



Parasitoid communities attacking externally feeding folivorous Lepidoptera in New Guinea rainforest

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Annotation

The host - parasitoid community of externally feeding folivorous Lepidoptera and their parasitoids was studied on 45 focal tree species in a New Guinea rainforest. The patterns of parasitation rate, parasitoid species richness and parasitoid host specificity are described.

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INDEX

INTRODUCTION	
Plant - herbivore - parasitoid food webs	1
Results of previous host - parasitoid studies	2
Purpose of this study	3
METHODS	4
Data gathering	4
Data analysis	5
RESULTS	6
General characteristics of the hosts	
General characteristics of the parasitoids	6
Data analysis	
Parasitation rate	13
Parasitoid species richness	
Dominance in parasitoid communities on particular hosts	14
Parasitoid host specificity	
DISCUSSION	16
Methodological issues	
Parasitation rate	17
Parasitoid species richness	19
Dominance in parasitoid communities on particular hosts	
Parasitoid host specificity	
CONCLUSIONS	
LITERATURE	23
APPENDIX A	
APPENDIX B	

APPENDIX C

INTRODUCTION

Plant - herbivore - parasitoid food webs

The study of food webs consisting of plants, their herbivores and parasitoids is a field of biology studying at least 75% or more of global terrestrial biodiversity (Price, 2002). Most of the global diversity which has been recently estimated at <10 million species of arthropods alone (Novotny et al., 2007), has not been described and catalogued, even though the biologists are systematically working on this from the times of Karl Linné (Godfray et al., 1999). Much more interesting and more laborious than mere cataloging of species is finding out how they interact in nature. Despite accelerating progress, this field is still in its early stage with many ideas how the species interactions should work, but severe limitation by the availability of experimental data (Godfray et al., 1999; Janzen, 1983). Even when we omit parasitoids and concentrate on the plant - herbivore interactions, the diversity is so huge that we can find only few larger systems (those which cover more than several species) which have been studied in detail, permitting generalisations (Dyer et al., 2007; Janzen, 1988; Novotny et al., 2002b). The few general patterns found can still be contradictory as they are often documented from very few sites (Dyer et al., 2007; Novotny et al., 2006). Such studies are bases on tens of thousands person-days spent collecting insects in the field, processing and identifying them (Novotny et al., 2002a).

The host - parasitoid interaction has proven even more difficult to study due to several factors. The greatest problem is sample size, simply because there are fewer individuals in higher trophic levels. The rearing of parasitoids is also complicated by often difficult species identification of immature hosts, which is however necessary for unambiguous coupling of parasitoid with its host. The difficulties are however balanced by the attractivity of parasitoids so there are no fewer studies concentrating on them than on herbivores.

The boom of the study of parasitoid - host interactions is usually dated to the 1880s when the vedalia beetle (a predator) was introduced in California for the biological control of the cottony cushion scale on citrus trees (Hawkins & Sheehan, 1994). This event started an intense interest in the use of natural enemies to control insect pests which continues at a somewhat lower pace also during the last decades. Since the pioneer studies by Askew (1961) and Price (1970) the emphasis is shifting towards studying complex communities in natural habitats (Hawkins & Sheehan, 1994).

Among the first communities studied were inhabitants of galls with their parasitoids (Askew, 1961; Price, 1970) and miners with their parasitoids (Memmott *et al.*, 1994; Rott & Godfray, 2000). Both systems have proven amenable to study for the relative ease with which it is possible to sample and identify the insects, which is also the reason why gall and miner communities account for most of the studied systems (Lewis *et al.*, 2002; Rauf *et al.*, 2000; Schonrogge & Crawley, 2000; Valladares *et al.*,

2001). Other studies concentrated on Macrolepidoptera (Barbosa *et al.*, 2001; Gentry & Dyer, 2002; Lill *et al.*, 2002; Sheehan, 1994; Stireman & Singer, 2003), Tortricidoidea (Mills, 1993), sawflies (Price & Pschornwalcher, 1988), aphids (Muller *et al.*, 1999), grass feeding chalcids (Dawah *et al.*, 1995; Tscharntke *et al.*, 2001) or solitary bees and wasps (Tylianakis *et al.*, 2007).

Distinctly different approach to the study of host - parasitoid interactions was pioneered by Hawkins (1994), whose meta-analytical research introduced a number of general patterns and serves an important background to which any new work can be related.

Results of previous host - parasitoid studies

The parasitoids occupy high positions in the food chain and the ecological and evolutionary forces affecting them mostly originate in lower levels of the food web (Price, 1992). Hawkins (1994) found the host feeding niche to be the single most important factor structuring host - parasitoid communities (see also Gentry & Dyer, 2002). Other factors were reported to be important, such as host plant (Lill *et al.*, 2002), host plant range of the herbivore, herbivore gregariousness, hairiness and aposematism (Stireman & Singer, 2003) and chemicals sequestered by the host (Gauld & Gaston, 1994; Gentry & Dyer, 2002). A correlation of climatic unpredictability with parasitation rate had also been suggested (Stireman *et al.*, 2005). The differences in parasitoid host use inspired important theoretical developments, such as the concept of koinobiont - idiobiont (Askew & Shaw, 1985) or the concept of parasitoid guilds (Mills, 1994).

The species in natural communities are highly interconnected (Lewis *et al.*, 2002) and therefore apparent competition has been suggested to be important is host - parasitoid communities (Godfray *et al.*, 1999; Holt & Lawton, 1993) It's existence was recently also confirmed experimentally (Morris *et al.*, 2004).

Interesting result emerge when it is possible to compare two or more food web datasets which are ordered along some gradient. Tylianakis *et al.* (2007) have shown in such study that the evenness of the interactions declined with increasing habitat modification while the species richness stays constant.

The community structure was found to be different even when Tscharntke *et al.* (2001) compared grass feeding chalcid wasp communities in Great Britain and Germany. They found the British communities non-saturated (consider the contrast of great and numerous British naturalists with the comparatively poor biodiversity in their homeland).

The knowledge about natural systems can be also used in predicting the potential of natural enemies for biological control (Dyer & Gentry, 1999) or for assessing impact of species introduced for biological control on the native communities (Henneman & Memmott, 2001).

The dynamics of host - parasitoid communities is very interesting, but it proved very hard to study. The data from studied system have to be usually pooled over several

years to produce one "snapshot" of the community with reasonable sample size. Moreover there is the problem of how to sample the community repeatedly without influencing its dynamics. Several community dynamics studies exist despite of these complications (Lewis et al., 2002; Muller et al., 1999; Valladares & Salvo, 2001) but extend only over 1, 2 or 3 years and therefore deal mostly with seasonal variation. The question whether there are differences between tropical and temperate host parasitoid communities is very intriguing (Godfray et al., 1999), but the studies of this problem have usually dealt only with parasitoid species richness (Noyes, 1989), focusing particularly on decreasing species richness of Ichneumonidae along the latitudinal gradient (Janzen, 1981; Owen & Owen, 1974; Sime & Brower, 1998). Such results are interesting, but tell us little about the structure of host - parasitoid communities. The tropical Lepidoptera hosts have also been suggested to be "nastier" for predators and therefore better targets for parasitoids than their temperate counterparts (Gauld & Gaston, 1994). The parasitoid species richness per host species tends to be higher in temperate regions for externally feeding hosts (Hawkins, 1994). In the study of Stireman et al. (2005) the parasitation rate did not significantly correlate with latitude. Lewis et al. (2002) found the tropical miner parasitoids to be highly polyphagous, which is the case also for temperate leaf miner parasitoids (Hawkins, 1994; Rott & Godfray, 2000). The evidence for either similarity or distinctness of tropical and temperate host - parasitoid communities is contradictory in overall and the need of more data for both regions is evident.

Purpose of this study

The purpose of this study is to describe patterns in parasitation of externally leaf feeding Lepidoptera reared in the mass rearing project of Novotny *et al.* (http://www.entu.cas.cz/png/).

The dataset is interesting in several aspects: (i) it is the first quantitative dataset covering both externally leaf feeding Macrolepidoptera and Microlepidoptera, (ii) both Hymenoptera and Diptera parasitoids are included and (iii) the study site lies in tropical rainforest with low seasonality. My aim is to describe parasitation rate, parasitoid species richness and parasitoid host specificity in this host - parasitoid community.

METHODS

Data gathering

The study area is in the vicinity of Madang town in Papua New Guinea. Average annual rainfall in this area is 3,600 mm, with a moderate dry season from July to September and mean air temperature 26.5°C (McAlpine *et al.*, 1983). The vegetation cover is species-rich evergreen rainforest. Fieldwork was conducted in primary and secondary lowland forests near Baitabag, Ohu and Mis Villages (145°41–7'E, 5°08–14'S, 0–200 m a.s.l.) during the years 1999-2004.

The insects were collected on 45 focal tree species (Appendix A) which were chosen to include representatives of main angiosperm lineages (monocotyledons,

basal eudicots, euasterids I and II, and eurosids I and II; APG II, 2003) as well as locally common plants from primary and secondary forest and riverine habitats (Leps *et al.*, 2001). All but one species were native, the exception being *Piper aduncum* which was introduced from the Neotropics, but has already attained caterpillar community indistinguishable from native trees (Leps *et al.*, 2002).

All Lepidoptera caterpillars feeding externally on leaves were collected from the vegetation by local collectors. Sampling effort was standardized to approximately 1500m2 of leaf area per plant species and each plant species was sampled over one year to control for seasonal effects. The number of tree inspections, that is, a particular tree sampled at a particular time, exceeded 1000 per plant species.

The caterpillars were brought to the rearing facility and provided with leaves of the plant they were collected on. Only the caterpillars that fed were retained, morphotyped by parataxomists and reared until a moth or a parasitoid hatched or the caterpillar died. Hyperparasitoids were not distinguished from parasitoids.

Adult moths were morphotyped by parataxonomists and later identified by taxonomists. The morphospecies thus correspond to species, albeit sometimes undescribed. The identification and especially the matching of sexes was aided by ~4000 mitochondrial CO I sequences (barcodes). Reared parasitoids were morphotyped by the author and than sent to taxonomists specialized to particular groups for identification (see acknowledgements for the list of taxonomists). The identifications of only two subfamilies of Braconidae (Cheloninae and Macrocentrinae) came back in time to be included in the analysis, while other identifications are based on my morphospecies identifications only. Several hundreds of mitochondrial CO I barcodes are planned to help with the parasitoid identifications. Both moth and parasitoid specimens are stored in USNM as well as other major museums.

The parasitoids were connected with the host through the caterpillar morphospecies code. All moth specimens reared from a particular caterpillar morphospecies code were checked and if at least 95% of them belonged to one species then the parasitoids

reared from caterpillars of that code were marked as parasitising the corresponding moth species.

In this way, 45.2% of parasitoid species and 45.5% of parasitoid specimens could be assigned with at least 95% confidence (usually much higher) to host species. Further 24.3% of species and 41.9% of parasitoid specimens could be safely assigned to host genera. Another 16.5% of species and 7.5% of specimens could be safely assigned to host family. Only 14.0% of species and 5.1% of specimens could not be safely associated with any host taxon. Such parasitoid species were mostly rare.

Data analysis

A simplified concept of "most probable host" was used in the analyses, associating the parasitoid with the moth which made up highest proportion of the specimens reared. This inevitably brought some factual error in the dataset, but greatly simplified the data analysis.

The variables were used as follows:

Parasitation rate as the proportion of parasitoid rearings from all successful rearings. Parasitoid species richness as the number of parasitoid species attacking a particular host.

Parasitoid host specificity as the number of hosts recorded for a parasitoid.

Caterpillar feeding mode as a factor with two levels: semi concealed and free living.

Leaf rolling and web making caterpillars were regarded as semi concealed (mostly Tortricidae, Crambidae, Thyrididae, Choreutidae, Pyralidae, Gelechiidae, Elachistidae and Immidae) and all others as free living (mostly Geometridae, Noctuidae, Lymantriidae, Arctiidae, Nolidae, Nymphalidae, Lycaenidae, Lacturidae, Limacodidae and Sphingidae). Appendix B gives the list of host species together with their feeding mode.

Host taxonomy as a factor with six levels corresponding to taxonomic groups shown in Fig.1.

All variables were log transformed prior to analysis. Untransformed variables were used in the figures.

Regressions were performed with lm function in R environment (R Development Core Team, 2006)

RESULTS

General characteristics of the hosts

Altogether 49,019 externally feeding caterpillars were collected from 45 focal trees (Appendix A). The overall rearing success was 34% leading in 15,001 Lepidoptera hosts and 1,602 Hymenoptera and Diptera parasitoids reared (total parasitation rate of 9.6%). The rearing success of the Lepidoptera species was highly variable with the mean of 30.6 ± 16.6 (SD).

A total of 274 host species from 28 families were reared (Appendix B). The most species rich groups were Pyraloidea (Crambidae + Pyralidae) with 48 species followed by Geometridae (43), Tortricidae (39) and Noctuidae (37). These four groups make up 61% of the host species and the next most common families significantly lag behind them (Thyrididae with 16 and Choreutidae with 13 species) (see Appendix C for the complete list of families). The taxonomic composition of species reared in this study is compared to other sites where mass rearing of externally feeding caterpillars took place in Fig. 1.

The abundance of individual species was highly unequal with only 42 species reaching over 100 individuals (with a maximum of 892) and 150 species having only 10 or less reared individuals.

Of the 274 host species, 134 were free living and 140 were semi concealed. Although the proportion of species was about 50% for each feeding mode, the semi concealed hosts were more much more common making 77.8% of reared caterpillar specimens, leaving only 22.2% to free living caterpillars. Also majority of common species were semi concealed feeders, so there were only ten free living species in the fifty most common hosts.

General characteristics of the parasitoids

Altogether 1,602 parasitoid specimens of 266 species were reared from 105 host species. About two thirds of them were Hymenoptera and the other third were Diptera: Tachinidae. The Hymenoptera were mostly Ichneumonoidea but several Chalcidoidea and Bethyloidea parasitoids were also reared. Only one tenth of the Ichneumonoidea were Ichneumonidae with the rest being different subfamilies of Braconidae. Table 1 details the number of specimens reared and the number of species for each taxonomic group.

Data analysis

The statistical analyses were performed with the assumption of the most probable host (explained earlier in the methods) and with datasets restricted to more common species. Table 2 summarizes the restrictions imposed to the datasets and shows the proportion of the data satisfying the criteria.

	Taxonomy		Specimens	Species
		Microgastrinae	581	86
		Agathidinae	123	20
		Cardiochilinae	88	1
Unimenentano	Braconidae	Orgilinae	41	9
Hymenoptera	Braconidae	Rogadinae	35	16
		Cheloninae	30	8
		Macrocentrinae	13	3
		Meteoridiinae	2	1
Hymenoptera	Ichneumonidae		99	19
Hymenoptera	Chalcidoidea		12	7
Hymenoptera	Bethylidae		8	2
Diptera	Tachinidae		570	94
			1602	266

Table 1. Taxonomic afiliation of reared parasitoids.

Table 2. Details for analysed datasets.

	Whole Dataset	Parasitation rate analysis	Parasitoid species richness analysis	Parasitoid host specificity analysis
the limit imposed		50+ rearings	50+ rearings, host species with no parasitoids excluded	5+ reared parasitoids
no. of host specimens	15001	11743	11336	9651
no. of parasitoid specimens	1602	1465	1465	1300
no. of host species	274	56	52	60
no. of parasitoid species	266	203	203	58

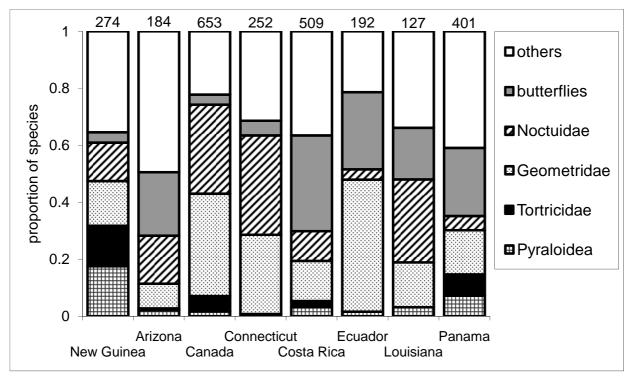


Figure 1. Taxonomic composition of reared species in the most extensive Lepidoptera rearing programs. The data used in this study are in the first column, the remaining data are from Dyer et al. (2007). Lepidoptera families representing less than 12% of species on the locality with their highest relative species richness were combined into category "others." Total number of species reared at each site is shown at the top of each bar.

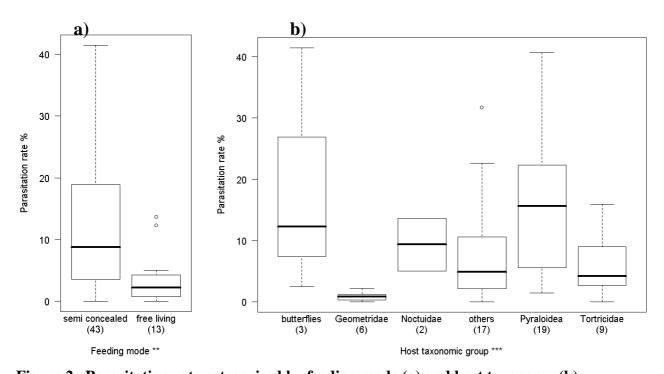


Figure 2. Parasitation rate categorised by feeding mode (a) and host taxonomy (b). The box shows first to third quartile with median as horizontal line, the whiskers show adjacent values and outliers are plotted as circles. Significance of a factor in linear model where the graphed factor is the

and outliers are plotted as circles. Significance of a factor in linear model where the graphed factor is the only explanatory variable is marked as follows: '***' p < 0.001 '**' p < 0.01 '*' p < 0.05 '(n.s.)' not significant. The number of moth species in each category is shown in parentheses under the category name.

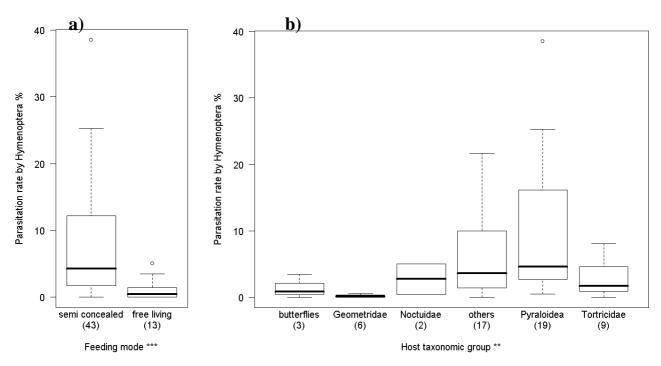


Figure 3. Parasitation rate by Hymenoptera categorised by feeding mode (a) and host taxonomy (b). The symbols are explained in legend to Fig. 2.

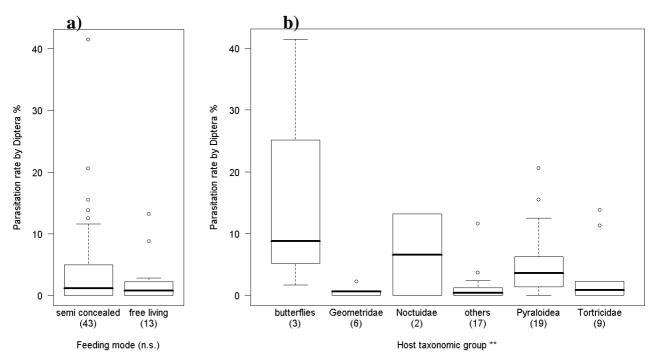


Figure 4. Parasitation rate by Diptera categorised by feeding mode (a) and host taxonomy (b). The symbols are explained in legend to Fig. 2.

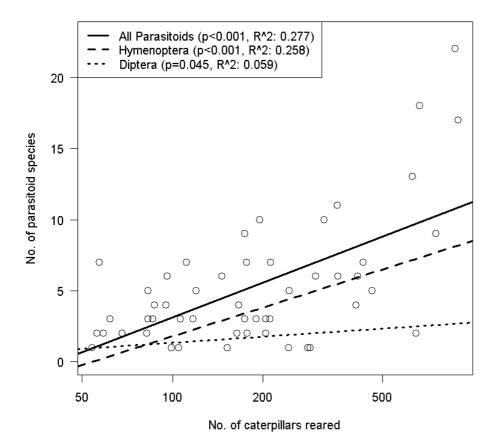


Figure 5. The relationship between sample size and parasitoid species richness. Both points and regression line are shown for total parasitoid species richness while only regression lines are shown for Hymenoptera and Diptera parasitoid species richness.

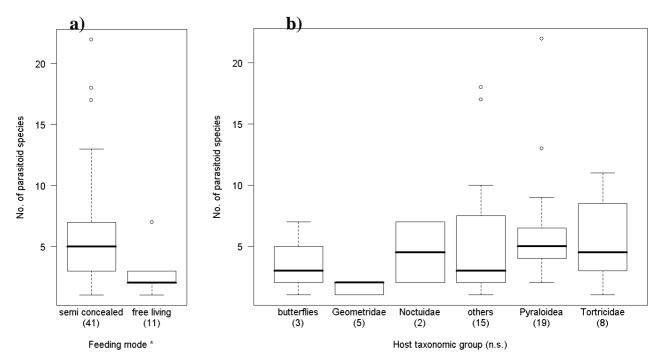


Figure 6. Parasitoid species richness categorised by feeding mode (a) and host taxonomy (b). The symbols are explained in legend to Fig. 2.

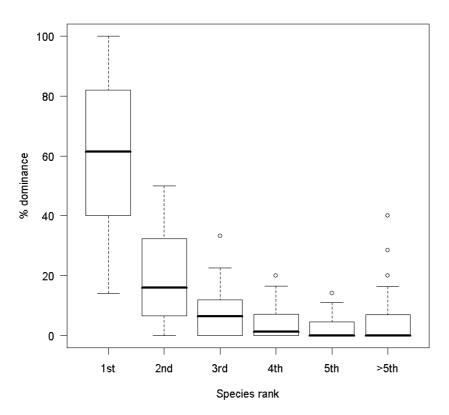


Figure 7. Dominance in parasitoid communities feeding on particular Lepidoptera host species. The proportion of individuals represented by the most abundant parasitoid species (1-5) and by all remaining species combined (rank > 5) is reported for 52 most common Lepidoptera host species (medians with first and third quartiles as boxes, adjacent values as whiskers, outliers as circles).

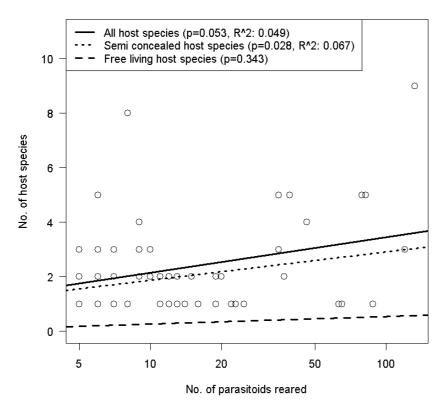


Figure 8. The relationship between sample size and parasitoid host specificity. Both points and regression line are shown for overall host specificity while only regression lines are shown for semi concealed and free living host specificity.

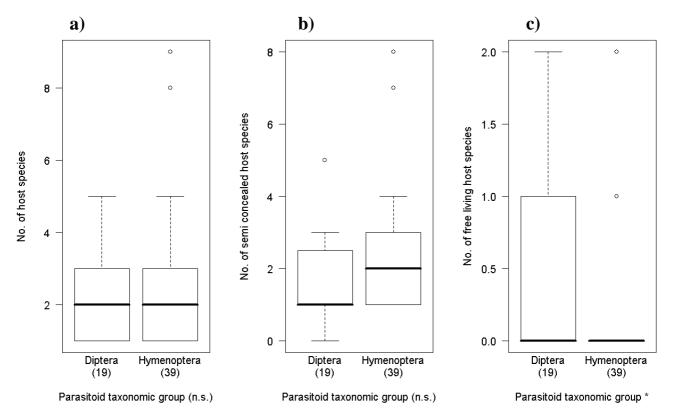


Figure 9. Host specificity (a), semi concealed host specificity (b) and free living host specificity (c) for different parasitoid taxa. The symbols are explained in legend to Fig. 2. Note different scale on y axes.

Parasitation rate

The overall parasitation rate was 5.6% (2.5 - 15.7, median with lower and upper quartile) and the rate caused by Hymenoptera (3.1%, 0.6 - 7.6) was significantly higher than that caused by Diptera (1.1%, 0.0 - 3.9) (p = 0.031, double sided Wilcoxon test).

The variable most strongly correlated with parasitation rate was number of parasitoid species (p<0.001, R^2 =0.438). Number of specimens reared from a moth species was not correlated with parasitation rate (p=0.578). The caterpillar feeding mode significantly influenced parasitation rate (p=0.002, R^2 =0.155) with semi concealed hosts suffering higher parasitation rate than free living (8.7%, 3.6 – 18.9 or 2.3%, 0.8 – 4.3 respectively, Fig. 2a). The effect of host taxonomy was highly significant (p<0.001, R^2 =0.271, Fig. 2b) with Geometridae being significantly different from all other groups at 0.05 significance level. The effects of host feeding mode and taxonomy were complementary to some degree, but the combined model was significantly better than either feeding mode or taxonomy alone (ANOVA, p<0.01 in both cases) and explained more variance than the single models (p<0.001, R^2 =0.351).

Parasitation rate caused by Hymenoptera was most strongly correlated with number of Hymenoptera parasitoid species (p<0.001, R²=0.580) and the effect of number of reared specimens was not significant (p=0.368). The caterpillar feeding mode significantly influenced Hymenoptera parasitation rate (p<0.001, R²=0.199) with semi concealed hosts suffering higher Hymenoptera parasitation rate than free living (4.3%, 1.7 - 12.2 or 0.5%, 0.0 - 1.4 respectively, Fig. 3a). The effect of host taxonomy was significant (p=0.002, R²=0.241, Fig. 3b). The effects of host feeding mode and taxonomy were highly complementary, so the combined model was not significantly better than either feeding mode or taxonomy alone (ANOVA, p=0.108 or p=0.127 respectively).

Parasitation rate caused by Diptera was most strongly correlated with number of Diptera parasitoid species (p<0.001, R²=0.512) and the effect of number of reared specimens was not significant (p=0.790). The caterpillar feeding mode did not significantly influenced Diptera parasitation rate (p=0.417) with semi concealed hosts suffering slightly higher Diptera parasitation rate than free living (1.1%, 0.1 – 5.0 or 0.8%, 0.0 – 2.3 respectively, Fig. 4a). The effect of host taxonomy was highly significant (p=0.005, R²=0.209, Fig. 4b). The combined model of host feeding mode and taxonomy showed same results as the single models alone.

Parasitoid species richness

The overall number of parasitoid species was 4 (2 - 7) and number of Hymenoptera species (2, 1 - 4) was significantly higher than number of Diptera species (1, 1 - 2) (p < 0.001, double sided Wilcoxon test).

Number of parasitoid species was most strongly correlated with number of caterpillars reared (p<0.001, R^2 =0.277, Fig. 5). The effect of parasitation rate was also significant and very strong (p<0.001, R^2 =0.271). These two effects combined into the effect of number of reared parasitoids (p<0.001, R^2 =0.596). This was found out by trying all combinations of the three variables in the models. The caterpillar feeding mode significantly influenced number of parasitoid species, but explained very low proportion of the variability (p=0.028, R^2 =0.075, Fig. 6a). The semi concealed hosts had more parasitoid species than free living (5, 3 – 7 or 2, 2 – 3 respectively). The feeding mode was still significant when considered together with number of caterpillars reared but not when considered together with both number of caterpillars reared and parasitation rate. The effect of host taxonomy was not significant (p=0.112, Fig. 6b).

Number of Hymenoptera parasitoid species showed the same relationships with number of caterpillars reared (p<0.001, R^2 =0.258, Fig. 5), parasitation rate (p<0.001, R^2 =0.185) and number of reared parasitoids (p<0.001, R^2 =0.470) as total number of parasitoid species. The effect of caterpillar feeding mode was highly significant and explained much bigger proportion of variance than in the case of number of parasitoid species (p<0.001, R^2 =0.193). The semi concealed hosts had more Hymenoptera parasitoid species than free living (3, 2 – 5 or 1, 1 – 1 respectively). The effect of host taxonomy was significant (p=0.018, R^2 =0.167) .The effects of host feeding mode and taxonomy were highly complementary, so the combined model was not significantly better than either feeding mode or taxonomy alone (ANOVA, p=0.685 or p=0.414 respectively).

Number of caterpillars reared had significant effect on number of Diptera parasitoid species, but explained very small proportion of the variability (p=0.045, R^2 =0.059, Fig. 5). The effect of parasitation rate was significant and strong (p=0.002, R^2 =0.165) and number of parasitoids reared explained significantly bigger proportion of variability than number of caterpillars reared and parasitation rate combined (p<0.001, R^2 =0.261). Neither caterpillar feeding mode nor host taxonomy were significant (p=0.772 or p=0.165 respectively).

Dominance in parasitoid communities on particular hosts

The proportion of individuals represented by the most abundant parasitoid species feeding on particular Lepidoptera host species is shown in Fig. 7. The most abundant parasitoid was responsible for 61.4% (40.0 - 80.2) of the total parasitation.

Parasitoid host specificity

The overall number of host species was 2 (1 - 3) and number of semi concealed species (2, 1 - 3) was significantly higher than number of free living species (0, 0 - 0) (p < 0.001, double sided Wilcoxon test).

The effect of number of parasitoids reared on parasitoid host specificity was not significant, but close to 0.05 significance level (p=0.053, $R^2=0.049$, Fig. 8).

Parasitoid taxonomy did not significantly influence the parasitoid host specificity (2, 1 - 3 for both groups, p=0.821, Fig. 9a).

Semi concealed host specificity was significantly influenced by number of reared parasitoids (p=0.028, R²=0.067, Fig. 8). The effect of parasitoid taxonomy was not significant (p=0.113, Fig. 9b), but Diptera had fewer species of semi concealed hosts than Hymenoptera (1, 1 - 2.5 or 2, 1 - 3 respectively).

Free living host specificity was not affected by number of parasitoids reared (p=0.343, Fig. 8), but the effect of parasitoid taxonomy was significant (p=0.016, R^2 =0.084, Fig. 9c) with Diptera having more species of free living hosts than Hymenoptera (0, 0 – 1 or 0, 0 – 0 respectively).

From the 19 Diptera species with more than 5 parasitoids reared 9 had only one host (6 semi concealed, 3 free living - but those had only 5 or 6 parasitoid specimens reared), 5 were confined to semi concealed hosts, none was confined to free living hosts and 5 parasitized both semi concealed and free living hosts.

From the 39 Hymenoptera species with more than 5 parasitoids reared 15 had only one host (all semi concealed) 19 were confined to semi concealed hosts,

none was confined to free living hosts and 5 parasitized both semi concealed and free living hosts.

DISCUSSION

Methodological issues

The studies of host - parasitoid interactions are hindered by many problems which lead to possible bias in their results.

Due to great diversity of both moths and parasitoids and the unevenness of their abundance with many species and interactions being very rare, it is largely impossible to sample all caterpillars and their parasitoids at any site and especially in a tropical rainforest. Even though it took tens of thousands of person days of work to amass this dataset, we still expect to find many new species and interaction if the collecting continues. It would we unimaginable to compile such dataset without the help of local collectors and parataxonomists (Basset *et al.*, 2004).

Main problem which complicates the understanding of general patterns in caterpillar parasitoid interaction is the bias to economically important species (Hawkins, 1994) and to the study of bigger host species i.e. Macrolepidoptera, despite the numerical dominance of Microlepidoptera in natural communities (Novotny *et al.*, 2006). I am not aware of any community study, other than ours, which quantitatively sampled parasitoids from both Macrolepidoptera and Microlepidoptera feeding externally on leaves. Leaf feeding caterpillars of Macrolepidoptera mostly forage freely on the vegetation while caterpillars of Microlepidoptera mostly feed in semi concealed situations (Powell *et al.*, 1999). Both groups interact through shared parasitoids and considering the former without the latter might lead to biased conclusions. The uniqueness of this study in this regard means also a lack of truly comparable results from other studies.

Other problems are common to all rearing surveys, the most serious of them being the reality that usually more than 50% of the caterpillars die in the rearing process. This severely lowers the yield / waste ratio and opens the possibility of skewed results due to possible differential survival of parasitized and parasitoid free caterpillars. Dissecting the dead caterpillars is a very labor intensive task and still leaves open the possibility that the parasitoid larva would be overlooked.

Further, the caterpillars are protected from parasitation from the moment of collection which again can skew the results (with the exception of possible accidental of introducing microtype eggs of Tachinidae, Stireman *et al.*, 2006). Eggs and pupae are rarely found and the pupation takes place in much wider range of microhabitats than the feeding. Current taxonomy of eggs and pupae often makes the species determination impossible. Due to all these reasons eggs and pupae were not sampled in our and similar studies. These effects limit the scope of the study to egg-larval, larval and larval-pupal parasitoids and the results underestimate both the total parasitation rate suffered by the host and number of parasitoid species attacking the host. Parasitoid life forms which attack mainly eggs and pupae are very rare in our

dataset and their general importance cannot be judged from our data, namely idiobionts (Askew & Shaw, 1985), ektoparasitoids and hyperparasitoids. As far as what can be inferred from the biology of parasitoid groups which were reared in this study, only a very small proportion could be hyperparasitoids (Bolton & Gauld, 1996), namely some Chalcidoidea and some Ichneumonidae.

Taxonomy of both hosts and parasitoids is a major challenge in rearing surveys and requires cooperation with many specialists. The species limits should be explored with both morphological and molecular methods (Hajibabaei *et al.*, 2006; Janzen *et al.*, 2005; Smith *et al.*, 2007). Our data match this standard in Lepidoptera taxonomy (Miller *et al.*, 2003), and we are working on the parasitoid taxonomy to meet the standard as well. However in this analysis only small proportion of parasitoid material was formally identified by specialists and the majority of the data is based on my morphospecies assignments.

Proper morphotyping of the caterpillars is needed for the parasitoid to be correctly associated with the host. The resulting 87.4% of parasitoid specimens being safely associated with at least host genera is satisfying when we consider the difficult taxonomy of microlepidoptera caterpillars.

The "most probable host" assumption which was used to circumvent the imperfect matching of parasitoids with hosts is a possible source of analytical bias, which however does not systematically decrease or increase the analyzed variables but brings some noise to the analysis (i.e. among closely related host species, some are analyzed as having more parasitoids than they probably do, but others are analyzed as having less parasitoids than they probably do).

Some possibly important factors were not yet analyzed which lowers the interpretational power of the study, the most important of them being the effect of the host plant (Lill *et al.*, 2002).

I report patterns of parasitism for Hymenoptera and Diptera, but it is important to keep in mind that the Diptera parasitoids come only from the family Tachinidae and the patterns reported for Hymenoptera are mostly driven by Ichneumonoidea and especially Braconidae (Table 1).

Parasitation rate

The overall parasitation rate reported in this study is one of the lowest reported for complex system of externally feeding caterpillars and their parasitoids (Stireman *et al.*, 2005). It becomes the lowest ever reported when we consider the fact that the parasitation rate reported in other papers is based mostly on Macrolepidoptera which are more comparable to our free living hosts. No clear hypothesis lends itself for the explanation of this fact. Our data point does not fit the negative correlation of

parasitation rate on climatic variability of Stireman *et al.*, (2005), scoring both low parasitation rate and low climatic variability. Latitude was not significant predictor of parasitation rate (Stireman *et al.*, 2005), and this issue cannot be solved without adding many more data points. Some other factors such as habitat or history should be also considered, although the parasitation rate on a site with climate similar to our study area was 26% (Gentry & Dyer, 2002; Stireman *et al.*, 2005) compared to 9.6% in our study.

Higher parasitation rate of the semi concealed caterpillars compared to free living caterpillars (Fig. 2a) was reported also in Gentry & Dyer, (2002). Similar relationship was reported also for parasitoid species richness by Hawkins (1994). The difference can be explained by the biology of these two groups of hosts. The semi concealed feeders should be better hosts for parasitoids for several reasons: (i) they are more common (Novotny *et al.*, 2006), (ii) they suffer lower predation (Jeffries & Lawton, 1984) (iii) they are less mobile and therefore more apparent to parasitoids since they tend to stay near the plant tissue they damage, which makes them more easily locatable by chemical signals released when the leaf is damaged (Gentry & Dyer, 2002; Hawkins, 1994).

The differential parasitation of Hymenoptera and Diptera where Hymenoptera parasitize mostly semi concealed feeders, while Diptera parasitize both types of hosts with very similar intensity (Fig. 3a and 4a) was reported before by Hawkins (1994) for parasitoid species richness and the part concerning Macrolepidoptera (mostly free living hosts) also by e.g. (Janzen, 1995; Sheehan, 1994). The minimal parasitism of free living by Hymenoptera can be explained by the experimental results of Gentry & Dyer (2002) that the Hymenoptera parasitoids are heavily deterred by the caterpillar's regurgitating, dropping and biting. The Hymenoptera parasitoids possess a piercing ovipositor which gives them the possibility to directly attack semi concealed hosts (Bolton & Gauld, 1996; Eggleton & Belshaw, 1993).

The Diptera parasitoids rarely have a piercing structure and have to rely on other means of reaching the host. Some oviposit on their host's integument and hatching larvae burrow into the host. Others oviposit or larviposit near a host, and are either consumed as eggs or search out their host as first instar larvae (Eggleton & Belshaw, 1993; Feener & Brown, 1997). We have to wait for the identifications to be more specific about the ovipositing behavior of Diptera in our study.

The Diptera reach very similar parasitation rates in semi concealed and free living hosts. This means that they fail to use the semi concealed hosts (who are generally better suited for parasitation) with higher efficiency. This is probably due to the limitations of the ovipositing behavior. On the other hand, the indirect oviposition of Diptera opens the way for them to parasitize free living hosts.

The taxonomic distribution of Diptera hosts gives indirect support to the assumption that Diptera have problems with attacking smaller hosts (Fig. 4b, note that category

"others" is composed almost exclusively of small sized caterpillars of Choreutidae, Gelechiidae and Thyrididae). This hypothesis needs to be tested directly with caterpillar body size. It brings up the question of what happens to the undersized host which eats a Tachinidae egg but is not big enough to support the parasitoid's development. This might be a parasitoid induced source of mortality for small semi concealed as well as free living hosts.

The active determent of the directly ovipositing parasitoid by the caterpillar together with the inability of Diptera to develop inside a small host would also explain the unusually low parasitation rate of Geometridae (Fig. 2b).

According to our results, the two principal parasitoid groups, Hymenoptera and Diptera, do not appear to be in direct competition as the lack of parasitation by one group is not compensated by the increase of the other. Stireman *et al.* (2005) also found the parasitation rate of Hymenoptera and Diptera uncoupled.

Parasitoid species richness

The strong correlation of parasitoid species richness with number of reared hosts (Fig. 5) is typical for mass rearing studies (Lewis *et al.*, 2002; Sheehan, 1994).

When the hosts are not sampled quantitatively it is usually regarded as sampling artifact (Hawkins, 1994). However in our study, considerable effort was spend to make the sampling effort constant over a tree species and therefore the number of caterpillars reared can be regarded as being close to the real caterpillar relative abundance on that tree (not the overall relative abundance in the habitat as the trees differ very much in the abundance, Novotny *et al.*, 2004) This suggests that the more common caterpillar species really do have more parasitoid species, probably because they represent a bigger resource than rare host species. This pattern is similar to that found for British tree species and their insect herbivores as tree species more common in Britain also host more herbivore species (Kelly & Southwood, 1999).

The parasitation rate and parasitoid species richness are strongly correlated in our data, which was shown by the regressions of one on the other. This pattern suggests that additional parasitoid species may increase overall parasitation rate.

The ecological variables explained low proportion of the variability in parasitoid species richness in both (Sheehan, 1994) and our study. Semi concealed hosts had more parasitoid species than free living hosts (Fig. 6a, Hawkins, 1994), the same pattern as with parasitation rate. The pattern with Hymenoptera having much more semi concealed host species than free living host species and Diptera having similar number of host species in both type of hosts is also a parallel to the same pattern found for parasitation rate. I expect the same forces (mentioned before) to drive this pattern for both parasitation rate and parasitation species richness. The insignificance of host taxonomy (Fig. 6b) in the analysis cannot be taken as a proof of nonexistent

differences, and would be better tested with balanced categories, which were however not provided by the quantitative sampling.

Dominance in parasitoid communities on particular hosts

The most abundant parasitoid on particular host was typically responsible for more than 50% of total parasitation of that host, leaving just about 20% of parasitations to the second most abundant parasitoid and about 10% to the third (Fig. 7). Interestingly, similar patter of high dominance of the most abundant species was found also in the communities of caterpillars feeding on a single host plant species (Novotny *et al.*, 2002c).

Parasitoid host specificity

The host specificity decreases very slowly with the number of reared parasitoids (Fig. 8), which suggests that we can't expect many more additional hosts for the parasitoids studied her even with additional sampling on the same tree species. I don't expect the common parasitoid species in our analysis to have regular hosts outside the studied community, as the Lepidoptera are by far the most common leaf feeding herbivores on the study site (Novotny *et al.*, 2002a) and miners reared from same tree species as the caterpillars in this study have completely different parasitoids (our unpublished data).

New hosts would be likely found if the sampling was extended to other plant species. The host specificity reported here is slightly underestimated due to the use of "most probable host" assumption in the analysis.

The finding that Hymenoptera and Diptera host specificity are identical (Fig. 9a) is novel and unexpected, although it was previously mentioned for Macrolepidoptera by Stireman *et al.* (2006) as a preliminary result of Janzen & Hallwachs (2005). However Janzen & Hallwachs's (2005) result refers mostly to free living caterpillars, where we found the Hymenoptera to be more host specific. This is possibly also due to very low parasitation rate of Hymenoptera on the free living hosts (Fig. 9c). Tachinidae are known to have wider host range than Hymenoptera (Eggleton & Belshaw, 1993; Feener & Brown, 1997; Stireman *et al.*, 2006) on the level of whole groups. It was generally assumed that they will be more generalist than Hymenoptera on the community level as well, but we show that this is not true for communities of externally leaf feeding Lepidoptera and their parasitoids. The Tachinidae could have easily been more generalist in the host use considering the diversity of the hosts studied (Appendix C), but they are not. The general idea that Hymenoptera are more host specific in caterpillar communities might be partially an artifact as many studies focused disproportionately on free feeding hosts.

Both Tachinidae and Hymenoptera have mechanisms to overcome the immunity reaction of the host, and the differences in this trait were thought to explain the lower host specificity of Tachinidae (Stireman *et al.*, 2006). Many Tachinidae form a

respiratory funnel which allows them to overcome the host's encapsulation response (Stireman *et al.*, 2006). On the other hand, Hymenoptera produce venoms and immune-suppressant substances such as polyDNA viruses (Bolton & Gauld, 1996; Qucke, 1997) which can be injected in the host with an ovipositor. The absence of the difference in host specificity reported here leads to the hypotheses that the way how the parasitoid overcomes the host's immunity reaction is either not important for the structure of host ranges in the studied system, or both groups of parasitoids are approximately equally good at it.

From the 58 parasitoid species with five or more reared specimens, nearly all species were either confined to semi concealed hosts or attacked both semi concealed and free living host. No Hymenoptera species was specialized to a free living host, and only three species specialized to free living hosts were found among Diptera. However, those three species had only 5 or 6 specimens reared and it is therefore probable that some semi concealed hosts would be recorded for them if the sampling continued.

The semi concealed hosts therefore seem to drive the host - parasitoid interaction of folivorous externally feeding Lepidoptera and their parasitoids. Generally, this is not very surprising as they are much more common in the nature and better suited for parasitation. This pattern can be also thought of as a case of apparent competition (Jeffries & Lawton, 1984) between two guilds of caterpillars. If this pattern is shown to be general it also implies that analyses of parasitation patterns based only on Macrolepidoptera are not appropriate, because they describe a pattern which is mostly a side effect of parasitation of semi concealed hosts. This in turn applies for instance to evolutionary considerations on the adaptive significance of oviposition behavior (Stireman *et al.*, 2006).

CONCLUSIONS

A number of important patterns in host - parasitoid interaction of folivorous externally feeding Lepidoptera and their parasitoids is reported based on extensive rearing survey in Papua New Guinea rainforest.

Feeding mode of the host caterpillar seems to be the most important determinant of host - parasitoid interactions in the studied system with semi concealed hosts (mostly Microlepidoptera) being much more common and having higher parasitation rate and more parasitoid species than free living hosts (mostly Macrolepidoptera).

The two principal parasitoid groups use semi concealed and free living hosts differently with Hymenoptera parasitising almost exclusively semi concealed hosts and Diptera using both groups of hosts with similar parasitation rate. This pattern is explained by (i) the overall dominance of semi concealed hosts in the nature, (ii) the effectivity of free living caterpillar defenses and (iii) the differences in parasitoid ovipositor and oviposition traits.

Host specificity was found to be the same in Hymenoptera and Diptera, despite the generally lower host specificity of Tachinidae reported in the literature, so the physiological mechanisms of overcoming the host's immunity reaction probably don't play as important role as expected in the differences in host specificity in the studied system.

Near absence of parasitoids specialized on free living hosts suggests that semi concealed hosts drive the host - parasitoid interaction in the studied system and the parasitation of free living hosts is mostly a side effect of parasitation of semi concealed hosts.

Further quantitative studies covering both Macrolepidoptera and Microlepidoptera are needed to evaluate the generality of these results.

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APPENDIX A. List of plant species sampled.

APPENDIX B. List of Lepidoptera species reared.

Moth Family	Moth Category	Moth Genus	Moth Species	Moth Author	Feeding Mode	Code
Arctiidae	others	Asura	pallida?	Rotschild	free living	XXXX073
Arctiidae	others	Chamaita	metamelaena	Hampson 1900	free living	LYMA035
Arctiidae	others	Darantasia	caerulescens	Druce	free living	ARCT002
Arctiidae	others	Eugoa	sp. near <i>perfasciata</i>	Rothchild	free living	ARCT010
Arctiidae	others	Spilosoma	niceta	Stoll	free living	NOCT049
Arctiidae	others	Trichalis	sp. near <i>aereoplagiata</i>	Rothchild	free living	ARCT011
Arctiidae	others	unknown	sp.		free living	ARCT012
Arctiidae	others	unknown	sp.		free living	LYMA073
Choreutidae	others	Brenthia	n. sp.		semi concealed	CHOR00
Choreutidae	others	Brenthia	sp.		semi concealed	CHOR00
Choreutidae	others	Brenthia	sp.		semi concealed	CHOR00
Choreutidae	others	Brenthia	sp.		semi concealed	CHOR01
Choreutidae	others	Brenthia	sp.		semi concealed	CHOR01
Choreutidae	others	Choreutis	basalis	(Felder & Rogenhofer)	semi concealed	TORT012
Choreutidae	others	Choreutis	chí?	(Durrant)	semi concealed	TORT013
Choreutidae	others	Choreutis	lutescens	(Felder & Rogenhofer)	semi concealed	TORT00
Choreutidae	others	Choreutis	sp.	- 3 /	semi concealed	CHOR01
Choreutidae	others	Choreutis	sp. cf. anthorma	(Meyrick)	semi concealed	TORT00
Choreutidae	others	Saphta	sp. cf <i>exanthista</i> & divitiosa	(Meyrick) / Walker	semi concealed	TORT00
Choreutidae	others	unknown	sp.		semi concealed	CHOR01
Choreutidae	others	unknown	sp.		semi concealed	CHOR01
Crambidae	Pyraloidea	Agrotera	ignepictoides	Rothschild	semi concealed	CRAM06
Crambidae	Pyraloidea	Agrotera	sp. 1 nr. <i>basinotata</i>		semi concealed	CRAM09
Crambidae	Pyraloidea	Agrotera	sp. nr. but not <i>effertali</i> s	Walker	semi concealed	PYRA01
Crambidae	Pyraloidea	Chalcidoptera	emissalis	(Walker)	semi concealed	CRAM06
Crambidae	Pyraloidea	Coelorhyncidia	nitidalis	Hampson	semi concealed	PYRA00
Crambidae	Pyraloidea	Coelorhyncidia	purpurea	Hampson	semi concealed	CRAM04
Crambidae	Pyraloidea	Coelorhyncidia	sp.		semi concealed	CRAM04
Crambidae	Pyraloidea	Cydalima	diaphanalis complex		semi concealed	CRAM06
Crambidae	Pyraloidea	Diaphania	indica	(Saunders)	semi concealed	CRAM06
Crambidae	Pyraloidea	Eutectona	sp.		semi concealed	PYRA00
Crambidae	Pyraloidea	Glyphodes	doleschalii	Lederer	semi concealed	CRAM01
Crambidae	Pyraloidea	Glyphodes	eurygania	Druce	semi concealed	CRAM01
Crambidae	Pyraloidea	Glyphodes	margaritaria	(Cramer)	semi concealed	CRAM00
Crambidae	Pyraloidea	Glyphodes	sp. cf. stolalis	Guenee	semi concealed	CRAM00
Crambidae	Pyraloidea	Haritalodes	adjunctalis	Leraut 2005	semi concealed	CRAM01
Crambidae	Pyraloidea	Herpetogramma	bractealis	(Kenrick)	semi concealed	PYRA02
Crambidae	Pyraloidea	Herpetogramma	nr. licarsisalis	(Walker) 1859	semi concealed	CRAM06
Crambidae	Pyraloidea	Musotima	sp.	(semi concealed	CRAM07
Crambidae	Pyraloidea	Nacoleia	octasema	(Meyrick)	semi concealed	PYRA02
Crambidae	Pyraloidea	Orthospila	sp. A	(Walker)	semi concealed	CRAM01
Crambidae	Pyraloidea	Orthospila	sp. C	(Walker)	semi concealed	CRAM05
Crambidae	Pyraloidea	Pagyda	nr. but not <i>ochrealis</i>	Whalley	semi concealed	PYRA01
Crambidae	Pyraloidea	Parotis	sp. nr. <i>marginata</i>	(Hampson)	semi concealed	GEOMO
Crambidae	Pyraloidea	Parotis	sp. m. marginata suralis	(Lederer)	semi concealed	CRAM03
Crambidae	Pyraloidea	Pleuroptya	sabinusalis	(Walker)	semi concealed	CRAM03
Crambidae	Pyraloidea		sellalis	(Guenee) 1854	semi concealed	CRAM01 CRAM07
Crambidae	Pyraloidea Pyraloidea	Pleuroptya Pseudocera	nr. trissosticha	(Guerree) 1004	semi concealed	CRAM07
	-			Hompson		
Crambidae	Pyraloidea Dyraloidea	Pycnarmon	argenticincta	Hampson	semi concealed	CRAM03
Crambidae	Pyraloidea	Pycnarmon	jaguaralis papualis	Munroe	semi concealed	CRAM02

Moth Family	Moth Category	Moth Genus	Moth Species	Moth Author	Feeding Mode	Code
Crambidae	Pyraloidea	Syllepte	ochrisalis	S. E. Miller	semi concealed	CRAM079
Crambidae	Pyraloidea	Talanga	deliciosa	(Butler)	semi concealed	CRAM008
Crambidae	Pyraloidea	Talanga	excelsalis moresbyensis	(Strand)	semi concealed	CRAM002
Crambidae	Pyraloidea	Talanga	polyzonalis	(Hampson)	semi concealed	CRAM009
Crambidae	Pyraloidea	Talanga	sexpunctalis	(Moore)	semi concealed	CRAM006
Crambidae	Pyraloidea	unknown	sp.	()	semi concealed	CRAM07
Crambidae	Pyraloidea	unknown	sp.		semi concealed	CRAM07
Crambidae	Pyraloidea	unknown	sp.		semi concealed	CRAM092
Elachistidae	others	gen. nr. <i>Peritomenta</i>	sp.		semi concealed	XXXX093
Elachistidae	others	Peritornenta	sp.		semi concealed	XXXX097
Elachistidae	others	unknown	sp.		semi concealed	TORT167
Elachistidae	others	unknown	sp.		free living	XXXX109
Elachistidae	others	unknown	sp.		semi concealed	XXXX117
Gelechiidae	others	Anarsia	sp.		semi concealed	XXXX116
Gelechiidae	others	Dichomeris	ochreoviridella	(Pagenstecher)	semi concealed	XXXX048
Gelechiidae	others	Dichomeris	sp.		semi concealed	XXXX068
Gelechiidae	others	Dichomeris	sp.		semi concealed	XXXX095
Gelechiidae	others	Idiophantis	sp. n. sp.		semi concealed	TORT163
Gelechiidae	others	unknown	sp.		semi concealed	XXXX120
Gelechioidea (sf)	others	unknown	sp.		semi concealed	TORT200
Gelechioidea (sf)	others	unknown	sp.		semi concealed	TORT202
Gelechioidea (sf)	others	unknown	sp.		semi concealed	XXXX126
Geometridae	Geometridae	Hypomecis	infaustaria	Walker	free living	GEOM02
Geometridae	Geometridae	Agathiopsis	maculata	Warren	free living	GEOM13
Geometridae	Geometridae	Amblychia	angeronaria	Guenee	free living	GEOM08
Geometridae	Geometridae	Catoria	delectaria	(Walker, 1866)	free living	GEOM00
Geometridae	Geometridae	Chrysochloroma	electrica or saturata	Warren	free living	GEOM12
Geometridae	Geometridae	Chrysocraspeda	rothschildi ?	Warren	free living	GEOM12
Geometridae	Geometridae	Chrysocraspeda	sp.		free living	GEOM11
Geometridae	Geometridae	Chrysocraspeda	sp. nr. <i>inundata</i>	Warren	free living	GEOM11
Geometridae	Geometridae	Cleora	decisaria	(Walker) 1866	free living	GEOM01
Geometridae	Geometridae	Cleora	repetita	Butler 1882	free living	GEOM02
Geometridae	Geometridae	Craspedosis	ovalis	Warren 1896	free living	GEOM10
Geometridae	Geometridae	Cyclophora	glomerata	Warren	free living	GEOM13
Geometridae	Geometridae	Derambila	stigicosta	Warren	free living	PYRA023
Geometridae	Geometridae	Dysgnathia	sp. near <i>albolineata</i>	Bethune- Baker), 1906	free living	GEOM10
Geometridae	Geometridae	Ectropis	bhurmitra	(Walker) 1860	free living	GEOM01
Geometridae	Geometridae	Eucyclodes	absona	(Warren)	free living	GEOM11
Geometridae	Geometridae	Eucyclodes	albilauta	(Warren) 1897	free living	GEOM02
Geometridae	Geometridae	Eucyclodes	sp. nr <i>griseonotata</i>	Warren	free living	GEOM10
Geometridae	Geometridae	Hyposidra	incomptaria	Walker 1866	free living	GEOM01
Geometridae	Geometridae	Hyposidra	talaca	Walker	free living	GEOM01
Geometridae	Geometridae	Oenospila	sp. nr. <i>flavilinea</i>		free living	GEOM15
Geometridae	Geometridae	Paradromula	xylinopa	Meyrick 1899	free living	GEOM05
Geometridae	Geometridae	Paradromulia	nr. but not lignifascia	Warren	free living	GEOM13
Geometridae	Geometridae	Perixera	ampligutta	Warren 1896	free living	GEOM03
Geometridae	Geometridae	Perixera	ceramis	(Meyrick)	free living	GEOM10
Geometridae	Geometridae	Pingasa	lariaria or nr.	(Walker)	free living	GEOM14
Geometridae	Geometridae	Pingasa	sp.	Stoll 1782	free living	GEOM00
Geometridae	Geometridae	Scopula	amala	Meyrick 1899	free living	GEOM05

Moth Family	Moth Category	Moth Genus	Moth Species	Moth Author	Feeding Mode	Code
Geometridae	Geometridae	Thalassodes (s.l.)	albifusa	(Warren) 1906	free living	GEOM013
Geometridae	Geometridae	Tiruvaca	subcostalis	(Walker)	free living	GEOM11
Geometridae	Geometridae	unknown	sp.	. ,	free living	GEOM07
Geometridae	Geometridae	unknown	sp.		free living	GEOM10
Geometridae	Geometridae	unknown	sp.		free living	GEOM10
Geometridae	Geometridae	unknown	sp.		free living	GEOM11
Geometridae	Geometridae	unknown	sp.		free living	GEOM11
Geometridae	Geometridae	unknown	sp.		free living	GEOM12
Geometridae	Geometridae	unknown	sp.		free living	GEOM13
Geometridae	Geometridae	unknown	sp.		free living	GEOM13
Geometridae	Geometridae	unknown	sp.		free living	GEOM14
Geometridae	Geometridae	unknown	sp.		free living	GEOM14
Geometridae	Geometridae	unknown	sp.		free living	GEOM15
Geometridae	Geometridae	Zeugma	sp. recusataria	Walker 1862	free living	GEOM10
Gracillariidae	others	unknown			semi concealed	XXXX111
Hesperiidae	butterflies	Chaetocneme	sp. <i>lunula</i>			HESP005
•				Oborthur 1979	free living	
Hesperiidae	butterflies	Notocrypta	renardi	Oberthur 1878	free living	HESP006 HESP007
Hesperiidae	butterflies	Sabera	sp.	-	semi concealed	
Hyblaenidae	others	Hyblaea	amboinae	Felder	semi concealed	HYBL003
Hyblaenidae	others	Hyblaea	constellata	Guenee	free living	HYBL001
Hyblaenidae	others	Hyblaea	sp. near <i>puera</i>	Cramer 1777	free living	HYBL002
Hypertrophidae	others	unknown	sp. nr. not	Mouriek	semi concealed	HYPE001
mmidae	others	Imma	campsigramma & crocozela	Meyrick	semi concealed	IMMI001
Immidae	others	Imma	sp.		semi concealed	TORT158
mmidae	others	Imma	sp.		semi concealed	TORT159
mmidae	others	Moca	congrualis	(Walsingham)	free living	TORT071
_acturidae	others	Lactura	sp. nr. <i>rhodographa</i>	Meyrick 1928	free living	LIMA030
Lacturidae	others	unknown	sp.		free living	LIMA029
Lecithoceridae	others	Scythropiodes	n. sp. near <i>perissa</i>	(Diakonoff)	semi concealed	XXXX090
imacodidae	others	Mambara	robigonosa ?	Hering 1931	free living	GEOM08
Limacodidae	others	unknown	sp.		free living	LIMA025
Lycaenidae	butterflies	Deudorix	epirus		free living	LYCA018
Lycaenidae	butterflies	Philiris	helena helena	(Snellen)	free living	LYCA006
Lycaenidae	butterflies	Philiris	moira	. ,	free living	LYCA001
Lymantriidae	others	Arctornis	sp. nr. <i>intacta</i>	Walker	free living	LYMA007
Lymantriidae	others	Artaxa	sp.	Walker	free living	LYMA015
Lymantriidae	others	Euproctis	sp.		free living	LYMA003
Lymantriidae	others	Nygmiini	sp. 2		free living	LYMA038
_ymantriidae	others	Olene	nr. <i>mendosa</i>	Huebner	free living	LYMA039
_ymantriidae	others	Somena	alba	(Bethune- Baker)	free living	LYMA060
_ymantriidae	others	Teia	nr. but not dewara	(Swinhoe) 1903	free living	LYMA001
_ymantriidae	others	unknown	sp.		free living	LYMA033
_ymantriidae	others	unknown	sp.		free living	LYMA045
_ymantriidae	others	unknown	sp.		free living	LYMA071
Noctuidae	Noctuidae	Achaea	janata	Linnaeus	free living	NOCT019
Noctuidae	Noctuidae	Anomis (s.l.)	sp.		free living	NOCT083
Noctuidae	Noctuidae	Asota	carica	(Fabricius)	free living	NOCT010
Noctuidae	Noctuidae	Asota	heliconia	(Linnaeus)	free living	NOCT002
Noctuidae	Noctuidae	Asota	plana	Walker	free living	NOCTOO
	Noctuidae	Asota	versicolor	F	free living	NOCT004
Noctuidae						
Noctuidae Noctuidae	Noctuidae	Avatha	pulcherima	(Butler) 1892	free living	NOCT051

Moth Family	Moth Category	Moth Genus	Moth Species	Moth Author	Feeding Mode	Code
Noctuidae	Noctuidae	Chasmina	tibiopunctata	Bethune-Baker	free living	LYMA062
Noctuidae	Noctuidae	Chrysodeixis	dinawa	(Bethune- Baker) 1906	free living	NOCT069
Noctuidae	Noctuidae	Ніроера	porphyrialis	(Pagenstecher 1900)	free living	NOCT053
Noctuidae	Noctuidae	Mecistoptera	franzwagneri	Lodl	free living	GEOM024
Noctuidae	Noctuidae	Mecistoptera	n. sp.		free living	XXXX092
Noctuidae	Noctuidae	Mocis	trifasciata	(Stephens)	free living	NOCT079
Noctuidae	Noctuidae	Ophyx	crinipes	Felder	free living	NOCT099
Noctuidae	Noctuidae	Parilyrgis	intacta	(Hampson)	free living	PYRA010
Noctuidae	Noctuidae	Piratisca	minax	Meyrick 1902	free living	GEOM06
Noctuidae	Noctuidae	Rusicada	nigritarsus xanthochroa	(Butler)	free living	NOCT077
Noctuidae	Noctuidae	Savara	pallidapex	Holloway 2005	free living	NOCT081
Noctuidae	Noctuidae	Spodoptera	litura		free living	NOCT067
Noctuidae	Noctuidae	Targalla	palliatrix	(Guenee) 1852	free living	NOCT064
Noctuidae	Noctuidae	unknown	sp.		free living	GEOM154
Noctuidae	Noctuidae	unknown	sp.		free living	GEOM15
Noctuidae	Noctuidae	unknown	sp.		free living	GEOM15
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT071
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT078
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT084
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT085
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT087
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT096
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT101
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT108
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT122
Noctuidae	Noctuidae	unknown	sp.		free living	NOCT123
Noctuidae	Noctuidae	unknown	sp.		free living	NOTO005
Noctuidae	Noctuidae	unknown	sp.		free living	THYR011
Noctuidae	Noctuidae	unknown	sp.		free living	TORT201
Nolidae	others	Barasa	cymatistis	Meyrick 1889	free living	NOCT065
Nolidae	others	Beara	falcata	Barlow	free living	LIMA024
Nolidae	others	Chora	huntei	Warren	free living	PSYC007
Nolidae	others	Earias	uniplaga	Bethune-Baker	free living	LYMA059
Nolidae	others	Giaura	leucophaea	Hampson	free living	GEOM13
Nolidae	others	Lophothripa	vitea	Swinhoe	free living	TORT137
Nolidae	others	unknown	sp.	Swinibe	free living	TORT157
Notodontidae	others	Chadisra	sp. striata	Rothschild	free living	NOTO004
Nymphalidae	butterflies	Cyrestis	acilia	Godart	free living	NYMP002
Nymphalidae	butterflies	Euploea	leucosticos	Gmelin	free living	NYMP002
Nymphalidae	butterflies	Mycalesis	duponchelii	Gillellin	free living	NYMP013
Nymphalidae	butterflies	Taenaris	sp. probably <i>myops</i>	C&R Felder, 1860	free living	NYMP012
Oecophoridae	others	Stathmopoda	sp. nr. <i>masinissa</i>	Meyrick	semi concealed	XXXX108
Oecophoridae	others	Stathmopoda	sp. m. masimosa		semi concealed	XXXX118
Oecophoridae	others	unknown	sp.		semi concealed	TORT150
Peleopodidae	others	Acria	sciogramma	Meyrick 1915	semi concealed	TORT130
Psychidae	others	unknown	sp.		free living	PSYC022
Pyralidae	Pyraloidea	Agrotera	coelatalis	Walker	semi concealed	PYRA018
Pyralidae Pyralidae	Pyraloidea	Macna	n. sp. nr. <i>atrirufalis</i>	Hampson	semi concealed	TORT149
Pyralidae Pyralidae	Pyraloidea	Macna	oppositalis	(Walker)	semi concealed	TORT148
Pyralidae Pyralidae	Pyraloidea	Macna		(walker)	semi concealed	TORT140
-	-		sp. melanoperalis	Hampson		
Pyralidae Dyralidae	Pyraloidea	Orthaga	melanoperalis	Hampson	semi concealed	PYRA002
Pyralidae	Pyraloidea	Orthaga	sp. nr. <i>percnodes</i>		semi concealed	NOCT020

Moth Family	Moth Category	Moth Genus	Moth Species	Moth Author	Feeding Mode	Code
Pyralidae	Pyraloidea	Pagyda	salvalis	Walker 1859	semi concealed	PYRA024
Pyralidae	Pyraloidea	Pycnarmon	glaucias	(Meyrick)	semi concealed	PYRA019
Pyralidae	Pyraloidea	Pycnarmon	praeruptalis	(Lederer) 1863	free living	PYRA027
Pyralidae	Pyraloidea	Unadophanes	trissomita	(Turner) Rothschild &	semi concealed	XXXX021
Sphingidae	others	Macroglossum	inspida papuanum	Jordan Rothschild &	free living	SPHI009
Sphingidae	others	Macroglossum	melas pullius	Jordan	free living	SPHI004
Thyrididae	others	Addaea	pusilla	(Butler)	semi concealed	TORT062
Thyrididae	others	Addaea	sp. near probolopsis	Meyrick	semi concealed	CRAM083
Thyrididae	others	Aglaopus	ignefissa	(Warren) 1908	semi concealed	THYR006
Thyrididae	others	Homodes	iomolybda	Meyrick 1889	free living	THYR009
Thyrididae	others	Mellea	sp.		semi concealed	THYR012
Thyrididae	others	Mellea	nitida	(Pagenstecher)	semi concealed	TORT083
Thyrididae	others	Mellea	ordinaria	(Warren)	semi concealed	THYR001
Thyrididae	others	Mellea	ramifera	(Warren)	semi concealed	TORT075
Thyrididae	others	Mellea	sp. near but not ramife	era and <i>nitida</i>	semi concealed	THYR016
Thyrididae	others	Pharambora	splendida	(Butler)	semi concealed	THYR003
Thyrididae	others	Rhodoneura	aurata	(Butler)	semi concealed	THYR005
Thyrididae	others	Striglina	asinina	Warren 1899	semi concealed	NOCT048
Thyrididae	others	Striglina	cinnamomea	(Rothschild)	semi concealed	THYR010
Thyrididae	others	unknown	sp.	· · ·	free living	THYR020
Thyrididae	others	unknown	sp.		semi concealed	THYR023
Thyrididae	others	unknown	sp.		semi concealed	THYR025
Tortricidae	Tortricidae	Adoxophyes	fasciculana	(Walker) 1866	semi concealed	TORT034
Fortricidae	Tortricidae	Adoxophyes	sp.	(Trainer) rooo	semi concealed	TORT131
Fortricidae	Tortricidae	Adoxophyes	sp. 11		semi concealed	TORT094
Fortricidae	Tortricidae	Adoxophyes	sp. 6A		semi concealed	TORT066
Fortricidae	Tortricidae	Adoxophyes	sp. 2 <i>nebrodes</i> , female	Diakonoff	semi concealed	TORT022
Tortricidae	Tortricidae	Adoxophyes	templana complex		semi concealed	TORT008
Tortricidae	Tortricidae	Adoxophyes	thoracica	Diakonoff	semi concealed	TORT044
Tortricidae	Tortricidae	Adoxophyes	tripselia	(Lower) 1908	semi concealed	TORT037
Tortricidae	Tortricidae	Ancylophyes	sp.		semi concealed	XXXX114
Tortricidae	Tortricidae	Archigraptis	chrysodema	(Diakonoff) 1952	semi concealed	TORT196
Fortricidae	Tortricidae	Dudua	n. sp. nr. <i>aprobola</i>	(Meyrick) 1886	semi concealed	TORT143
Tortricidae	Tortricidae	gen. nov. nr. <i>Loboschiza</i>	sp. nov.		semi concealed	TORT172
Tortricidae	Tortricidae	Heleanna	sp. 1		semi concealed	TORT065
Tortricidae	Tortricidae	Holocola	n. sp.		semi concealed	TORT170
Fortricidae	Tortricidae	Homona	aestivana	(Walker) 1866	semi concealed	TORT085
Fortricidae	Tortricidae	Homona	mermerodes	Meyrick 1910	semi concealed	TORT040
Fortricidae	Tortricidae	Homona	phanaea	Meyrick	semi concealed	TORT051
Tortricidae	Tortricidae	Homona	salaconis group	(Meyrick) 1912	semi concealed	TORT086
Tortricidae	Tortricidae	Homona	trachyptera	Diakonoff	semi concealed	TORT067
Tortricidae	Tortricidae	Isotenes	sp. nr. but not <i>miserana</i>	(Walker)	semi concealed	TORT061
Fortricidae	Tortricidae	Macrothyma	sanguinolenta	(Diakonoff) 1941	semi concealed	TORT098
Fortricidae	Tortricidae	Nycteola	indicatana	(Walker)	free living	TORT145
Tortricidae	Tortricidae	Ophiorrhabda	deceptor	Diakonoff	semi concealed	TORT142
Tortricidae	Tortricidae	Sorolopha	cyclotoma	Lower	free living	TORT183
Tortricidae	Tortricidae	Sorolopha	sp.		semi concealed	TORT147
Tortricidae	Tortricidae	Sorolopha	sp. 8		semi concealed	TORT117
Tortricidae	Tortricidae	Sorolopha	sp. probably caryochlora	Diakonoff	semi concealed	TORT184
Tortricidae	Tortricidae	Statherotis	leucapsis	(Meyrick) 1902	semi concealed	TORT129

Moth Family	Moth Category	Moth Genus	Moth Species	Moth Author	Feeding Mode	Code
Tortricidae	Tortricidae	unknown	sp.		semi concealed	TORT130
Tortricidae	Tortricidae	unknown	sp.		semi concealed	TORT144
Tortricidae	Tortricidae	unknown	sp.		semi concealed	TORT15
Tortricidae	Tortricidae	unknown	sp.		semi concealed	TORT16
Tortricidae	Tortricidae	unknown	sp.		semi concealed	TORT18
Tortricidae	Tortricidae	unknown	sp.		free living	TORT197
Tortricidae	Tortricidae	unknown	sp.		semi concealed	TORT20
Tortricidae	Tortricidae	unknown	sp.		semi concealed	TORT204
Tortricidae	Tortricidae	unknown	sp.		semi concealed	TORT20
Tortricidae	Tortricidae	unknown	sp.		semi concealed	TORT20
Tortricidae	Tortricidae	Xenothictis	n. sp.		semi concealed	TORT03
XXXX	others	unknown	sp.		semi concealed	XXXX11
XXXX	others	unknown	sp.		semi concealed	XXXX130
XXXX	others	unknown	sp.		semi concealed	XXXX13
XXXX	others	unknown	sp.		free living	XXXX13
XXXX	others	unknown	sp.		free living	XXXX13
XXXX	others	unknown	sp.		semi concealed	XXXX13
XXXX	others	unknown	sp.		semi concealed	XXXX150

Family	Species	Parasitised Species	
Geometridae	43		6
Tortricidae	39		14
Crambidae	37		20
Noctuidae	37		ç
Thyrididae	16		6
Choreutidae	13		8
Pyralidae	11		7
Lymantriidae	10		Ę
Gelechiidae	9		Ę
Arctiidae	8		2
Nolidae	7		2
unknown	7		
Elachistidae	5		
Immidae	4		2
Nymphalidae	4		2
Hesperiidae	3		
Hyblaenidae	3		
Lycaenidae	3		
Oecophoridae	3		
Lacturidae	2		2
Limacodidae	2		
Sphingidae	2		
Gracillariidae	1		
Hypertrophidae	1		
Lecithoceridae	1		
Notodontidae	1		
Peleopodidae	1		
Psychidae	1		
Grand Total	274		105

APPENDIX C. Overview of number of Lepidoptera species reared from each family and number of species for which parasitoids were recorded.