit, semi- or explicit measures will have the same effect. In both examples, the advance of ecological theory is undoubtedly hampered by the use of vague terminology.

Consequently, the accepted theory behind parasitoids regulating host populations if they or their hosts are sufficiently aggregated, in terms of statistical heterogeneity, may not hold true for higher dimensions of spatial heterogeneity that are potentially more biological realistic descriptors of the host-parasitoid interaction. In the same manner, only one dimension of spatial heterogeneity of a species occurrence may promote species coexistence (i.e. as shown by Stoll & Prati 2001). Any pattern of statistical heterogeneity or spatial structure in a species occurrence will not necessarily have an influence on its coexistence with other species. The importance of the correct use and specifying of measures used in all biological fields where spatial heterogeneity is of theoretical importance is thus highlighted. This has implications for the traditional view of quantifying aggregation in ecology. Future studies will have the opportunity to test the consequences of how aggregation is quantified and interpreted.

This raises the important question of which measure gives the most correct description of spatial heterogeneity. Ultimately, the measure used to describe spatial heterogeneity should depend on the organism or interaction being studied (Wiens 2000), which in turn is dependent on the objective of the study. For example, the number of pupae per tree and the proportion of them parasitised describe an interaction between host and parasitoid. Considering parasitoid biology, theoretically the quantification of spatial heterogeneity, i.e. the spatial aggregation of hosts, is of vital importance in determining the existence of density dependent parasitism (Pacala & Hassell 1991; Gross & Ives 1999; Hassell 2000; Chapter 4). Because the type of spatial aggregation, regularity or randomness shown by pupae, number parasitised and parasitism rate was shown to be dependent on the measure of spatial heterogeneity used, it is vital that the correct form of spatial heterogeneity be recorded. In the case of *G. postica*, host

abundance represents a patchy resource for foraging parasitoids because pupae occur on trees that are irregularly spaced, and only a few single occurring trees have many pupae per tree (significant patch of high pupal abundance on a single tree), while the majority have few. Therefore, spatial heterogeneity in pupal abundance that is spatially explicit (locational) will include relevant spatial information not available from spatially non-explicit, or even semi-explicit categories.

In the future it is proposed that the quantification of aggregation in biology takes the data type, objectives, and the biology of the process under investigation in consideration. First, the type of data gathered should be classified as either abundance or occurrence data. Second the dimension of spatial heterogeneity relevant to the biological process being studied, as well as suitable for addressing the objectives needs to be chosen. Only hereafter is a specific associated measure chosen to quantify the form of spatial heterogeneity (i.e. Table 1). This procedure, as well as using specifically assigned terminology, will ensure that conclusions about the form of spatial heterogeneity can be compared between studies.

In summary this study illustrates that statistical heterogeneity and spatial structure are complimentary to spatial non-randomness. For example, statistical heterogeneity gives some information on aggregation at a scale smaller than at which the data was collected. Therefore, spatial non-randomness should be seen as another addition to the list of methods available to ecologists to describe spatial heterogeneity (see Dutilleul & Legendre 1993). However, the empirical comparison of spatially non-explicit, semi-, and explicit to approaches to the measurement of spatial heterogeneity in this study, highlights the need for specific definition of spatial heterogeneity and aggregation. Here the potential value of spatially explicit approaches for the re-evaluation of theory developed using more traditional methods has been highlighted. In the future the dimensionality of spatial heterogeneity should thus be considered when quantifying aggregation in ecological data.

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Appendix. Number of *Gonometa postica* pupae and the percentage parasitised at surveyed sites (Gen. = generation). The number of pupae, number of parasitised pupae as well as percentage parasitised (individual species or all combined) per plot is given. The number of trees (maximum 100) with at least one pupa or parasitised pupa, as well as the percentage of host occupied trees with at least one parasitised pupae is also shown.

Locality	Gen.	Number of		Parasitoid species or category	Number of parasitised		Percent parasitised	
		pupae	trees		pupae	trees	pupae	trees
Vryburg1	1	202	53	?*Palexorista* sp.	117	40	57.9	75.5
				All species	150	46	74.3	86.8
Vryburg2	1	426	55	*Brachymeria* sp.	69	23	16.2	41.8
				P. semitestacea	83	34	19.5	61.8
				All species	192	42	45.1	76.4
Gabane	1	505	60	*Brachymeria* sp.	36	17	7.1	28.3
				P. semitestacea	37	18	7.3	30.0
				All species	100	35	19.8	58.3
	2	439	56	*Brachymeria* sp.	64	25	14.6	44.6
				P. semitestacea	31	15	7.1	26.8
				All species	128	32	29.2	57.1
Kumukwane	1	252	51	?Tachinidae sp.	27	18	10.7	35.3
				P. semitestacea	23	17	9.1	33.3
				All species	75	34	29.8	66.7
Kopong	1	92	38	*P. semitestacea*	10	9	10.9	23.7
				All species	20	16	21.7	42.1

CHAPTER 4

Spatially explicit host-parasitoid relationships: density dependence revisited

INTRODUCTION

The realisation of the importance of space in species interactions and their responses to resources has increased significantly over the last decade (Ives & Klopfer 1997; Godfray *et al*. 2000; Stewart *et al*. 2000; Liebhold & Gurevitch 2002; McGeoch & Price 2004). Spatial variation in the densities of individuals of one species may result in higher order aggregation in others (e.g. interactions between herbivores and their host plants, or predators and their prey) (Logerwell *et al*. 1998; Bohan *et al*. 2000; Wiens 2000; Winder *et al*. 2001; Brewer & Gaston 2002). One well known example is the marked effects spatial variation in a species' abundance can have on the mortality levels imposed by its natural enemies (Hassell & May 1974; Godfray *et al*. 2000; Hassell 2000), i.e. when host (prey) individuals are aggregated, natural enemies may concentrate their search in high density areas (Hassell & May 1974; Dolman & Sutherland 1997; Godfray *et al*. 2000). For example, randomly searching parasitoids are thought to have lower attack rates when hosts are aggregated because search time is wasted by foraging in empty patches (Murdoch & Stewart-Oaten 1989; Hassell and Pacala 1990). By contrast, a non-random search relative to host density will result in increased attack rates when hosts are aggregated (Hassell and Pacala 1990, Kareiva 1990). Inverse and direct patterns of density dependent parasitism therefore result under these conditions.

Despite obvious selective advantages to natural enemies in targeting high abundance patches (i.e. reduced search time within patches and travel time between patches) (Charnov 1976, Cook & Hubbard 1977), patterns of natural enemy-induced mortality of insect herbivores have frequently been found to be density independent (Hassell & May 1974; Lessells 1985; Stilling 1987; Walde & Murdoch 1988; Norowi *et al*. 2001). Few natural

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enemy-host interactions have been more extensively examined than herbivore insect-parasitoid interactions. Review of the frequency of detecting density dependence in parasitism rates demonstrates that approximately half of these relationships were density independent, while the remainder equally divided between direct and inverse density dependence (Lessells 1985; Stilling 1987; Walde & Murdoch 1988). The low frequency of density dependence is not necessarily unexpected, as the factors influencing interactions between herbivores and their parasitoids are numerous (Hassell & May 1974; Lessells 1985; Godfray *et al*. 2000). For example, the absence of density dependent parasitism has been considered to be a consequence of a wide array of factors, including the absence of an aggregative response by the parasitoid (Loch & Zalucki 1998), interference between parasitoids (Sutherland 1983; Visser *et al*. 1999), sequential parasitism (Lessells 1985), mortality inflicted by hyperparasitoids (Loch & Zalucki 1998) or other natural enemies of parasitoids (Strong 1989), host spatial distribution (Iwasa *et al*. 1981; Lessells 1985; Driessen *et al*. 1995), low and variable host abundance (Hails & Crawley 1992), egg-laying potential (Hassell 1982; Lessells 1985), and finally, parasitoid searching capacity (Loch & Zalucki 1998).

Studies conducted at inappropriate scales for the search behaviour of the natural enemy concerned, have also been shown to be responsible for the failure to detect density dependence (Heads & Lawton 1983; Ray & Hastings 1996). Density dependence may not be detected if studies are conducted at the 'wrong' spatial scale (extent of the study arena) (Ray & Hastings 1996). The scale at which parasitism rates are investigated has also been shown to influence the type of density dependence detected (Heads & Lawton 1983; Hails & Crawley 1992; Norowi *et al*. 2000; but see, Walde & Murdoch 1988; Freeman & Smith 1990; Rothman & Darling 1990; Stiling *et al*. 1991). Generally, when scale increases from the 'plant part' to 'whole plant' to 'several plant' scales, density dependent parasitism changes from inverse to direct density dependence to density independence (Norowi *et al*. 2000). However, although the range of densities increases with increasing scale, the number of replicates in studies tends to decline, making it difficult to distinguish statistical artefact from ecological reality when investigating the detection of density dependence (Hails & Crawley 1992). Nonetheless, for appropriately scaled studies ("scale at which natural enemies recognize and respond to changes in host density" *sens*u Hails & Crawley 1992) density dependence should be detected if present (Ray & Hastings 1996) and reflect a biologically realistic response (Heads & Lawton 1983).

Finally, the failure to detect spatial density dependence has also been attributed to the low statistical power (Type II errors) of tests used (Hails & Crawley 1992; Dolman & Sutherland 1997). For example, binomial regression, one method of detecting density dependence in parasitism rates, has acceptable Type I error levels, but runs a greater risk of making a Type II error, especially when underlying density dependence is weak (Hails & Crawley 1992). Furthermore, recent advances in the analysis of spatial data and in describing spatial heterogeneity (Legendre *et al*. 2002; Perry *et al*. 2002) highlight some issues that suggest that the quantification of host-parasitoid relationships (HPR's) warrant reconsideration. First, the spatial non-independence of host density counts (i.e. the sample points) (and the resulting increase in Type I error rates; see Legendre & Legendre 1998) in HPR's dictate that the spatial position of counts must be considered in such analyses. Second, because density dependence is specifically a proportional response of a parasitoid species to the spatial pattern of aggregation of its host (Hassell & May 1974), a biologically relevant, spatial measure of aggregation is most appropriate (see Perry 1998). Therefore, there is clearly a need to explicitly consider the spatial position of hosts (i.e. spatial references of sampling point) when examining HPR's, and the inclusion of spatial information in such analyses (i.e. spatially explicit analyses) may provide further insight into density dependent relationships.

Host-parasitoid relationships

Several types of HPR's have been used to quantify patterns of density dependent parasitism (Table 1). The behavioural and population functional responses investigate individual and population attack rates in relation to host density, whereas the aggregative response quantifies the tendency for parasitoids to aggregate in areas of high host density (Table 1). The proportion of parasitised hosts (rather than number) per patch can also be used, providing an indirect description of parasitoid response to host density (Hassell 1982). In the HPR literature, the term ‘spatial density dependence’ has become synonymous with the latter relationship, i.e. between the proportion of parasitised hosts and host density across patches (Lessells 1985; Stilling 1987; Walde & Murdoch 1988; Pacala & Hassell 1991) (Table 1). This arose from the more commonly investigated relationship between host density and overall site parasitism over time, i.e. temporal density dependence (Holyoak 1994; Hunter & Price 1998)

Table 1. Different types of host-parasitoid relationships (HPR's) used to quantify patterns of parasitism as a function of host density, divided into spatially explicit and non-explicit relationship categories. The applications of these relationships are also indicated. Numbers in superscript denote source of terminology or example of recent use. DD, density dependence; DI, density independence.

Types of HPR's Different forms of a HPR	Host-parasitoid interaction	Synonyms	Application
	Spatially non-explicit relationships		
Behavioural functional response [1]	Relationship between the attack rate of an individual parasitoid and host density on one or a few plants [1, 2, 3]	-	Behavioural studies [1]; Optimal foraging models [4]
Population functional response [1]	Relationship between average parasitoid attack rate and mean host density among plants in a study arena [1]	-	Modelling host-parasitoid dynamics [1]; Studies on population dynamics [1]
Type I curve [5]	Parasitoid attack rate increases linearly with increasing host density but ceases to increase after some threshold density	-	Density independence (at high host densities)
Type II curve [5]	Parasitoid attack rate decelerates with increasing host density	-	Inverse DD
Type III curve [5]	Parasitoid attack rate accelerates with increasing host density but decelerates after some threshold density	-	Direct DD (at low host densities)

Table 1. continued

Types of HPR's Different forms of a HPR	Host-parasitoid interaction	Synonyms	Application
Aggregative response [6]	Relationship between numbers of foraging parasitoids the density of the host per patch [2, 6]	Spatial distribution of foraging parasitoids [6]	Modelling of parasitoid foraging behaviour [2]
Spatial density dependence [5, 7, 8, 9]	Relationship between proportion of parasitised hosts per patch and host density, across patches [6] (Positive correlation between parasitism rate and host density across patches [5])	Pattern of parasitism [6]; Aggregative response* [7]; Spatial aggregation of deaths [9]; Type of parasitoid aggregation [10]	Traditional method of detecting DD [5, 7, 8, 9]
Direct density dependence [6]	Proportion parasitised per patch increases with increasing host density [6]	Density dependent aggregation [10, 11]	
Inverse density dependence [6]	Proportion parasitised per patch decreases with increasing host density [6]	Inverse density-dependent aggregation [10, 11]	
Density independence [6]	Proportion parasitised per patch is unaffected by host density [6]	Density-independent aggregation [10, 11, 12]	

Table 1. continued

Types of HPR's Different forms of a HPR	Host-parasitoid interaction	Synonyms	Application
	Spatially explicit relationship		
Spatially associated density dependence	Degree of spatial association between parasitism rate and host abundance	Spatially explicit matching	Proposed new method of detecting DD
Significant association	Matching in spatial pattern of proportion parasitised and host density greater than expected by chance	-	Indicates direct DD
Significant dissociation	Spatial mismatching between proportion parasitised and host density greater than expected by chance	-	Indicates inverse DD
Non-significant association or dissociation	Matching or mismatching between proportion parasitised and host density is no different from expected by chance	-	Indicates density independence

[1] Ives *et al*. 1999; [2] Sutherland 1983; [3] Montoya *et al*. 2000; [4] Iwasa *et al*. 1981; [5] Walde & Murdoch 1988; [6] Hassell 1982; [7] Heads & Lawton 1983; [8] Hassell *et al*. 1987; [9] Hails & Crawley 1992; [10] Klopfer & Ives 1997; [11] Gross & Ives 1999; [12] Pacala & Hassell 1991; * denotes authors use term interchangeably.

Although the population functional response (based on the individual functional response of each parasitoid in the population) (Table 1) has resulted in valuable insights on how variability in individual parasitoid behaviour and spatial pattern of host abundance influence resulting patterns of parasitism (Hassell 1982; Gross & Ives 1999; Ives *et al.* 1999), such investigations are logistically difficult and may be hampered by scale limitations (Ives *et al.* 1999). In addition, despite the aggregative response being important for understanding non-random parasitoid search behaviour, the number of foraging parasitoids does not impact on host population dynamics directly (Hassell 1982; Sutherland 1983; Lessells 1985). By contrast, spatial density dependence depends on the aggregative response (Hassell 1982, Heads & Lawton 1983), behavioural and population functional responses (Hassell 1982; Gross & Ives 1999), parasitoid interference (Sutherland 1983), patch residence time and travel time between patches (Hassell & May 1974; Driessen *et al*. 1995), as well as the foraging strategy employed (Waage 1979; Iwasa *et al*. 1981; Driessen & Bernstein 1999). Therefore, because the proportion of parasitised hosts provides a summary of all factors that may influence mortality as a function of host density, and because it is readily measured, it is most often used when examining HPR's for density dependent parasitism (Hassell 1982; Pacala & Hassell 1991, Hassell 2000).

Spatial density dependence is considered to reflect between-patch variation in the risk of parasitism between individuals in a host population, i.e. 'host density dependent heterogeneity' (patch parasitism risk dependent on host density) *sensu* Hassell (2000). This depends on the frequency distribution of the number of hosts and parasitoids per patch (Hassell 2000). For example, models of direct spatially density dependent parasitism assume that parasitoids will aggregate where hosts are aggregated, the number of hosts per patch being described by the negative binomial distribution (Pacala & Hassell 1991; Hassell 2000). Importantly, however, the spatial positions of these patches relative to each other are not considered. This measure of aggregation (spatial heterogeneity *sensu* Wiens 2000), represented by the frequency distribution of counts, is a spatially non-explicit measure of the degree of aggregation (Perry & Hewitt 1991; Perry 1998). The effect of explicitly considering the spatial positions of these count data on the relationship between the proportion of parasitised hosts per patch and host density across patches (spatial density dependence) has not previously been investigated.

Spatially explicit aggregation in host abundance

Lloyd (1967) first proposed that the detection of density dependence was a function of the importance of host crowding (which is a measure of aggregation). Traditionally, aggregation in host abundance has only been defined by the frequency distribution of number of hosts per patch (e.g. May 1978; Pacala & Hassell 1991). However, the spatial explicitness of the measure used to quantify spatial pattern has been shown to affect if aggregation is present (Chapter 4). For example a spatially non-explicit measure such as an overdispersed frequency distribution indicates only that the count size associated with sample points are aggregated, but not physically where in the study arena this aggregation occurs (Perry *et al*. 1999). The spatial position of aggregation is, however, biologically highly relevant in the detection of density dependence. For example, a patch with low host abundance may be more heavily parasitised if it occurs close to a neighbouring patch with high host abundance that attracts parasitoids to the area. Failure to consider spatial position may in such instances weaken the quantified relationship, and the likelihood that significant spatial density dependence is detected.

Spatial Analysis by Distance Indices is a measure that identifies spatially explicit aggregation (Chapter 4). This measure has greater power to detect departures from random spatial pattern by using all available spatial information (Perry 1998). Although not applied in this context previously, this method also permits the biologically relevant matching of the physical position of aggregation in host density with that of parasitism rate, i.e. spatially associated density dependence (Table 1). Spatial association is a method that is able to determine overall and local (spatially explicit) matching in spatial pattern such as this (Perry & Dixon 2002). By determining the strength of spatial association a test for density dependence is made spatially explicit (Table 1). Furthermore, because spatial association compares the degree of spatial pattern at a shared position of the counts of two variables, instead of only the counts themselves, this method has been empirically shown to have greater power to detect significant relationships between spatially referenced variables (Winder *et al*. 2001). To date no other method has considered the aggregation of hosts (i.e. host density) other than non-explicitly. Even the improvement made by Roland and Taylor (1997) on the binomial regression method, by allowing for spatial non-independence in parasitism rate, does not account for spatial non-independence in, or physical position of host density.

The question that remains unanswered in HPR's, is therefore, does data on the physical spatial position of hosts, in addition to their abundance, affect the type of density dependence observed at a given scale? Using field data on insect-host abundance and parasitism rate, this study tests if a spatially explicit description of host aggregation differs from the traditional, spatially non-explicit methods of detecting dependent parasitism. This is done by comparing spatially non-explicit (spatial density dependence) and explicit (spatially associated density dependence) methods of detecting density dependence, in the type (i.e. direct, indirect or density independence) of density dependence quantified. To my knowledge this will be the first empirical test of spatially explicit density dependence in a HPR. Therefore, this study will indicate whether or not considering host abundance at a sampling point relative to neighbouring points is important for the detection of density dependence.

METHODS

Study Area

Gonometa postica populations were examined at five localities within the known (historic and recent records) outbreak range of this species, spanning a distance of 400km between the two furthest localities. The localities were Vryburg (26°59'S, 24°40'E) and Hotazel (27°15'S, 23°03'E) in North-central South Africa and Gabane (24°37'S, 25°46'E), Kumukwane (24°38'S, 25°40'E), and Kopong (24°31'S, 25°48'E) in South-Eastern Botswana. The dominant woody host species utilized by *G. postica* at the first two localities was *Acacia erioloba* Meyer and at the remainder, *Acacia tortillis* Hayne (both Mimosaceae) (Veldtman *et al*. 2002).

One site was selected at each locality, with two at Vryburg (~ 1.5 km apart). Sampling was standardized by delimiting an approximately rectangular area incorporating 100 trees at each site to compensate for possible tree-density differences between host-plants and localities. An initial minimum of 40 first-generation cocoons per site was a prerequisite for site selection.

G. postica is bivoltine and overwinters in pupal diapause. When diapause is broken in early spring (September to October), emerging moths mate and lay eggs to form the first generation, which start pupating after two months (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), which pupate in early autumn (March to April). The un-emerged first generation pupae and second generation pupae enter diapause, emerging only the following spring. Generations are readily distinguishable based on cocoon appearance. New cocoons are covered in a dense layer of setae 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.

Surveys of sites commenced in winter (June to July, 2000) and were repeated in mid summer (January, 2001). During the first survey, the number and fate of overwintering pupae were recorded. With the second survey the resulting fate of those individuals that were alive in the first survey as well as the number of new first generation pupae were recorded. Similarly, the fate of these first generation pupae was followed (two subsequent surveys repeated at same periods as above) till mid summer of the following year (January 2002).

Cocoon sampling

Within each site every tree was carefully searched for cocoons. Cocoons were inspected to determine if the pupa inside the cocoon was i) parasitised, ii) alive, iii) dead as a result of unknown causes or iv) had successfully emerged. This was indicated respectively by the i) presence or ii) absence of small emergence hole(s), iii) light weight of the cocoon or iv) a single large anterior emergence hole. Parasitoid species responsible for parasitism may be identified from the shape and size of emergence holes left in the cocoon wall of a parasitised pupa (Veldtman *et. al* 2004.). Consequently, the number of pupae and number of pupae parasitised by each parasitoid species, per tree were counted.

The position of each tree within a site was measured at the main trunk of the tree with a hand held Global Positioning System (GPS). For trees in close proximity to each other the direction and distance between the two trees were noted and assigned to one of three categories (half, quarter and a tenth of the third (last) decimal of a minute) based on hand drawn maps which specifically documented this fine scale distribution of trees. These spatial co-ordinates were used in all spatial analyses.

For the investigation of density dependence, only sampling points (trees) with at least one pupa were included in analyses, as parasitism events can logically not be observed if there are no pupae. At each site, pupae parasitised by different species of parasitoid were either analysed individually, or collectively ('all species') as a measure of total parasitoid mortality (see also Heads & Lawton 1983; Williams *et al*. 2001).

Although all the parasitoids species considered here parasitise the final instar larvae of *G. postica*, we assume that pupal abundance is a good approximation of final instar abundance. This assumption is based on support from field observations that final instar larvae have a low probability of leaving their final food plant to pupate. Final instars were seldom observed moving between plants, approximately 90% of all pupae are found on the larval host plant, and large quantities of larval frass have been observed under trees with high numbers of pupae. However, if this assumption were incorrect we would not expect any direct density dependent relationships regarding parasitism rate. Using the pupal stage also has advantages. Because parasitised larvae cannot be identified in the field, larvae would have to be collected in order to determine the exact relationship between host abundance and parasitism rate. However, premature removal may prevent an unknown number of parasitism events. A study of density dependent pupal parasitism should thus be seen as a practical surrogate for determining the impact of larval parasitoids on this host species. However, at within tree-level analyses this assumption may easily be violated.

Quantification of host parasitoid relationships

Five methods of detecting density dependence were used in this study to allow the quantified relationships of spatially non-explicit and spatially explicit methods to be compared (Table 2). In the following sections these methods and their previous use in the test of density dependence are described.

Spatial density dependence

The relationship between parasitism rate and host density has most commonly been quantified using simple linear regression after arcsine square-root transformation of the proportion of hosts parasitised (Zar 1984; Williams *et al*. 2001, and Lill *et al*. 2002). However,

Table 2. Methods for quantifying traditional spatial density dependence and spatially associated density dependence. LS, Least squares; ML, Maximum likelihood; SADIE, Spatial Analysis by Distance IndicEs; expo, exponential; log, logarithmic; a and b are constants.

Method	Estimation method	Dependent variable		Independent variable/s		Examples of use
		Y	Form	X	Form	
Spatial density dependence						
1. Arcsine square-root	LS	Proportion of parasitised hosts	$\sin^{-1}\sqrt{y}$	Number of host individuals	untransformed	1, 2, 3
2. Regression function comparison	ML	Number of parasitised hosts	*linear*: y *expo*: y *log*: $\log_e y$ *power*: $\log_e y$	Number of host individuals	*linear*: a + bx *expo*: $\exp^x$ *log*: log a + bx *power*: x^b	4, 5
3. Binomial regression	ML	Proportion of parasitised hosts	log(y/(1 - y)	Number of host individuals	untransformed	6, 7, 8
4. Binomial regression with spatial terms	ML	Proportion of parasitised hosts	log(y/(1 - y)	i. Number of host individuals; ii. Patch location	i. untrans-formed ii. significant 3rd order polynomial terms of locality co-ordinates	9
Spatially associated density dependence						
5. Spatial association	SADIE	Rounded integer of proportion	proportion multiplied by 10	Number of hosts	untransformed	this study

[1] Zar 1984; [2] Williams *et al*. 2000; [3] Lill *et al*. 2002; [4] McCullagh & Nelder 1989; [5] Srivastava & Lawton 1998; [6] Trexler *et al*. 1988; [7] Hails & Crawley 1992; [8] Crawley 1993; [9] Roland & Taylor 1997.

this transformation may not be adequate to meet least squares assumptions for proportion parasitised data (Crawley 1993).

Alternatively, a relationship between two variables can be identified as accelerating, decelerating or constant by fitting different regression functions (Savage 1996) and determining the model with the best fit (Srivastava & Lawton 1998). Because several models may fit such a relationship (May 1975), a model that fits significantly better than alternatives (after penalisation for multiple terms; McGill 2003) has to be identified. Linear, exponential, logarithmic and power functions were fitted to each data set using generalized linear modeling (assuming a Poisson or negative binomial distribution as appropriate) by using different combinations of the untransformed and transformed dependent (link functions either identity or natural logarithm) and independent variables (untransformed or natural logarithm) (McCullagh & Nelder 1989; Srivastava & Lawton 1998). The best fitting model was identified by comparing the log likelihood ratio statistic (difference in log-likelihood score of two competing models against the expectation of the chi-squared distribution; see Dobson 2002, p76) of competing models. All regressions were done using the SAS (PROC GENMOD) (SAS Institute Inc., Cary, New York).

Generalised linear models assuming a binomial error distribution provide a statistically superior option for the regression of percentage parasitism data (Hails & Crawley 1992; Crawley 1993), even when percent parasitism can be successfully transformed to meet the assumption of normality (Quinn & Keough 2002) and after stabilising the variance (Collett 1991). When the numbers of successes, for example parasitism events, are bounded between 0 and the number of hosts available in a patch, a binomial probability model should be used (Trexler *et al*. 1988). A generalized linear model assuming a binomial error distribution was used to determine the relationship between parasitism rate and host density (Trexler *et al*. 1988; Hails & Crawley 1992; Crawley 1993).

This method was also modified to take spatial non-independencies of samples into account by adding spatial terms identified by trend surface analysis (Roland & Taylor 1997). Spatial terms that significantly contributed to explaining variation in parasitism rate (significant terms from the 3rd order polynomial of latitude and longitude records of each tree) were first added in the model. Hereafter host density was added to the model and the estimate of this variable was determined.

Spatially associated density dependence

Just as a linear regression between number of parasitised hosts and available hosts cannot be negative, significant positive spatial association between these two counts will be an artefact of the analysis because number of pupae parasitised is a proportion of the number of pupae (see Brett 2004). To adjust for this, proportions were transformed to integers after multiplying with a constant and rounding to the nearest integer, such that the standard SADIE method can be used with proportional data (Perry *et al*. 1999). The proportion of parasitised pupae (from here on parasitism rate) was subsequently multiplied by 10, a constant that rendered the proportion comparable to the number of hosts (usual maximum range was 20 pupae). We propose that density dependent parasitism can be inferred when the proportion of parasitised pupae is spatially associated with the number of hosts. We refer to this relationship as spatially associated density dependence (Table 1).

Significance of associations was determined by comparing X to critical values for the randomised distribution of overall association, using the 97.5^{th} and 2.5^{th} centiles for a desired 95% confidence interval (Perry & Dixon 2002), and the maximum critical value (derived from the number of simulations (153 times) multiplied by the number of sample points in the data) to determine significance at $p < 0.001$. SADIE clustering and association statistics may be affected by the number and spatial position of patches in data sets (Xu & Madden 2003). However, the implications for multi-patch patterns, as found in this study, are limited (Xu & Madden 2003), and the issues these authors raise therefore do not affect the results we report. The degree of matching between two sets of count data sharing a set of spatial references was determined with spatial association statistics using SADIEShell v. 1.21 software (http://www.rothamsted.bbsrc.ac.uk/ pie/sadie/SADIE_downloads_software_page) (Winder *et al.* 2001, Perry & Dixon 2002).

RESULTS

Only four parasitoid species resulted in more than 5% parasitism in *Gonometa postica* (Table 3). Sites with high pupal abundance did not have higher parasitism rates than low abundance sites (Table 3). On average (± SE) there were 319 (± 66) pupae per site occupying

Table 3. Number of *Gonometa postica* pupae and the percentage parasitised at surveyed sites. The number of pupae, number of parasitised pupae as well as percentage parasitised (individual species or all combined) per site is given for parasitoid species responsible for more than 5% parasitism. The number of trees with at least one pupa or one parasitised pupa (out of 100 trees), as well as the percent of host occupied trees with at least one parasitised pupae is also given.

Locality	Gene-ration	Number of		Parasitoid species or category	Number of parasitised		Overall % parasitised	
		pupae	trees		pupae	trees	pupae	trees
Vryburg1	1	202	53	?*Palexorista* sp.	117	40	57.9	75.5
				All species	150	46	74.3	86.8
Vryburg2	1	426	55	*Brachymeria* sp.	69	23	16.2	41.8
				P. semitestacea	83	34	19.5	61.8
				All species	192	42	45.1	76.4
Gabane	1	505	60	*Brachymeria* sp.	36	17	7.1	28.3
				P. semitestacea	37	18	7.3	30.0
				All species	100	35	19.8	58.3
	2	439	56	*Brachymeria* sp.	64	25	14.6	44.6
				P. semitestacea	31	15	7.1	26.8
				All species	128	32	29.2	57.1
Kumukwane	1	252	51	?Tachinidae sp.	27	18	10.7	35.3
				P. semitestacea	23	17	9.1	33.3
				All species	75	34	29.8	66.7
Kopong	1	92	38	*P. semitestacea*	10	9	10.9	23.7
				All species	20	16	21.7	42.1

52 (± 3) trees. Single parasitoid species parasitised an average of 50 (± 10) pupae on 22 (± 3) trees, while all parasitoids together parasitised 111 (± 25) pupae on 34 (± 4) trees per site. The number of pupae was usually unequally distributed over the site with few trees with high abundance and many with few pupae, resulting in marked differences in host abundance at the between plant scale.

Quantification of host density-parasitism relationships

Spatial density dependence

Using the arcsine square root method, five significant relationships between parasitism rate and host density were found (Table 4). All five had positive slopes (although small) and therefore indicated direct density dependence (e.g. Fig. 1). With regression function comparison, linear and power models generally provided a significantly better fit to the relationship between number of pupae and parasitised pupae than exponential or logarithmic models (Table 4). Therefore, relationships were identified as exclusively density independent (linear or exponent of power model equal to zero) by this method, when it was possible to discriminate statistically between the four alternative models (e.g. Fig. 2). The fit of binomial regression models to parasitism rate, without (standard) or with the inclusion of spatial terms, was adequate (deviance per degree of freedom close to unity, McCullagh & Nelder 1989) in most cases (Table 4). Using standard binomial regression, three significant relationships were identified, all of which were inversely density dependent and weak, with pupal density explaining only between 7-11 % of the deviance in parasitism rate (e.g. Fig. 3). Binomial regression with spatial terms, however, only indicated one significant inversely density dependent relationship with the other two relationships identified by standard binomial regression becoming non-significant.

Table 4. Relationship between parasitism rate and pupal density quantified with alternative methods. Method 2 results with different letters in superscript denote significant differences and rank with respect to best fitting curve (a > b > c). Method 3 results show percentage deviance explained followed by the sign of the relationship in brackets. Method 4 results show the percentage deviance explained by host density after removing significant locational (spatial) terms. Method 5 results show significant overall association (*X*) (ranging between 1 (perfect association) and –1 (perfect disassociation)) and maximum simulated association value from randomisation procedure. Values in bold denote significant density dependence; *, ** and *** are $p < 0.05$, 0.01 and 0.001.

Site (sample size)	Methods										
	1. Arcsine square-root		2. Regression function comparison				3. Binomial regression	4. Binomial regression with spatial terms		5. Spatial association	
			% Deviance explained (DE)								
	F statistic	slope	Linear	Exp	Log	Power	% DE	Spatial terms	% DE by host density	*X*	Max. simul. value
Vryburg1 (n = 53)											
?*Palexorista* sp.	0.14	0.008	73.4 [a]	62.5 [b]	60.0 [c]	73.7 [a]	2.45	x^2	0.71	**0.310***	0.393
All species	0.00	0.000	82.8 [a]	71.9 [b]	67.4 [c]	82.9 [a]	3.19	x^2, y	0.46	0.207	0.390
Vryburg2 (n = 55)											
Brachymeria	**12.47*****	0.018	52.3 [a]	32.2 [c]	45.2 [b]	49.6 [a]	0.09	-	0.09	0.242	0.294
P. semitestacea	0.38	0.005	55.1 [a]	46.6 [b]	43.1 [c]	55.2 [a]	0.34	x^2	0.20	0.092	0.343
All species	2.01	0.012	80.1 [a]	58.9 [c]	66.5 [b]	80.0 [a]	0.26	-	0.26	0.253	0.329

Table 4. continued

Site (sample size)	1.	2.				3.	4.		5.	
	F statistic	slope	% Deviance explained (DE)				% DE	Spatial terms	% DE by host density	*X*	Max. simul. value
			Linear	Exp	Log	Power					
Gabane (generation 1, n = 60)											
Brachymeria	1.34	0.004	47.0 [a]	48.3 [a]	25.8 [b]	50.5 [a]	**10.46**(-)**	x^2	3.32	0.071	0.291
P. semitestacea	**5.84***	0.007	50.0 [a]	38.0 [b]	33.0 [b]	50.4 [a]	2.85	-	2.85	**0.307*****	0.269
All species	2.55	0.007	66.6 [a]	59.9 [b]	42.9 [c]	68.5 [a]	**11.37**(-)**	x^2, y	2.24	-0.112	-0.371
Gabane (generation 2, n = 56)											
Brachymeria	**15.00*****	0.014	66.2 [a]	43.5 [c]	55.5 [b]	63.5 [a]	0.55	-	0.55	-0.036	-0.345
P. semitestacea	**4.95***	0.008	54.1 [a]	44.9 [b]	37.2 [b]	56.7 [a]	5.26	-	5.26	**0.418*****	0.305
All species	**9.44****	0.017	81.3 [a]	79.3 [b]	78.3 [c]	82.3 [a]	**7.55*(-)**	-	**7.55*(-)**	**0.307***	0.525
Kumukwane (n = 51)											
?Tachinidae sp.	0.37	-0.008	21.8 [a]	22.3 [a]	23.0 [a]	21.9 [a]	4.98	-	4.98	0.180	0.371
P. semitestacea	0.00	0.000	14.5 [a]	14.6 [a]	14.9 [a]	14.5 [a]	1.43	-	1.43	0.307	0.347
All species	1.08	-0.019	36.1 [a]	32.7 [a]	33.0 [a]	36.2 [a]	3.64	-	3.64	0.210	0.369
Kopong (n = 38)											
P. semitestacea	0.67	0.031	17.9 [a]	15.3 [a]	19.2 [a]	17.5 [a]	0.02	-	0.02	**0.453*****	0.348
All species	3.11	0.071	37.9 [a]	24.5 [b]	43.3 [a]	34.4 [ab]	0.04	-	0.04	**0.581*****	0.399

Underlined values indicate loss of significance after column-wide step-up false discovery rate correction (at α=0.05) (García 2004). The large difference in the % deviance explained between methods 2 and methods 3 and 4 is attributable to the necessarily positive relationship between number of parasitised and total hosts (method 2), being taken into account by expressing number of parasitised hosts as a proportion of the total number of hosts in method 3 and 4.

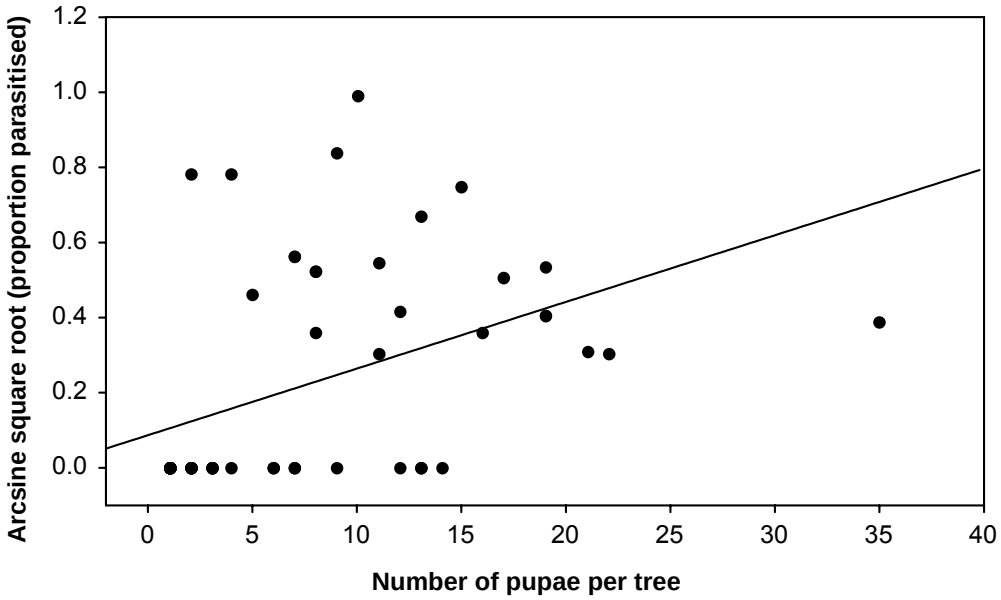

Figure 1. Arcsine square root method: transformed proportion pupae parasitised by *Brachymeria* sp. at Vryburg 2 positively related to pupal density (number of pupae per tree). The quantified linear relationship was weak (R^2 = 19.04%), indicating that the linear fit .should be interpreted with caution.

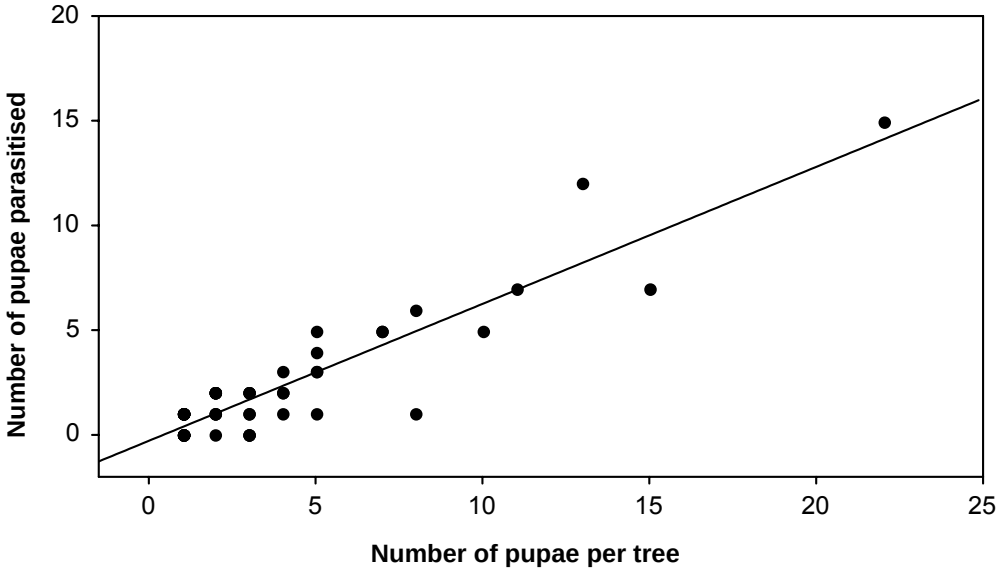

Figure 2. Regression function comparison: number of pupae parasitised by ?*Palexorista* sp. at Vryburg 1 with a constant positive relationship with pupal density. See Table 4 for strength and significance of depicted relationship.

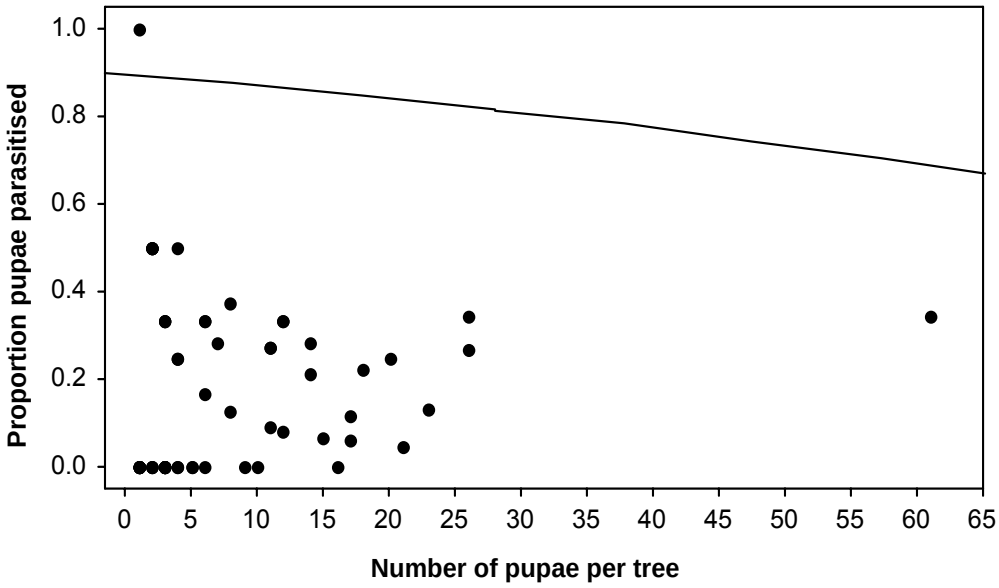

Figure 3. Binomial regression: proportion of pupae parasitised by all parasitoid species at Gabane (generation 1) determined by binomial regression with a negative relationship with pupal density. The quantified negative relationship was very weak (% deviance explained [%DE] = 11.37%), indicating that the slope .should be interpreted with caution.

Spatially associated density dependence

Spatial association identified six cases in which parasitism rate was significantly spatially associated with pupal density (Table 4). In all six cases of spatially associated density dependence the relationship was direct (positive) and in four cases highly significant (e.g. Fig. 4). Spatial association was not limited to certain localities, with usually at least one case (e.g. one parasitoid species) of significant positive association present at each locality. In three out of five cases the parasitism rate of *Pimelimyia semitestacea* was significantly associated with the number of available pupae (Table 4). By contrast, the parasitism rate of *Brachymeria* sp. was never (three cases) spatially associated with pupal density. Considering all parasitoid species at each locality together, significant spatial association was present twice. However in both cases *P. semitestacea* parasitism rate was spatially associated at the same site.

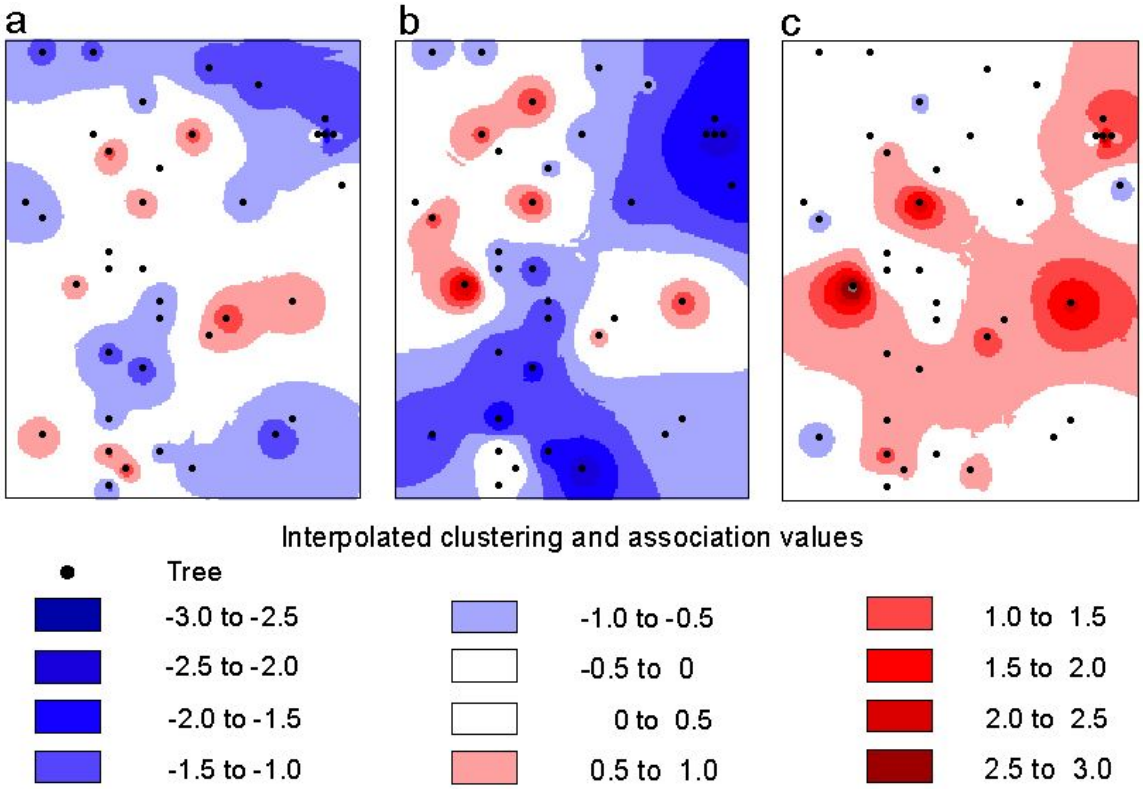

Figure 4. Example of method used to detect spatially associated density dependence. Interpolated (least distance weighted, Perry *et al*. 1999) spatial clustering and spatial association of wild silk moth pupae and parasitism rate by the fly, *Pimelimyia semitestacea*, on trees at Kopong. a) Spatial clustering of pupae (I_a = 0.94; p > 0.05). b) Spatial clustering of *P. semitestacea* parasitism rate (I_a = 1.16; p > 0.05). In both a. and b. areas coded > 1.5 denote areas of significant positive, and areas < -1.5 areas of significant negative, clustering. c) Spatial association between number of pupae and *P. semitestacea* parasitism rate (X = 0.453; p < 0.001). Areas coded as > 0.5 are significantly positively associated at the between-patch scale, while those < -0.5 are significantly negatively associated (Winder *et al*. 2001).

The results of the five methods were thus markedly different, not only in the prevalence of density dependence identified, but also in the sign of significant relationships. Spatial association identified significant density dependence in three instances where relationships were not significant using the other methods (Table 5). By contrast, the regression function

Table 5. Summary of patterns of density dependent (DD) parasitism shown by *G. postica*'s pupal parasitoids using spatially non-explicit methods (1-4) and a spatially explicit method (SADIE association test). 'ind', 'dir' and 'inv' refer to independent, direct, or inverse density dependence respectively. '?' indicates where the type of density dependence could not be determined. 'ns' non-significant after false discovery rate correction (García 2004). * indicates a poor fit (R^2 or %DE < 22%); while (+),and (+++) indicate weak and strong DD respectively.

Site	Parasitoid species	Spatial DD				Spatially associated DD
		1. Arcsine square-root	2. Regression function comparison	3. Binomial regression	4. Binomial regression with spatial terms	5. Spatial association
Vryburg1	?*Palexorista* sp.	ind	ind	ind	ind	dir (ns)
	All species	ind	ind	ind	ind	ind
Vryburg2	*Brachymeria* sp.	dir (+)*	? (not inv)	ind	ind	ind
	P. semitestacea	ind	ind	ind	ind	ind
	All species	ind	ind	ind	ind	ind
Gabane (gen 1)	*Brachymeria* sp.	ind	ind	inv (+)*	ind	ind
	P. semitestacea	dir (ns)*	ind	ind	ind	dir (+++)
	All species	ind	ind	inv (+)*	ind	ind
Gabane (gen 2)	*Brachymeria* sp.	dir (+)*	ind	ind	ind	ind
	P. semitestacea	dir (ns)*	ind	ind	ind	dir (+++)
	All species	dir (+)*	ind	inv (ns)*	inv (ns)	dir (ns)
Kumu-kwane	?Tachinidae sp.	ind	?	ind	ind	ind
	P. semitestacea	ind	?	ind	ind	ind
	All species	ind	?	ind	ind	ind
Kopong	*P. semitestacea*	ind	?	ind	ind	dir (+++)
	All species	ind	? (not dir)	ind	ind	dir (+++)

comparison was least sensitive to density dependence, with all relationships identified as density independent. All three significant standard binomial regression relationships were inversely density dependent (however, when including spatial terms, the contribution of host density became non-significant for two of these), and two of these were not identified as significant by the other methods. The arcsine square root method and spatial association were unique in being the only methods that identified direct density dependence. However, these two methods only shared three cases of direct density dependence.

Due to the marked differences between methods in detecting density dependence, only density dependence identified by spatial association is considered valid because of its advantages over traditional, spatially non-explicit approaches. Of *G. postica*'s parasitoids, two Tachinidae species, *P. semitestacea* and ?*Palexorista* sp., were the only parasitoid species that caused density dependent parasitism. *Brachymeria* sp. and the unknown Tachinidae species never resulted in density dependent parasitism.

DISCUSSION

The five methods used to detect density dependence in the parasitism rates of *Gonometa postica*'s parasitoids did not give similar results with regard to the form of density dependence detected. The spatially explicit method, spatial association, which uses more of the biological relevant information than traditional spatially non-explicit methods, is consequently regarded as the superior method of analysing density dependence in parasitism rates. Only spatial association indicated that *Pimelimyia semitestacea* repeatedly resulted in direct density dependent parasitism rates. Therefore, if this method was not used, the potential importance of this parasitoid for *G. postica* population dynamics (Chapter 1) would not have been correctly predicted.

Spatial association revealed that density dependence was usually weak at the site scale, and only indicated strong density dependence at isolated trees within a site. The magnitude of the strongest relationship quantified at this scale, using overall spatial association, was 0.58, while the theoretical maximum is 1.00. This confirms that the density dependence in pupal parasitism rates were relatively weak in this study. Nonetheless, overall association values of

positive relationships in biological data usually range between 0.05 and 0.60 (Thackray *et al*. 2002), and 0.7 may represent a biological realistic maximum in ecological associations. For example, it is generally accepted that R^2 values of 70% indicate a very strong relationship in ecology. An overall association value of 0.58 is thus in fact very large. However, local association values were significant (2.5 and greater), for only a few single trees. Thus, the strength of density dependent parasitism observed in *Gonometa postica* populations is highly variable at the site scale, i.e. between trees. No other method was able to provide information on the pattern of density dependence in such spatial detail.

Two biological reasons for density independent parasitism rates have been proposed. First, analysing the spatial pattern of parasitism of more than one parasitoid species simultaneously might obscure the detection of density dependent parasitism (Heads & Lawton 1983). In this study, *P. semitestacea* and ?*Palexorista* sp. were the only parasitoid species to show spatially explicit density dependence. Combinations of all parasitoid species rarely exhibited spatially associated density dependence, even if specific species on their own were found to be density dependent. Therefore, when parasitism rates of different parasitoid species are lumped for analyses (Williams *et al*. 2001) or are indistinguishable (Heads & Lawton 1983), the true type of density dependent relationship between individual parasitoid species and their host may thus be obscured. Second, density independent parasitism rates may be due to sequential parasitism. Lessells (1985) previously illustrated how direct density dependence may be missed when different parasitoid species parasitise the host sequentially. In this study it may be the case as *P. semitestacea* is suspected to parasitise final instar larvae first and other parasitoid species to follow thereafter. This may be a plausible explanation for why density dependence was only detected for this species.

Another potential reason for the form of density dependence detected is the scale of investigation (Heads & Lawton 1983; Ray & Hastings 1996). In this study all tests for density dependence were conducted at the between-plant scale. It has further been suggested that density independent parasitism rates will be the norm for insect herbivores varying in abundance at the between-plant scale (Norowi *et al*. 2000). However, this study found both density dependence and density independence in parasitism rates when using the same parasitoid species and method. This suggests that scale is not responsible for the form of density dependence identified at the between-plant scale in this study.

However, as illustrated by this study, the method used can also severely affect the form of density dependence detected. Traditional (spatially non-explicit) methods of detecting density dependence may be especially prone to missing significant density dependence when attack rates are below 10% and the host's abundance is low (Trexler *et al*. 1988). Generally, and as found in this study, curve fitting methods perform especially poorly, not being powerful enough to distinguish the form of density dependence (Trexler *et al*. 1988; McGill 2003). Binomial regression, on the other hand, tends to indicate density independence much more often than density dependence and, in the latter, usually weak inverse density dependence is detected (Hails & Crawley1992; Norowi *et al.* 2000; this study). Therefore, when using binomial regression, although host density may account for some variance in the proportion of parasitised hosts, this amount is usually small. A large proportion of parasitism risk is thus not accounted for by host density (e.g. Norowi *et al.* 2000, and this study). The high probability of making a Type II error when using this method, limits it value in detecting density dependent parasitism under field conditions, which are likely to be weak (see also Hails & Crawley1992). In contrast, spatial association does not violate statistical assumptions of spatial independence, incorporates what is known to be biologically relevant spatial information in host abundance, and is more sensitive (has greater power; Winder *et al*. 2001) to the detection of weak density dependent relationships, it offers an advantageous alternative to traditional methods. Thus, using a spatially explicit method of detecting density dependence is not similar to using spatially non-explicit methods.

The explicit inclusion of spatial information in ecological models is being increasingly adopted (Legendre *et al.* 2002; Perry *et al.* 2002), although it is still rare in analyses of density dependence (e.g. Dolman & Sutherland 1997; Hassell 2000; Berryman 2003). In two examples (Roland & Taylor 1997; Loch & Zalucki 1998) where spatial referenced data are used in density dependent (parasitism) investigations, spatial information was not used in the quantification of aggregation in host abundance and the spatial pattern described was not location-specific. Trend surface analysis (Roland & Taylor 1997) or testing for spatial autocorrelation in parasitism rate (Roland & Taylor 1997; Loch & Zalucki 1998) is an incomplete solution, because although it accounts for the spatial variance or the spatial structure in parasitism rate, it does not quantify the spatial relationship with host abundance. In this study, in the absence of spatial autocorrelation in host abundance (see Chapter 3), spatial

association was still able to match isolated (single sample point) areas of high host abundance and high parasitism rate.

The value of using spatially explicit abundance data to investigate insect predator-prey cycles (by determining spatial association over time) has been illustrated previously (Bohan *et al*. 2000; Ferguson *et al*. 2000; Winder *et al*. 2001). In these studies delayed temporal density dependence is inferred from quantifying the degree to which predator densities temporally track prey densities. No studies to date have, however, investigated the spatially explicit relationship between host density and mortality rate, allowing a direct test for the presence of spatially explicit (associated) density dependence. Using *Gonometa postica* and its parasitoids as a case study, we have illustrated that spatial association between host abundance and parasitism rate measured in one generation can be used to detect spatially-explicit density dependence. By defining spatial patchiness in the most biologically relevant manner (Perry 1998), the search for spatial density dependence was made more powerful.

The results of this study show that the degree of spatial explicitness determines if, and what form, of density dependence is detected. This has implications for decades of work on the detection of density dependence in parasitism rates of insect herbivore parasitoids (1941-1987, reviewed by Stilling 1987, and Walde & Murdoch 1988). In these studies the spatially explicit pattern of host abundance (position of sample points and neighbours) was not considered. By omitting spatial data the frequency of density dependent parasitism may have been underestimated. Although studies on density dependent parasitism refer only to patterns in mortality and not to the processes that cause them, exploring the use of spatial explicit data in other HPR's (e.g. population functional response, see Table 1) may provide further insight into processes that lead to density dependence. Furthermore, the quantification of the density dependence in parasitism rates has been, and still is, an important topic in host-parasitoid population dynamics (Hassell 2000; Haak 2002). Natural enemies are thought to only regulate prey populations when they induce density dependent mortality (Crawley 1992). Density dependence has thus profound implications for our current understanding of population regulation.

The fact that markedly different conclusions on the prevalence and form of spatial density dependence are reached with alternative methods, calls for a re-evaluation of its statistical definition. In summary, spatial association does not violate statistical assumptions of

spatial independence, incorporates biologically relevant spatial information on host density and parasitism risk, and has greater power to detect weak density dependent relationships than other methods (Winder *et al*. 2001; Perry & Dixon 2002). This method is thus the superior method for detecting spatial density dependent parasitism or other relationships. While the debate on the consequences of density dependence for host population dynamics continues (Godfray & Hassell 1997; Berryman 2003), the statistical definition and quantification of density dependent relationships remain fundamental to the field of population ecology (Haak 2002). Given that density dependent processes form part of all five of the so-called 'principles' of population ecology (geometric growth, cooperation, competition, interacting species and limiting factors; Berryman 2003), the ability to detect density dependence, in general, is an issue of vital importance.

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CHAPTER 5

Variability in cocoon size in southern African wild silk moths: implications for sustainable harvesting

INTRODUCTION

In addition to the domesticated or mulberry silkworm, *Bombyx mori* (Lepidoptera: Bombycidae), many indigenous wild silk moth species have been utilized for over 2000 years (Peigler 1993). Although *B. mori* silk currently satisfies 95 - 99 % of the demand for commercial silk (Peigler 1993; Scoble 1995), the low volume of wild silk supplies an exclusive niche market where scarcity and naturalness is highly valued.

Southern Africa has two indigenous silk moth species, *Gonometa postica* Walker and *G. rufobrunnea* Aurivillius (Lepidoptera: Lasiocampidae), that produce high quality silk (Nagaraju & Jolly 1988). *Gonometa* silk is slightly coarser than *B. mori* silk, but finer than other wild silk moth species (Hartland-Rowe 1992, Freddi *et al.* 1993), has a natural gold colour and dyes well (Hartland-Rowe 1992). The cocoons of both species are thus considered a valuable natural resource.

Despite similar cocoon characteristics, there are marked differences between the two *Gonometa* species. *G. postica* is polyphagous (hosts include *Acacia erioloba*, *A. tortillis*, *A. mellifera*, *Burkea africana*, *Brachystegia* spp. and the alien, *Prosopis glandulosa*), whereas *G. rufobrunnea* feeds only on *Colophospermum mopane* (Scholtz & Holm 1985; Hartland-Rowe1992). The distributions of the species also differ (Fig. 1) (Pinhey 1975; Hartland-Rowe1992). Male and female adults of *G. postica* have brown fore wings, while those of *G. rufobrunnea* are red (Pinhey 1975). Although the general biologies of both species are reasonably well known (Pinhey 1975; Scholtz & Holm 1985; Hartland-Rowe 1992), the ecology of neither has been studied. For example, the spatial and temporal variation of natural

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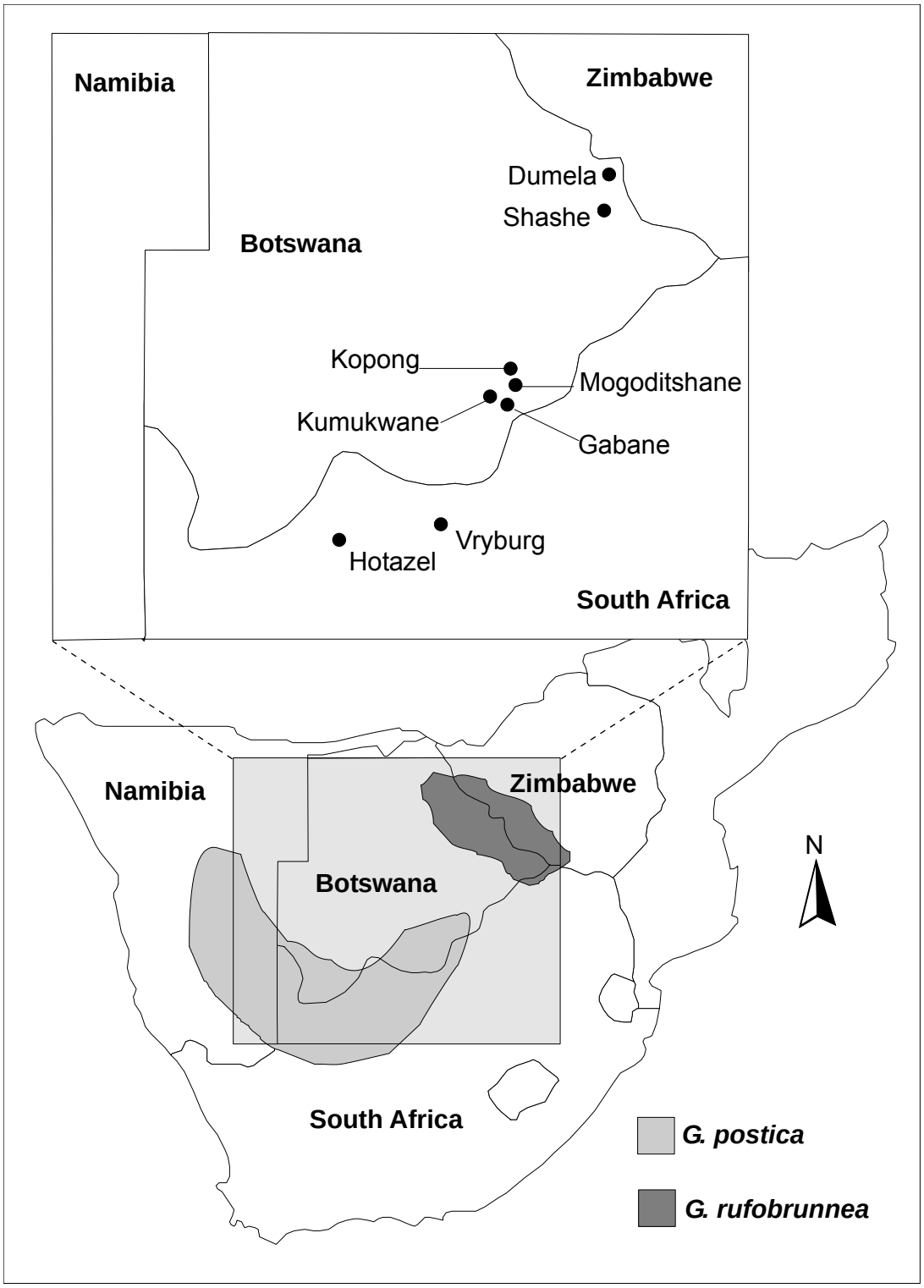

Figure 1. Known distribution ranges of eruptive phases (as from previous published and historic reports, as well as personal observations) of *Gonometa* species in southern Africa, as well as sampled localities.

population sizes, and the impacts of natural enemies, host plant distribution and quality, are not known. Despite this, harvesting of *G. rufobrunnea* has been extensive. Between 1986 and 1987, 430 tonnes of cocoons containing live pupae (here after referred to as 'occupied cocoons') were collected by inhabitants of the Francistown area (Botswana) and sold to Shashe Silk Ltd. (Hartland-Rowe 1992). A decrease in cocoon abundance and a fall in the international silk price coincided with the abrupt end of this enterprise (McGeoch 2000). However, because the population dynamics of the species are unknown, the decline in abundance could not be unequivocally attributed to over harvesting.

Presently, empty cocoons (i.e. from which adults have emerged) are being collected from natural populations of *G. postica* in the North West Province of South Africa. Although this practice may be sustainable, the quality and market value of silk extracted from empty cocoons, which are usually older and with the cocoon surface ruptured by emergence holes (caused by the moth itself or parasitoids), is lower than that from occupied cocoons. There is thus still extensive potential pressure on natural populations of *Gonometa* from harvesting of occupied cocoons, and additional information on the species is required to develop a sustainable harvesting programme.

One component of this information is the identification of *Gonometa* species and sex using cocoons in the field, as well as identifying additional patterns of variability in cocoon size. This not only has implications for the estimation of silk yields, but also for extracting biological information, such as sex ratio and population density, from cocoons in the field. Studying the pupal stage has a number of advantages. Cocoons are sessile, conspicuous and therefore more readily measured and monitored than mobile stages. Cocoons are also the raw material for silk production, and variation in their size is thus important. With as many as 670 cocoons of *G. rufobrunnea* needed to produce one kilogram of raw silk (Hartland-Rowe 1992), variation in cocoon size of naturally harvested populations could markedly affect silk yields. In addition to reported cocoon size sex and species differences (Nagaraju & Jolly 1988; Hartland-Rowe 1992), variability in host-specific populations and geographically separated localities may exist. The frequency of dwarfism (significantly smaller than average cocoons) that has been observed in populations is also unknown. Bivoltinism in these species may also result in cocoon size differences between generations.

Although occupied cocoon mass (OCM) (as a measure of cocoon size) has been shown to be positively correlated with cocoon volume in other Saturniidae (Tripathi *et al.* 1988), using OCM to study size variability has three disadvantages. It requires destructive sampling, cocoon mass is highly influenced by the status of the pupa (live, dead or parasitised), and although pupal (and thus cocoon) mass is often related to fecundity in Lepidoptera species (Wickman & Karlsson 1989, Garcia-Barros 2000), it is not always so (Leather 1988). Cocoon length is proposed as an alternative size measurement that is accurate and practical, and may in fact be a better measure of potential reproductive effort (Leather 1988, although see Robison *et al.* 1998).

The aims of this study were thus to determine: 1) if these *Gonometa* species are significantly sexually dimorphic in cocoon length, width and shape and if sex can be determined using these measurements; 2) whether cocoon length is a suitable surrogate measure for occupied cocoon mass, and can be used to estimate cocoon silk yield; 3) the sex ratios of the species within and between generations and localities; 4) the frequency of observed dwarfism in populations of both *Gonometa* species and whether this varies between generations; 5) whether cocoon length differs between populations on different host plants, between localities and between the first and second generations.

MATERIAL AND METHODS

G. postica was sampled in North-central South Africa (Vryburg and Hotazel) and South-Eastern Botswana (Gabane, Kumukwane, Mogoditshane and Kopong), while *G. rufobrunnea* was sampled from North-Eastern Botswana (Shashe and Dumela) (Fig. 1; Table 1). Sites were selected based on cocoon abundance, with a minimum of 30 first-generation cocoons per site required for site selection. Sampling was standardized by delimiting an approximately rectangular area incorporating 100 trees at each site (from here on referred to as a grid). This was done to compensate for possible tree-density differences between host-plants and between geographically separated sites (see Table 1). Cocoons were found on all above-ground parts of the tree, and occasionally on herbs growing directly beside the tree trunk. Every cocoon on each tree of each grid was counted and its length measured. At least three grids per host plant

were selected. Sampling of grids started in winter when all larvae had pupated to over-winter. Cocoons formed during this period are hereafter referred to as the first generation. Two months after adult emergence in spring, newly formed cocoons were sampled again at the same grids, which are hereafter referred to as the second generation.

Table 1. Localities where both *Gonometa* species were sampled (first and second generation) and associated host-plants. A grid refers to the sample area incorporating 100 trees.

Species	Host plant	Locality	Co-ordinates	No. grids	Grid area (m^2)	#1st	#2nd
G. postica	*Acacia erioloba*	Hotazel	27° 15' S 23° 03' E	1	9750	1	1
		Vryburg	26° 59' S 24° 40' E	2	6726 ± 2*	2	2
	Acacia tortillis	Gabane	24° 37' S 25° 46' E	1	2500	1	1
		Kumukwane	24° 38' S 25° 40' E	1	3105	1	1
		Mogoditshane	24° 34' S 25° 50' E	1	2243	1	0
		Kopong	24° 31' S 25° 48' E	1	1679	1	1
G. rufobrunnea	*Colophospermum mopane*	Shashe	21° 31' S 27° 24' E	3	380 ± 31*	3	3
		Dumela	21° 07' S 27° 32' E	2	444 ± 73*	2	2

* = mean grid area (± S.E.) for a locality where more than one grid was sampled; #1st = number of first generation surveys, conducted from June to August 2000; #2nd = number of second generation surveys, conducted from January to February 2001. The second generation cocoons of *G. postica* at Mogoditshane could not be sampled due to destruction of the habitat.

To establish the relationship between other cocoon size variables, i.e. length, width and mass, at least 50 occupied cocoons (referred to as harvested cocoons) were removed from trees in areas at least 0.5 km away from each grid. Grids closer than 2 km apart, shared the same sample, while separate samples were taken for those more than 2 km apart. Cocoons were collected during sampling of both the first and second generations. The longest axis of a cocoon was taken as length, while width was measured at the widest section of the cocoon perpendicular to its length. Dimension measurements were taken with a digital caliper accurate to 0.01 mm, while mass was determined with an electronic balance accurate to 0.01 g. Simple and multiple regressions of cocoon length and width with mass were done separately for the sexes of each species because of the marked differences between males and females.

To determine the validity of classifying males and females based on cocoon size and shape alone, the shape of approximately 300 harvested first generation cocoons of each species' was quantified by examining the length-width ratio (LWR). Individuals were categorized as dead, parasitised, emerged, or not yet emerged (cocoon occupied). Dwarfs were defined as individuals smaller than approximately two standard deviations of mean male cocoon length. On emergence, adult moths show marked sexual dimorphism (Pinhey 1975). First generation pupae that failed to emerge were sexed (using the two rounded genital scars on abdominal segment eight and nine of females and the single scar on segment nine of males; see Scoble 1995, p. 131-132). As insufficient time had elapsed for second generation emergence only pupae of this generation, falling in the length- and width-overlap range of the first generation, were sexed. However, it is likely that all sex identification errors were determined because no sex identification errors were made outside of the sex-size overlap range.

Analysis

Differences in cocoon size between sexes, species, generations and localities were determined using generalized linear models (maximum likelihood technique) that have no strict normality assumption for the dependent variable (McCullagh & Nelder 1989). This made it possible to simultaneously investigate differences between separate species-sex combinations. Because of the marked sexual dimorphism in both species, male and female cocoon size data were analysed separately. Thus when considering factors such as generation, host-plant (*G. postica* only) and locality, a model explaining cocoon length was built separately for species

and sexes. Only one host species was found per locality, and localities with a specific host species were closer to each other than to those with other host species. This constraint on the sampling design resulted from a shortage of sampling sites where cocoons were sufficiently abundant. Because *G. postica*'s two host plant species were not found at the same localities, the possible effect of host plant and /or locality on cocoon size could not be separated in this study. However, if no consistent differences in cocoon size are found between localities on which the species occur on different host plant species, then the conclusion may be drawn that host plant species does not affect cocoon size.

RESULTS

Both *Gonometa* species were sexually dimorphic with regard to cocoon mass, length, width and colour. The cocoons of *G. postica* are white with brown setae, whereas *G. rufobrunnea* has red cocoons with red setae. Although mean OCM of *G. postica* and *G. rufobrunnea* only differed significantly between females ($F_{3,620}$ = 1629.46; P < 0.001; R^2 = 88.7%), all species-sex combinations were significantly different from each other with regard to length and width ($F_{3,620}$ = 960.90; P < 0.001; R^2 = 82.2% and $F_{3,620}$ = 1034.02; P < 0.001; R^2 = 83.2% respectively) (Table 2).

Table 2. Mean (± S.E.) cocoon mass (occupied), and length and width of male and female cocoons of both *Gonometa* species. Different letters (superscripts) indicate a significant difference of P < 0.05 between means.

Species	Sex	n	Mass (g)	Length (mm)	Width (mm)
G. postica	male	248	2.85 ± 0.02 [a]	36.00 ± 0.11 [a]	16.41 ± 0.05 [a]
	female	227	6.81 ± 0.06 [b]	45.87 ± 0.17 [b]	21.34 ± 0.08 [b]
G. rufobrunnea	male	55	2.72 ± 0.04 [a]	35.17 ± 0.24 [c]	15.81 ± 0.10 [c]
	female	94	5.13 ± 0.07 [c]	41.82 ± 0.21 [d]	19.26 ± 0.13 [d]

Cocoon length explained approximately 45 % and 60 % of the variation in OCM of both *Gonometa* species males and females respectively. Cocoon length generally explained more of the variation in OCM than cocoon width, but together length and width explained 11 % to 18 % more of the variation in mass than length alone (Table 3). When comparing males and females, cocoon length and width, separately and together consistently explained more (7 % to 22 %) of the variation in mass of females than of males (Table 3). These parameters also generally explained more of the variation in mass of *G. rufobrunnea* than of *G. postica* (ranged from 1 % less to 13 % more) (Table 3).

Table 3. R^2 (%) for simple and multiple (corrected R^2) regressions of length and width on occupied cocoon mass of both *Gonometa* species. Each species-sex combination was analysed separately. All relationships were significant at $P < 0.001$.

Species	Sex	n	Length	Width	Length & width
G. postica	male	248	42.2	40.3	59.6
	female	227	55.2	56.2	72.2
G. rufobrunnea	male	55	48.4	48.1	58.3
	female	93	68.2	55.4	80.1

Males and females of *G. postica* were generally longer than those of *G. rufobrunnea* (Fig. 2a & b). Also, the length overlap range between males and females was smaller for *G. postica* (2 %) than *G. rufobrunnea* (17 %) (Fig. 2a & b). When comparing the differences in cocoon length between sexes and between species, sex differences ($F_{1,3969} = 12566.608$, $P < 0.01$) were far greater than between-species differences ($F_{1,3969} = 1265.649$, $P < 0.01$), although both were highly significant (Table 4).

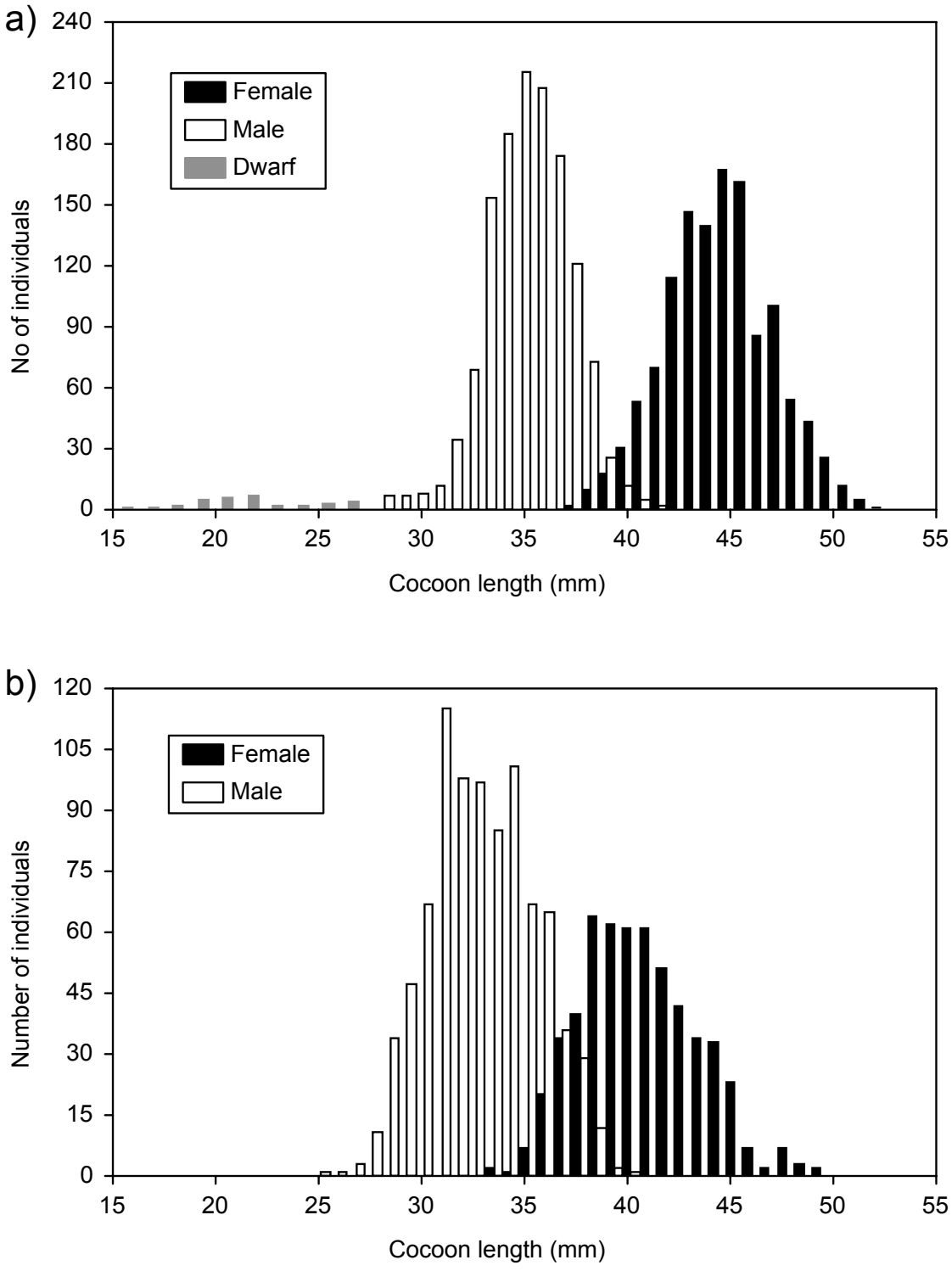

Figure 2. Cocoon length frequency distribution of all field-measured cocoons of a) *Gonometa postica* and b) *G. rufobrunnea*. Note the presence of dwarf individuals for *G. postica*.

Table 4. General linear models of cocoon length on species and sex. Mean (± S.E.) cocoon length differences between *G. postica* and *G. rufobrunnea* and between males and females of both *Gonometa* species are indicated. $P < 0.01$ is denoted by **.

Species	Sex	
	Female	Male
G. postica	44.57 ± 0.07	35.12 ± 0.06
G. rufobrunnea	40.66 ± 0.12	32.94 ± 0.09

Whole model: $R^2 = 79\%$, $F_{2,3969} = 7341.527$**

The length-width ratio (LWR) of males and females of both *Gonometa* species generally had the same range (Fig. 3a & b), but the slopes of the sexes of *G. postica* differed more between each other than those of *G. rufobrunnea* (slopes for the sexes of both species differed significantly at $P < 0.001$ and $P < 0.01$ respectively). Also for both species the rate of increase of LWR with an increase in length was greater for males than for females (Fig. 3a & b). One second-generation *G. postica* female cocoon was malformed (cocoon shape not ovoid) and its length and width (33.67 mm and 15.53 mm respectively) was more typical of a male cocoon than a female. Although this individual fell in the middle of the male LWR against cocoon length scatter, it still emerged successfully as a female and even oviposited a number of eggs. However as a general rule, where length or width overlap occurs, sex identification is still possible because male cocoons are narrower than females at the same length.

The harvested cocoons of *G. postica* had smaller length and width overlap ranges, and a smaller proportion of the population fell in this range compared to *G. rufobrunnea* (Table 5). Also for OCM, *G. postica* had a greater range of no mass overlap between the sexes (males < 3.64 g and females > 3.75 g) than those of *G. rufobrunnea* (males < 3.39 g and females > 3.41 g). Although fewer sex identification errors were made for *G. postica* than *G. rufobrunnea*, when standardised for the proportion of the population in the overlap range, the percentage sex identification errors made was similar for both species (Table 5).

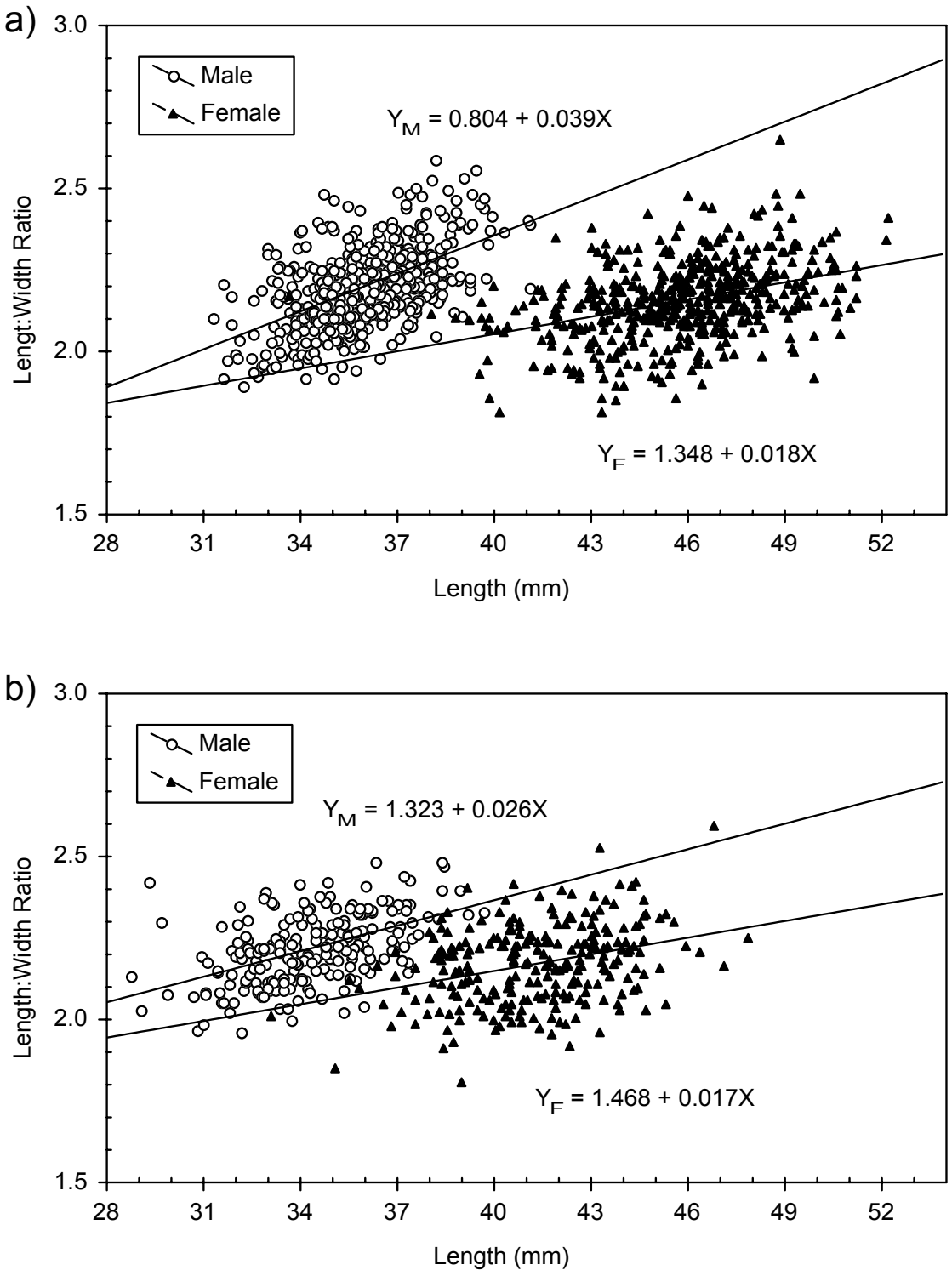

Figure 3. Cocoon length-width ratio against cocoon length and linear regression equations for a) *Gonometa postica* and b) *G. rufobrunnea*.

Table 5. Comparison of the overlap range of male and female cocoons of both *Gonometa* species and subsequent accuracy of sexing.

Species	N	Overlap range (mm)				IDE	% pop.	% IDEOR
		Width	Length	n	% pop.			
G. postica	978	17.50 – 19.00	38.00 – 41.50	20	2.04	3	0.31	15.00
G. rufobrunnea	472	16.40 – 18.50	33.00 – 40.00	79	16.74	10	2.11	12.70

% pop. = percentage of population; IDE = number of identification errors; % IDEOR = percentage of Identification Errors made in Overlap Range.

A sex ratio of 1:1 was expected for both species and this was the case in 19 out of 23 surveys (not 24 due to destruction of a grid, see Table 1). Exceptions included (χ^2 = 1 df): Mogoditshane ($P < 0.05$), Dumela1 and Dumela2 (both $P < 0.001$) first generation surveys, as well as Gabane second generation survey ($P < 0.001$). In all these cases the sex ratio was male biased.

G. postica was the only species with dwarf individuals (Fig. 2a). For this species there was no consistent difference in the frequency of dwarfism found for the first and second generation, but more dwarfs were found on *Acacia erioloba* than on *A. tortillis* (75 % and 25% dwarfs respectively). In only one case, namely first generation cocoons of *G. postica* with *A. tortillis* as host plant, were no dwarfs recorded. The frequency of dwarfism was low and in most cases occurred in approximately 1.5 % of the sampled population. Dwarf cocoons ranged between 15.13 - 27.31 mm in length (n = 32).

When considering each species-sex combination separately there were no significant differences between the lengths of first- and second-generation cocoons, except for *G. rufobrunnea* males where the second generation was longer than the first. In contrast, lengths differed significantly between localities for all four species-sex combinations (Table 6). *G. postica* males and females were the only groupings where host-plant type may potentially affect cocoon size. Despite significant differences between *G. postica* localities, they were not consistent between host specific localities and differed between males and females. The only pattern that emerged was that Gabane and Mogoditshane had the highest mean male and

female cocoon lengths, while Vryburg and Hotazel had the lowest values (Table 7). Comparing localities of *G. rufobrunnea*, Dumela had a highly significant lower mean male and female cocoon length than Shashe.

Table 6. General linear models of cocoon length on generation and locality for each species-sex combination.

Species-sex combinations	R^2	d.f.	F	P	Variable	d.f.	F	P
G. postica	0.06	6	15.082	< 0.001	Generation	1	3.779	0.052
females					Locality	5	17.896	< **0.001**
G. rufobrunnea	0.22	2	79.253	< 0.001	Generation	1	2.587	0.108
females					Locality	1	158.476	< **0.001**
G. postica	0.04	6	9.279	< 0.001	Generation	1	1.486	0.223
males					Locality	5	11.132	< **0.001**
G. rufobrunnea	0.28	2	166.842	< 0.001	Generation	1	9.236	**0.002**
males					Locality	1	333.084	< **0.001**

Table 7. Mean (± S.E.) cocoon lengths of both *Gonometa* species' males and females for generations, localities and host plants. Different letters (superscript) indicate a significance of $P < 0.01$. See Table 6 for analyses.

Category	Type	Cocoon length (mm)			
		Female	n	Male	n
G. postica					
Generation	1st generation	44.62 ± 0.09 [a]	850	35.12 ± 0.07 [a]	826
	2nd generation	44.46 ± 0.12 [a]	390	35.13 ± 0.10 [a]	485
Locality					
A. erioloba	Vryburg	43.84 ± 0.14 [a]	328	34.78 ± 0.11 [a]	268
	Hotazel	44.05 ± 0.14 [ab]	260	34.64 ± 0.12 [a]	242
A. tortillis	Gabane	45.35 ± 0.14 [c]	386	35.61 ± 0.10 [b]	481
	Kumukwane	44.51 ± 0.19 [abd]	145	34.88 ± 0.16 [a]	147
	Mogoditshane	45.44 ± 0.25 [cd]	69	35.25 ± 0.16 [ab]	109
	Kopong	45.05 ± 0.33 [bcd]	52	35.02 ± 0.28 [ab]	64
G. rufobrunnea					
Generation	1st generation	40.66 ± 0.12 [a]	542	32.93 ± 0.09 [a]	846
	2nd generation	40.54 ± 0.37 [a]	14	33.26 ± 0.27 [b]	26
Locality	Shashe	41.79 ± 0.15 [a]	321	34.57 ± 0.12 [a]	339
	Dumela	39.11 ± 0.14 [b]	235	31.89 ± 0.09 [b]	533

DISCUSSION

Marked size differences were found between *G. postica* and *G. rufobrunnea*, with all cocoon size measurements differing significantly between species. These differences, as well as species cocoon colour differences, make species identification in the field based on cocoon morphology possible. Cocoon size differences between sexes were greater for *G. postica* than *G. rufobrunnea*. This is to be expected from allometric scaling of sexually dimorphic species where females are the larger sex (see Fig. 1, Fairbairn 1997). As species become larger so do the intra-specific differences between the sexes, as well as the deviation from the expected isometric scaling constant (Fairbairn 1997).

Sexing cocoons based on shape was found to be acceptable because males were generally narrower (high LWR) than females (low LWR) at the same cocoon length. Simultaneously, male width decreased at a faster rate than female cocoon width with an increase in cocoon length. However, the accuracy of sexing harvested cocoons of both *Gonometa* species was occasionally compromised when males were longer and females shorter than usual. Consequently, for *G. rufobrunnea* more sex identification errors were made. However, standardising the number of identification errors for the proportion of the population, the rate of misidentification was approximately equal for both species. Thus the proportion of the population in this range, and not the size of the length and width overlap range, influenced the number of sex identification errors. Despite these complications in sex identification, both species' cocoons were found to be sexually dimorphic and could be sexed with reasonable confidence in the field (99.7 % accuracy for *G. postica* and 98 % for *G. rufobrunnea*).

Although length-mass regressions of each species-sex combination in this study were significantly positive, the R^2-values were only approximately 50 %. Using both cocoon length and width approximately 15 % more of the variation in OCM was explained. Therefore, although it is possible to estimate silk yield from cocoon length, these estimates will have limited accuracy. There is however no information to date that suggests that cocoon mass would provide more accurate estimates of silk yield. In the single study that examined the latter relationship, no measures of variability were provided (Nagaraju & Jolly 1988). Further research is thus needed to quantify the relationships between pupal mass, cocoon length and silk yield. Based on the results presented here, it is nonetheless possible to use cocoon length

of individuals at a site to determine the size distribution of individuals in the population and to estimate (with a measured degree of accuracy) the potential silk yield of that plot.

Gonometa species from southern Africa were found to have an equal sex ratio, with exceptions being male biased. These exceptions did, however, not occur at the same locality or in both generations, which suggests that they were chance deviations caused by unknown factors in some populations (see for example Jiggins *et al.* 1998, Myers *et al.* 1998).

As dwarfism occurred only in *G. postica* in approximately 1.5 % of the total population on either of the host plant species affected, concerns related to harvesting cocoons from natural populations are apparently unfounded. When dwarfs occur at such low frequencies they should have no effect on the average silk yield per cocoon of harvested natural populations. The cause of dwarfism in *G. postica* or the sex of these individuals is presently unknown. No occupied dwarf cocoons have ever been observed in the field, and it is thought that these cocoons do in fact not contain viable pupae.

Cocoon length variability between populations on different host plant species, from different localities, or of different generations, may also affect the patterns of utilisation, should harvesters select larger cocoons. However, this study showed no significant differences in length between *G. postica* cocoons from its two host plant species between generations. Although locality differences were found for both species, there was much less variation in the cocoon length of *G. postica* between localities than *G. rufobrunnea*. The opposite may have been expected because *G. postica* was found on two host plant species over a wider geographical range than *G. rufobrunnea.* This suggests that host plant species plays little role in determining cocoon size.

The extent of quantitative cocoon size differences between species, sexes, host-plants, localities and generations, as well as their relative importance, has now been described for the first time. The findings presented here thus form the first component of information necessary to estimate silk yields as part of a sustainable utilisation program for harvesting *Gonometa* spp. in southern Africa.

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CHAPTER 6

Fine-scale pupal abundance and distribution patterns of *Gonometa postica* and *G. rufobrunnea* (Lepidoptera: Lasiocampidae)

INTRODUCTION

The spatial distribution of herbivorous insects is not simply a random phenomenon. A large body of literature has demonstrated that insect herbivores may exhibit oviposition preferences, niche partitioning, utilisation of enemy free space, and microclimate preferences that are likely to result in non-random patterns in their distribution (e.g. Dethier 1959; Strong *et al*. 1984; Bernays & Chapman 1994; Price 1997). At a between-host plant scale, the distribution of insect herbivores may be influenced by host plant density (Dubbert *et al*. 1998; Williams *et al*. 2001; Ohashi & Yahara 2002), distance from the edge of the site (Murchie *et al*. 1999; McGeoch & Gaston 2000), habitat structure (Ellingson & Anderson 2002), direct or plant-mediated interactions between herbivores (Riihimäki *et al.* 2003), avoidance of conspecifics (Stamp 1980) or spatial escape from natural enemies (Williams *et al*. 2001). Alternatively, host selection may be based on host plant size or quality characteristics (Floater 1997; Hodkinson *et al*. 2001), as well as previous levels of attack (Gilbert *et al*. 2001). At a within-host plant scale, spatial distribution may be affected by heterogeneity in plant quality (Orains & Jones 2001), niche partitioning (Dubbert *et al*. 1998; McGeoch & Price 2004), density of conspecifics (Cappuccino 1988; Cappuccino *et al*. 1995) or the presence of, or interactions with, other species (Bernays & Chapman 1994; Faeth & Hammon 1996, 1997), larval behaviour (Anstey *et al*. 2002), thermal regime (Stamp & Bowers 1990; Klok & Chown 1998, 1999) or avoidance of natural enemies (Stamp & Wilkens 1993; Wermelinger 2002). Although several factors therefore clearly influence herbivore insect distribution, some of these are likely to be most important determinants of spatial distribution for specific insect herbivore species. Identifying what these factors are for particular species forms an important component

of understanding the population dynamics of the species, as well as the habitat requirements necessary for their conservation (Ranius 2001).

Species that differ in life history strategy may also be expected to have different distribution patterns (Wallner 1987; Ribeiro *et al*. 2003). For example insects with latent population dynamics have a strong relationship between oviposition site preference and larval performance, and therefore larval distribution will closely track host plant quality (Price *et al*. 1990). In contrast, eruptive insects that show limited oviposition choice may not be able to judge host quality and plant quality is therefore unlikely to determine egg and early instar distribution for such species (Leyva *et al*. 2003). In cases like these larvae are left to locate suitable feeding sites (Dodge & Price 1991), and distance of oviposited eggs from a suitable host plant may determine the number and distribution of surviving larvae (Dethier 1959). Eruptive species are also often poorer dispersers than latent insects (Hunter 1995), and as a result eruptive species tend to have more aggregated distributions with latent species more evenly distributed among plants (Ribeiro *et al*. 2003). Insect herbivores that differ in host specificity, secondary compound tolerance, defence characteristics and microclimate preferences are also expected to have different, non-random distributions (e.g. Strong *et al*. 1984; Holmes & Schultz 1988; Stork *et al*. 2001; Kessler & Baldwin 2002). For example aposematic species are likely to have distributions that differ from those of cryptic species, because they are protected from natural enemies (Brower 1958). Instead, other factors, such as solar radiation, may be major determinants of their distribution (Casey 1993). Monophagous species may be able to utilise chemically defended high quality host plant leaves near the tip of the plant, but polyphagous species may be limited to feeding on older, low quality leaves near the base (Kessler & Baldwin 2002). Polyphagous species are also expected to have a more even distribution across plant species polycultures, while monophagous species are likely to be more aggregated and associated only with stands of their host plant (Strong *et al*. 1984).

Furthermore, different life stages are subject to different mortality factors and the selection imposed by them is likely to result in different behaviours and preferences (Price 1997). For example, early Lepidoptera instars may be unable to move to more nutritious plant parts if dispersal is costly (Kessler & Baldwin 2002) and their distribution thus largely follows female oviposition choice. In contrast, larger instars may move freely to conspecific hosts plants (i.e. upon defoliation of their host plant) depending on available food resources (Floater

1997). Galling-insects and leafminers are a particular group of herbivore insects where increased performance on high quality hosts or host plant parts, results in strong selection for the use of such high quality resources (Price *et al*. 1990; Scheirs *et al*. 2004). Consequently these insect herbivores are often non-randomly distributed as a function of oviposition preference for high host quality (Price *et al*. 1995; Faeth & Hammon 1996, 1997, but see Valladares & Lawton 1991). In contrast, the pupae of insect herbivores may have distributions that maximise their survival, because selection for pupation sites by larvae largely determines pupal survival probability (Ruszczyk 1996). Pupal survival can in turn be influenced by both abiotic (e.g. solar radiation) and biotic factors (e.g. natural enemy attack) (Nowbahari & Thibout 1990; Kukal 1995; Ruszczyk 1996; Irwin & Lee 2003). However, when pupal survival is not affected by the distribution of the pupae, patterns may simply reflect oviposition or larval movement patterns, or track the availability of pupation sites at within or between plant scales (Batzer *et al*. 1995).

Finally, tree size and oviposition load may have marked affects on the distribution of the pupal stage (Batzer *et al*. 1995). At densities where larval mortality is no longer subject to inverse density dependent mortality, the amount of foliage and number of conspecifics determines the degree of defoliation (Floater 2001; Rhainds *et al*. 2002). When the primary host tree is defoliated, a secondary host plant has to be selected or larvae will starve. Although larvae may be able to find secondary hosts, dispersal may be extremely costly when host plants are far apart or co-occur with non-host plants (Floater 2001; Steinbauer *et al*. 2001; Hódar *et al*. 2002). Consequently large host plants have a greater probability of sustaining larger numbers of final instars, while those larvae defoliating small hosts may not find suitable replacements and die of starvation (Dethier 1959). In cases were host defoliation is rare and pupae are not subject to density dependent mortality, most larvae will remain and pupate on plants, especially when these plants are large (Batzer *et al*. 1995). However, if some natural enemy preferentially utilises final instar larvae or pupae found on the host plant (Guildford 1992), one may expect the use of non-host plants, leaf litter, or the soil itself as pupation sites. Thus pupal distributions may be influenced by; defoliation level, use of natural enemy free sites, background colour and microclimate requirements (Batzer *et al*. 1995; Lyon & Cartar 1996; Ruszczyk 1996; Hazel *et al*. 1998).

The pupal cocoons of two wild silk moth species native to southern Africa, *Gonometa postica* Walker and *Gonometa rufobrunnea* Aurivillius (Lepidoptera; Lasiocampidae), have great economic value. Cocoons can be degummed to produce high quality silk, which rivals the silk produced from *Bombyx mori* (Veldtman *et al*. 2002). Currently, the pupal stage is the target of harvesting practices that are totally dependent on the availability of pupae from natural populations (Veldtman *et al*. 2002). These pupae almost exclusively occur on the branches and stems of woody plant species (Hartland-Rowe 1992). Because of the harvesting demand, and poor knowledge of the species biology, there is thus substantial interest in the distribution of pupae among and within trees for both *Gonometa* species. Therefore, this study investigates if between and within-tree pupal distributions in these two species are non-random, and if so, if there are relationships between pupation site use and tree characteristics such as tree size, available pupation space and branch position.

METHODS

Study Area

Gonometa postica and *G. rufobrunnea* populations were examined at six and five sites respectively within the known (historic and recent records) eruptive range of these species, spanning a distance of 400km between the two furthest localities for *G. postica*, and 60km for *G. rufobrunnea*. The localities included Vryburg and Hotazel (North-central South Africa) and Gabane, Kumukwane, and Kopong (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* Meyer and at the final three, *Acacia tortillis* Hayne (both Mimosaceae). *G. rufobrunnea* only utilizes *Colophospermum mopane* Kirk ex Benth. (Caesalpiniaceae).

Sampling was standardized by delimiting an approximately rectangular area incorporating 100 trees at each site, to compensate for possible tree-density differences between host-plants and localities (see Veldtman *et al*. 2002). An initial minimum of 40 first-generation cocoons per plot was a prerequisite for site selection. At least three sites per host plant were thus selected.

Surveys of plots 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. Newly formed pupae counted in the first, second, third and final survey are referred from here on to as generation one, two, three and four respectively.

Cocoon sampling

For each of the 100 trees per plot, the tree's species, maximum height, number of branches and spatial position were recorded. Tree species used for pupation were divided into three functional groups namely, primary larval host plant species, non-host plant without thorns, and non-host plant with thorns, as the use of each represents a different pupation strategy. Remaining on the host plant to pupate can guarantee that the right host is oviposited on (Bernays & Chapman 1994). On the other hand using non-host plant can disrupt the search image of natural enemies (Guilford 1992). Tree height was measured to the nearest 0.25 m and divided into three categories, i.e. small (< 1.75 m), medium (1.75 – 3.00 m) and large (> 3.00 m). The number of branches per tree was determined by counting the number of tree sub-units (branches). A primary host plant tree of 0.75 m (smallest sampled) was taken to represent one branch. Counting the number of branches in this manner standardises the three-dimensional differences in tree size between different hosts. Consequently, counts of number of branches per tree were only comparable between sites with similar primary host species. The position of each tree within a plot was measured at the main trunk of the tree with a hand held Global Positioning System (GPS: Garmin Etrex). For trees in close proximity to each other the direction and distance between the two trees were noted and assigned to one of three categories (half, quarter and a tenth of the third (last) decimals of a minute), based on hand drawn maps documenting this fine scale distribution of trees within the site. These spatial co-ordinates were used in all spatial analyses.

Every tree was carefully searched and all pupae of the present generation were counted. For each pupa, its sex (see Veldtman *et al*. 2002), cocoon size, height in the tree (to the nearest 5cm), distance from the main tree trunk (to the nearest 10cm), branch position and aspect were recorded. Branch position was divided into seven categories: edge (E) within 15 cm from terminal branch end; edge middle (EM) 15-30 cm from terminal branch end; edge stem (ES)

terminal branch attached directly to stem; middle edge (ME) start of terminal branch 60 cm from edge; middle (M) middle branch; middle stem (MS) start of main branch; and stem (S) on main tree trunk (Fig. 1a, b). Aspect was determined with a compass, dividing measured directions into four sectors, each centred on a cardinal compass direction, i.e. north (N), east (E), south (S) and west (W). At the start of the study, the number of pupae per aspect was not recorded directly in the first generation, but the number of first generation cocoons found in the second survey were counted instead. Consequently, the site sample sizes for which data on aspect use were available could be lower than for other variables, if some pupae became detached and were not resampled in the second survey.

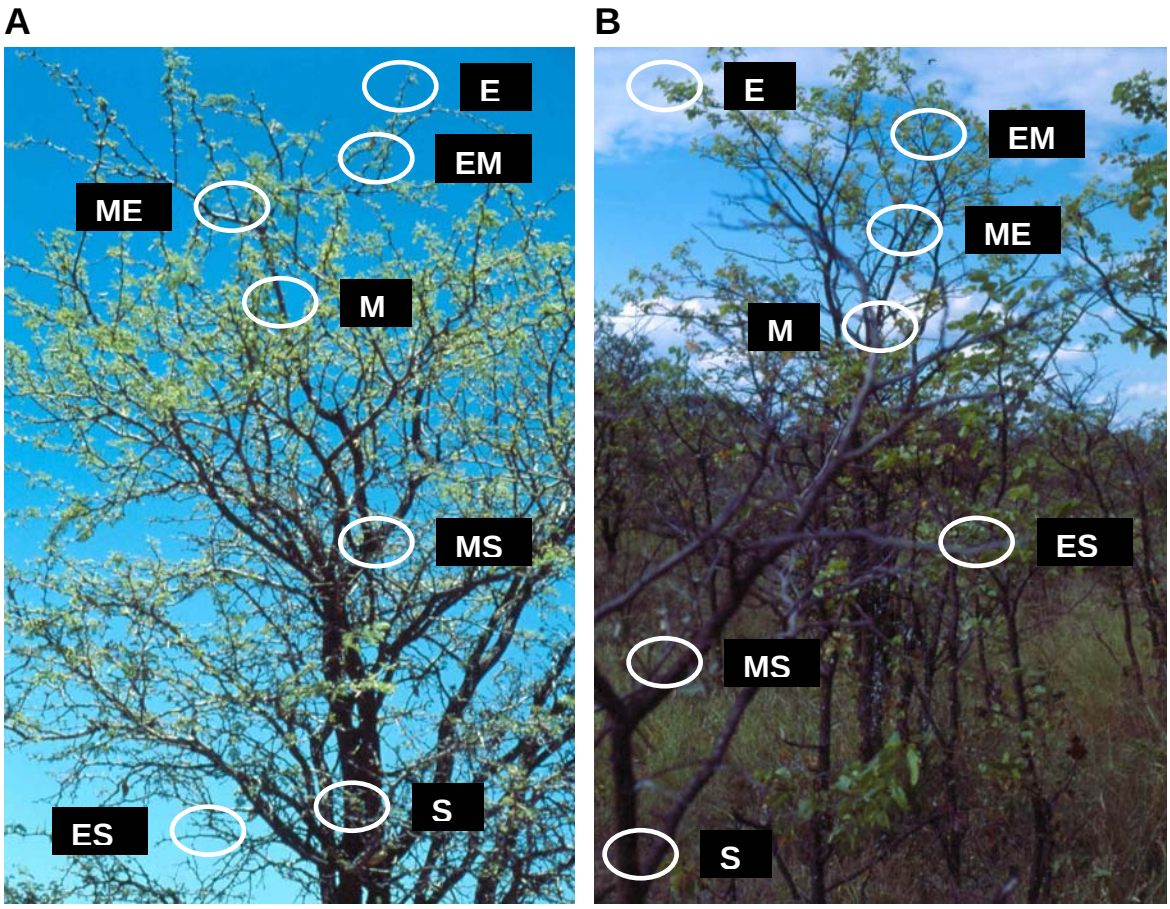

Figure 1. Branch position categories (edge (E) within 15 cm from terminal branch end; edge middle (EM) 15-30 cm from terminal branch end; edge stem (ES) terminal branch

attached directly to stem; middle edge (ME) start of terminal branch 60 cm from edge; middle (M) middle of branch; middle stem (MS) start of main branch; and stem (S) on main tree trunk) assigned to pupae, shown for A) one of *G. postica*'s larval host plants (*Acacia erioloba*) and B) for *G. rufobrunnea*'s larval host plant (*Colophospermum mopane*). Codes shown left or right of encircled area denotes the branch position that will be assigned to cocoons if found within this area.

Data analysis

The relationship between the mean and the variance of the frequency distribution for number of branches per tree counts were quantified by the Poisson index of dispersion (s^2/m) count data (Perry & Hewitt 1991). This index was calculated by dividing the sample variance by the sample mean (Perry & Hewitt 1991). If this index is close to unity the data have a Poisson distribution. When the index is smaller or greater than 1.0 this indicates that the distribution is under- and over dispersed and the data are best fit by a binomial or negative binomial distribution (or another over-dispersed distribution, e.g. gamma distribution) respectively (Bliss & Fisher 1953). Significant departures from randomness were determined by calculating $(n-1)*(s^2/m)$ and comparing them to the X^2_{n-1} distribution (Perry & Hewitt 1991). Alpha level corrections for multiple testing were preformed using the step-up false discovery rate (FDR) procedure shown to be the least over corrective of current alpha level correction methods (García 2004).

Between-tree patterns

The objective was to determine if between-tree variation in pupal abundance could be explained by tree characteristics such as plant functional group (primary host plant, non-host plant, non-host plant with thorns), tree size (for all trees and the primary host plant only), or by across-tree aggregation patterns. First, whether the functional group to which an individual tree belongs influences the number of pupae found was examined. Second, the importance of the frequency of primary larval host-plant trees in different height categories is sufficient to explain the utilisation by pupae, was investigated. To determine if tree functional types or size classes (primary host functional group) had a greater or lower proportion of the pupae than

expected from their recorded frequencies, Chi-square goodness of fit analyses were performed (Zar 1984). If the ratio of observed to expected pupae is greater than one, over utilisation is indicated, while ratios less than one indicate under utilisation. Trees were divided into groups based on functional type (primary larval host plant (H); non-larval host plant (N); non-larval host plant with thorns (T)). Although, there were low numbers of pupae for N and NT categories, as long as expected pupal frequencies were greater than five, the data could be analysed. Primary host plant trees were also divided into three size classes (small (S) < 1.75 m; medium (M) 1.75 - 3.00 m; large (L) > 3.00 m). For both groupings three categories were generally available for comparison. In cases were some groups did not have sufficient pupae to allow analysis a two-way category comparison was done (bias in Chi-square analysis occurs if there are expected frequencies less than one or more than 20% of frequencies below 5, Zar 1984).

Third, it was determined if the number of pupae counted per tree and their location within the site, was significantly different from a pattern expected by chance. Spatial analysis by distance indices (SADIE) methodology (Perry 1995) was used to quantify the degree of departure from spatial randomness for the spatially-referenced (X,Y) branch and pupal count data in this study. Spatial non-randomness is based on the distance to regularity (minimum cumulative distance to achieve a regular distribution of counts, thus when all sample counts are equal to the mean) that can be quantified for the data set as a whole (overall aggregation) or indicate the contribution of each sample point (degree of clustering) to local departures from randomness within the data set (Perry & Dixon 2002). The significance of overall aggregation was tested by dividing the observed distance to regularity by the average distances of randomisations of the sample counts, to give the index of aggregation (I_a) (Perry 1995). This index summarises the spatial arrangement of the counts relative to each other (Perry *et al*. 1999; Perry & Dixon 2002). Although significance is actually tested, values of I_a of approximately 1.5 and greater indicate significant aggregation (Perry *et al*. 1999).

Provided there is evidence of overall aggregation, the degree of clustering in count data can be quantified (Perry & Dixon 2002). The index of clustering, v, provides information on the degree of clustering for each spatially referenced point based on the magnitude of the count and its occurrence in relation to neighbouring counts. Clustering occurs in two forms, namely patches (counts greater than the sample mean, v_i) and gaps (counts smaller than the sample

mean, v_j). For random arrangements of counts, v_i and v_j have expected values of 1 and -1. Values greater than these expected values indicate membership by the count of a patch ($v_i > 1$) or gap ($v_j < -1$). Non-randomness is formally tested by comparing mean v_i and mean v_j values with their expected values of 1 and -1 for random arrangements (Perry *et al*. 1999). If mean v_i and mean v_j are not significant, the lack of overall, strong clustering into patches and gaps is indicated (Perry *et al*. 1999; Perry & Dixon 2002).

For each site-generation combination, I_a, mean v_i and mean v_j were calculated if pupae were found on more than 20% of the trees. At densities lower than this (e.g. mean count per tree < 0.2), it is not possible to quantify overall aggregation and spatial clustering (Winder *et al*. 2001). The maximum ratio of non-zero values to total number of measured values that still allows the detection of significant spatial clustering (sufficient power) has been shown to be 4: 25 (Korie *et al*. 2000). In this study the lowest ratio (1: 4) was well within this limit. Spatial non-randomness was also calculated for tree size, using number of branches per tree as counts. All non-randomness statistics were calculated with SADIEShell v. 1.21, red-blue analysis.

Hereafter spatial matching between the spatial patterns of pupal abundance and number of branches was determined. The degree of matching between two sets of count data sharing a set of spatial references may be determined with spatial association statistics (Winder *et al*. 2001, Perry & Dixon 2002). Spatial association is based on comparing the local clustering indices (described above) of two variables measured at each shared spatially referenced point (Perry & Dixon 2002). A local association value can be calculated based on the matching between the two clustering indices at each of these points. For each set of clustering indices allowance for small-scale spatial autocorrelation has to be made by detrending the data set if necessary with the method of Dutilleul (1993). Failure to do so will inflate the significance of the association (Perry & Dixon 2002). Overall spatial association (X) is then calculated as the mean of these local association values. Significance is determined by comparing an actual overall association value to the critical values of a randomisation distribution of overall association. The randomisation distribution is determined by randomly placing the counts of both data sets and then quantifying the strength of each generated data set's association. Overall spatial association is significant at $p < 0.05$ when larger than the critical value of the 97.5^{th} percentile (see Perry and Dixon 2002). All spatial association analyses between number of pupae and the proportion of parasitised pupae were made using the Association analysis

option of SADIEShell v. 1.21 software. SADIE clustering and association statistics may be affected by the number and spatial position of patches in data sets (Xu & Madden 2003). However, the implications for multi-patch patterns, as found in this study, are limited (Xu & Madden 2003), and the issues these authors raise therefore do not affect the results reported.

Finally, the amount of variation explained by spatial and tree variables when considered collectively were determined and the most important explanatory variables were identified. To determine the amount of variability in pupal abundance explained by spatial and environmental variables (tree variables), trend surface analysis and stepwise model building approaches to analysing spatially referenced biological data were applied (Legendre & Legendre 1998). Trend surface analysis was first applied to determine the best fit of spatial variables that significantly contributed to explaining variation in pupal abundance (significant terms from the 3rd order polynomial of latitude and longitude records of each tree, see Legendre & Legendre 1998). Hereafter a stepwise model building procedure (generalised linear model, Poisson distribution, log link function) was used to determine the additional variation explained by tree variables (number of branches, tree height and tree functional group) after spatial non-independencies were accounted for. A major critique of stepwise regression is that the order in which variables are added influences which variables are included in the final model (Abraham *et al*. 1999; Randic 2001). To counter this problem best subset analyses of only tree variables were done. This allowed likelihood scores to be calculated that were used to rank tree variables in order of importance in explaining variation in pupal abundance. The tree variables were sequentially added to the spatial model according to rank until the percentage of deviance explained was not increased significantly or all tree variables were included. By subtracting the amount of variation explained by the spatial model from the total model, the pure environmental contribution of sequentially added host tree variables was determined (Legendre & Legendre 1998).

Within-tree patterns

The objective was to quantify within-tree patterns in pupal abundance, and to determine how much of the within-tree distribution in pupal abundance is explained by pupal and tree variables, including branch position, aspect, standardised cocoon height, cocoon height and distance from the tree trunk. First, the number of pupae for each branch position and aspect

category was compared within each category. This was done for each site-generation combination separately and for each *Gonometa* species in total. The significance of differences in the numbers of pupae between different branch positions or aspects was determined by Chi-square goodness of fit (Zar 1984). Expected frequencies were calculated as the product of the proportion of trees of a category with the sites' total pupal abundance. For branch position, given the physical space constraints in the number of possible pupation sites in tree shape, all positions farther than 30cm from the tree's outer edge was lumped into one category. Consequently the assumption was made that E, EM and all other categories combined would have equal frequencies of pupae by chance. Different aspects were expected to have equal frequencies of pupae, because there were no noticeable or consistent differences in number of branches between aspects. For both branch position and aspect, the influence of sex was also taken into account with Chi-square analysis of two-way contingency tables (Zar 1984). Equal numbers of female and male pupae were expected for each category of branch position and aspect.

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

Finally, potential factors responsible for within-tree distribution patterns of pupal abundance of *G. postica* and *G. rufobrunnea* were identified by determining how much of the variation in cocoon height and distance of the cocoon from the tree trunk could be explained by cocoon position attributes or tree characteristics. Functional group and height of tree, as well as branch position of the cocoon and sex were used as explanatory variables for cocoon height. Only tree functional group, tree height, and cocoon sex were used as explanatory variables for distance to trunk because branch position was logically correlated with distance to trunk. For

the analysis of both continuous dependent variables, a generalised linear model assuming a normal distribution (log link function) was used.

RESULTS

Sites differed in the absolute and mean (±SE) number of branches, as well as tree height, between sites and degree of overdispersion (Table 1), and thus offered a range of conditions to investigate pupal abundance patterns. In all but a few cases counts of the number of branches per tree were randomly distributed within sites (Table 1). Mean tree height for sites with *G. postica* or *G. rufobrunnea* was 2.40 ± 4.86 m and 2.19 ± 3.83 m, and significantly different ($t = 3.333$, $P < 0.001$). At all plots, the primary host plant accounted for 60% or more of the trees found (on average 86.3 % for *G. postica* and 82.8 % for *G. rufobrunnea*) (Table 1). Consequently, the number of non-host plant trees per plot was low. Considering only host plant trees, most trees were in the medium height class (Table 1).

Between-tree variability

Significant patterns of over and under utilization were observed, after accounting for differences in the number of trees per site for each functional group (Table 2). For *G. postica* abundance the host plant was frequently significantly over-utilised (ratio of observed to expected number of pupae greater than one) and only under-utilised (ratio of observed to expected number of pupae smaller than one) in one case. In contrast, the host plant of *G. rufobrunnea* was under-utilised, but never over utilised (Table 2). Both non-host functional groups were significantly under-utilised by *G. postica* in most cases (only two cases of over utilisation). In contrast, either non-hosts with or without thorns were always significantly over-utilised by *G. rufobrunnea* (Table 2). Thus, *G. postica* pupated mostly on its primary host plant, while *G. rufobrunnea* tended to pupate on non-host plants, both those with and without thorns. More *G. rufobrunnea* females were found on non-host plants relative to males, and both sexes were significantly larger if occurring on non-host plant species (Table 3). *G. postica* showed similar trends, but both sex ratio and cocoon size were only significantly greater in non-hosts species in one case each.

Table 1. Vegetation characteristics of sites (consisting of a 100 trees each) where *G. postica* and *G. rufobrunnea* were sampled. The frequency of trees according to functional type (primary larval host plant (H); non-larval host plant (N); non-larval host plant with thorns) and primary host plants according to tree size (small (S) < 1.75 m; medium (M) 1.75 - 3.00 m; large (L) > 3.00 m) is given. * and *** denote significant difference at P < 0.05 and 0.001, while ** indicates P > 0.90. s^2/m = variance to mean ratio; I_a = Index of overall aggregation.

	Number of branches				Tree height	Functional group			Primary host size class		
Locality	Total	mean ± SE	s^2/m	I_a	mean ± SE	H	N	NT	S	M	L
G. postica											
Vryburg1	697	7.0 ± 0.6	5.20***	1.03	3.50 ± 0.14	92	4	4	13	20	59
Vryburg2	888	8.9 ± 0.8	6.94***	1.16	2.63 ± 0.13	82	18	0	15	25	42
Hotazel	342	3.4 ± 0.3	2.04***	0.79	1.75 ± 0.12	71	8	21	15	36	20
Gabane	649	6.5 ± 0.9	13.19***	1.10	2.25 ± 0.11	84	15	1	22	43	19
Kumukwane	572	5.7 ± 0.5	3.65***	0.68*	2.25 ± 0.09	90	4	6	22	59	9
Kopong	321	3.2 ± 0.1	0.70**†	1.97***	2.00 ± 0.06	99	0	1	30	68	1
G. rufobrunnea											
Shashe1	1136	11.4 ± 1.3	7.33***	1.12	1.75 ± 0.11	60	39	1	24	21	15
Shashe2	778	7.8 ± 0.4	2.81***	1.03	2.00 ± 0.06	83	13	4	14	63	6
Shashe3	657	6.6 ± 0.3	2.44***	1.10	2.38 ± 0.07	76	21	3	11	57	8
Dumela1	1110	11.1 ± 0.5	2.48***	1.06	2.50 ± 0.08	99	1	0	5	77	17
Dumela2	1175	11.8 ± 0.7	4.83***	1.52*	2.00 ± 0.08	96	0	4	28	60	8

† Variance was significantly less than the mean. Underlined values lost significance after correction with step-up FDR at the 0.05 .α-level.

Table 2. Difference between observed and expected host plant use of trees grouped according to functional type (host plant (H); non-host plant without (N) and with thorns (NT)) for *G. postica* and *G. rufobrunnea*. *, ** and *** denote significant difference at P < 0.05, 0.01 and 0.001. '-' indicates not available; † and ††, denote expected frequencies with more than 20% < 5 and any < 1. Step-up FDR at the 0.05 level, did not change significance.

Locality	Gen	n	Ratio of observed to expected number of pupae			Chi-Square
			H	N	NT	Sum
G. postica						
Vryburg1	1	202	1.07	0.12	0.25	11.71**
	4	157	1.09	0.00	0.00	13.65**
Vryburg2	1	426	1.21	0.03	-	88.70***
	2	91	1.22	0.00	-	19.98***
	4	342	1.22	0.00	-	75.07***
Hotazel	1	288	1.34	0.31	0.12	81.30***
	2	281	1.35	0.22	0.12	83.64***
	3	83	1.37	0.00	0.11	28.56***
	4	587	1.40	0.00	0.02	231.00***
Gabane	1	505	1.03	0.91	0.00	5.98
	2	442	0.96	1.31	0.00	11.60**
	3	76	0.77	2.37	0.00	24.80***
	4	84	1.02	0.96	0.00	0.04
Kumukwane	1	252	1.04	1.19	0.26	8.92*
	2	72	0.97	0.69	1.62	†
	4	67	1.06	0.00	0.75	†
Kopong	1	92	0.98	-	3.26	††
	2	31	0.94	-	6.45	††
G. rufobrunnea						
Shashe1	1	204	0.67	1.52	0.49	34.92***
Shashe2	1	253	0.64	0.33	10.57	968.79***
Shashe3	1	214	0.59	2.51	0.78	130.69***
Dumela1	1	561	0.97	4.10	-	54.45***
	2	36	1.01	0.00	-	††
	4	65	1.01	0.00	-	††
Dumela2	1	281	0.92	-	2.85	39.94***
	4	73	0.98	-	1.37	††

Table 3. Difference between the primary host plant and non-host plants of *G. postica* (*A. erioloba* and *A. tortillis* sites) and *G. rufobrunnea* in the female to male ratio and cocoon size. Underlined values represent sex ratio observed on all plants. ** and *** denote significant difference between groups at P < 0.01 and 0.001. Different letters denote significant differences in cocoon length between groups (†, P < 0.05; ††, P < 0.001).

Species	Sex ratio		Cocoon length (mm)			
Plant site type	N	Expected	Female		Male	
Host plant type	% N	Female/Male	n	Mean ± SE	n	Mean ± SE
G. postica						
A. erioloba (3 sites)	914	1.21/1.00				
Primary	97.9	1.20/1.00 ^{ns}	466	43.77 ± 0.12 ^{a}	394	34.49 ± 0.10 ^{a}
Non-host	2.1	2.17/1.00 ^{ns}	13	44.32 ± 0.58 ^{a}	6	35.98 ± 0.96 ^{a}
A. tortillis (3 sites)	849	1.00/1.02				
Primary	89.6	1.00/1.09 ^{ns}	356	45.26 ± 0.14 ^{a}	393	35.60 ± 0.10 ^{a}
Non-host	10.4	1.75/1.00**	55	46.13 ± 0.34 ^{b†}	32	35.52 ± 0.35 ^{a}
G. rufobrunnea						
C. mopane (5 sites)	1513	1.00/1.56				
Primary	72.7	1.00/1.96***	353	40.02 ± 0.15 ^{a}	719	32.46 ± 0.09 ^{a}
Non-host	27.3	1.12/1.00***	218	41.34 ± 0.18 ^{b††}	195	34.09 ± 0.17 ^{b††}

Categorising tree height of only host plant trees, marked differences in utilisation were found between height classes, even after standardising for frequency differences (Table 4). In all cases large trees were over-utilised while small trees were consistently under-utilised. Where medium sized trees formed the largest category (Kopong), this size class was over-utilised (Table 4). Thus the largest of trees available within the site were over-utilised, independent of the actual size of the plant.

Table 4. Difference between observed and expected host plant use of primary host trees grouped according to tree size (small (S) < 1.75 m; medium (M) 1.75 - 3.00 m; large (L) > 3.00 m) for *G. postica* and *G. rufobrunnea*. ** and *** indicate significant difference between-tree size classes at P < 0.01 and 0.001 respectively. † denote expected frequencies < 1. Column-wide step-up FDR at the 0.05 level, did not change significance.

Locality	Gen	n	Ratio of observed to expected number of pupae			
			S	M	L	Chi-Square
G. postica						
Vryburg1	1	199	0.04	0.21	1.48	82.81***
	4	157	0.00	0.47	1.40	47.96***
Vryburg2	1	424	0.01	0.48	1.66	205.83***
	2	91	0.00	0.43	1.69	48.09***
	4	342	0.02	0.55	1.62	149.62***
Hotazel	1	272	0.00	0.39	2.85	369.40***
	2	269	0.00	0.68	2.32	203.20***
	3	81	0.00	0.29	3.02	131.17***
	4	583	0.01	0.75	2.19	372.89***
Gabane	1	436	0.08	0.64	2.88	474.18***
	2	355	0.06	0.65	2.88	386.55***
	3	49	0.00	0.44	3.43	86.11***
	4	71	0.00	0.91	2.37	48.88***
Kumukwane	1	236	0.02	1.20	2.12	91.17***
	2	63	0.00	1.16	2.38	28.50***
	4	64	0.00	1.26	1.72	21.86***
Kopong	1	89	0.26	1.24	6.67	†
	2	29	0.11	1.36	3.41	†
G. rufobrunnea						
Shashe1	1	82	0.00	0.45	3.37	156.13***
Shashe2	1	135	0.31	0.89	3.79	88.25***
Shashe3	1	96	0.14	1.10	1.48	13.23**
Dumela1	1	538	0.00	0.70	2.66	320.81***
	2	36	0.00	0.82	2.10	10.23**
	4	65	0.00	0.83	2.06	17.29***
Dumela2	1	249	0.10	0.93	4.67	340.22***
	4	69	0.05	1.16	3.13	45.37***

In terms of spatial non-randomness, pupal abundance of both species was normally not aggregated across trees but was rather random (Table 5). Furthermore, with two exceptions the quantified spatial pattern (*sensu* Chapter 4) was not consistent with other generations sampled at the same site. Although there was thus little evidence for overall aggregation in pupal abundance at the site scale, local clustering indices identified certain trees as contributing significantly to the formation of patches of pupal abundance (e.g. at Gabane, Fig 2b-d). Spatial association between number of pupae and number of branches was significant in almost all cases for *G. postica*, while few significant cases were found for *G. rufobrunnea* (Table 5). Local spatial association values were usually significant for only a few single trees (e.g. at Gabane, Fig 3a-d). This suggested that the selection of trees for pupation sites was not for areas of great tree size, but rather showed individual selection of large trees, irrespective of the size of neighbouring trees.

Table 5. Spatial clustering of *Gonometa postica* pupae and association between number of pupae and number of branches of a sample tree. Significant positive association (5% level, two tailed test) was determined using SADIE. I_a, v_i, v_j and X are the overall index of aggregation, mean clustering values of patches and gaps and overall association value. The inflation factor (IF) reports the degree of correction for autocorrelation between data sets. The maximum simulated value (MSV) is the greatest randomised association-value for a data set.

Locality	Gen	N	I_a	v_i	v_j	X	IF	MSV
G. postica								
Vryburg1	1	53	1.62**	1.71**	-1.67**	0.106	1.00	0.300
	4	44	1.00	0.69	-1.01	0.288**	1.00	0.272
Vryburg2	1	55	1.14	1.12	-1.20	0.519***	1.01	0.270
	2	33	0.84	0.83	-0.94	0.556***	1.06	0.273
	4	57	1.12	1.27	-1.31	0.197	1.01	0.336
Hotazel	1	42	1.06	1.17	-1.02	0.288**	1.10	0.302
	2	49	1.19	0.94	-1.17	0.334***	1.09	0.276
	3	23	1.00	0.90	-1.00	0.434***	1.17	0.290
	4	53	0.86	0.93	-0.88	0.396***	1.18	0.263

Table 5. continued

Locality	Gen	N	I_a	v_i	v_j	X	IF	MSV
Gabane	1	60	1.13	1.06	-1.07	0.678***	1.15	0.343
	2	56	0.87	0.91	-0.89	0.492***	1.14	0.292
	3	29	1.06	1.12	-1.07	0.642***	1.26	0.253
	4	38	0.76	0.92	-0.77	0.512***	1.13	0.251
Kumukwane	1	51	0.91	0.69	-0.95	0.294***	1.07	0.206
	2	36	1.03	1.10	-1.08	0.573***	1.19	0.245
	4	36	1.27	1.27	-1.32	0.367***	1.05	0.340
Kopong	1	38	1.09	1.09	-1.17	0.303***	1.02	0.271
	2	27	0.97	0.85	-0.95	0.028	1.07	0.291
G. rufobrunnea								
Shashe1	1	46	1.24	1.15	-1.52*	0.236	1.24	0.212
Shashe2	1	59	1.58**	1.36	-1.54*	0.133	1.08	0.250
Shashe3	1	60	0.84	0.97	-0.88	0.178	1.00	0.305
Dumela1	1	81	0.91	0.94	-0.89	0.194	1.04	0.263
	2	25	0.91	0.89	-0.89	0.198	1.09	0.254
	4	45	1.77**	1.74**	-1.82**	0.206*	1.07	0.267
Dumela2	1	60	0.86	0.92	-0.88	0.390**	1.13	0.440
	4	36	0.96	0.98	-0.97	0.517***	1.05	0.213

Number of pupae for each generation of a locality as specified in Table 2. Underlined values were non-significant after column wide correction with step-up FDR at the 0.05 α-level.

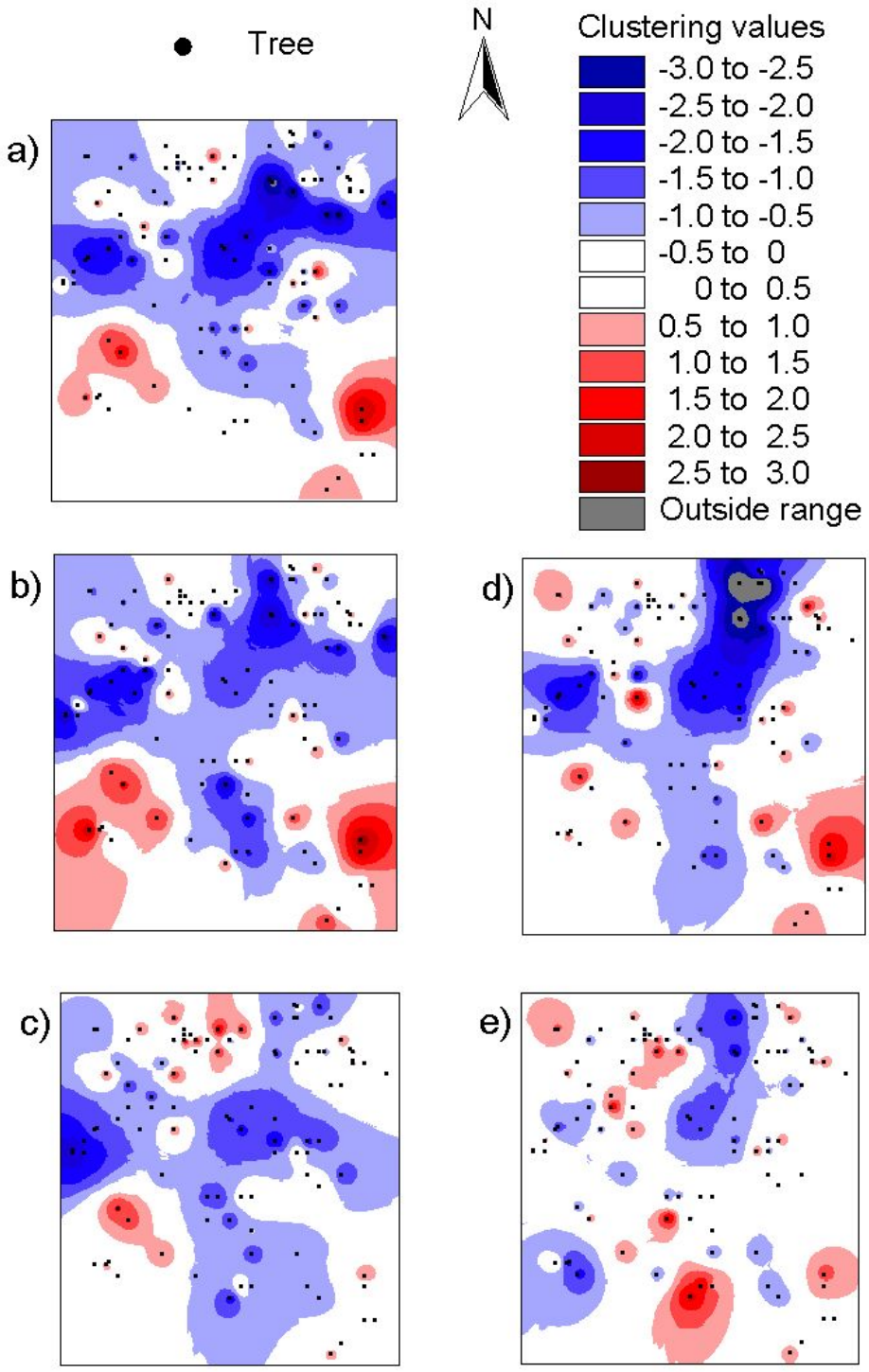

Figure 2. Least distance weighted interpolation of clustering indices of a) number of branches and the number of pupae in the b) first, c) second, d) third and e) fourth generation at Gabane. Areas coded > 1.5 denote areas of significant positive, and areas < -1.5 areas of significant negative, clustering. See Table 5 for specific case statistics.

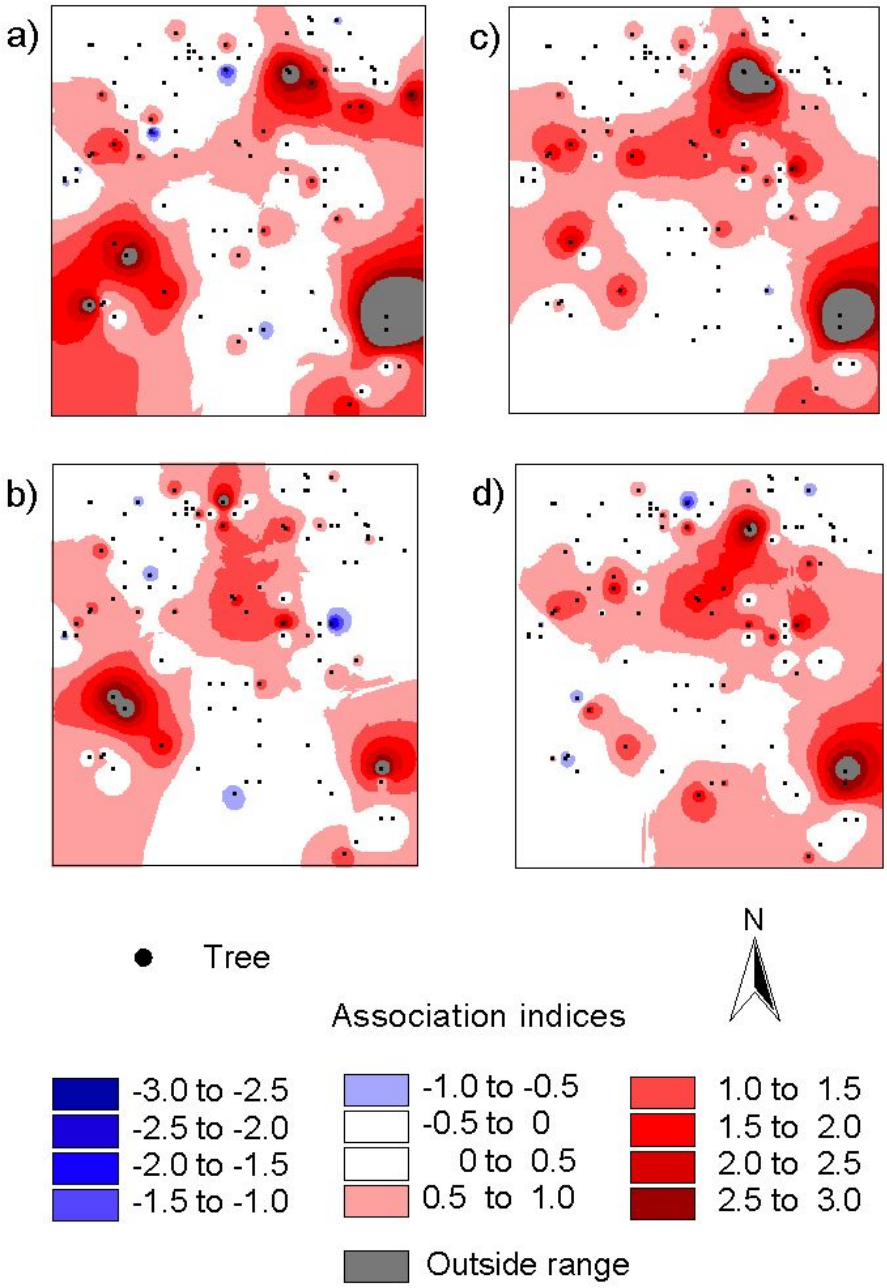

Figure 3. Least distance weighted interpolation of local spatial association indices between number of pupae of the a) first, b) second, c) third and d) fourth generation and number of branches at Gabane. Areas coded as > 0.5 are significantly positively associated at the between-patch scale, while those < -0.5 are significantly negatively associated. See Table 5 for specific case statistics.

The total percentage deviance in pupal abundance explained for *G. postica* and *G. rufobrunnea* ranged between 15-69% and 19-75 % (Table 6). For both species the spatial component contributed little to explaining pupal abundance in most cases, explaining more than 20% of the deviance in only two out of 26 cases. In contrast, generally more than 30% of the deviance was explained by the pure environmental component (spatial non-independence taken into account) (Table 6). For *G. postica* in particular, number of branches added the most to the percentage deviance explained, followed by tree height and tree functional group. Thus, number of branches was the most important variable explaining the pupal abundance of *G. postica* between trees. For *G. rufobrunnea* this pattern was not as general, with functional group and tree height adding greater percentages of explained deviance in several data sets. For both species, number of branches and/or tree height was positively related to pupal abundance in all cases (Table 6). There was, however, a major difference between the species in the relationship between the functional group and pupal abundance. For *G. postica*, pupal abundance was significantly higher on its primary host plant than other groups in both *Acacia* veld types, whereas *G. rufobrunnea* pupal abundance was significantly lower on its host plant (Table 6). In some cases non-host plants and non-host plants with thorns either had higher or lower numbers of *G. postica* pupae than expected. Even though functional group added significantly to the percentage of explained deviance in 10 cases for *G. postica*, in half of these the coefficients were non-significant. In contrast, in four out of five cases functional group coefficients were significant for *G. rufobrunnea* (Table 6). Tree size seems thus to largely explain between-tree variation in pupal abundance for *G. postica*, while functional group was also important for *G. rufobrunnea*.

Table 6. Forward stepwise regression of pupal abundance used to determine the percentage of deviance explained (DE) by spatial and environmental (sample tree) variables. The total %DE by the spatial component (pure spatial and spatially structured environmental; see Legendre & Legendre 1998), as well as the increase %DE by sequentially added significant tree variables (additively the pure environmental component) is shown. The order of adding significant tree variables and their respective coefficients is also shown. BR = number of branches; HGT = tree height; FGRP = functional group (H = host, N = non host, T = non host with thorns).

Locality	Gen	Residual deviance	df	Scaled dev/df	Percentage of explained deviance					Entry sequence of significant biological terms	Coefficients
					Total	Spatial	BR	HGT	FGRP		
G. postica											
Vryburg1	1	226.37	96	0.964	46.4	23.2	18.1	5.1	ns	BR; HGT	+; +
	4	212.38	95	0.833	43.1	9.3	33.8	ns	ns	BR	+
Vryburg2	1	341.24	95	0.909	59.5	8.9	44.0	4.6	2.0	BR; HGT; FGRP	+; +; ns
	2	112.34	96	0.880	56.7	2.5	52.2	2.0	ns	BR; HGT	+; +
	4	375.15	96	0.725	46.1	3.0	39.2	3.9	ns	BR; HGT	+; +
Hotazel	1	272.26	92	0.588	68.0	5.3	49.6	11.7	1.4	BR; HGT; FGRP	+; +; ns
	2	269.66	93	0.829	57.3	7.1	36.7	12.2	1.2	BR; HGT; FGRP	+; +; ns
	3	128.23	95	0.826	58.7	11.1	36.4	9.7	1.5	BR; HGT; FGRP	+; +; ns
	4	446.50	94	0.874	68.6	4.6	49.3	10.5	4.2	BR; HGT; FGRP	+; +; +(H)
Gabane	1	556.95	94	0.594	43.6	5.5	20.4	11.1	6.5	BR; HGT; FGRP	ns; +; +(H)
	2	588.91	92	0.773	38.9	4.3	21.9	8.5	4.2	BR; HGT; FGRP	ns; +; ns
	3	113.16	96	0.736	56.7	5.2	43.7	7.8	ns	BR; HGT	+; +
	4	132.60	95	0.867	30.9	2.1	ns	22.7	6.0	HGT; FGRP	+; -(N)

Table 6. continued

Locality	Gen	Residual deviance	df	Scaled dev/df	Percentage of explained deviance					Entry sequence of significant biological terms	Coefficients
					Total	Spatial	BR	HGT	FGRP		
Kumukwane	1	265.49	93	0.795	48.2	4.6	25.7	ns	17.8	BR; FGRP	+; +(N)-(T)
	2	91.74	94	0.976	49.7	6.6	30.9	ns	12.2	BR; FGRP	+; +(N)-(T)
	4	96.36	95	0.867	38.2	6.3	18.8	ns	13.1	BR; FGRP	+; +(T)
Kopong	1	158.34	97	0.773	27.8	3.9	ns	23.9	ns	HGT	+
	2	70.96	98	0.861	15.2	ns	ns	15.2	ns	HGT	+
G. rufobrunnea											
Shashe1	1	239.59	93	0.905	52.3	5.9	16.3	1.6	28.4	BR; HGT; FGRP	ns; +; -(H)+(N)
Shashe2	1	184.55	94	1.001	74.9	31.0	2.8	11.9	29.2	FGRP; HGT; BR	-(H); +; +
Shashe3	1	385.74	93	0.752	24.0	3.9	16.3	2.2	1.5	BR; HGT; FGRP	+; ns; ns
Dumela1	1	321.94	95	1.036	51.7	9.1	ns	38.7	3.9	HGT; FGRP	+; -(H)
	2	91.14	98	0.930	19.2	ns	19.2	ns	ns	BR	+
	4	79.98	96	1.000	31.5	11.5	ns	20.0	ns	HGT	+
Dumela2	1	210.75	95	1.006	61.9	2.2	40.8	11.7	7.2	BR; HGT; FGRP	+; +; -(H)
	4	98.64	96	0.946	44.4	5.9	32.4	6.1	ns	BR; HGT	+; +

Number of pupae for each generation of a locality is similar as specified in Table 2.

Within-tree variability

For each site-generation combination, the difference between expected and observed numbers of pupae per branch position was significant in most cases, with the E and/or EM categories usually being over-utilised by pupae, while the grouped remaining branch positions were under-utilised (Table 7). *G. postica* had 5 exceptions (28%) which showed the opposite pattern. *G. rufobrunnea*, however, showed no exceptions and, in general, differences between branch positions were stronger (Table 7). There were also significant differences between males and females in the frequencies of branch position occupied. For both species, males usually significantly over-utilised the edges of terminal branches (E), and in a few cases near edges of branches (EM), while females mostly over-utilised the grouped remaining branch positions (Table 7). Sex differences were significant for *G. postica* in 14 cases (61%) and for *G. rufobrunnea* in 3 cases (38%) (Table 7). The same utilisation patterns for *G. postica* and *G. rufobrunnea* were evident when the total number of male and female cocoons per branch position was compared across the entire study. The percentage female cocoons in the 'rest' category was greater than that for males for both *G. postica* (Figure 4a & b) and *G. rufobrunnea* (Figure 5a & b).

Table 7. Observed versus expected within-host plant use in branch position for each *Gonometa* species generation at a site (sample size as in Table 2), quantified for all pupae within a site, and between males and females separately. E, EM and rest (ES, ME, M, MS), and S denote edge, near edge, (stem edge, edge of branch, middle of branch, start of branch) and main stem respectively). 'no diff' indicates non-significant sex differences; *, ** and *** denote $P < 0.05$, 0.01 and 0.001 level. Underlined values were non-significant after step-up FDR at the 0.05 α-level.

Locality	Gen	Ratio of observed to expected number of pupae			Chi-Square	Dominant sex			Chi-Square
		E	EM	Rest	Sum	E	EM	Rest	Sum
G. postica									
Vryburg1	1	1.77	0.74	0.49	61.6***	M	no diff	F	6.58*
	4	0.88	1.38	0.75	11.6**	ns	ns	ns	2.7
Vryburg2	1	2.00	0.77	0.23	233.3***	M	F	F	13.90***
	2	1.25	1.15	0.59	7.7*	M	no diff	F	9.50**
	4	1.10	1.19	0.71	14.9***	M	F	F	19.10***
Hotazel	1	1.87	0.89	0.24	127.7***	ns	ns	ns	4.84
	2	1.38	1.28	0.34	61.3***	M	no diff	F	8.45*
	3	0.54	1.73	0.72	22.9***	ns	ns	ns	2.18
	4	1.20	1.44	0.36	125.0***	M	F	F	28.35***
Gabane	1	1.79	0.81	0.40	171.4***	M	F	F	22.26***
	2	1.22	1.15	0.62	31.5***	M	M	F	13.99***
	3	0.75	0.83	1.42	6.8*	M	M	F	5.58
	4	1.08	1.01	0.90	0.5	ns	ns	ns	4.09
Kumukwane	1	1.13	1.15	0.72	10.5**	M	no diff	F	14.74***
	2	0.63	0.92	1.46	8.6*	ns	ns	ns	4.8
	4	0.54	1.03	1.43	9.0*	M	M	F	10.87**
Kopong	1	0.95	0.59	1.47	12.0**	ns	ns	ns	3.14
	2	0.39	1.16	1.45	6.3*	ns	ns	ns	1.9

Table 7. continued

Locality	Gen	Ratio of observed to expected number of pupae			Chi-Square	Dominant sex			Chi-Square
		E	EM	Rest	Sum			E	EM
G. rufobrunnea									
Shashe1	1	1.64	0.76	0.60	42.3***	M	F	F	12.57**
Shashe2	1	2.03	0.66	0.31	138.9***	ns	ns	ns	1.32
Shashe3	1	2.03	0.73	0.24	122.7***	M	F	F	8.14*
Dumela1	1	1.36	1.37	0.27	150.6***	ns	ns	ns	3.84
	2	1.17	0.92	0.92	0.5	ns	ns	ns	0.9
	4	1.43	0.83	0.74	6.1*	ns	ns	ns	1.79
Dumela2	1	1.88	0.65	0.47	110.1***	M	M	F	32.05***
	4	1.19	1.19	0.62	5.4	ns	ns	ns	1.81

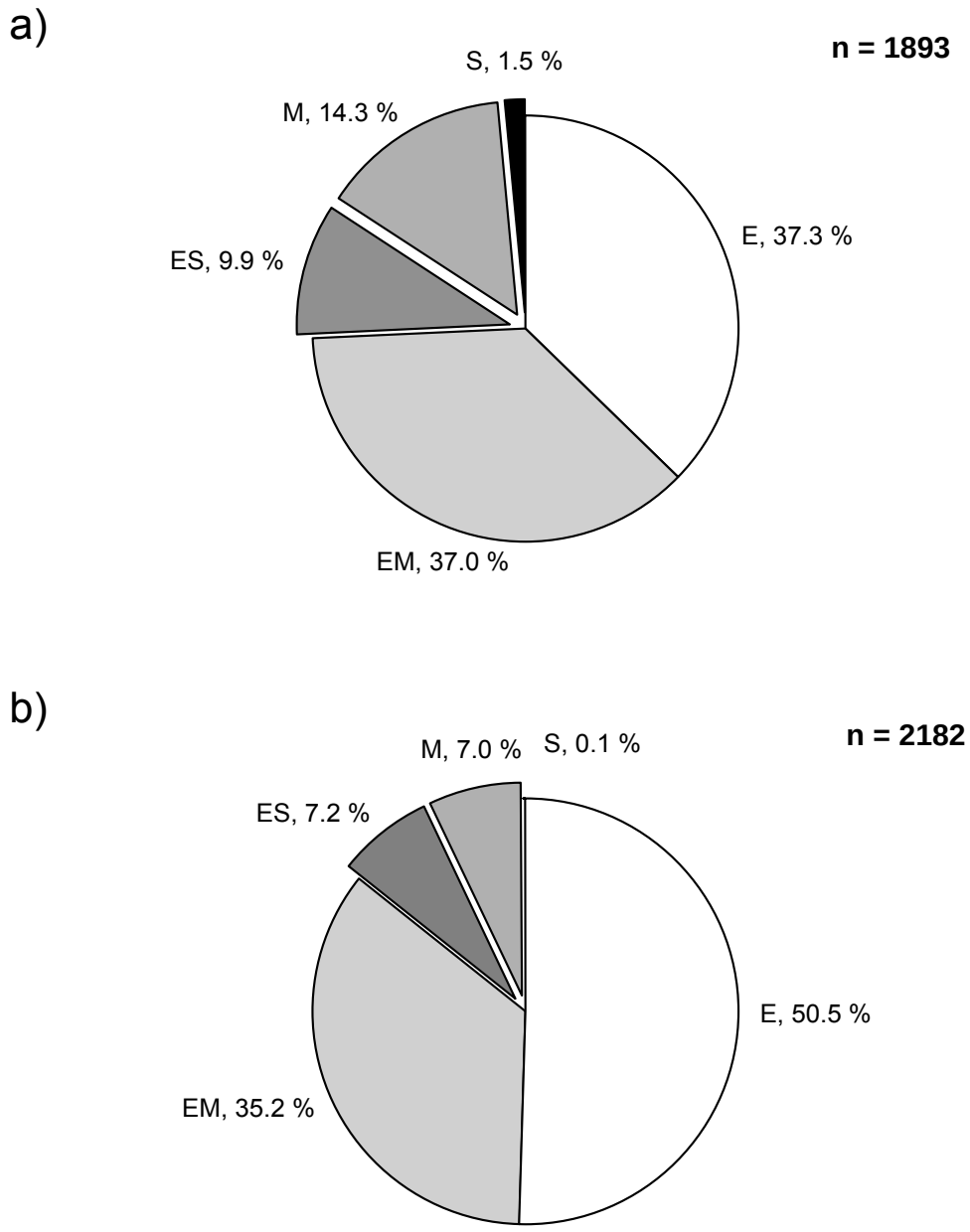

Figure 4. Percentage a) female and b) male cocoons for each branch position for *G. postica* at all sites. E, EM, ES, M (including ME and MS), and S denote edge, near edge, stem edge, middle of branch and main stem respectively.

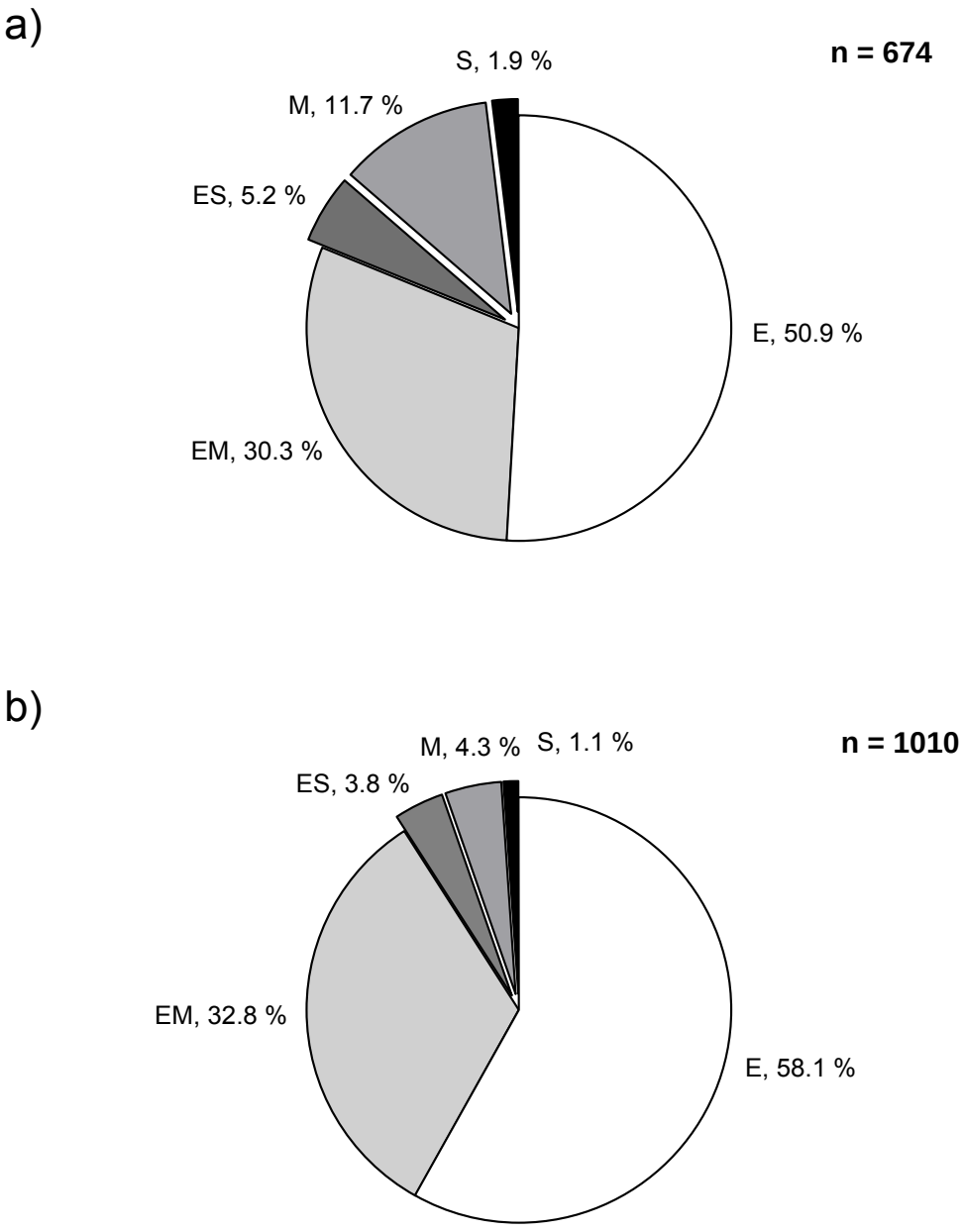

Figure 5. Percentage a) female and b) male cocoons for each branch position for *G. rufobrunnea* at all sites. Notation same as for Figure 4.

The difference between expected and observed numbers of pupae between aspects was significant in most cases for *G. postica* (81%), but not *G. rufobrunnea* (25%) (Table 8). Where such differences were significant, N and/or E aspects were over-utilised, while S and/or W aspects were under-utilised (Table 8). The same pattern was evident for *G. postica* and *G. rufobrunnea* when the total number of male and female cocoons per aspect was considered across the entire study (Figure 6a & b). There were, however, no significant differences in the frequencies of males and females with respect to aspect (Table 8).

Table 8. Observed versus expected within-host plant use according to aspect (N, E, S and W) for all *G. postica* and *G. rufobrunnea* pupae as well as the influence of sex. *, ** and *** denote $p < 0.05$, 0.01 and 0.001 level. '-', not available; † analysis with expected values < 1. Step-up FDR at the 0.05 α-level, did not change significance.

Locality	Gen	n	Ratio of observed to expected number of pupae				Chi-Square Sum statistics	
			N	E	S	W	All pupae	Females vs. males
G. postica								
Vryburg1	1	-					-	-
	4	155	1.47	1.14	0.88	0.52	19.0***	6.84
Vryburg2	1	-					-	-
	2	88	1.23	1.86	0.73	0.18	33.9***	0.02
	4	341	1.09	1.48	0.87	0.56	37.9***	2.05
Hotazel	1	69	0.87	1.74	0.99	0.41	15.8**	1.32
	2	266	1.13	1.25	1.01	0.62	15.0**	5.32
	3	83	1.35	1.01	0.72	0.92	4.3	3.73
	4	580	1.23	1.11	0.80	0.86	18.6***	5.39
Gabane	1	414	1.10	1.49	0.64	0.77	44.6***	0.18
	2	441	1.00	1.45	0.71	0.84	34.6***	6.18
	3	76	1.74	1.47	0.47	0.32	28.7***	1.44
	4	83	1.35	0.96	1.16	0.53	7.7	2.76
Kumukwane	1	159	1.21	1.13	1.18	0.48	14.6**	2.06
	2	70	0.74	1.49	0.57	1.20	9.2*	4.81
	4	65	1.54	1.54	0.49	0.43	18.9***	1.93
Kopong	1	55	0.95	1.82	0.51	0.73	13.6**	0.50
	2	31	0.90	1.29	0.90	0.90	0.9	1.94

Table 8. continued

Locality	Gen	n	Ratio of observed to expected number of pupae				Chi-Square Sum statistics	
			N	E	S	W	All pupae	Females vs. males
G. rufobrunnea								
Shashe1	1	78	1.59	0.87	0.87	0.67	9.6*	6.01
Shashe2	1	30	0.93	1.07	1.20	0.80	0.7	3.82
Shashe3	1	78	1.23	1.18	0.72	0.87	3.5	3.49
Dumela1	1	33	1.21	0.85	0.97	0.97	0.6	3.64
	2	36	1.00	1.00	0.89	1.11	0.2	1.82
	4	65	1.42	1.05	0.80	0.74	4.6	0.16
Dumela2	1	27	1.19	1.19	1.19	0.44	2.8	1.50
	4	72	1.28	1.72	0.67	0.33	20.8***	14.03**†

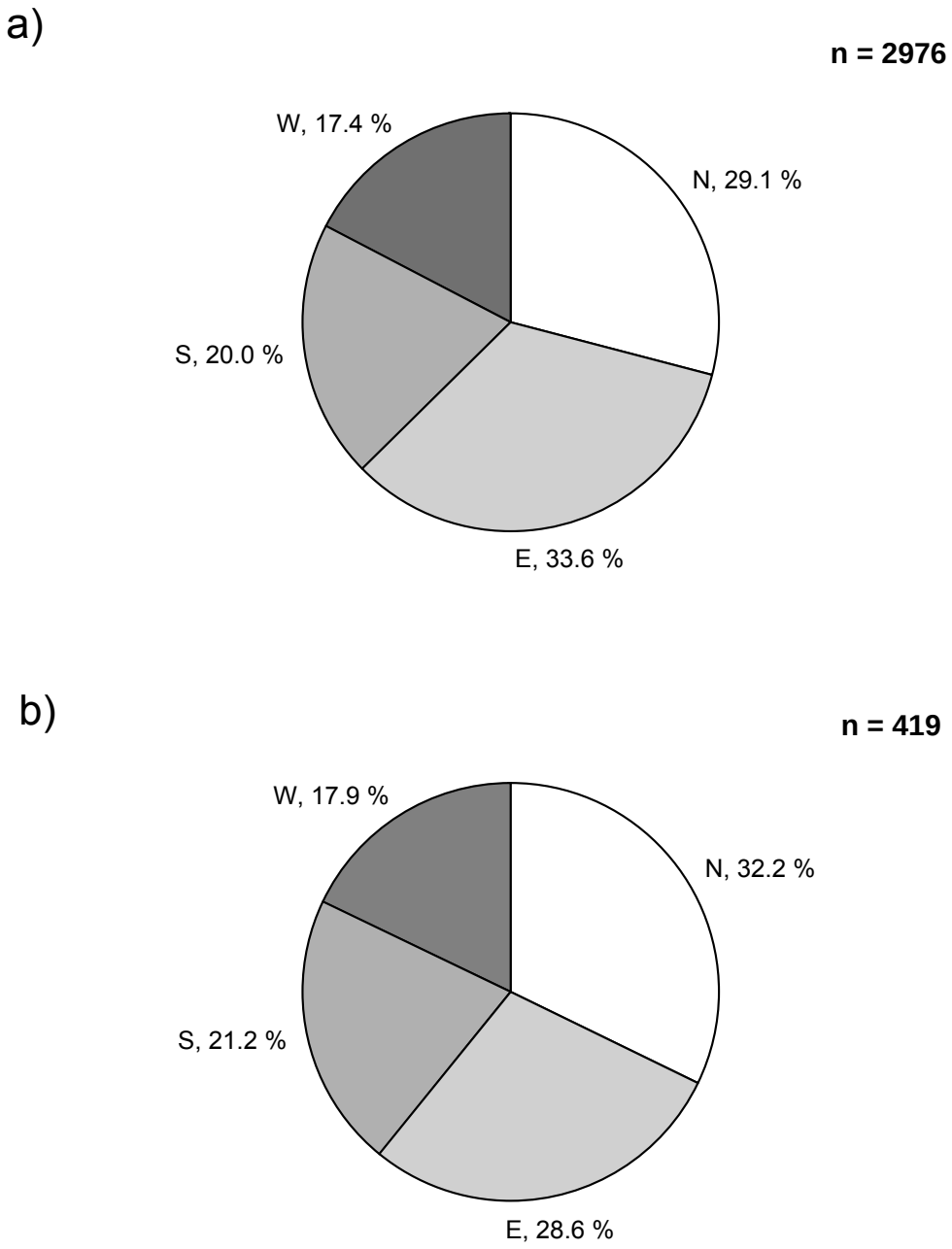

Figure 6. Percentage of cocoons found in each aspect for a) *G. postica* and b) *G. rufobrunnea* at all sites.

The distribution of standardised cocoon height (standardised for tree size) showed marked between-species differences, as well as within-species differences in *G. postica*. *G. postica* at sites with *Acacia erioloba* had a normal cocoon height distribution, with most cocoons just above mid-tree height (Fig 7a). At sites with *Acacia tortillis* cocoon height had a left skewed distribution, but in this case most cocoons were found just below mid-tree height (Fig 7b). In contrast, *G. rufobrunnea* had a right skewed distribution with most individuals at the two-thirds tree height mark (Fig 7c). However, in all cases the height classes at which most pupae was found, were below the height where the greatest available canopy volume of the primary host plant was expected to occur (Fig. 7a-c).

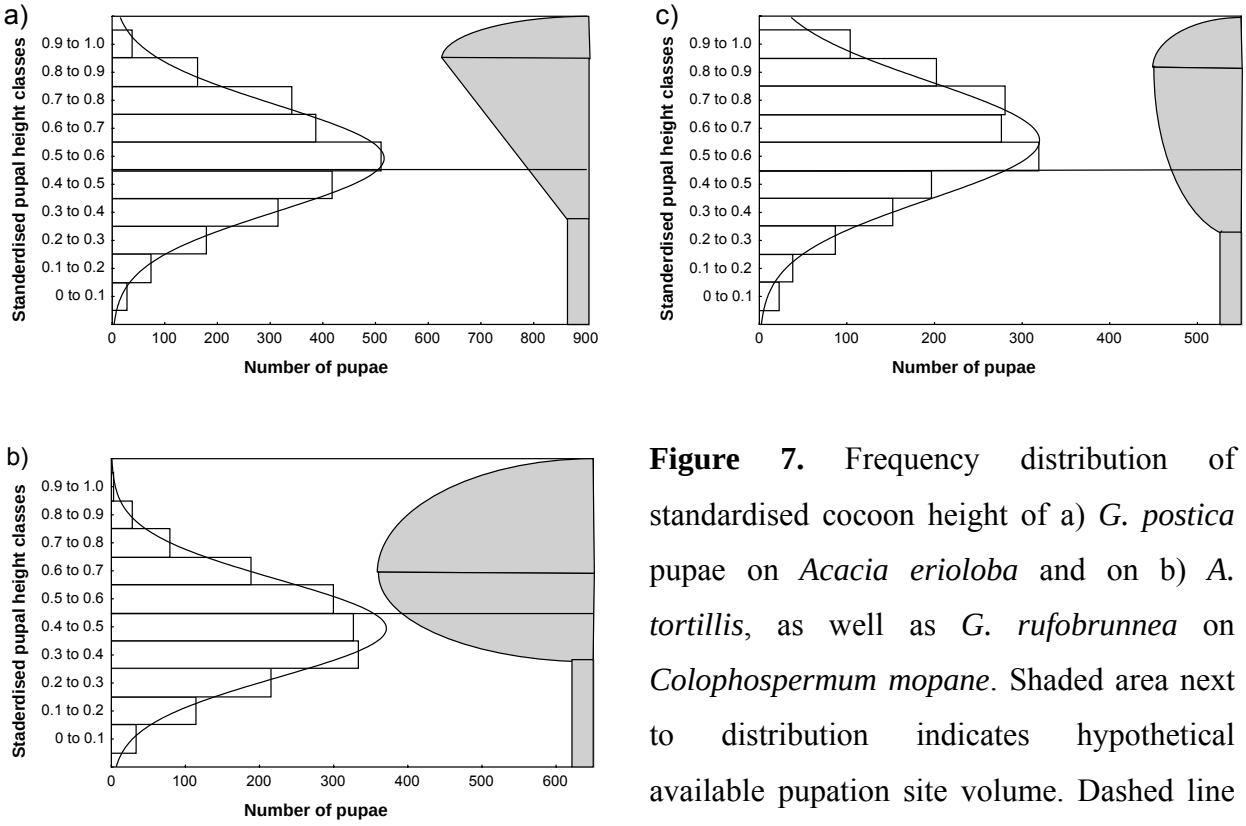

Figure 7. Frequency distribution of standardised cocoon height of a) *G. postica* pupae on *Acacia erioloba* and on b) *A. tortillis*, as well as *G. rufobrunnea* on *Colophospermum mopane*. Shaded area next to distribution indicates hypothetical available pupation site volume. Dashed line indicates mid tree height.

In all cases the relationship between cocoon height and tree height was significantly positive (Table 9). Cocoon height revealed that in all cases branch position, functional group and tree height, but not sex, contributed significantly to the percentage of deviance explained for *G. postica* (on both host plants) and *G. rufobrunnea* (Table 9). Cocoons with branch position category E, EM or ME consistently pupated higher, while cocoons found on S were significantly lower. With respect to functional group, in all three regressions the cocoons on primary host trees were significantly higher than they were on non-hosts (Table 9). For cocoons of *G. postica* on *A. tortillis* and *G. rufobrunnea*, cocoons on undefended non-host plants were significantly lower. This indicates that even when tree height is accounted for, tree functional group may still influence pupation height.

For both *Gonometa* species distance of a cocoon to the tree trunk always had a significant positive relationship with tree height (Table 9). *G. postica* cocoons were significantly further from the tree trunk if on one of its primary host plants, while functional group did not explain distance of *G. rufobrunnea* cocoons from the trunk significantly, although tending to be closer if on a non-host without thorns. *G. postica* on *A. erioloba* and *G. rufobrunnea* were significantly closer to the trunk if cocoons were female, while for *G. postica* on *A. tortillis*, sex had no significant effect (Table 9).

Table 9. Generalised linear regression of the height and distance from the tree trunk where pupation occurred for *G. postica* (for both host plants) and *G. rufobrunnea*. The fit and percentage deviance explained (DE) by the total model as well as the significance of independent variables is shown. Branch position: E, EM, ES, ME, M, MS, and S; denote edge, near edge, stem edge, edge of branch, middle of branch, start of branch, and main stem respectively. Sex: female (F) and male (M); Functional group: primary host (*A.e.* = *A. erioloba*; *A.t.* = *A. tortillis*; *C.m.* = *C. mopane*), non-host no thorns (nhn) and non-host with thorns (nht).

Dependent variable	df	Scaled dev/df	Total % DE	Independent variables	Slope ± SE	Log likelihood	χ^2	P
G. postica* on *A. erioloba								
Cocoon height	2444	1.004	26. 5	Branch position	+ (E, EM, ME, M) – (S)	-13931	232.8	< 0.001
				Functional group	+ (*A.e.*)	-13826	24.04	< 0.001
				Sex	ns	-13815	1.08	0.300
				Tree height	+	-14026	422.71	< 0.001
Distance to trunk	2450	1.002	9.9	Functional group	+(*A.e.*)	-7843.3	37.70	< 0.001
				Sex	– (F)	-7843.6	38.26	< 0.001
				Tree height	+	-7896.4	143.93	< 0.001
G. postica* on *A. tortillis								
Cocoon height	1609	1.007	45.5	Branch position	+ (E, EM, ME)	-8826.3	103.29	< 0.001
				Functional group	+ (*A.t.*) – (nhn)	-8821.1	92.96	< 0.001
				Sex	ns	-8775.1	0.84	0.657
				Tree height	+	-9131.6	713.78	< 0.001
Distance to trunk	1613	1.004	34. 0	Functional group	+ (*A.t.*)	-5770.1	218.36	< 0.001
				Sex	ns	-5674.6	27.32	< 0.001
				Tree height	+	-5974.3	626.80	< 0.001

Table 9. continued

Dependent variable	df	Scaled dev/df	Total % DE	Independent variables	Slope ± SE	Log likelihood	χ^2	P
G. rufobrunnea								
Cocoon height	1673	1.007	52.6	Branch position	+ (E, EM, ME) – (S)	-9349.2	442.49	< 0.001
				Functional group	+ (*C.m.*) – (nhn)	-9181.4	106.98	< 0.001
				Sex	ns	-9128.2	0.65	0.420
				Tree height	+	-9442.7	629.55	< 0.001
Distance to trunk	1682	1.003	12.3	Functional group	– (nhn)	-4216.0	4.48	0.106
				Sex	– (F)	-4218.6	9.61	0.002
				Tree height	+	-4299.7	171.85	< 0.001

DISCUSSION

Between-tree patterns in the pupal abundance of *Gonometa* species were random in terms of absolute spatial position, but markedly non-random in terms of tree characteristics. Most *G. postica* pupae were found on large primary host trees, while *G. rufobrunnea* used large primary host trees as well as non-host trees irrespective of their size. Indeed, very few *G. postica* pupae were found on non-host plants, while almost a third of all *G. rufobrunnea* pupae were found on non-hosts. Also, tree size explained more of the variation in *G. postica* pupal abundance, and had a stronger positive spatial relationship with abundance (i.e. areas with large numbers of branches had high pupal abundance) than *G. rufobrunnea*. Nonetheless, for both species pupal abundance patterns were not explained by the spatial position of trees, but rather specific properties of the tree (i.e. size and functional group). This suggests that trees used as pupation sites are individually selected irrespective of their position relative to other trees (see also Rodeghiero & Battisti 2000). The strong trend in *G. rufobrunnea* towards more females and larger pupae in general on non-host plants is a curious result. It is possible that large larvae are more likely to disperse, or have greater dispersal distances, from the host plant before pupation (see also Gutierrez & Menendez 1997; Etienne & Olff 2004; Ness *et al*. 2004). As a result the pupae found on non-host plants will be larger and have a greater probability of being female. Therefore, at the between-plant scale the two *Gonometa* species differed only in the extent to which non-larval-host plants were used for pupation, as well as the importance of tree size in explaining pupal abundance.

Although several possible mechanisms can lead to more pupae on taller trees, as well as those with more branches, there are two reasons that suggest that oviposition behaviour of *Gonometa* species are responsible for this pattern. First, host plant apparency is known to affect the oviposition patterns of Lepidoptera (Courtney 1982). For example, the oviposition pattern of *Imbrasia belina* (Saturniidae), an ecologically similar species to *G. rufobrunnea*, is related to the apparency of the host plant quantified as tree size and the proximity of neighbouring host plants (Wiggins 1997). During oviposition site selection, location of host plants is partly visual in most butterflies, and if the host plant is conspicuous oviposition is usually limited to host plants (Wiklund 1984). The primary hosts of both *Gonometa* species were highly apparent, generally the largest trees at the site, and most abundant. Large trees

may thus be more apparent to ovipositing females and consequently receive more egg batches (Courtney 1982; Batzer *et al*. 1995; Wiggins 1997). Second, larvae may not survive if the eggs they emerged from are located on small hosts or non-host plants. The first instar larvae of Lepidoptera that often do not oviposit on host plants (generally species that overwinter as eggs or small larvae) use silk threads to 'select' host plants (Bernays & Chapman 1994). Consequently larvae will only have a high probability of survival if a suitable host plant is in close proximity (Leyva *et al*. 2003). *Gonometa postica* early instar larvae have been observed to drop with a silk thread from defoliated branches of potted hosts in a green house. This suggests that if females oviposit on non-hosts, first instars may only be able to disperse to suitable hosts directly next to the host plant. Based on the large distances between the primary host plants of *Gonometa* species, larvae are unlikely to successfully disperse to suitable hosts if oviposited on non-hosts. Furthermore, oviposition on the host plant is typical of southern African Lasiocampidae (Scholtz & Holm 1985).

Pupation patterns of *Gonometa* species are less likely the result of secondary host plant selection by larvae that are still feeding. Although Lepidoptera larvae are more likely to move to an object the bigger it appears to them visually (Bernays & Chapman 1994), dispersal success to alternative hosts is usually low (Floater 2001). The low number of pupae relative to available foliage on host plants suggests that defoliation by *Gonometa* is rare and remaining on the host plant will be less costly than moving to a secondary host (Batzer *et al*. 1995). There is thus little evidence to suggest that density dependent dispersal of larvae to secondary host plants occurs (see Rhainds *et al*. 2002), and oviposition site selection by adult females is therefore thought to be the primary determinant of pupal distributions in *Gonometa* species.

However, the frequent use of non-host plants by *G. rufobrunnea* suggests that a secondary mechanism is required to explain why final instar larvae actively seek out non-host plants. The use of non-host plants by *G. rufobrunnea* pupae, which are very vulnerable to bird predation (Chapter 1), may serve as a form of enemy free space. Predators, especially vertebrates, using visual cues may not only select high-density prey patches, but also form search images of prey against certain backgrounds (Guilford 1992). Using non-host plants may thus be a method of escaping bird predation, by disrupting the search image of the predator (Brower 1958). The distribution of apparent *G. postica* pupae, which appear to be virtually immune to predation (Chapter 1), were seldom found on non-host plants, supporting this

hypothesis. Evidence for selection of crypsis in swallowtail butterfly pupae, which experience lower predation levels when successfully matching their background when pupating high up on their host plant, provides further support (Hazel *et al*. 1998). Furthermore, when host plants have high larval densities, pupating on the same host plant will decrease the effectiveness of cocoon crypsis as an anti-predator defence (Brower 1958). Thus non-host trees may be used especially at medium to high site pupal abundances (i.e. as found for first generation sites). Thus, *G. rufobrunnea* between-tree pupal abundance is not only dependent on oviposition patterns, but may also be a consequence of the selection of enemy free space for pupation by final instars.

At a within-plant scale the pupae of *G. postica* and *G. rufobrunnea* showed similar patterns of branch position and aspect (to a lesser extent) use, as well as cocoon height (non-standardised) and distance from trunk patterns. Most pupae were found on the edge or near the edge of branches, on the eastern and northern sectors of trees, and occurred higher and further away from the stem if on larger trees. The low number of pupae for which aspect data was available for *G. rufobrunnea* in the first generation, may explain the absence of significant differences between aspects, compared with the significant differences commonly found for *G. postica*. Nonetheless, for both *Gonometa* species across study within-tree aspect use was similar. Thus, similarities in within-tree use for *Gonometa* species suggest that these patterns have a common explanation. Although there are more pupation sites on terminal branches, within-tree pupation patterns were not simply a matter of resource size, as more exposed branch positions were used than expected. Differences in solar radiation possibly explain these patterns. The shade provided by trees reduces the solar radiation and long wave radiation from the ground (Kotzen 2003). Branch positions near the trunk will receive the least solar radiation because of maximum shading by tree branches, while terminal branch positions will receive minimum shading (Kotzen 2003). Within their host plants caterpillars may expose themselves to maximum radiation at low temperatures, and move to more shaded areas as the temperatures increases (Casey 1993). Therefore, it is possible that the cooler microclimate of more heavily shaded branch positions near the tree trunk are less favourable for the development of a pupa into an adult, compared to those on the edge of branches that are most likely to receive oblique, early morning radiation (see Bryant *et al*. 2002). Differential aspect use within trees may also be explained by differences in thermal microclimate properties (Stork *et al*. 2001). In the

Southern Hemisphere, northern and eastern aspects of trees will receive more solar radiation in the morning than southern and western aspects, while the reverse is the case in the afternoon (see Kotzen 2003). Therefore, pupae positioned to receive maximum morning radiation may warm up more quickly, while decreased exposure to afternoon radiation could prevent pupae experiencing maximum temperatures potentially detrimental to their survival. Because pupal metabolic rate is positively related to temperature, avoidance of high midday temperatures may also be a strategy to conserve energy usage in overwintering pupae (e.g. Bennett *et al.* 2003; Irwin & Lee 2003).

These explanations for these within-tree pupation tree patterns were further supported by standardised cocoon height patterns. Differences between *Gonometa* species in cocoon height standardised for tree height corresponded with differences in the shape of the primary host plants. The difference between *G. postica* populations on different host plants may also be explained by tree shape. Large *Acacia tortillis* trees are typically umbrella shaped and *A. erioloba* trees have a wide spreading crown, while *C. mopane* typically occurs as upright shrubs or trees, widening only close to its crown (Palgrave 1977). Although tree shape is a measure of the three-dimensional space available for pupation, the maximum frequency height classes of *G. postica* and *G. rufobrunnea* corresponded to regions below the maximum canopy volume of their host species. Thus pupation site availability itself was not a major determinant of the relative height of pupae within trees. Alternatively, using the shaded pupation sites just below the maximum canopy volume may provide a more buffered and cooler microclimate, particularly at midday (see Kotzen 2003). Therefore, at the within-tree scale branch position, aspect and tree shape may influence pupation site choice by providing microclimate conditions for which pupating *Gonometa* larvae have a particular preference, and which optimises pupal survival, energy usage, or adult development rate.

However, sex differences in pupation site use suggest alternative explanations for within-tree pupation patterns. Branch position categories and distance to trunk were significantly different between males and females. In contrast, aspect and cocoon height did not show significant sex differences. The causes of these sex differences are unknown, but appear to be less important than the broad trend of more pupae on the edge of branches. It has been observed (pers. obs.) that males usually emerge at midday while females emerge at dusk. Males are stronger fliers (Chapter 1) and may be less vulnerable to predators than females that

fly mostly at night. Males typically start wing fluttering upon emergence compared to females that remain inactive for extended periods after emergence. Therefore, using terminal branch edges is possibly advantageous for the rapid, post-eclosion dispersal in males, while more sheltered branch positions allow cover until nightfall in females. Nonetheless, the stronger patterns in within-tree pupation site use suggest that microclimate differences with respect to received solar radiation is the major factor explaining within-tree pupal distribution.

This study highlights the value of documenting between tree and within tree patterns as a first step to explaining pupation site selection, as well as identifying possible evolutionarily selective factors in the species, and generating testable hypotheses from these. Subsequent experiments on female oviposition choice, larval dispersal, and pupal survival under different levels of natural enemy attack at the between-tree scale, and microclimatic conditions at the within-tree scale, may now be conducted to test the proposed hypotheses. The marked differences between *Gonometa* species at a between-tree scale, but strong similarities at a within-tree scale, emphasises the fact that factors influencing herbivorous insect distributions are scale dependent (see also Hamid *et al*. 1999). Therefore, studying the distribution of herbivorous insects at more than one scale provides more information when comparing species, and reduces the risk of missing possible mechanistic explanations for the patterns observed (e.g. McGeoch & Price 2004).

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GENERAL CONCLUSION

"One of the most ubiquitous phenomena of all natural populations is their variability in numbers in space and time. One of the major challenges in population and community ecology is to explain and understand this variety and to find underlying rules...."

Lundberg *et al*. 2000

Understanding the cause of spatial and temporal variability in abundance of Southern Africa's wild silk moths is crucial for their sustainable utilisation. However, insect herbivore population dynamics are the result of complex interaction between bottom-up and top-down effects as well as stochastic factors such as weather (Andrewartha & Birch 1954; Berryman 1996; Lundberg *et al*. 2000). Using current theory about herbivorous insects and how they respond to plant quality, natural enemies and climate as a guide (Strong *et al*. 1974; Bernays & Chapman 1984; Price *et al*. 1990; Dyer & Gentry 1999; Brewer & Gaston 2002; Ribeiro *et al*. 2003), population data for *G. postica* and *G. rufobrunnea* were collected to identify which of these factors were important for their population dynamics. This study is the first to quantify the spatial and temporal variability in pupal abundance, as well as the percentage mortality caused by natural enemies for both *Gonometa* species. Some research has previously been done on the biology and types of natural enemies of *G. rufobrunnea* (Hartland-Rowe 1992). However, quantifying differences and similarities between *G. postica* and *G. rufobrunnea* has proven valuable for identifying factors that potentially explain observed population size patterns at different scales. For example, despite differences in the impact of natural enemies, both species showed similar population size trends. This suggests that top-down effects are not likely to be the cause of observed patterns, but rather climate. Similarly, within trees, the smallest scale considered, the microclimate properties of the trees seem to be the major explanation for observed patterns for both species. On the other hand, at a between-tree scale host plant size was the likely cause of patterns observed for *G. postica*, while bird predation was important for *G. rufobrunnea*. The implications of this study for current and future utilisation of *Gonometa* species are discussed.

Implications for utilisation methods

In southern Africa the utilisation of *Gonometa postica* and *G. rufobrunnea* has bearing, nationally and internationally, on natural harvesting-managers, cocoon processors, silk refiners and silk marketing and retail, as well as scientific researchers. The Liberty Life Trust Wild Silk Workshop held on Tuesday, the 5th of November 2002, brought these role players together. Two of the main conclusions were that better communication was required between different interested parties, and that applied published research was urgently required to guide the utilisation process (Liberty Life Trust Wild Silk Workshop Summary Document, compiled by M.A. McGeoch).

Current utilisation of both *Gonometa* species consists solely of harvesting pupal cocoons from natural populations (Veldtman *et al.* 2002). Consequently, variation in pupal abundance in space and over time will determine the harvestable quantity and, consequently, the economic sustainability of this utilisation method. Chapter one shows that although *Gonometa* species population sizes are highly variable in space and time, this variation is less than for classic eruptive species, consistent with their less extreme eruptive life history traits. This provides further support for the practical utility of using life history to predict a pest or commercial species dynamics (Nylin 2001). The broad-scale spatial synchrony observed in pupal abundance suggests climate is the major factor controlling spatial and temporal variability. If climate is indeed the cause of population fluctuations, cocoon yields will continue to be erratic. However, if the timing of eruptions and population declines can be accurately predicted, cocoons could be stored during favourable times and processed during periods of low availability. Spatial synchrony in population size presents another potential concern, because the pattern (Chapter 1) potentially predicts that cocoon abundance could drop simultaneously across an entire region. Furthermore, this study also suggests that although cocoons may be harvestable over large regions in years of high pupal abundance, at a fine scale (a few kilometres) high pupal abundance sites may be difficult to find. Also, as with other commercially valued species, destructive harvesting during high abundance years may lead to human driven extinction during low abundance phases (McGeoch 2002). Seeding may be used as an alternative strategy during these times by establishing populations in different geographic regions with more favourable climates. Alternatively, if the first few instars are disproportionately at risk from this density independent factor, rearing the first few instars

under more controlled conditions and then seeding them on suitable host plants may increase harvestable quantities.

The extent of natural enemy-induced mortality for these species is likely to further contribute to the high temporal variability observed in abundances under field conditions. Bird predation (in addition to parasitism) resulted in significantly lower proportions of *G. rufobrunnea* pupae surviving to adulthood than *G. postica* (less susceptible to bird predation) and which might explain *G. rufobrunnea*'s greater temporal variability. Natural enemies may not only decrease the number of surviving pupae, but the damage caused to a cocoon during predation or parasitoid emergence (i.e. *Palexorista* sp., see Veldtman *et al*. 2004) may make these cocoons unprofitable or unsuitable for degumming. Natural enemy responses may also have implications for other utilisation strategies such as seeding or mass rearing, which require consideration when these strategies are implemented. For example, preventing bird predation in small plots of natural *Colophospermum mopane* veld could increase the survival of *G. rufobrunnea* pupae during its eruptive phase. However, trials are needed to ascertain how the parasitism levels will respond to such a management practise.

Chapter two indicated that the parasitoids responsible for parasitism can easily be determined from the emergence holes left, making rapid assessments of field parasitism possible (Veldtman *et al*. 2004). The ease of species identification will make it possible for future studies to document possible geographic variation in the occurrence and parasitism rates of *Gonometa* species parasitoids. The ease of determining species-specific parasitism will also allow parasitoid responses to seeding and artificial rearing programs to be monitored.

The spatial variability in pupal abundance and parasitism observed in Chapter three indicates a standardised surveying method is necessary. One major constraint in the natural harvesting of *Gonometa* species is a predictable cocoon supply (Veldtman *et. al*. 2002, 2004). Although sampling at a scale of 100 trees per site (Veldtman *et. al*. 2002) revealed considerable spatial pattern in both pupal abundance and parasitism, this survey method is unlikely to detect broader spatial patterns outside the site. Also the intensity of sampling makes this method unpractical for population size estimation. An alternative surveying method (multi-directional transect, Appendices A, B, C & D) was consequently developed (by R. Veldtman and M.A. McGeoch) for the estimation of *Gonometa* species pupal densities by natural harvesters and resource managers. This method allows greater area coverage, reduced sampling

effort (only 41 trees surveyed per site), and directional spatial trends to be identified. This method was tested in the field (Ibo Zimmermann, Polytechnic of Namibia) and subsequently improved.

Chapter four identified *Pimelimyia semitestacea* (Tachinidae) as a parasitoid species that was likely to result in spatial density dependence in *G. postica* populations. Although natural enemies may not cause population fluctuations, natural enemy induced mortality may contribute to spatial variability in population size between neighbouring sites. Monitoring of species that result in density dependent parasitism, predation, etc. is thus important. Further study of *P. semitestacea*'s ecology may be important in identifying the precise mechanism that results in density dependent parasitism. Such work could potentially illuminate why other parasitoid species did not cause density dependent mortality. In general, natural enemies that cause density dependent mortality are likely to respond positively (increased parasitism and population size) to artificial increases in *Gonometa* species abundance during seeding or artificial rearing.

Chapter five indicated that cocoon length is an acceptable surrogate for silk yield and can replace occupied cocoon mass as a non-destructive quantitative size measurement (Veldtman *et al*. 2002 and Appendix E). Potential yields at sites can consequently be estimated from mean cocoon length. The geographic variability documented in cocoon size is the first data available for southern African *Gonometa* species. However, it is stressed that much broader geographic scales need to be considered and sampled representatively before broad scale patterns may be identified. For example, *G. rufobrunnea* cocoons collected from the Kruger National Park, Northern Province (Mopane camp) during an outbreak in October 2003 are more comparable to the length quantified for *G. postica* than for other *G. rufobrunnea* populations (Appendix F). Considerable variation may thus still remain undescribed across southern Africa. Only after representative multi-regional data on cocoon length is available will it be possible to propose and test mechanisms for these patterns. If the range of quantified cocoon size differences between localities is even larger at such a broad spatial scale, targeting localities with the greatest mean cocoon sizes may have a dramatic effect on the silk yield and consequently economic profitability of harvesting.

Chapter six showed that it is possible to predict the number of pupae available for harvesting and where these pupae are likely to be distributed from tree characteristics (i.e. as a

surrogate for pupal abundance). These results can thus guide within-site harvesting practices. For example, harvesters should include non-host plants when searching for *G. rufobrunnea* pupae, while non-hosts can largely be ignored for *G. postica*. Also, especially in the case of *G. postica*, large trees (greater than three meters) are more likely to contain pupae than smaller equivalents. At a within-tree scale pupae will be most plentiful on the ends of branches just below the maximum width of the tree crown, especially on the northern and eastern aspects of trees. Described patterns also make it now possible to recommend how to naturally distribute pupae used for seeding, to ensure high probability of survival and fulfilment of microclimatic requirements.

By concentrating on the pupal stage this research could focus on several aspects of *Gonometa* species ecology as well as gathering information of direct value for the utilisation of these species. The data gathered can be used as a base line to plan more detailed investigations into the causes of the patterns quantified here and for testing the mechanisms suggested. With base-line information now available, several avenues of research can be explored to aid in the utilisation of *Gonometa* species.

Future research

Quantifying the genetic structure of *Gonometa* populations may provide unique information to understand the ecology of these species. For example, the dispersal ability and population connectivity is important in population studies but no published information exists for either *Gonometa* species. Preliminary data on the genetic structure of *G. postica* populations in North West and Northern Cape Provinces have identified high levels of similarity between populations, suggesting a high degree of dispersal and provides evidence for the existence of metapopulation dynamics in this species (Delport *et al*. 2003). If dispersal results in high population connectivity between neighbouring populations, this may explain the observed fine-scale variation in pupal abundance between neighbouring sites.

Understanding pupal diapause termination in *Gonometa* species is yet another important, yet unexplored, research aspect (Hartland-Rowe 1992). Preliminary trials have indicated that emergence is not simply related to temperature and photoperiod, but that considerable geographical and between individual variation exists (e.g. Tammaru *et al*. 1999; Menu *et al*. 2000; Pieloor & Seymour 2001). Understanding the mechanism of diapause termination will

greatly aid in non-harvesting utilisation methods were rearing sufficient numbers of individuals is the key to success. This will also allow mass moth emergence to be timed with optimal climatic conditions and foliage availability, some of the major constraints in artificial rearing and seeding.

Another research focus should be to test if host quality determines cocoon size, by affecting larval performance. The results such investigations will indicate whether host quality can result in geographic cocoon size variation. The importance of other alternative, abiotic factors such as climatic conditions for pupal size variation can also subsequently be investigated. For example, rainfall can indirectly influence larval performance by speeding up leaf flush of the host plant. If leaves are available earlier, leaf quality may remain high longer, resulting in greater final instar and pupal size (Dixon 2003; White 2004). Such research could also have direct applied value. Investigating the performance (growth rate and size) of larvae under different host fertilisation and watering regimes would indicate if optimal rearing conditions exist (see Floater 1997). Similarly, a test of whether trees repeatedly fed on by larvae show an increase in inducible defences (negatively affects larval growth), could suggest whether this is a potential mechanism explaining pupal size variation. The information gathered could thus be used to optimise larval growth during rearing and help improve seeding strategies to avoid inducible defences.

Seeding as an utilisation strategy also requires further research to fully explore the potential of this utilisation method. Although there is evidence that pupal seeding is the best strategy (Hartland-Rowe 1992), density of pupae, attachment techniques and the benefits of enclosures, needs further research (Hartland-Rowe 1992; see also Okelo 1978). However, the initial and long-term dependency on naturally collected material needs to be monitored. The response of natural enemies to this method must also be monitored, as seeding operations may increase natural enemy densities and negatively affect natural populations.

Recommendations

As with the utilisation of any natural resource, monitoring of its availability is crucial to ensure its sustainable and efficient use (Goodland 1995; Hilborn *et al*. 1995). Due to the scale of temporal variation in cocoon abundance and the spatial range of the two species, a long-term site-monitoring network will be key in identifying the viability of *Gonometa* populations and

their potential for harvesting across southern Africa. Also, finding alternative populations for utilisation will improve the availability of cocoons. This will require cooperation between the southern Africa countries were *Gonometa* species occur. With such a large scale of scientific investigation, the population fluctuations of these species across southern Africa will be better understood. As more data becomes available the potential of successfully predicting the availability of cocoons may also be improved.

Long-term monitoring will also ensure the conservation of this commercially important species (McGeoch 2002). Even though empty cocoons are collected at present (Veldtman *et al*. 2002), some individuals are still collected by accident, or for seeding trails. A potential danger of overexploitation or severe disturbance of natural populations thus remains. The wide geographic range of especially *G. postica* may pose further problems. Metapopulations of different geographic regions may have unique genetic composition (see Delport *et al*. 2003). To ensure the conservation of the genetic identity of populations from different regions, strict monitoring of the collection and seeding of occupied cocoons should be practised. Cocoons should only be seeded from local regions where they were collected, although artificial rearing operations can use material from other regions, provided no moths or parasitoids can escape from collected material. As the present utilisation of the species is totally dependent on natural populations the conservation of both species habitat is also important.

The prospect of sustainably utilising *Gonometa* species in southern Africa is one of promise. In contrast to the mopane worm, *Imbrasia belina*, where the resource is the final instar larva itself, wild silk utilisation may indeed be sustainable. The present practice of harvesting only cocoons from which adults have emerged is an effective rule of thumb to prevent over-harvesting. However, this practice has not traditionally been applied in Botswana, where the collection of *G. rufobrunnea* cocoons (for ankle rattles) is practised indiscriminately. Although silk reeled from intact cocoons is highly valued, it is recommended that only cocoons produced during artificial rearing be used in this manner. The temporal and spatial variability in cocoon abundance makes the harvesting of occupied *Gonometa* cocoons from natural populations an ecologically unsound practise.

The research presented here considers *G. postica* and *G. rufobrunnea* over multiple generations and a large geographic area, thereby providing quality baseline information for both species. Additionally, this research advances the basic ecological understanding of

southern Africa *Gonometa* species population dynamics. Thus, a scientific basis for the sustainable exploitation and conservation of these species has been provided.

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Appendix A: Description of *Gonometa* Density Survey method.

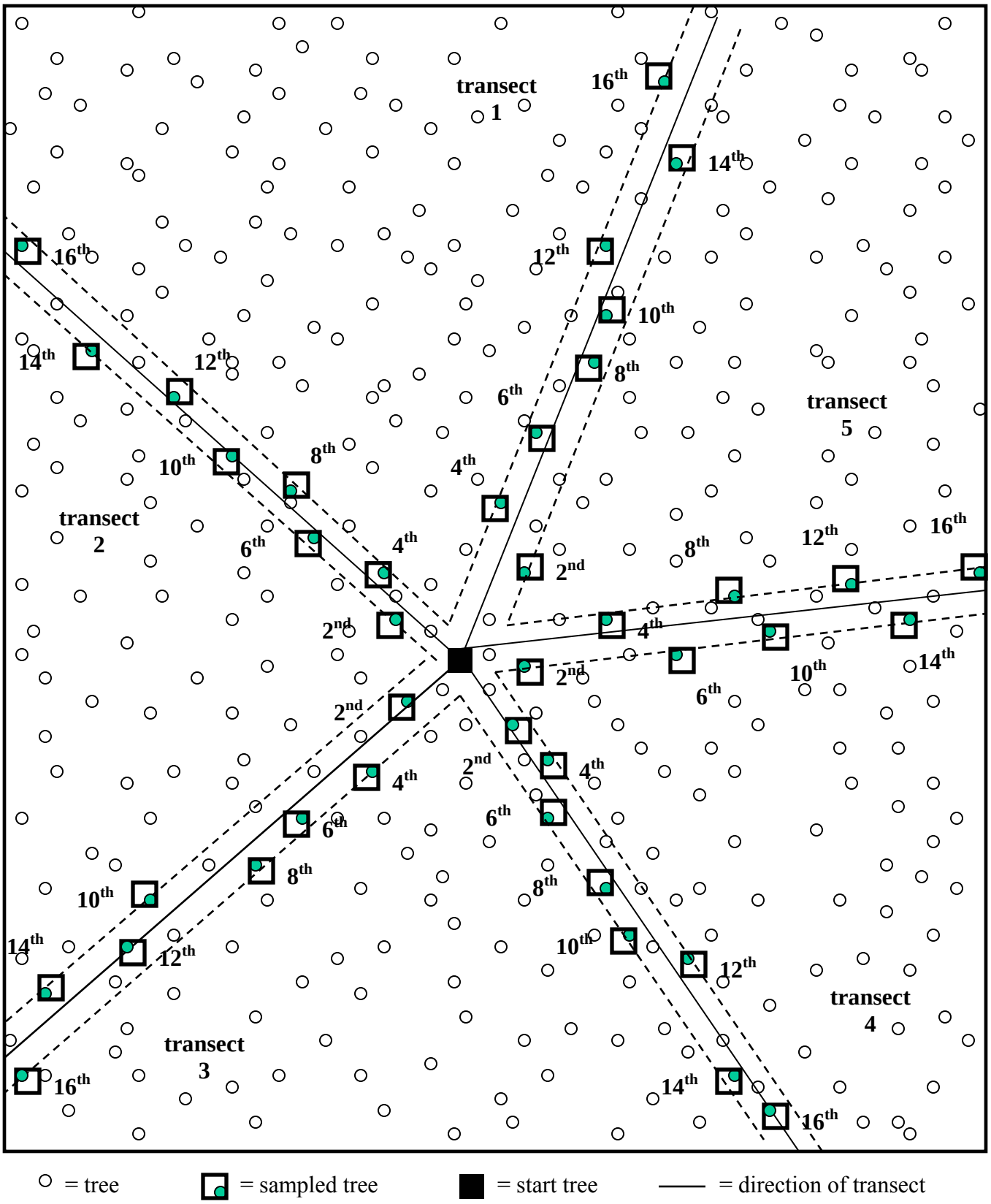
The following description is illustrated in the diagram in Appendix B.

1. Forty-one trees are sampled in each survey, and the selection process and position of these trees is described here and illustrated below. *Only trees greater than 1m in height are included in the survey.*
2. The first tree (called the START TREE) is chosen by finding any tree with at least one cocoon on it, and that is at least 25 trees away from the edge of the site. Mark this tree, e.g. with danger tape.
3. All the details for the start tree are filled in on the data sheet (in the shaded row).
4. Five transects are then walked in 5 different directions away from the START TREE. Each direction will represent a sampling transect (Fig.1.).
5. Pick one transect to be transect 1 and number the others consecutively.
6. The 2nd tree from the START TREE in transect 1 and every second tree in this transect thereafter (4th, 6th, 8th, etc.) is sampled. The same details recorded as for the START TREE are then recorded for this tree and filled in on the data sheet. *Trees must be sampled regardless of whether they have any cocoons on them or not. If they do not have cocoons, zeros are filled in on the data sheet under the three cocoon columns.*
7. This process is repeated until the 16th tree distant from the START TREE in transect 1 (8 trees in transect) has been sampled.
8. The same procedure is then followed for transects 2-5.
9. All the data for one survey are filled in on a single data sheet. The number of surveys to be conducted at a locality will be determined by the size of the locality and discretion of the surveyor. However, no surveys should be conducted within 0.5 km from the edge of any other survey.

Equipment Needed to Conduct Survey

1. Handheld Global Positioning System (GPS)
2. 2 m long stake
3. Danger tape for marking START TREE
4. Pencil, clipboard and data sheet

Appendix B: Graphical representation of *Gonometa* Density Survey.



Appendix C: Instructions for completing the *Gonometa* Density Survey Data Sheet

Description of data entry details

1	Date:	The day/month/year on which the survey is conducted.
2	Locality:	The farm/property name.
3	City/Town:	The closest city, town or village to the survey site.
4	Surveyor:	The name of the principle person conducting the survey.
5	Organisation:	The organization/institution that the surveyor represents.
6	Tree no:	41 trees are examined per survey. No data are filled in here.
7	Transect:	There are five transects plus the start tree per survey. No data are filled in here.
8	Tree position:	After the start tree, the 2nd, 4th, 6th, 8th, 10th, 12th, 14th and 16th tree from the start tree are sampled in each transect.
	GPS Reading:	Three values are recorded under here:
9	X:	Latitude
10	Y:	Longitude
11	Z:	Altitude
	Tree	Three entries are recorded under here:
13	Species:	The scientific name of the tree species (standard abbreviations can be used, e.g. A.ERI for *Acacia erioloba* /Camel thorn.
14	Height:	An estimate of the tree height (m) is made to the nearest meter (Stand a 2 m long stake upright against the tree. Walk 10 m away from the tree (within site of the stake). Use the length of the stake from where you are standing to estimate 2 m lengths above the stake and work out tree height.)
15	Canopy:	The width of the tree canopy is estimated by pacing the maximum extent of the canopy.
	Cocoons	Three values are recorded under this section:
16	Total:	The total numbers of cocoons on the tree are counted.
17	Old:	The number of old cocoons (sun-bleached with no hairs) on the tree.
18	New:	The number of new cocoons (many dark hairs visible) on the tree.

Appendix D: *Gonometa* Density Survey Data Sheet

Date:……. Locality:…… Village……..…

Landscape:……..…. Altitude: …… Transect width…….

Surveyor:…….……..… Organisation:…….…...…

Tree no.	Transect		Tree Pos.	GPS Readings		Tree			Cocoons			
	No	Dst		S	E	Species	Height	Canopy	Old	New	Ground	Total
1		0m	Start									
2	1		2									
3	1		4									
4	1		6									
5	1		8									
6	1		10									
7	1		12									
8	1		14									
9	1		16									
10	2		2									
11	2		4									
12	2		6									
13	2		8									
14	2		10									
15	2		12									
16	2		14									
17	2		16									
18	3		2									
19	3		4									
20	3		6									
21	3		8									
22	3		10									
23	3		12									
24	3		14									
25	3		16									
26	4		2									
27	4		4									
28	4		6									
29	4		8									
30	4		10									
31	4		12									

Appendix D: continued

Tree no.	Transect		Tree Pos.	GPS Readings		Tree			Cocoons			
	No	Dst		S	E	Species	Height	Canopy	Old	New	Ground	Total
32	4		14									
33	4		16									
34	5		2									
35	5		4									
36	5		6									
37	5		8									
38	5		10									
39	5		12									
40	5		14									
41	5		16									

APPENDIX E:

Quantified relationship between cocoon size (length and width) and silk yield (empty cocoon mass) for southern African *Gonometa* species. R^2 (%) for simple and multiple (corrected R^2) regressions of length and width on empty cocoon mass. Each species-sex combination was analysed separately. All relationships were significant at $P < 0.001$. Method of analysis similar to that used by Veldtman *et al* 2002.

Species	Sex	n	Length	Width	Length & width
G. postica	male	245	23.6	35.1	43.0
	female	220	46.7	52.5	62.7
G. rufobrunnea	male	55	37.6	54.6	56.8
	female	89	58.8	50.5	71.8

APPENDIX F:

Gonometa rufobrunnea cocoons sampled from a recent (October 2003) reported outbreak at Mopane Camp in the Kruger National Park, Northern Province, South Africa (sample size: 41 females and 29 males). This represents the most southern locality where cocoon size has been quantified for this species.