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.

TABLE OF CONTENTS

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

1

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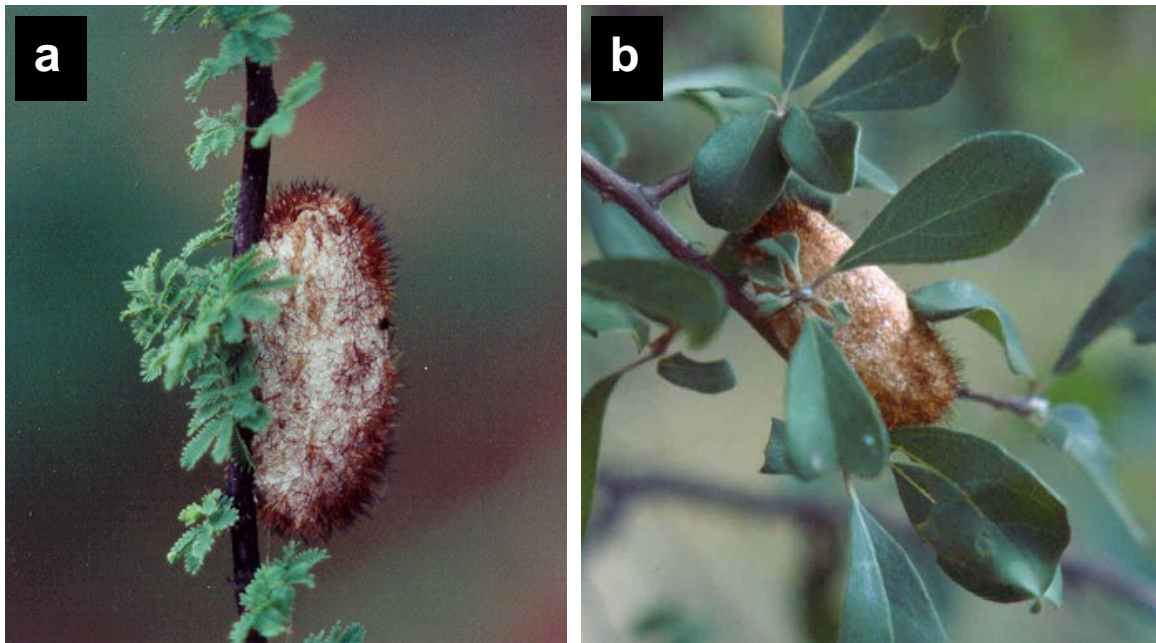
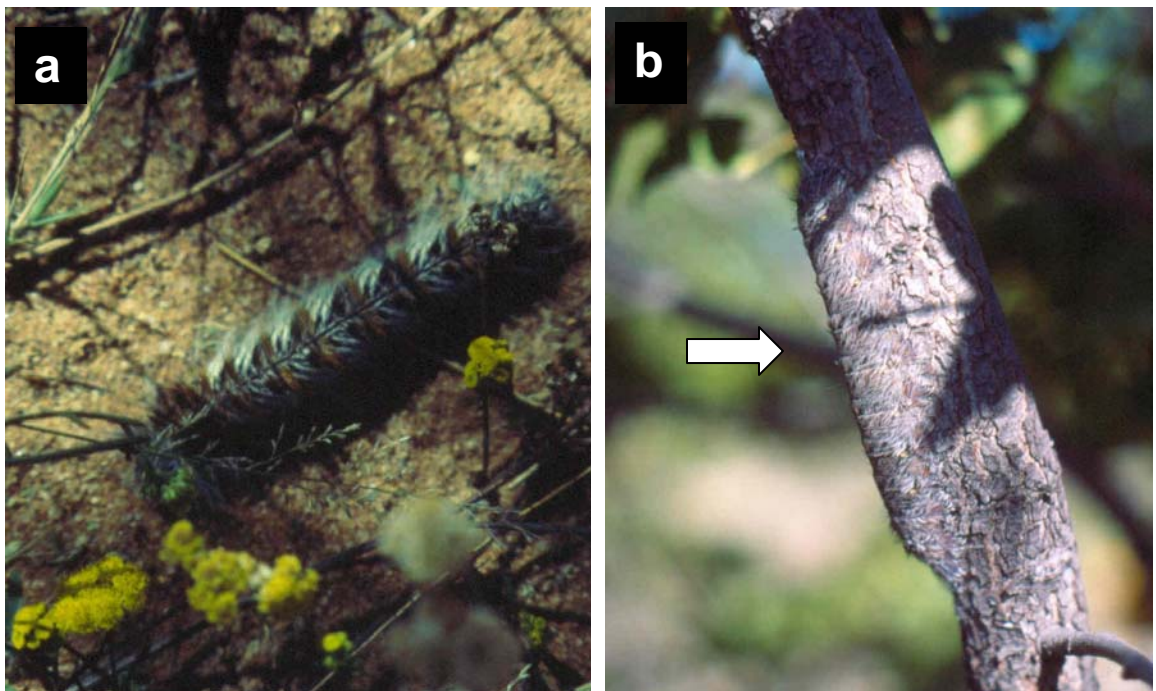**Figure 1.** Occupied pupal cocoons of a) *G. postica* and b) *G. rufobrunnea*.

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).
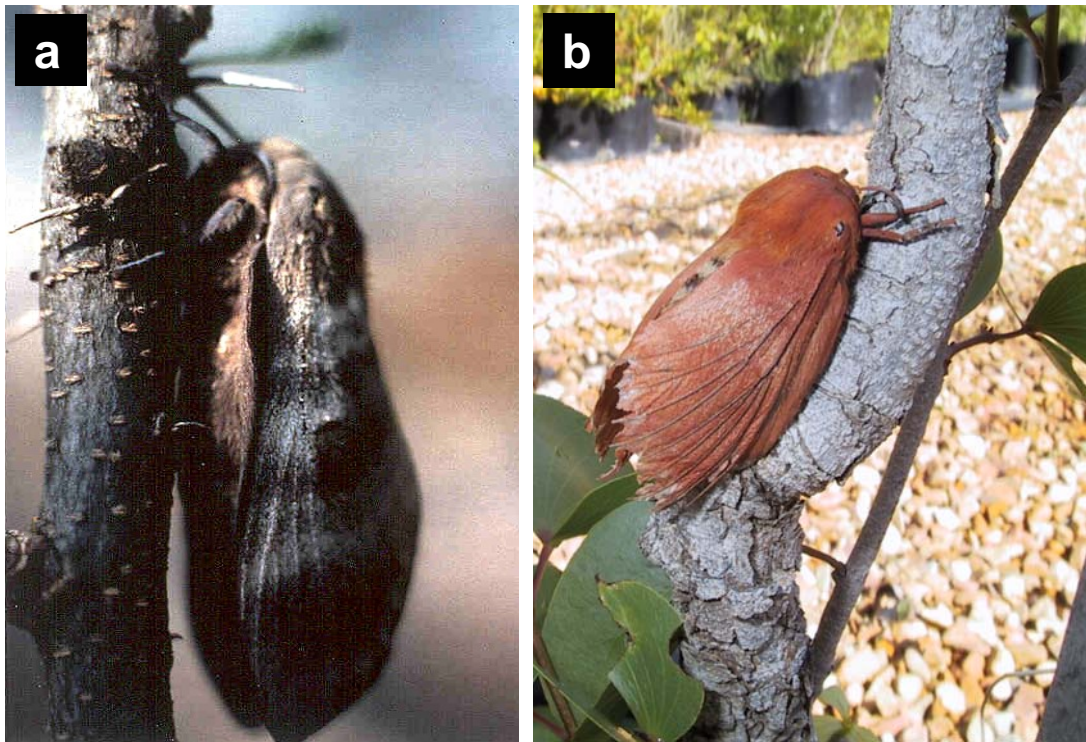
8

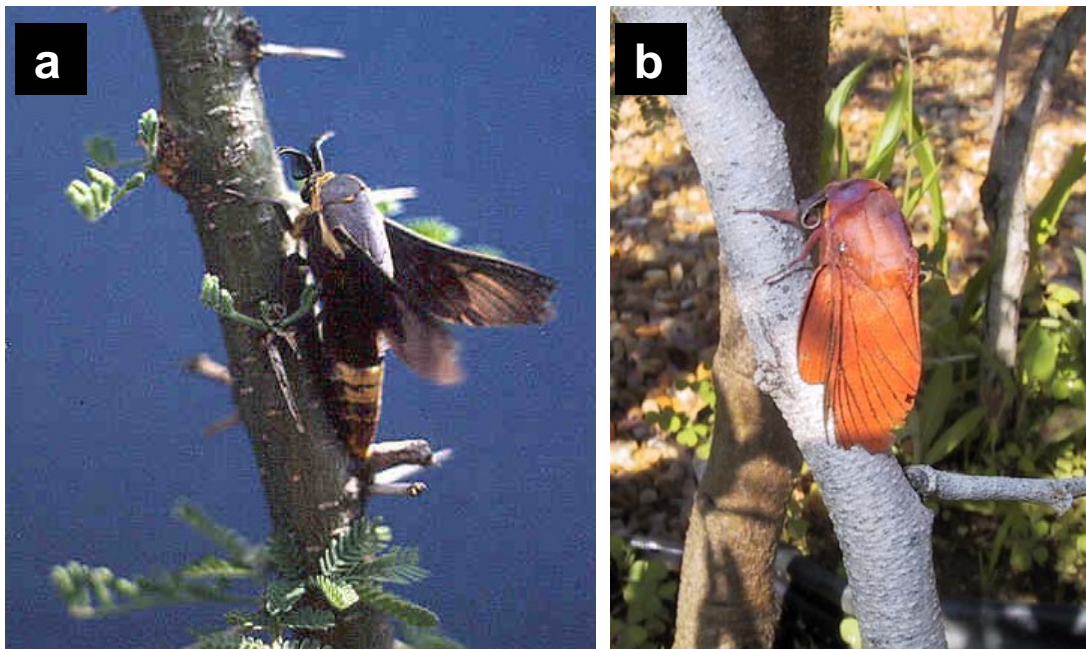**Figure 3.** Adult female moths of a) *G. postica* and b) *G. rufobrunnea*

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).

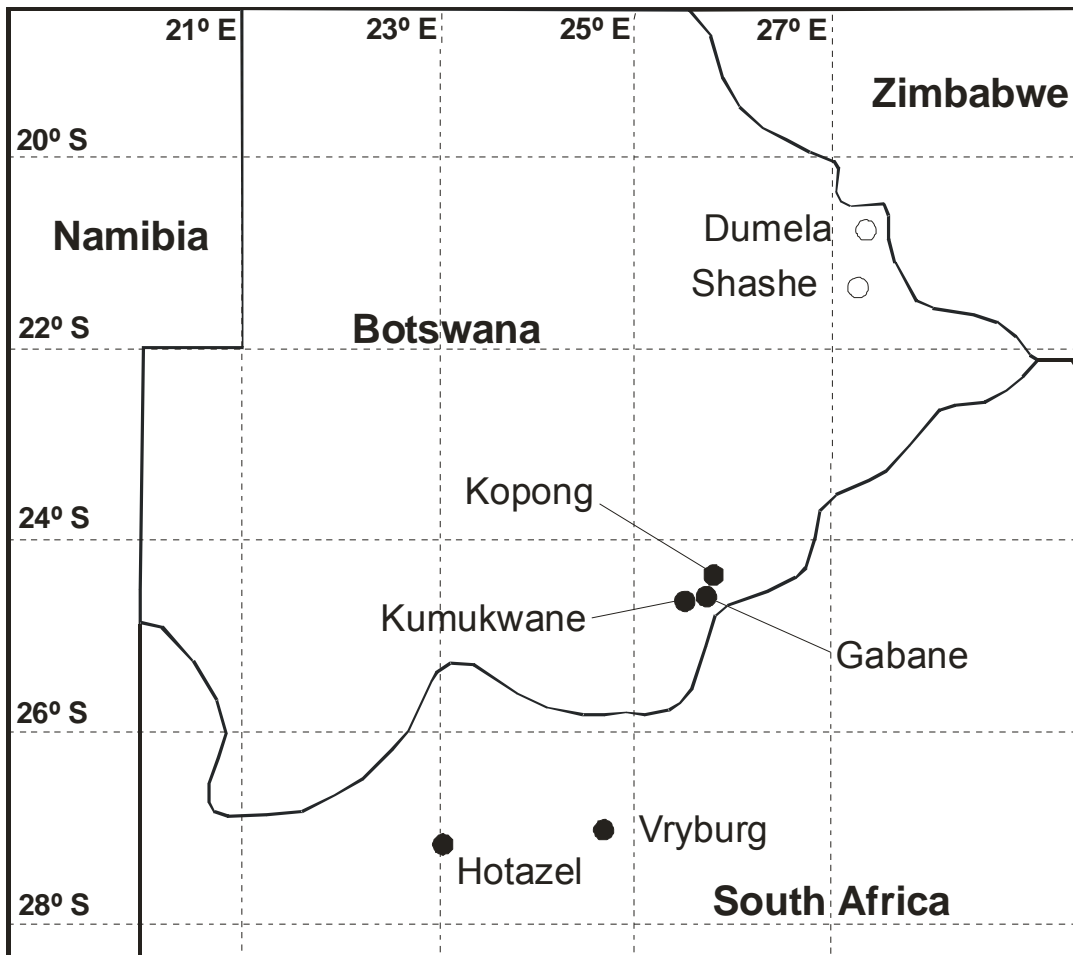**Figure 5.** Localities in South Africa and Botswana where *G. postica* (filled circles) and *G. rufobrunnea* (open circles) were sampled.

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

13

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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