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.

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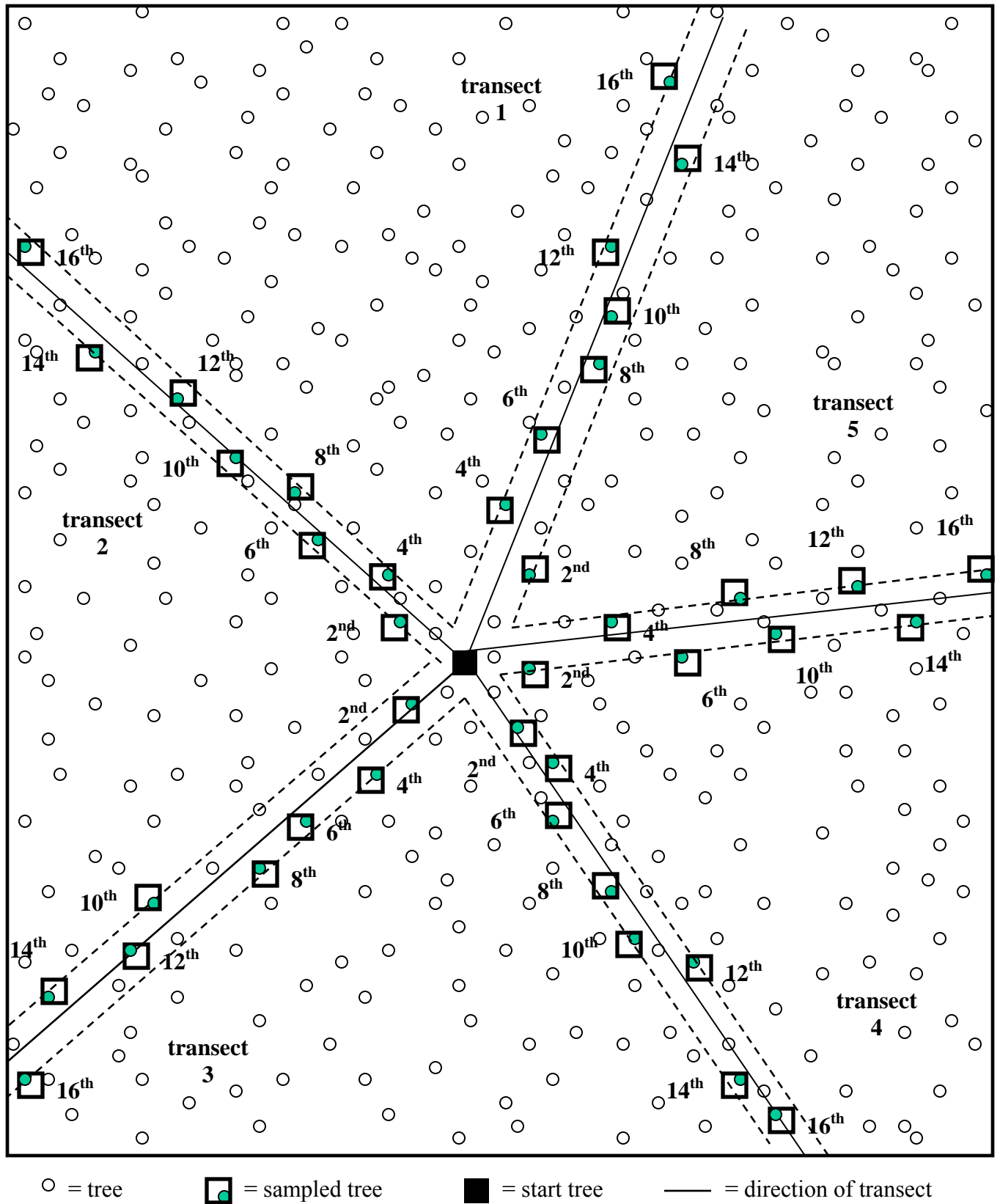**Appendix A:** Description of *Gonometa* Density Survey method.

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.