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SWEET OR SAVOURY? ADULT FEEDING PREFERENCES OF LEPIDOPTERA ATTRACTED TO BANANA AND PRAWN BAITS IN THE ORIENTAL TROPICS

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ABSTRACT. — A survey of Lepidoptera using pairs of baited traps, one with fermenting banana and one with rotting prawn heads, was conducted for just over a year at five sites at the Genting Tea Estate in Pahang, Malaysia. All individuals were collected and identified at least to morphospecies and mostly to species. 519 species were recorded. The results are presented using the most recent classification for the Order. Striking differences at higher taxonomic levels were noted, with over twice as many species and more higher taxonomic groups being taken in the prawn traps. Comparisons are made with data for moths obtained at banana bait in Sabah, Malaysia, and with records for butterflies made in Sabah and Vietnam. Comparison is also made with an experiment using sugar and banana baits in Bavaria. The results are related to observations made in Southeast Asia of other facets of adult feeding behaviour such as fruit-piercing, feeding at tear fluids in the eyes of mammals (lacryphagy), blood-sucking, and mud-puddling. Possible relationship to larval host-preference is explored. Comments are made on sex ratios involved across the range of feeding behaviour, and also on the utility of bait-trapping for assessing diversity in tropical Lepidoptera.

KEY WORDS. — Malaysia, Vietnam, moths, butterflies, fruit-piercing, lacryphagy, blood-sucking, mud-puddling

INTRODUCTION

There has been a long tradition for using baits to collect Lepidoptera. Guides to temperate Macroheterocera such as South ([1907] to 1961) contain recipes for sugaring mixtures that involve the boiling up of coarse brown sugar, treacle, beer or other alcoholic beverages and the addition of various fruit essences. They provided instructions for deployment of the mixture on tree-trunks, fences etc., or hanging up rags or ropes that had been soaked in it. Indeed, this was probably the main method of collecting nocturnal moths until the advent of powerful light-traps, though Alfred Russel Wallace (1869) was an early advocate of the value of a good light source for attracting moths in the tropics, and the fourth edition of South cited above also gives details of the Robinson-pattern light-trap.

Early butterfly collecting in Malaysia also benefited from the use of baits, and essential ingredients of collecting forays consisted of rotting prawns and red wine, the former to bring in the quarry and the latter to sustain the spirits of the hunters. Fermentation was also important in ensuring that banana baits were in optimum condition.

In more recent times there has been an increasing trend to quantify the diversity of insects in various parts of the world and to monitor the impact of human activity on this diversity. A. S. Corbet, from his assiduous collecting of butterflies in Malaysia, made a significant contribution to this in one of the classic papers in the developing of a more statistical approach to measurement of diversity (Fisher et al., 1943). Data from light-trapping have continued to make a significant contribution to such studies for moths but, for butterflies, fruit-baiting has also provided a major means for study of diversity in the tropics, though primarily for the family Nymphalidae, e.g., by DeVries et al. (1997, 1999, 2011) in the Neotropics, Molleman et al. (2005a, 2005b, 2005c) in Africa and, in Southeast Asia, Beck & Schulze (2000), Schulze et al. (2001), and Tangah et al. (2004). The moth data from Sabah presented here are derived from a further such study (Benedick et al., 2006, 2007, 2009).

Quantification of moth data from bait collecting for diversity studies has also involved red wine, but as an ingredient of a banana bait and in temperate localities in central Europe (Süssenbach & Fiedler, 1999), and this study is used to provide a useful comparison with the results of our tropical surveys in assessing whether baiting may also have a role in assessing diversity in lowland sites.

The studies we present here may well break new ground in two ways. First, we provide a choice at each study site between a fruit bait (banana) and a savoury one (prawn), offering essentially different substances to adult Lepidoptera, sugars on the one hand and proteins and salts on the other, though fruit is not devoid of protein and can also be a rich source of amino acids (Molleman et al., 2005a; Beck, 2007). However, choice between a range of savoury baits was provided for butterflies in Sabah by Beck et al. (1999), and Molleman et al. (2005c) used pairs of traps with fermenting banana or rotting fish in Africa as a preliminary way of identifying butterflies relevant to their study of puddling behaviour in species attracted to carrion. Second, we have tried to assess in detail the extent to which the very considerable higher taxonomic diversity of Lepidoptera present in the tropics responded to the two bait types. In doing the latter, we have had the benefit of the considerable advances that have occurred over the past two decades in developing a phylogenetic classification of the Order, mainly, but not entirely, through DNA sequencing. These are reviewed in more detail in the next two sections and are utilised in the ordering of the results.

Much general information on adult feeding in Lepidoptera (including the lack of it in some groups) has accumulated over the last two centuries as reviewed by Scoble (1992), but only in recent time has a considerable effort been devoted to studying: the physiological requirements involved that may not have been fully achieved by the resource-building undertaken by the larval stage; the adult feeding behavioural aspects of gaining these requirements; and morphological adaptations that have occurred to facilitate their acquisition.

The work of Wilhelm Büttiker and, with particular relevance to Southeast Asia, Hans Bänziger amongst others has been to the forefront in this, particularly with regard to both sweet, the development of fruit-piercing behaviour, and savoury, the development of lachryphagy and blood-sucking, all in moths. Our results will be compared and contrasted with observations of these aspects in our discussion.

One aspect of adult feeding where our study falls short is with regard to nectaring, obvious in most butterflies but hard to assess in mainly nocturnal insects such as most moths. It could be assumed that any moth with a well-developed proboscis (seen mainly in the Ditrysia) will take nectar, but no means is yet available for quantifying the extent of nectaring behaviour in the huge diversity of moths in a manner similar to that of the baiting exercise we report on here.

MATERIAL AND METHODS

The Genting survey. — Pairs of bait traps, one using banana bait and one using prawn bait, were operated at five sites at Genting Tea Estate, Pahang, W. Malaysia, between 693–754 m asl on the Pahang side of the Genting Sempah Pass, some 30 km north east of Kuala Lumpur, close to the Karak Highway. The traps used were BugDorm pop-up butterfly bait traps (DC0018) consisting of a nylon net cylinder 40 cm in diameter and 100 cm in height with a bait tray at the bottom; these were suspended from branches at about human waist-height (Fig. 1).

All traps were operated twice a week by HSB and HKL, the banana baits from 16 Dec.2011 and the prawn baits from 8 Jan.2012, in both cases till 30 Jan.2013. Traps were baited in mid-morning and collected in the middle of the following morning. The baits were renewed after each collection.

The trapping work was done in conjunction with an exercise set up specifically to trap butterfly species of the genus *Mycalesis* for study by Paul Brakefield and Ullasa Kodandaramaiah (Brakefield & Kodandaramaiah, studies of the seasonal biology of mycalesine butterflies, in prep.).

Rainfall, temperature and humidity records were maintained during the trapping period, all three parameters measured at HKL's quarters; additionally, humidity recordings were made at Site 2. Details are available from HKL if required. Humidity at Site 2 was close to 100% much of the time.

Fig 1. Trap at Site 5 being checked by HSB and HKL.

Rainfall for the calendar year 2012 was 2638 mm, slightly above the recent average.

The baits used were as follows: Banana – About half a cupful of mashed banana that had been allowed to ferment was placed in a small plastazote container on the base of the trap. Prawn – 3 stale raw prawn heads as above.

Location and details of Genting trapping sites: Site 1 –03°21.585'N, 101°47.571'E, 693 m asl. About 2 m away from a small stream, in advanced secondary vegetation, primarily bamboo. Frequent disruption of both traps, but more frequently prawn trap, from monkeys and/or otters. Site 2 –03°21.615'N, 101°47.581'E, 702 m asl. The opposite side of the same stream, about 50 m away, closer to a smaller, tributary stream in secondary vegetation of bamboo, but with advanced secondary forest immediately adjacent. Disruption as for site 1 above. Site 3 – 03°21.571'N, 101°47.368'E, 717 m asl. Upstream of sites 1 & 2, but still adjacent to the stream, where there was a small amount of secondary vegetation along the stream, but the main catchment area was periodically mown coarse grasses planted with small dipterocarp saplings. Little if any disruption from monkeys and otters. Site 4 – 03°21.540'N, 101°47.274'E, 740 m asl. On the side of the valley, about 200 m from the stream, in advanced secondary vegetation of 15 year old dipterocarps and other forest trees. Little if any disruption from monkeys and none from otters. Site 5 – 03°21.489'N, 101°47.429'E, 754 m asl. Further up the same side of the valley, secondary vegetation similar to site 4, but less advanced and more open. Little if any disruption from monkeys and none from otters.

The Sabah survey. — Moth data from Sabah relate to 'by-catch' from a butterfly sampling project conducted by Benedick et al. (2006, 2007, 2009), following an earlier one on the effects of selective logging (Hamer et al., 2008), to assess the effects of lowland forest fragmentation on butterflies in Sabah, both in relation to overall diversity and in relation to genetic diversity in *Mycalesis orseis*, a species also taken in the Genting survey.

Banana bait traps were deployed at ten forested sites in Sabah, two with continuous forest, two with large forest fragments (>27000 ha), two with medium forest fragments (4294 and 6735 ha) and four with small forest fragments (120–720ha). Data were also collected from two sites within an oil palm plantation (2700+ ha) and the catches pooled. Details and locations of these sites have been published elsewhere (Benedick et al., locs. cit.), so will not be repeated here, as the data are presented mainly to provide a comparison with macroheteroceran catches from Genting.

It is, of course, possible that some of the captured insects recorded in both surveys were not attracted to the baits but had entered the traps to roost during the period of the day when they were not active. We suspect that any such event will be rare, but this could easily be tested in future by deployment of unbaited traps as controls.

Identification and taxonomy. — Material from the Genting survey was identified by HSB with some later input from JDH; the non-pyraloid Microlepidoptera were kindly identified by Kevin R. Tuck. Subsequent to this, the raw data sheets were processed and analysed by JDH. The data will be finalised in spreadsheet format and made available online. The Sabah moth material was processed and identified by J. K. Hill and CVK, again with some input from JDH.

The biosystematic order used in this paper is based on that for the Lepidoptera as a whole compiled by Nieukerken et al. (2011). Each clade listed (Results and Table 1) reflects the pectinate structure of the current classification (e.g., in Regier et al., 2009; Mutanen et al., 2010), and is nested within the preceding clades. The butterfly classification mostly follows that of Corbet & Pendlebury (1992) and Vane-Wright & de Jong (2003), but the classification of the Nymphalidae has been modified to reflect the phylogeny derived by Wahlberg et al. (2009). The order for the Macroheterocera is generally as in the Borneo checklist of Holloway (2011), which itself draws heavily on the molecular phylogenies for the Geometridae of Yamamoto & Sota (2007) and Sihvonen et al. (2011) and for the Noctuoidea of Zahiri et al. (2011, 2012, 2013a, 2013b), though it is here modified slightly to reflect the results of the later Zahiri works. Subfamilies for the Notodontidae follow Schintlmeister & Lourens (2010). Subfamilies in the Pyraloidea are based on the phylogeny of Regier et al. (2012).

Author names have been omitted for the sake of brevity and simplicity, but can be found in the above references, primarily Corbet & Pendlebury (1992) and Holloway (2011). For groups where a mix of banana and prawn records occur, the species in the following text are followed by the numbers of individuals recorded at each bait in the format (B:P).

RESULTS

The total sample for the Genting survey was of approximately 2670 individuals from 519 species or morphospecies. 267 (just over 51%) of these species were only represented by single individuals and a further 86 (just over 17%) were only represented by two, a total of 68%. This suggests, from a crude application of the Chao1 richness estimator (e.g., Colwell & Coddington, 1994; Holloway, 2011: 455; Basset et al., 2013), that just over 400 species in the locality of the survey remain to be collected by these baiting methods; thus they have so far only captured just over half the potential species total estimated at just over 900. This can be placed in the context of the total of about 5000 Lepidoptera recorded at the Genting locality over more than 40 years, mostly by light-trapping, but including 442 butterflies, representing 42% of the total recorded for Peninsular Malaysia (Barlow, unpublished).

As will be seen from the following sections, not all groups of Lepidoptera come to feed at these baits, most obviously those where the adults do not feed, but also major groups such as

Table 1. The numbers of species recorded at each site for the two bait types for the more significant families, together with (in **bold**) the total species for each bait type and the overall total.

Superfamily	Family	B1	B2	B3	B4	B5	**B**	P1	P2	P3	P4	P5	**P**	**B+P**
Clade Apoditrysia														
Gelechioidea	Lecithoceridae +	1	–	–	–	1	**2**	5	1	–	–	1	**6**	**8**
Immoidea	Immidae	3	4	4	5	1	**13**	2	9	–	–	–	**10**	**16**
Tortricoidea	Tortricidae	–	–	–	–	–	**–**	14	21	–	4	–	**30**	**30**
Clade Obtectomera														
Thyridoidea	Thyrididae	–	–	–	–	–	**–**	7	7	1	2	1	**14**	**14**
Calliduloidea	Callidulidae	–	–	–	–	–	**–**	1	1	–	1	–	**1**	**1**
Pyraloidea	Crambidae	4	3	3	3	2	**14**	46	56	25	24	4	**95**	**99**
Papilionoidea	Hesperiidae	–	–	–	–	–	**–**	4	5	9	10	4	**25**	**25**
	Lycaenidae	–	–	–	–	–	**–**	3	5	3	4	5	**13**	**13**
	Nymphalidae	21	20	20	25	25	**44**	11	12	18	10	16	**42**	**64**
Clade Macroheterocera														
Drepanoidea	Drepanidae	1	–	–	1	1	**2**	5	6	4	5	1	**9**	**10**
Geometroidea	Uraniidae	–	–	–	–	–	**–**	–	3	–	1	–	**4**	**4**
	Geometridae	–	–	1	1	1	**3**	28	57	11	21	11	**74**	**77**
Noctuoidea	Notodontidae	–	–	–	–	–	**–**	3	3	1	1	1	**5**	**5**
	Erebidae	30	38	44	43	39	**111**	7	18	10	16	12	**39**	**132**
	Noctuidae	1	1	4	3	3	**4**	1	2	2	–	2	**7**	**9**
ALL LEPIDOPTERA		61	66	77	82	75	**197**	139	209	85	100	59	**382**	**519**

the butterfly families Pieridae and Papilionidae that readily take nectar from flowers and form the major component of 'mud-puddle clubs' (see also Beck et al., 1999). The species totals for each bait type and site in Table 1 show that the diversity recorded by the prawn traps is about double that recorded by the banana traps, though these totals include a minority of species that was attracted to both baits. The catches at individual sites also vary between the two baits. Diversity at the prawn traps ranks the sites, in descending order of richness, P2>P1>P4>P3>P5, an apparent correlation with the diversity of vegetation at each. Diversity ranking for the banana traps, B4>B3>B5>B2>B1, suggests that this bait is favoured more by species characteristic of biotopes with some degree of disturbance, with earlier successional stages present.

Even for the most notable groups in terms of diversity recorded by the Genting survey such as the ennomine Geometridae and the herminiine and erebine Erebidae, the Chao richness estimator still only indicates that the results represent just over half of the number of species potentially collectable by these baiting methods. The only exception to this is the subfamily Satyrinae of the Nymphalidae, where the richness estimator suggests that only about six species might be added to the 39 sampled. This projected total of 45 is 80% of the currently recorded total for the extended Genting locality of 56 (Barlow, unpublished). The total for central Peninsular Malaysia is 83 (Corbet & Pendlebury, 1992).

All Lepidoptera trapped except for two Tineidae have been from the Clade Apoditrysia of the Suborder Glossata. Only the superfamilies Immoidea and Tortricoidea were recorded in significant numbers amongst the basal superfamilies of this clade, though small numbers of Gelechioidea, a few Zygaenoidea and single Carposinoidea and Pterophoroidea were also recorded. The majority of records present in South-east Asia is from Clade Obtectomera, with most superfamilies being represented to a greater or lesser degree, exceptions being the small superfamily Hyblaeoidea, and the Lasiocampoidea and Bombycoidea where the adult moths, with the exception of some Sphingidae of the Bombycoidea, are non-feeding. Attraction to prawn bait proved to be much more general across these groups than did attraction to banana bait, this being more or less restricted to Immoidea, Papilionoidea and Noctuoidea (Table 1). In the second and third of these groups, the families showing this are all relatively distal in the phylogeny of their superfamilies, so a fruit-feeding strategy would appear to have been adopted independently three times, maybe more if several minor instances in other groups are included.

Basal Ditrysia. — Singletons of two species of the genus *Monopis* (Tineoidea: Tineidae) were recorded at each of P1 and P2.

Apoditrysia. — Eight species of Gelechioidea were recorded in small numbers, perhaps mainly from the family Lecithoceridae, six from prawn and two from banana, most from Site 1 (Table 1). The single pterophoroid was recorded at B3 and the only carposinoid, a species of Copromorphidae, was from P1. The remaining superfamilies of the basal Apoditrysia are discussed in the next three sections.

Immoidea. — Perhaps 16 species of the only constituent family, Immidae, were sampled, the majority as singletons, and with no species represented by more than eight individuals. Six species were recorded from both bait types, and the figures suggest a slight but probably not significant preference for banana (Table 1). Most immids were only identified to morphospecies, the exceptions being *Imma flavibasa* (0:1) and *I. homocrossa* (1:2).

Tortricoidea. — This superfamily consists solely of the family, Tortricidae. 30 species were recorded, all from the subfamily Olethreutinae, and entirely from the tribes Enarmoniini (7) and Olethreutini (14) for species identified to this level. In the Olethreutini, the genera *Dactylioglypha*, *Phaecasiophora*, *Sorotropha*, *Statherotis*, *Sycacantha*, and *Teleta* have been identified with certainty. No species was represented by more than 8 individuals, and most (21) were single records. All were from prawn bait and only from Sites 1, 2 and 4 (Table 1).

Zygaenoidea. — The Zygaenidae are the only species-rich family of this superfamily to have a well-developed proboscis, but only three specimens came to the trap, two from the tribe Artonini of subfamily Procridinae to prawn and one from the subfamily Chalcosiinae to banana: *Artona zebraica* and a possible *Homophylotis* species (0:1); *Chalcosia phalaenaria* (1:0).

Thyridoidea. — This and the next are two of the three smaller superfamilies in the Obtectomera clade outside the Macroheterocera. A third, the Hyblaeoidea, is represented in Southeast Asia but was not recorded. All three contain a single family.

Sixteen species of Thyrididae were recorded, all exclusive to the prawn traps. They were drawn from three of the subfamilies. In the Thyridinae, three species of *Dysodia* were recorded: *D. rufiflava* (0:1) and two not identified to species, a singleton and one with four specimens. In the Striglininae, five species were recorded from Site 1 as singletons: *Striglina buergersi*, *S. asinina* or *lilacina*, *S.* sp.; *Aglaopus decussata*; *Banisia flavidiscalis*. In the Siculodinae, eight species were recorded, six from the tribe Siculodini and two from the tribe Rhodoneurini, all except one of the former as singletons: *Calindoea atripunctalis*, *Microbelia canidentalis*, *Pharambara splendida*, *P.* sp., *Collinsa decoratalis* and another probable *Collinsa* with two specimens. The Rhodoneurini were *Rhodoneura pudicula* (0:7) and *Mellea tetragonata* (0:5). Most thyridid records were from Sites 1 and 2.

Calliduloidea. — One species of the Callidulidae was recorded at prawn baits only: *Tetragonus catamitus* (0:6).

Pyraloidea. — This is the third most diverse superfamily amongst the moths, exceeding the Tortricoidea but falling short of the macroheteroceran Geometroidea and Noctuoidea. Over 100 morphospecies were recorded but only 44 of these could be identified to genus or species. All of these were in the family Crambidae and most of these were in the subfamily Spilomelinae, with single representatives of the Acentropinae (*Orgyraetis* sp. (0:1)), Musotiminae (*Musotima ?suffusalis* (0:1)) and Odontiinae (*Pitama hermesalis* (0:2)). Almost all species were recorded primarily or only from the prawn traps, particularly at Sites 1 and 2 (Table 1). 17 of the morphospecies were represented by five or more individuals. The following Spilomelinae genera and species were recorded (figures given only for named species), ordered as in Robinson et al. (1994), with nomenclature updated from Nielsen et al. (1996): *Pagyda calida* (0:20); *Hydriris*; *Xanthomelaena schematias* (0:2); *Heterocnephes lymphatalis* (1:9); *Glyphodes badialis* (0:2) and two other species; *Omiodes*; *Stemorrhages amphitritalis* (0:1); *Palpita picticostalis* (0:1); *Tyspanodes exathesalis* (0:7); ?*Coptobasis*; *Pleuroptya* ?*punctimarginalis* (0:2); *Bocchoris*; *Botyodes*; *Gadessa*; *Dichocrocis xuthusalis* (1:5), *zebralis* (0:1) and one other; *Conogethes punctiferalis* (0:1) and one other; *Nevrina procopia* (0:1); *Lipararchis tranquillalis* (0:2); *Nosophora triguttalis* (0:12), *chironalis* (0:2), *scotacula* (0:2) and four others; *Pycnarmon quintula* (1:1) and *abraxalis* (0:2); *Prophantis*; *Catachena*; *Herpetogramma*, three species; *Cnaphalocrocis patnalis* (0:1); *Sygamia*; *Metroea* ?*punctata* (0:2).

Papilionoidea. — Three of the six families found in Southeast Asia were not recorded at any of the traps: Papilionidae, Pieridae and Riodinidae. The first two are extremely diverse in the study area and are known to indulge extensively in nectaring for sugars and mud-puddling for salts, the latter behaviour shown predominantly by males (Holloway, 1984; Corbet & Pendlebury, 1992; Beck et al., 1999), though this is also seen to a lesser extent in the other families. These two families and the Nymphalidae are also notable for migratory behaviour.

Of the three families recorded in the bait traps, two, the Hesperiidae and Lycaenidae, were noted only at the prawn traps. The Nymphalidae were by far the most abundant group sampled in this study, rivalled only by the Erebidae of the Noctuoidea.

Hesperiidae. — Only two of the three subfamilies found in South-east Asia were recorded at the baits: the Coeliadinae and the Hesperiinae. The Pyrginae, with similar diversity to the Coeliadinae, were not collected. The greatest diversity was observed at Sites 3 and 4, but, of the 25 species noted (Table 1), less than half were recorded from any one site. All were taken in the prawn traps (Table 1). All except seven species have been identified to at least genus. Only seven were represented by more than one individual, and the most abundant was *Ampittia dioscorides* with 12 individuals, all except one taken at Site 3. Site 3 and Site 4 were about twice as species-rich as the other three (Table 1).

The Coeliadinae were represented by *Bibasis oedipodea* (2), *B. etelka*, *B. harisa* (3), *B. gomata* (5), *Hasora leucospila* and *Choaspes plateni*. The Hesperiinae trapped were *Ampittia dioscorides* (12), *Halpe zema* (3), two other *Halpe* species, *Iambrix salsala*, *Ancistroides nigrita*, *Notocrypta paralysos*, *N. clavata*, *Erionota acroleuca*, *Potanthus omaha* (2), *Telicota besta* and *Iton semamora*.

Lycaenidae. — The Lycaenidae were also only recorded from the prawn traps, the 13 species being spread evenly over the sites with no more than five recorded at any one (Table 1). Five were only recorded singly, the most abundant

Table 2. Numbers of species in various subgroups for the three principal families recorded in the survey, set out as in Table 1.

Family	Subfamily: tribe or group	B1	B2	B3	B4	B5	**B**	P1	P2	P3	P4	P5	**P**	**B+P**
NYMPHALIDAE														
	Satyrinae: Satyrini	12	9	9	11	11	**18**	3	5	8	4	8	**14**	**21**
	Satyrinae: Morphini	8	10	5	11	9	**15**	2	5	1	2	3	**11**	**18**
	Limenitidinae	1	1	4	2	4	**7**	1	1	6	2	3	**8**	**14**
	Remainder	–	–	2	1	1	**4**	5	1	3	2	2	**9**	**11**
GEOMETRIDAE														
	Larentiinae	–	–	–	–	–	**–**	4	6	1	1	3	**8**	**8**
	Sterrhinae	–	–	1	–	1	**2**	3	3	2	2	1	**4**	**6**
	Oenochrominae	–	–	–	–	–	**–**	1	2	–	1	–	**2**	**2**
	Geometrinae	–	–	–	–	–	–	1	2	1	–	1	**5**	**5**
	Ennominae: Ennomini group	–	–	–	1	–	**1**	6	18	–	5	2	**20**	**21**
	Ennominae: Boarmiini group	–	–	–	–	–	**–**	13	25	7	12	4	**34**	**34**
EREBIDAE														
	Herminiinae	18	16	12	15	16	**44**	1	1	–	1	–	**3**	**45**
	Boletobiinae: Boletobiini	2	5	3	3	–	**8**	–	1	–	–	–	**1**	**8**
	Lithosiinae	–	–	5	–	2	**7**	–	–	–	–	3	**3**	**8**
	Erebinae	9	14	18	17	16	**32**	3	5	6	8	4	**14**	**36**
	Scoliopteryginae	–	–	1	1	1	**3**	2	5	3	3	3	**8**	**9**
	Remainder	1	3	5	7	4	**17**	1	6	1	4	2	10	26

being *Jamides celeno* with 11. All except two were from the subfamily Lycaeninae, most in the genera *Jamides* and *Nacaduba*.

The Miletinae were represented by *Taraka hamada* (2) and the Curetinae by *Curetis bulis* (7, split between Sites 3 and 5). The Lycaeninae records were of *Caleta elna*, *Megisba malaya*, *Jamides bochus* (2), *J. celeno* (11), *J. pura* (2), *J. caeruleus*, *J. virgulatus*, *Nacaduba pactolus* (4), *N. beroe*, *N. berenice* (3) and *Cheritra freja*.

Nymphalidae. — This family was recorded in the greatest numbers and diversity of all three butterfly families trapped in the survey, with 64 species in all, and two-thirds of these were noted at each trap type. However, individual banana traps had consistently more species than the prawn traps, only approaching equality at Site 3 (Table 1). Seven subfamilies were recorded, ranking as follows: Satyrinae (39); Limenitidinae (14); Charaxinae (4); Danainae, Biblidinae and Nymphalinae (2); Heliconiinae (1). The Satyrinae (Table 2) were split more or less evenly between the Morphini (18) and Satyrini (21). Whilst both Satyrinae tribes were relatively evenly diverse across the five sites for each bait type with slight predominance at banana at individual sites and overall, the records for the remaining tribes were concentrated in Sites 3, 4 and 5, with slightly greater representation at prawn.

The less well represented subfamilies did not include any really abundant species and had a spread of bait preference: Danainae, with *Parantica aspasia* (1:2) and *Ideopsis gaura* (0:2); Heliconiinae, with *Terinos terpander* (0:1); Biblidinae, with *Ariadne isaeus* (0:4) and *Laringa castelnaui* (0:2); Nymphalinae, with *Symbrenthia hypselis* (0:1) and *Rhinopalpa polynice* (2:3); Charaxinae, with *Prothoe franck* (1:0), *Polyura athamas* (0:1), *P. delphis* (0:1) and *Charaxes bernardus* (1:0).

Limenitidinae. — The species of this subfamily (Table 2) fall into three tribes, Neptini, Limenitidini and Adoliadini. The first two are mostly recorded from prawn traps, whereas the last showed a slight preference for banana. Only one species had more than 10 individuals (Table 3), and most were represented by singletons: the Neptini with *Neptis duryodana* (1:0), *N. clinia* (1:0), *N. hylas* (0:15), *N. nata* (0:1), *N. leucoporos* (0:1) and *N. ilira* (0:1); the Limenitidini with *Athyma cama* (0:3), *A. nefte* (0:1) and *Moduza procris* (0:1); the Adoliadini with *Tanaecia munda* (1:0), *T. iapis* (1:1), *Euthalia monina* (6:4), *Dophla evelina* (3:0), and *Lexias pardalis* (5:0). The first two tribes were mostly taken at the more disturbed sites, 3 and 5, whereas the third was more evenly spread.

Satyrinae*: *Morphini. — This tribe shows a much stronger preference for banana than the Satyrini, though three species, two singletons and a doubleton, were only taken at prawn bait. Four of the species are listed in Table 3. The records were for *Melanitis leda* (6:1), *M. phedima* (124:2), *M. zitenius* (14:0), *Elymnias panthera* (1:0), *E. patna* (0:1), *E. nesaea* (1:0), *E. casiphone* (1:0), *Neorina lowii* (9:0), *Xanthotaenia busiris* (3:0), *Amathusia phidippus* (3:1), *A. perakana* (5:2), *Amathuxidia amythaon* (9:1), *Zeuxidia amethystus* (19:1), *Z. doubledayi* (8:0), *Z. aurelius* (8:0), *Discophora sondaica* (0:2), *D. timora* (4:2) and *Enispe intermedia* (0:1).

Satyrinae*: *Satyrini. — This group includes the genus *Mycalesis* that provided the stimulus for the bait-trapping project. 12 of the 21 species belong to the genus, with a total of about 360 individuals sampled, mostly from the banana traps, as follows (see also Table 3): *M. fusca* (13:0), *M. mnasicles* (65:1), *M. janardana* (40:4), *M. perseus* (7:0), *M. perseoides* (29:4), *M. mineus* (11:0), *M. intermedia* (75:9), *M. visala* (46:4), *M. orseis* (41:0), *M. maianeas* (3:0), *M. oroatis* (3:0) and *M.* sp. (2:2). 17 species in total are known

Table 3. Distribution over the sites and baits of numbers of individuals of species with a total of 10 individuals or more in the family Nymphalidae.

Group	Genus & species	B1	B2	B3	B4	B5	P1	P2	P3	P4	P5	TOTAL
SATYRINAE:	SATYRINI											
	Erites argentina	2	7	–	–	–	2	3	–	–	–	**14**
	Ypthima pandocus	–	–	–	–	1	–	–	6	–	4	**11**
	Mycalesis mineus	1	–	–	5	5	–	–	–	–	–	**11**
	Mycalesis perseoides	1	–	18	4	6	–	–	3	1	–	**33**
	Mycalesis orseis	3	2	14	13	7	–	–	–	–	–	**41**
	Mycalesis visala	1	–	8	28	9	–	1	1	1	1	**50**
	Mycalesis mnasicles	2	13	–	37	3	–	1	–	–	–	**66**
	Mycalesis janardana	4	4	6	15	11	1	–	2	–	1	**44**
	Mycalesis intermedia	–	–	25	27	23	–	–	3	1	5	84
	Orsotriaena medus	–	1	17	2	2	–	–	10	1	–	**33**
SATYRINAE:	MORPHINI											
	Melanitis phedima	12	18	33	48	13	–	–	1	–	1	**126**
	Melanitis zitenius	4	4	1	4	1	–	–	–	–	–	**14**
	Amathuxidia amythaon	7	4	–	7	1	–	1	–	–	–	**20**
	Zeuxidia amethystus	7	4	–	7	1	–	1	–	–	–	**20**
LIMENITIDINAE												
	Euthalia monina	–	–	1	4	1	–	1	2	1	–	**10**
	Neptis hylas	–	–	–	–	–	–	–	14	–	1	**15**

from Peninsular Malaysia (Corbet & Pendlebury, 1992). Most of the species were commonest at Sites 3, 4 and 5, some more or less restricted to them.

Other species recorded (see also Table 3) were *Lethe europa* (1:1), *L. mekara* (0:1), *Orsotriaena medus* (22:11), *Erites argentina* (9:5), *Coelites epiminthia* (1:3), *Ragadia makuta* (9:0), *Ypthima horsfieldii* (0:2), *Y. savara* (0:4), *Y. pandocus* (1:10). In contrast to *Mycalesis*, 15 out of 16 individuals of *Ypthima* were recorded at prawn baits, but also at Sites 3 and 5. In contrast, all of the forest-frequenting *Ragadia makuta* were captured with banana at Sites 1 and 2.

Clade Macroheterocera. — This clade contains almost all the larger moths and includes the other major superfamily where extensive fruit bait feeding was detected. It also produced most of the moth captures made as a by-product of butterfly sampling in the Bornean state of Sabah studied by CVK who is continuing to sample moths in this manner and will include prawn baits in future. The species caught show considerable commonality with the Genting study as indicated by asterisks in the sections following, one (*) for presence, (**) two for 10 or more individuals.

Two of the five superfamilies that form this terminal clade consist mainly of families where the adults do not feed and have a reduced proboscis or have lost it completely: Lasiocampoidea and Bombycoidea. Only the Sphingidae amongst the latter have adults that take nectar, and that in only two of the three subfamilies: Sphinginae and Macroglossinae. This can involve (e.g., *Macroglossum*) hovering in front of a flower, drawing nectar with a long proboscis, often co-adapted for tubular flowers. Most moths in both subfamilies are large, and their life strategy was studied in detail by Janzen (1984) in the Neotropics, and assessed in relation to Southeast Asia by Holloway (1987). Only one sphingid species was trapped during this study, the macroglossine *Eupanacra elegantulus*, a singleton trapped at banana at Site 4.

Drepanoidea. — This superfamily is very much smaller than the final two, with only the family Drepanidae being widely distributed and relatively diverse. The largest subfamily, Drepaninae, was the only one recorded in this study, and most records were made in the prawn traps (Table 1). Three species were quite common and are detailed in Table 4. The ten species recorded are *Teldenia specca* (0:14), *Euphalacra semisecta** (4:1), *Pseuderosia desmierdechenoni* (0:1), *Monoprista* sp. near *mecasa* (0:1), *Drapetodes matulata* (0:3), *D. mitaria* (0:3), *D. nummularia* (0:14), *D. fratercula* (0:10), *Microblepsis renifera* (1:10), *Callidrepana gelidata* (0:6; all at Site 4). The Sabah survey also recorded *Hyalospectra pustularia* with banana.

Geometroidea. — Both the Uraniidae and the Geometridae were represented in the Genting data (Table 1), but only the latter featured in the Sabah data. The superfamily as a whole showed a virtually complete (three geometrid exceptions) preference for prawn baits in the Genting data, but many of the geometrid groups were taken at banana bait in Sabah, though rarely in numbers.

Uraniidae. — Three of the four subfamilies were represented, the Uraniinae by *Urapteroides astheniata* (0:4 at Site 2), the Microniinae by *Micronia pluviosa* (0:7 at Site 2) and the Epipleminae by *Dysaethria plicata* (0:3 at Site 4) and *Chionoplema ?paradeicta* (0:1 at Site 2). The appearance of site specificity is reinforced by the fact that the records consist only singletons and one doubleton taken over a range of dates.

Table 4. Distribution over the sites and bait types of individuals of the commonest species in the families Drepanidae and Geometridae as in Table 3.

Group	Genus & species	B1	B2	B3	B4	B5	P1	P2	P3	P4	P5	TOTAL
DREPANIDAE												
	Teldenia specca	–	–	–	–	–	2	2	2	5	3	**14**
	Drapetodes nummularia	–	–	–	–	–	5	2	2	9	–	**18**
	Drapetodes fratercula	–	–	–	–	–	1	5	1	2	–	**9**
GEOMETRIDAE												
STERRHINAE												
	Zythos turbata	–	–	–	–	–	4	8	3	3	2	**20**
	Scopula urnaria	–	–	–	–	–	2	14	–	3	–	**19**
OENOCHROMINAE												
	Eumelea florinata	–	–	–	–	–	5	10	–	1	–	**16**
ENNOMINAE												
	Achrosis fulvifusa	–	–	–	–	–	2	8	–	–	–	**10**
	Borbacha bipardaria	–	–	–	–	–	1	11	–	–	–	**12**
	Xeropteryx columbicola	–	–	–	–	–	3	12	–	–	–	**15**
	Oxymacaria temeraria	–	–	–	–	–	6	3	2	1	–	**12**
	Chiasmia albipuncta	–	–	–	–	–	5	9	–	–	–	**14**
	Chiasmia nora	–	–	–	–	–	–	5	2	–	4	**11**
	Xerodes ypsaria	–	–	–	–	–	9	5	1	1	–	**16**
	Amblychia infoveata	–	–	–	–	–	14	21	4	7	2	**48**

Geometridae. — Recent DNA-sequencing work (Yamamoto & Sota, 2007; Sihvonen et al., 2011) has indicated a separation of a sister-pair of subfamilies, Larentiinae and Sterrhinae, from a well-supported clade containing all the rest. Most of the records made in both surveys fall within this second grouping (Table 2), though two species of tribe Scopulini of the Sterrhinae have been taken in some numbers (Table 4). Twice as many species were recorded from Site 2 as from Site 1, with species numbers from Sites 3 and 5 only just reaching double figures.

Larentiinae. — Three tribes were represented by a total of eight species, none in high numbers, with records mostly in Sites 2 and 1 (Table 2). The records were as follows: Trichopterygini with *Goniopteroloba solivaga* (0:1), *Tristeirometa mesogrammata* (0:1) and *Sauris abnormis* (0:2); Eupitheciini with *Collix stellata* (0.1) and *Scintillithex glaucisparsa* (0.2); Xanthorhoini with *Xanthorhoe saturata* (0.2), *Visiana ?sordidata* (0:4), and *Gonanticlea aversa* (0:6). The Sabah survey recorded only one eupitheciine, *Eupithystis infuscata*.

Sterrhinae. — The subfamily splits into two clear lineages, supported by morphological (Holloway, 1997) and molecular (Sihvonen et al., 2011) evidence: the Timandrini lineage and the Scopulini lineage (see also Holloway, 2011). The limited records in the Genting survey were split on these lines with the two Cosymbiini in the first lineage noted from banana, *Chrysocraspeda planctogramma* (1:0) and *C. rubraspersa* (1:0), and four Scopulini in the second lineage all recorded from prawn, *Zythos turbata** (0:20), *Z. strigata* (0:1), *Z. obliterata* (0:2) and *Scopula urnaria** (0:19). However, the two most abundant of the latter, as indicated by asterisks, were recorded from banana in the Sabah survey as well as *Perixera argyrommoides* from the Cosymbiini.

Oenochrominae. — Two species referable to this subfamily were recorded. One, from the Oenochromini, was *Sarcinodes vultuaria* (0:1). The other was *Eumelea florinata** (0:16, Table 4, mostly at Sites 1 and 2), a member of the tribe Eumeleini, originally described in the subfamily Desmobathrinae by Holloway (1997), but now shown to be weakly associated with the Oenochromini by DNA results (Sihvonen et al., 2011). Four specimens were taken at banana in the Sabah survey. No Desmobathrinae were recorded in either survey.

Geometrinae. — Only four species of this subfamily were recorded, all except one as singletons. Two were Dysphaniini, *Dysphania sagana* and *D. malayanus*, and the remaining two were from the Hemitheini, *Berta chrysolineata* (0:2) and a possible *Hemithea* species. The Sabah survey yielded only a single *Ornithospila bipunctata* in a genus of uncertain tribal placement but with larvae possibly specialist dipterocarp feeders.

Ennominae. — The DNA analysis of Sihvonen et al. (2011) supported the grouping of the tribes Boarmiini, Cassymiini, Eutoeiini and Macariini by Holloway (1993[4]) but added the Abraxini to this. Most of the other Ennomini tribes were grouped together in one large but weakly supported clade and two small outlying groups, including the Ennomini, so this latter could be called the Ennomini group as distinct from the Boarmiini group. The Genting survey recorded half as many species again in the Boarmiini group, but Site 2 was the most species-rich in both groups (Table 2). All except one of the 55 species in total were recorded exclusively in prawn traps, but many of the species were taken at banana in the Sabah survey as the asterisks in following sections will show. The Sabah survey recorded 29 species.

Ennomini group. — The Hypochrosini were represented by seven species, all except two by singletons, *Achrosis fulvifusa* (0:10, Table 4), *A. lithosiaria* (0:8), *Loxomiza herberti*, *Fascellina viridicosta, F. meligerys*, *F. castanea**, and *F. celata*. The Sabah survey also yielded *F. inconspicua* and *F. quadrata*, with the additional genus *Hypochrosis* represented by *H. binexata* and *H. waterstradti*.

The tribes Scardamiini, Baptini and Lithinini were each represented by single species at Genting, respectively *Scardamia iographa* (0:5), *Lomographa luciferata* (0:3) and *Entomopteryx amputata* (0:1), but they were not recorded in the Sabah survey.

The tribe Deveniliini was represented by five species in three genera and included the only species recorded from banana, albeit singly, *Curbia martiata*; it was not recorded in Sabah. The other two genera were recorded in both surveys: *Parasynegia sundastriaria** (0:4), *P. fortilineata** (0.1) and *P. lineata* (Sabah only); *Borbacha punctipardaria** (0.1), *B. bipardaria** (0:12, Table 4) and *B. altipardaria* (Sabah only).

The Caberini were represented only by the *Petelia* group where all larval records are from Rhamnaceae: *Petelia medardaria* (0:2), *P. paroobathra* (0:5), *P. distracta* (Sabah only) and *P. tuhana* (Sabah only); *Astygisa vexillaria* (0:1). Representation of the Thinopterygini was marked, given the size of the group, with *Thinopteryx crocopterata* (0:6), *Xeropteryx columbicola* (0:15, Table 4) and *Pareumelea eugeniata* (0:1) recorded at Genting and *Stalagmia guttaria* in Sabah.

Boarmiini group. — No records of the Cassymini or Abraxini were noted in either survey, but the Eutoeini, Macariini and Boarmiini were recorded at both, with some significant overlap in genera and species.

Eutoeini: *Calletaera jotaria* (0:1), *Probithia exclusa* (0:3), *P. imprimata* (0:1), *Eutoea heteroneurata* (0:1), *Luxiaria hyalodela** (0:2).

Macariini: *Hypephyra terrosa* (0:4), *Oxymacaria temeraria* (0:12, Table 4), *Chiasmia albipuncta* (0:14, Table 4), *C. nora* (0:11, Table 4), *C. avitusaria** (0:1), *C. translineata** (0:3) and *C. khasiana* (0:1).

Boarmiini: *Dalima subflavata** (0:5), *Hyposidra picaria* (0:1), *Racotis hollowayi* (0:1), *R. boarmiaria* (Sabah only), *Xerodes ypsaria* (0:16, Table 4), *Coremecis incursaria* (0:1), *C. maculata* (0:2), *Amblychia infoveata** (0:48, Table 4), *A. hymenaria** (0:7), *Cleora determinata* (0:1), *C. contiguata* (0:3), *C. inoffensa* (0:4), *C. pupillata* (0:2), *Ruttellerona pseudocessaria* (0:2), *R. pallicostaria* (0:7), *Ophthalmitis clararia* (0:1), *O. viridior** (0:6), *O rufilauta** (0:1), *Catoria olivescens* (0:1), *Alcis periphracta* (0:4), *Marobia dentigerata* (0:1), *Abaciscus* ?*paucisignata* (0:1), *Diplurodes* sp. (0:2). Genera and species only recorded from Sabah were *Lassaba vinacea*, *Ectropis bhurmitra*, *Pseudalcis catoriata*, *Hypomecis subdetractaria*, *H. tetragonata* and *Necyopa subtriangula*; *Ectropis bhurmitra* was the only species in Sabah to be recorded in double figures (19).

Noctuoidea. — The Noctuoidea include about a quarter of the known global Lepidoptera fauna according to the figures in Nieukerken et al. (2011). The faunas of Borneo and Peninsular Malaysia are very similar, and about 2850 noctuoid species are known from the former (Holloway, 2011). About 150 noctuoid species have been recorded in the Genting survey (Table 1), about 30% of the total recorded, compared to 20% for each of the butterflies and Crambidae and 16% for the Geometridae. Almost 90% of these noctuoids belong to one family, the Erebidae, much higher than the 65% that they contribute to the Bornean Noctuoidea in terms of species (1857).

The Erebidae are one of four related families sharing a derived character of the forewing where four, rather than three, veins are clustered around the posterior distal angle of the forewing cell (an area of lamina in the centre of all wings entirely or almost entirely enclosed by venation), giving the name 'quadrifid families' to this quartet, the other three being the Euteliidae, Nolidae and Noctuidae. Sister to this quartet is the family Notodontidae, with a trifid (three-veined) set of veins around that angle of the cell. This condition is also seen in the small, most basal family in the Noctuoidea, the Oenosandridae, endemic to Australia (Zahiri et al., 2011, 2012, 2013a, 2013b).

Notodontidae. — Only five species have been recorded, all except one in small numbers, all to prawn in the Genting survey. Two are currently in the subfamily Scranciinae and three are in the Dicranurinae in the system of Schintlmeister & Lourens (2010). The Scranciinae are *Gargetta* ?*divisa* (0:15, Table 5) and *G. curvaria* (0:1), and the Dicranurinae are *Omichlis rufitincta* (0:1), *Somera viridifusca* (0:2) and *S. virens* (0:1).

Euteliidae and Nolidae. — These two families have yielded four species to the Genting survey, all represented by singletons, the Euteliidae only by *Penicillaria simplex* on prawn. The Nolidae consisted of two Chloephorinae on prawn, *Calymera albimargo* and *Dilophothripa alopha*, and one Risobinae on banana, *Risoba basalis*. The Sabah survey recorded two more Chloephorinae, *Calymera elaeospila* and *Chloroplaga pallida*.

Erebidae. — Not all of the subfamilies in Southeast Asia of this highly diverse family were represented. The large subfamily Lymantriinae has non-feeding adults so was obviously not represented, and only the Lithosiini of the Arctiinae were recorded. The Arctiini are of low diversity apart from the conspicuous genus *Nyctemera*, as are the Syntomini, but the latter were recorded in Sabah with singletons of *Amata elisa*, *A. apicelisa* and *A. cinctelisa*. The sister-subfamilies Aganainae and Herminiinae are related to the Arctiinae and are both represented, with the Herminiinae yielding more species (45) than any other subfamily. The Scoliopteryginae, Calpinae (in Sabah at least), Boletobiinae

Table 5. Distribution over the sites and bait types of individuals of the commonest species in the families of the Noctuoidea.

Group	Genus & species	B1	B2	B3	B4	B5	P1	P2	P3	P4	P5	**TOTAL**
NOTODONTIDAE												
	Gargetta ?divisa	–	–	–	–	–	1	12	1	–	1	**15**
EREBIDAE												
HERMINIINAE												
	Bertula rufosa	5	7	1	–	1	–	1	–	–	–	**15**
	Adrapsa ereboides	–	6	5	4	1	–	–	–	–	–	**16**
	Adrapsa thermesia	5	12	2	8	–	–	–	–	–	–	**27**
	Adrapsa orgyoides	7	5	2	2	–	–	–	–	–	–	**16**
BOLETOBIINI												
	Drepanorhina shelfordi	4	7	–	2	–	–	1	–	–	–	**14**
EREBINAE												
	Sypnoides infernalis	40	44	4	21	5	17	38	1	5	1	**176**
	Erebus caprimulgus	36	55	21	21	3	4	1	3	1	–	**135**
	Erebus ephesperis	23	14	12	20	–	1	–	1	–	–	**71**
	Trigonodes hyppasia	–	6	14	–	–	–	–	–	–	–	**20**
	Thyas coronata	–	2	7	1	5	–	–	1	–	–	**16**
	Ommatophora luminosa	–	6	23	8	1	–	–	–	1	–	**39**
	Hypopyra pudens	5	6	11	16	9	–	–	1	–	1	**49**
	Hexamitoptera lawinda	13	9	–	6	–	–	–	–	–	–	**27**
	Anisoneura aluco	2	2	1	8	4	–	–	–	1	–	**18**
	Anisoneura salebrosa	1	3	1	2	43	–	1	–	–	–	**12**
EULEPIDOTINAE												
	Anticarsia irrorata	–	–	–	–	–	1	–	8	1	–	**10**
NOCTUIDAE												
ERIOPINAE												
	Callopistria emiliusalis	–	1	6	2	2	–	–	–	–	–	**11**
	Callopistria ventralis	1	–	6	8	7	–	–	–	–	–	**22**

(especially tribe Boletobiini) and Erebinae were the other subfamilies rich in records, the last with the second highest total (36) and probably the highest number of individuals (e.g., species in Table 5).

Other subfamilies were represented in ones and twos as follows: Pangraptinae, *Poliofoca gebenna* (0:1), *Vestura minereusalis* (1:0) and, in Sabah only, *Pangrapta lasiophora*, *P. macariata* and *Acharya franconia*; Hypeninae, *Hypena* sp. (0:1) and *Euphiuche picta* (Sabah only); Hypenodinae, *Luceria bakeri* (3:1), *Luceria*/*Schrankia* sp. (9:1); Anobinae, *Plecoptera recta* (1:0); Eulepidotinae, *Anticarsia irrorata* (0:11, Table 5). Three small subfamilies present in the fauna were not taken: Rivulinae, Hypocalinae and Tinoliinae. A genus of uncertain placement, *Dierna strigata*, was taken twice at prawn bait.

Most groups showed a significant preference for banana, but this trend was reversed in the Scoliopteryginae and the single species of Eulepidotinae. Records were mostly distributed evenly over the five sites at Genting.

Lithosiini. — 10 species were recorded at Genting, mostly in low numbers, the commonest with seven individuals. Most species and individuals were taken at banana bait, and at Sites 3 and, to a lesser extent, 5, as follows: *Poliosia* sp. (0:1), "*Eilema*" *pulvereola* (0:1), *Cyana tettigonioides* (1:1), *Lyclene peloa* (2:0), *Eugoa bipuncta* (6:1), *E. uniformis* (1:0), *Orieosia orientalis* (0:1), *Neoduma ectozona* (3:0), *Trischalis* sp. (1:0), Unidentified (1:0).

Aganainae. — Most records, all from banana, are for the genus *Mecodina*, only recently associated with the traditional Aganainae (Zahiri et al., 2012), as follows: *Mecodina albodentata* (1:0), *M. praecipua* (2:0), *M. viridacea* (3:0) and *M. poaphiloides* (Sabah only). The only traditional aganaine, *Asota heliconia*, was recorded singly in the Sabah survey.

Herminiinae. — 17 of the 31 genera recorded for Borneo (Holloway, 2011) were collected in the Genting survey (one more was added by the Sabah data), the 36 species coming almost entirely to banana traps evenly across the sites (Table 2), though the commonest species (Table 5) were almost absent from Site 5; indeed, all the 16 species recorded there were as singletons only. The records were as follows: *Bertula* sp. near *willotti* (2:0), *B. tespisalis* (1:0), *B. inconspicua* (5:0), *B. carta* (1:0), *B. crucialis** (5:0), *B. depressalis* (Sabah only), *Raphiscopa undulata* (1:0), *R. hirsuta* (3:0), *Mosopia kononenkoi* (1:0), *Hepsidera ferruginea* (3:0), *Alelimma pallidifusca* (1:0), *Idia ocellata* (1:0), *Hydrillodes toresalis** (1:0), *Echanella temperata* (1:1), *Adrapsa alsusalis* (4:0), *A. ereboides*** (22:0, Table 5), *A terroides* (7:0), *A. thermesia* (27:0, Table 5), *A. geometroides** (5:0), *A. orgyoides* (16:0, Table 5), *A. quadrilinealis* (1:0), *Bocana manifestalis***

(7:0), *B. silenusalis** (1:0), *Simplicia discosticta* (1:0), *S. cornicalis** (1:0), *S. variegata* (1:0), *S. griseolimbalis* (2:0), *S. rufa* (Sabah only), *Polypogon nothusalis* (1:0), *P. kurokoi* (2:0), *P. longisaccus* (2:0), *Hipoepa biasalis* (4:0), *Progonia oileusalis* (1:0), *P. fonteialis* (0:1), *Naarda* ?*laufellalis* (2:0) and three other probable *Naarda* species (1:0). The Sabah survey also recorded *Egnasides rudmuna*. Fig. 2 illustrates several species of *Adrapsa* and *Bocana* feeding from a cut *Boletus* fruiting body in Sabah.

Scoliopteryginae. — Nine species from five genera definitely belonging to this group were recorded at Genting, mostly from prawn, as follows: *Ossonoba torpida* (0:5), *Falana sordida* (1:7), *Savara anomioides* (0:2), *S. contraria* (0:2), *S. pallidapex* (0:2), *Rusicada fulvida* (1:1), *Arthisma mutilata* (1:0), *A. rectilinea* (0:2) and *A. amisa* (0:4). Two further *Rusicada*, *prima* and *nigritarsis*, together with *Anomis lyona* and *A. scitipennis*, were recorded from banana in the Sabah survey. So it may be that members of the *Anomis* group of genera have a general preference for banana. Two species of *Dinumma*, *combusta* (7:0) and *spiculata* (1:0), were also taken only on banana in the Genting survey, but this genus is only tentatively placed in the Scoliopteryginae (Holloway, 2005) and may prove to belong elsewhere.

Calpinae. — Only three individuals of two species of this group were taken, all from banana traps. The species were from the tribes Ophiderini and Phyllodini (Zahiri et al., 2012), *Eudocima phalonia** (2:0) and *Phyllodes eyndhovii* (1:0). However, the Sabah survey recorded six more *Eudocima* (*discrepans*, *dividens*, *homaena*, *jordani*, *smaragdipicta* and *srivijayana*) and one more *Phyllodes* (*verhuelli*).

Boletobiinae. — This is another diverse subfamily consisting of several tribes, but its internal structure requires further resolution (Zahiri et al., 2012). Records to baits were all from the tribes Boletobiini and Aventiini, but the latter are definitely not monophyletic and were treated as a temporary resting place of convenience for many genera by Holloway (2011), and all records in the baiting survey of known species are from the *Saroba* group of genera of Holloway (2005). Eight species of Boletobiini and six of the Aventiini were recorded in the Genting survey, the former favouring banana.

Boletobiini: *Drepanorhina shelfordi** (13:1, Table 5), *Panilla homospila* (1:0), *Diomea* ?*roydsi* (1:0), *D. hirdi* (2:0), *D.* sp. (1:0), *D. diffusifascia* (Sabah only), *D. lignicolora* (Sabah only), *Caduca albopunctata** (1:0), *C. phronimus* (1:0), *Maguda santubong* (1:0).

Aventiini: ?*Saroba* sp. (1:1), *Lopharthrum comprimens* (0:1), *Tamba cosmoloma* (1:0), *T. apicata* (0:1), *T. ionomera* (Sabah only), *T. dichroma* (Sabah only), *T. mniomera* (Sabah only), and two unidentified species (2:1 and 0:1).

Erebinae. — Species in the group include most of the largest moths recorded in both surveys, and most of the abundant ones (Table 5). All tribes known from Borneo except the Catocalini, Catephiini, Pandesmini, Pericymini and Amphigoniini were noted, though the Pandesmini (*Polydesma boarmoides*) were represented in Sabah. All these 'missing' tribes only contain a few Southeast Asian species, and these are mostly uncommon. The records are as follows:

Acantholipini: *Ugia disjungens** (1:0), *Heterospila fulgurea** (1:0), *Tochara creberrima* (1:0).

Sypnini: *Sypna albilinea*** (2:0), *S. martina* (0:1), *Sypnoides infernalis* ** (114:62, Table 5), *Hypersypnoides borneensis* (0:1), *Pterocyclophora ridleyi** (1:0).

Erebini: *Erebus caprimulgus*** (135:9, Table 5), *E. ephesperis*** (69:2, Table 5), *E. macrops** (1:0), *E. hieroglyphica* (Sabah only), *Lygniodes schoenbergi* (Sabah only).

Cocytiini: *Serrodes campana* (1:0).

Euclidiini: *Trigonodes hyppasia* (20:0, Table 5), *T. disjuncta* (1:0), *Mocis frugalis* and *M. undata* (Sabah only).

Ophiusini: *Artena dotata** (1:0), *A. convergens* and *A. inversa* (Sabah only), *Thyas honesta*** (3:0) *T. coronata*** (15:1, Table 5), *Ophiusa tirhaca* (1:0), *Ophisma gravata* (Sabah only).

Poaphilini: *Achaea serva** (2:0), "*Parallelia*" *calefaciens* (1:0), *Bastilla absentimacula* (0:1), *B., fulvotaenia** (2:0), *B. arcuata* (Sabah only), *Pindara illibata** (2:1), *Chalciope mygdon* (Sabah only).

Ercheiini: *Ercheia cyllaria** (1:1).

Ommatophorini: *Ommatophora luminosa*** (38:1, Table 5).

Hulodini: *Hulodes caranea** (0:3), and, from Sabah only, *Lacera noctilio*, *L. uniformis*, *Ericeia elongata*.

Hypopyrini: *Spirama helicina* (1:0), *Hypopyra pudens*** (47:2, Table 5), *H. pallidigera*** (2:1), *H. lactipex*** (4:0), *Hexamitoptera lawinda*** (27:0, Table 5).

Unplaced to tribe: *Anisoneura aluco*** (17:1, Table 5), *A. salebrosa*** (11:1, Table 5), *Ischyja inferna*** (8:0), *I. manlia*** (2:0), *I. marapok*** (2:0), *I. paraplesius* (1:0) and, from Sabah only, *I. gynnis*, *I. hagenii*, *I. hemiphaea*, *I. manlioides* and *I. subreducta*, *Platyja ciacula* (0:1), *P. acerces* (1:0), *Fodina oriolus* (0:1). Further records from Sabah only are for *Papuacola albisigillata* and *Sarobacala albopunctata*.

Noctuidae. — Only nine Noctuidae species were recorded in the Genting survey, but two, both in the genus *Callopistria*, were collected in significant numbers at banana, mostly at Sites 3, 4 and 5 (Table 5). All except one of the other records were from prawn or both baits. Six subfamilies were involved as follows: Dyopsinae, *Arcte modesta* (1:0); Plusiinae, *Ctenoplusia albostriata* (0:1), *Thysanoplusia orichalcea* (0:1); Eustrotiinae, ?*Pseudodeltote* nr. *vexillifera* (0:1); Agaristinae, *Sarbanissa transiens* (0:1); Condicinae, *Condica illecta** (4:0); Eriopinae, *Callopistria emiliusalis** (11:0), Table 5), *C. ventralis** (22:1, Table 5) and *C. maillardi** (0:1). The Sabah survey also recorded *Ortopla nulliusinverba* in the Pantheinae.

Sex ratios. — During the course of the Genting survey some attempt was made to sex the larger moths trapped, and a significant difference was noted between the two bait types, with those taken at prawn bait being almost exclusively male and those taken at banana bait having a male to female ratio of about three to two. Most of the females recorded at prawn were those of large erebines that were otherwise recorded mainly on banana. Two out of six of the callidulid *Tetragonus catamitus* taken exclusively on prawn were female, as was one of the four of the uraniid *Urapteroides astheniata*. The singleton of the geometrid *Hyposidra picaria* was female.

Indication of habitat preference and general diversity. — Some comments have been made in the preceding sections on site preferences, if any, in the Genting survey. The Sites could be ranked subjectively in the order: 1+2; 4; 3+5 in terms of decline of forest diversity and forest development, and increase of open habitats and herbaceous vegetation. The moths generally reflected this in various ways (Tables 1, 2), with groups such as Tortricidae, Thyrididae, Crambidae and Geometridae being significantly more diverse in Sites 1 and 2, particularly the latter, and showing the lowest diversity in Site 5. Other groups, such as the butterfly families and the Erebidae, showed a much more even distribution of diversity.

At an individual level of abundance, most satyrine Nymphalidae species were commoner in Sites 3, 4 and 5 (Table 3), and several geometrid species were more or less restricted to Sites 1 and 2 (Table 4). Commoner Erebidae (Table 5), generally favoured sites 1 and 2 but were uncommon in Site 5. Exceptions were *Trigonodes hyppasia*, *Ommatophora luminosa*, and *Anticarsia irrorata,* all legume-feeders as larvae, with the *Trigonodes* also feeding on grasses. In the Noctuidae, the two most abundant species, both in the genus *Callopistria* (Table 5), favoured sites 3 to 5, as did the third most abundant, *Condica illecta*, the first two being fern-feeders as larvae, and the third feeding on herbaceous Compositae. Three butterflies, *Ampittia dioscorides*, *Jamides celeno*, and *Neptis hylas* (Table 4), were all more abundant at Site 3. The *Ampittia* is a larval grass-feeder, but the other two feed on Leguminosae. Potential larval host influence on patterns of abundance across higher taxa revealed by these surveys will be discussed later.

Diversity variation in the records of the Sabah survey has not been studied in detail, but a few general observations can be made. First, the lowest catches were made in the two sites in large areas of continuous forest, totalling only 19 species altogether. Only one species, *Ommatophora luminosa*, was represented by more than 10 individuals, and this species represented more than a quarter of the total individuals sampled across all the sites.

The oil palm samples yielded similarly low diversity with 23 species and only one, *Mocis undata*, with over 10 individuals. Several species were only taken in oil palm, and these were mostly species characteristic of disturbed and open habitats, all Erebidae, with six Erebinae (*Mocis frugalis*, *M. undata*, *Bastilla arcuata*, *Chalciope mygdon*, *Ericeia elongata* and *Polydesma boarmoides*) and three Scoliopteryginae (*Anomis lyona*, *A. scitipennis*, and *Rusicada prima*). Not one of these was recorded in the Genting survey. *Mocis*, *Ericeia* and *Polydesma* larvae feed mainly on Leguminosae and Gramineae, *Bastilla* and *Chalciope* feed on Euphorbiaceae, and the scoliopterygines are mostly on Malvaceae.

The samples from forest fragments of different sizes were generally more species-rich and with more abundant species, though the medium fragment sites were the lowest in richness rather than the four small ones, though these also had the highest number of species (8 in three of them) with ten or more individuals, perhaps an indication of a greater dominance effect. The greatest diversity was recorded in the large fragment at Tabin with 57 species, 7 with over 10 individuals.

All except one of the species with 10 individuals or over was an erebid, with 21 Erebinae, one Pangraptinae and one Boletobiini. The exception was the ennomine geometrid, *Ectropis bhurmitra* with 19 individuals, but, this was only recorded in one of the small fragments.

DISCUSSION

These surveys have provided a wide perspective on adult feeding behaviour and preference in Lepidoptera, both in terms of its presence and intensity, and in terms of its nature. Conducting them in the tropics has ensured that an extensive array of higher taxa has been presented with an opportunity to exploit the two bait types. Obviously this is not an option for groups with non-feeding adults, but we have found great variation amongst groups where they do feed.

Scoble (1992: 19–26) provided a review of adult feeding in Lepidoptera, and indicated that most information on this had been gained from general field observations. He stated that four main substances are sought: water, sugars, salts and amino acids, and listed the wider range of sources, citing Adler (1982), from which these substances have been observed to be frequented by Lepidoptera.

Water, of course, provides a solute for the other three substances, and it may be difficult to ascertain when it is being imbibed per se or as a source of these (Beck et al., 1999); mud-puddling and feeding from sweat and ash is probably mostly for the latter, particularly salts, because water is sometimes seen to be ejected from the abdomen by drinking Lepidoptera that are obviously extracting and concentrating some other component of the fluid (Bänziger, 1973; Beck et al., 1999). The Genting study offered a choice between sugars on the one hand (banana) and perhaps a combination of salts and amino-acids on the other (prawn carrion), and this discussion will later review how its results relate to other observations in the Southeast Asian tropics, particularly with regard to fruit-piercing for sugars, and lacryphagy and mud-puddling for salts and protein. Büttiker (1997b) compared variation in the incidence of lacryphagy in Lepidoptera groups in the three major regions of the tropics, with Noctuoidea predominating in Africa and Geometridae in S. America.

Nectaring, of course, is a significant means of obtaining sugars (Beck & Fiedler, 2009), and is exhibited by a much wider range of Lepidoptera than those recorded at banana baits by this study. It is general to butterflies and occurs in a wide range of moths, particularly hawk moths of the subfamilies Sphinginae and Macroglossinae, large moths with rapid flight, used by Scoble (1992) to typify high energy demands amongst the Order. As most moths are nocturnal, observations of nectaring are much more patchy than those for butterflies, so nectaring behaviour could be only be considered briefly here as being probably more widely present than fruit-feeding.

Microlepidoptera. — In the Tortricoidea and Pyraloidea, records were all from the prawn baits and probably restricted to one major grouping in each, the Olethreutinae and Spilomelinae (Crambidae) respectively. Both groups represent the major source of widespread pest species in their particular superfamilies and perhaps therefore have more of an r-selected, early stage successional character and are particularly associated with open, disturbed habitats in the tropics.

Twelve genera of Spilomelinae have been recorded feeding from mammalian lachrymal secretions in the Oriental tropics (Büttiker, 1967, 1969; Bänziger, 1973, 1992), but there are no records for other crambid subfamilies or from Pyralidae. Only five of those genera (asterisked) are also recorded from prawn in the Genting survey: *Botyodes**, *Bradina*, *Filodes*, *Glyphodes**, *Herpetogramma**, *Mabra*, *Pagyda**, *Paliga*, *Paratalanta*, *Pyrausta*, *Synclera*, and *Tyspanodes**.

Other Apoditrysian groups such as the Gelechioidea (mainly Lecithoceridae) and Immoidea, and Obtectomeran groups such as Calliduloidea and Thyridoidea are of low global diversity generally. Three are entirely or predominantly recorded from prawn bait. The exception is provided by the Immoidea, but little is known of their biology (Common, 1990; Robinson et al. 2001). The Lecithoceridae and some other Gelechioidea are leaf-litter feeders as larvae, with adults often encountered in the forest understorey, features also seen in the Herminiinae and perhaps Boletobiini of the Erebidae.

Butterflies. — The five butterfly families fall into three categories, but all exhibit general nectaring behaviour, though Molleman et al. (2005b) made some distinction of nectaring and fruit-feeding guilds in the African tropics. The Papilionidae and Pieridae did not come to baits, but are perhaps the major exponents of mud-puddling behaviour, often found in swarms on river banks and by puddles and involving many different species, as noted in Borneo by Holloway (1984: 97–99), who also recorded some Nymphalidae, particularly Charaxinae and Cyrestinae, and a smaller number of Lycaenidae. Males predominate in this behaviour (e.g., Beck et al., 1999; Molleman et al., 2005c).

The Lycaenidae and Hesperiidae were exclusively recorded at prawn bait and may generally be more attracted to carrion, as a few species of both families were recorded at fish fragments and patches of blood by Holloway (1984). Beck et al. (1999) also distinguished differences between the families in investigating whether mud-puddling was for obtaining minerals or proteins, noting that Nymphalidae, Hesperiidae, and particularly Lycaenidae preferred a protein resource (albumin), whereas Papilionidae and Pieridae favoured sodium chloride. Their records of Lycaenidae (28 species) were more numerous than in the Genting survey, with six species (the *Caleta*, *Cheritra*, *Megisba* and species of *Nacaduba* and *Jamides*) in common. Their Hesperiidae consisted of only four species, including *Potanthus omaha* from the Genting survey.

The Nymphalidae were the only family to exploit the banana bait and, for the Satyrinae at least, showed a far fuller representation of the local fauna than any other group in the study. Both bait types were favoured, often by the same species, and the taxa recorded showed significant overlap with those noted at fruit bait in Vietnam (Monostyrskii, 2011) and Borneo (e.g., Beck & Schultze, 2000, Tangah et al., 2004). The records from savoury baits made in Borneo by Beck et al. (1999) included no Satyrinae, but did include several of the genera (asterisked) in other subfamilies listed below, with the addition of *Phalanta* and *Vindula* in the Heliconiinae and *Euripus* in the Apaturinae. Proboscis modifications in fruit-feeding Nymphalidae are discussed in a separate section below.

Even in just these few studies, fruit baiting has yielded a high proportion of nymphalid genera (about 80%) and species in Southeast Asia, with the exception of the Danainae. Such genera, using the system of Wahlberg et al. (2009), are:

Limenitidinae: *Parthenos*, *Neptis**, *Pantoporia*, *Athyma**, *Moduza**, *Tanaecia*, *Euthalia*, *Dophla*, *Lexias*, *Bassarona*.
Heliconiinae: *Algia* (*Paduca**), *Cirrochroa**, *Cupha*.
Pseudergolinae: *Amnosia*, *Dichorragia*, *Stibochiona*.
Apaturinae: *Herona*, *Rohana*.
Biblidinae: *Ariadne*, *Laringa*.
Cyrestinae: *Cyrestis**, *Chersonesia**.
Nymphalinae: *Rhinopalpa**, *Kallima*, *Symbrenthia*, *Junonia*, *Kaniska*, *Hypolimnas*.
Charaxinae: *Charaxes**, *Polyura**, *Agatasa*, *Prothoe*.
Satyrinae, Morphini: *Xanthotaenia*, *Neorina*, *Penthema*, *Melanitis*, *Elymnias*, *Faunis*, *Discophora*, *Enispe*, *Thaumantis*, *Amathusia*, *Zeuxidia*, *Thauria*, *Aemona*, *Stichophthalma*.
Satyrinae, Satyrini: *Mycalesis*, *Orsotriaena*, *Ypthima*, *Lethe*, *Ragadia*, *Coelites*, *Erites*, *Zipaetis*, *Neope*.

Macroheterocera. — In the Macroheterocera, the Drepanidae of the Drepanoidea were recorded mainly at prawn baits; the one species favouring banana, *Euphalacra semisecta*, was the only species recorded in the Sabah survey. The species were all from the subfamily Drepaninae. No other feeding records for this group in Southeast Asia have been located, but Bänziger (1988b, 1992) recorded two species of the more robust-bodied noctuid-like subfamily Thyatirinae as feeding from lachrymal secretions of mammals in Thailand, the genera being *Chaeopsestis* and *Neotogaria*. Bänziger (1992) also recorded a sphingid in the genus *Rhagastis* drinking from the human eye nostrils and mouth, and the genera *Acosmeryx* and *Cechenena* have also been recorded from excreted mammalian fluids. All are from the subfamily Macroglossinae.

In the Geometroidea, almost entirely prawn-feeding in the Genting survey, no other records for Uraniidae have been found, though Common (1990) noted day-flying Uraniinae in Australia as nectaring.

Though almost all the Geometridae recorded were at prawn bait, several of the genera and species were recorded from banana in the Sabah survey. The genera were: Sterrhinae, *Scopula* and *Zythos*; Oenochrominae: *Eumelea*; Ennominae: *Fascellina*, *Parasynegia*, *Borbacha*, *Luxiaria*, *Chiasmia*, *Dalima*, *Amblychia* and *Ophthalmitis*.

Genera uniquely recorded in the Sabah banana survey were *Eupithystis* (Larentiinae), *Perixera* (Sterrhinae: Cosymbiini), *Ornithospila* (Geometrinae) and, from the Ennominae, *Hypochrosis* (Hypochrosini), *Stalagmia* (Thinopterygini), *Lassaba*, *Ectropis*, *Pseudalcis*, *Hypomecis* and *Necyopa* (Boarmiini). A species of *Ectropis*, *ischnadelpha*, was frequently observed at night drinking at streams and bamboo gutters in forests at middle altitudes on G. Kinabalu (Holloway, 1976), and Beck (unpublished) has made similar observations for other Bornean geometrids.

Lacryphagy. — Records of feeding from mammalian lachrymal secretions by geometrids have been described in detail by Büttiker (1967), Bänziger (1973), and Bänziger & Fletcher (1988) from: the Scopulini of the Sterrhinae (*Scopula*, *Problepsis*, *Somatina*); the Pseudoterpnini of the Geometrinae (*Pingasa*); both lineages of the Ennominae, Hypochrosini (*Achrosis* [as *Sabaria*], many species of *Hypochrosis*) in the ennomine lineage, and Cassymini (*Peratophyga*) and Macariini (many species of *Chiasmia*) in the boarmiine lineage. A day-flying species of *Dysphania* (Geometrinae: Dysphaniini) was observed mud-puddling and feeding from wet ash in Borneo (Holloway, 1996: 186).

Records from the Noctuoidea are primarily from the Erebidae as indicated earlier, but several species of Notodontidae were taken in the Genting survey, primarily at prawn bait. This family has also been frequently observed feeding at mammalian lachrymal secretions in Southeast Asia (Bänziger, 1988a, 1989, 1992), but the species show no correspondence with the Genting records, being mostly species from the Ceirinae now placed in the genus *Ramesa* (Schintlmeister & Pinratana, 2007) and from the Dudusinae (*Dudusa*), though Schintlmeister & Pinratana did then place *Gargetta* in the Ceirinae rather than the Scranciinae as in Schintlmeister & Lourens (2010).

Two of the three Nolidae were recorded from prawn, and Büttiker (1967) and Bänziger (1983) have recorded species of three genera in the family as mammalian eye-frequenters: *Etanna* (Sarrothripini, as *Nanaguna*); *Arcyophora* (Westermanniinae) and *Lobocraspis* (subfamily uncertain). Bänziger (2007) stated that both sexes of *Arcyophora* and *Lobocraspis* were lachryphagous, whereas in other Lepidoptera this was seen in males only. A few Erebidae have also been recorded drinking at lachrymal secretions in Bangladesh and Thailand (locs. cit. and Büttiker, 1969) in the genera *Hypena* (Hypeninae), *Calyptra* (Calpinae), *Mocis* (Erebinae) and *Blasticorhinus* (subfamily uncertain). Only *Hypena* was recorded in the Genting survey, singly, from prawn, but *Calyptra* will be discussed further below.

Fruit-piercing in Erebidae. — There is considerable overlap between the Erebidae recorded at Genting and the moths observed piercing and feeding from fruit in the Oriental tropics (Büttiker, 1962, 1997a; Bänziger, 1982, 1983, 1986, 1987). These fruit-feeders fall into just three of the erebid subfamilies: Scoliopteryginae, Calpinae and Erebinae. Bänziger (1982) distinguished between primary fruit piercers where the moth is able to penetrate tough or thick skins or rinds of fruit, ranking them according to the toughness of the skin they could penetrate, and secondary piercers that mostly feed from soft fruit or exploit the entry holes made by primary piercers in tough fruit. The modifications of the proboscis (sharpened tip with erectile barbs) that facilitate the piercing of tough rinds and skin of fruit are very similar in genera of the first two groups, leading to the hypothesis that they might be closely related. However, DNA-sequencing results (Zahiri et al., 2012) show clearly that this is not the case and that the proboscis modifications have arisen independently. Bänziger (1982) considered that all genera now assigned to the Erebinae are only capable of piercing soft-skinned intact fruit, except for the Ercheiini and Pericymini where the proboscis tip is sclerotized and sharp; the Pericymini also have erectile barbs.

The relatively low abundance of Scoliopteryginae and Calpinae at the banana baits in the Genting survey is, at first sight, perhaps surprising, though the Sabah survey did yield a much higher diversity of *Eudocima* species in the Calpinae. But it may be that the more capable primary piercers spurn soft fruit that is rotting or fermenting.

In the Scoliopteryginae, there was some distinction between taxa known to Bänziger (1982) as fruit-piercers and suckers such as in the *Anomis* group of genera (*Anomis*, *Gonitis* and *Rusicada*), where records at banana were made (mostly in Sabah), and genera where no records of fruit-piercing have been made such as *Arthisma*, *Falana*, *Ossonoba* and *Savara* which were taken almost entirely at prawn baits. However, Büttiker (1997a) has noted that *Scoliopteryx libatrix*, the type of the subfamily and probably related to *Ossonoba* (Zahiri et al., 2012), pierces fruit in Europe. Bänziger (1986) has described proboscis modifications in members of the *Anomis* group and in *Scoliopteryx*, and see below for modifications of the proboscis in butterflies.

In the Calpinae, records for banana were only made from the Ophiderini (*Eudocima*) and Phyllodini. No records for either bait were made of species of Calpini in the genera *Calyptra*, *Oraesia* or *Plusiodonta*, all present at Genting and in lowland Sabah. Species of *Calyptra* might have been expected to visit prawn bait, as many species of the genus are facultatively skin-piercing to suck the blood of mammals (Bänziger, 1983, 2007). Bänziger (2007) suggested that these species required both fruit sap and salts to ensure longevity; only males sucked blood but could survive for merely a few days on blood and/or water. Their behaviour in piercing the skin of mammals was the same as for piercing fruit, and this behaviour was the same as that in other Calpini that feed on fruit alone, leading Bänziger to suggest that the blood-sucking habit was derived from the more widely exhibited fruit-piercing one in Calpinae These observations have been placed in a phylogenetic context by Zaspel et al. (2012). They suggested that this phylogeny indicated a directional addition of feeding types from nectaring to fruit-piercing to skin-piercing and blood-feeding.

The genera of Erebinae listed by Bänziger (1982, 1987) show considerable overlap with those recorded at banana bait at Genting and in Sabah: *Erebus*, *Serrodes*, *Mocis*, *Artena*, *Thyas*, *Ophiusa*, *Ophisma*, *Achaea*, *Bastilla*, *Pindara*, *Ercheia*, *Hulodes*, *Ericeia*, *Spirama*, *Hypopyra*, *Ischyja*, *Platyja*, and *Sarobacala* (as *Saroba*). Other Erebinae genera recorded by Bänziger are likely to be added if the trapping at Genting is continued, such as *Pericyma*, *Buzura*, *Grammodes*, *Oxyodes* and *Sympis*, but two, *Sphingomorpha* and *Facidina* (allied to *Platyja*), are not yet recorded in Malaysia. Bänziger (1982) also referred to *Ommatophora*, *Dierna*, and *Simplicia* in a third category of fruit-feeders where piercing does not occur but juice is obtained by abrasion of the thin skin of soft, ripe fruit. *Ommatophora luminosa* was one of the most abundant species in both surveys. *Dierna* was taken twice at Genting at prawn bait. *Simplicia* will be discussed in the next section. Bänziger also noted *Focillistis sita* (as *F. salsoma*) as a fruit-sucker, now a member of the Pangraptinae (Holloway, 2011). As seen earlier, the Pangraptinae also generally favour banana, but not exclusively.

There is some concentration of banana feeding in the Boletobiinae, particularly in the Boletobiini, but unrecorded in the Eublemmini. Also, the only group in the Arctiinae, the Lithosiini, shows a similar preference, but the other major erebid group showing a strong preference for banana is the Herminiinae. These groups and the few Noctuidae discussed next, are of particular interest to a later section of this discussion, when the role of larval resources is considered.

Fruit-piercing in Noctuidae. — One of the very few Noctuidae recorded at Genting was a species of *Arcte*, a genus that Bänziger (1982) noted as a fruit-piercer in Japan; single specimens of *Arcte modesta* were taken at each bait type at Genting. Several other records were of singletons at prawn bait, but three species recorded in both surveys were taken in some numbers at banana. The two most numerous were related species of *Callopistria* in the small subfamily Eriopinae. The genus is one of the few in the Lepidoptera that specialises in larval fern-feeding.

Fruit-piercing in butterflies. — Molleman et al. (2005b) noted two different feeding techniques employed by fruit-feeding nymphalid butterflies in the African tropics that perhaps parallel those in the Erebinae. They described the distinctly different proboscis modifications involved. They identified the two techniques as piercing and sweeping the latter involving sucking up fluids from the surfaces of bruised or damaged fruit. Piercing is characteristic of the Charaxinae, perhaps the most the robust members of the Nymphalidae, as are the Erebinae and Calpinae in the Erebidae. In the Charaxinae, the proboscis is similarly robust, thick and apically sharp.The two types of sensilla are short, the sensilla styloconica restricted to the apex and widely spaced in a single row on each side. The sweepers are the Satyrinae and the traditional, broad concept of Nymphalinae as in Corbet & Pendlebury (1992). In these, the proboscis is slender, more flexible, with long sensilla styloconica that are denser and may occur in more than one row, forming a brush adapted to sweep up fluids on the surface of fruit.

Larval diet specialism. — The incidence on banana bait of several species of Noctuidae from a genus with fern-feeding larvae raises the possibility of larval diet being a factor in determining the degree of adult feeding. Certainly, some of the groups recorded here have specialist diets where some nutrient levels may be unusually low and require some kind of supplement from adult feeding. Fern-feeding has just been mentioned, and there are three other instances where fern-feeding (in the broadest sense) specialists have been recorded in the Genting survey. *Ragadia makuta* (Nymphalidae: Satyrini) on *Selaginella*; *Entomopteryx amputata* (Geometridae: Lithinini) and *Tetragonus catamitus* (Callidulidae) on ferns generally. The *Ragadia* was taken quite frequently at banana bait, and the *Entomopteryx* was recorded singly at prawn bait. The Callidulinae are fern specialists as a family (Holloway, 1998), and it is surprising that neither of the two other species (including a second *Tetragonus*) recorded in the Genting locality was taken; all the *Tetragonus* individuals were taken at prawn bait.

Ragadia is the only member of the Satyrinae that does not feed on monocotyledons. The rest feed variously on grasses, including bamboos, and palms, with *Xanthotaenia* on gingers (Zingiberaceae). Most of the Drepaninae recorded belong to a generally palm-feeding group within the subfamily but with *Drapetodes* also on Zingiberaceae (Holloway, 1998). The Hesperiinae also feed generally on Gramineae, with some, such as *Ancistroides* and *Notocrypta*, also on Zingiberaceae. But other grass-feeding groups with abundant species such as the Leucaniini and lineages of *Spodoptera* (Prodeniini) in the Noctuidae have not been recorded, and the bulk of the palm-feeding Notodontidae in the Ceirinae, with the exception of *Ramesa*, a tear-drinker, are also notable for their absence. The groups that feed on monocotyledons and do feed as adults seem mostly to prefer savoury substances with the exception of the Satyrinae, and even amongst these, the genus *Ypthima* showed a preference for prawn in the Genting survey.

Within the Erebidae, there are three groups that show a preference for banana that also have unusual diets as larvae. The Lithosiini are generally algal or lichen feeders, usually browsing on these on the trunks, branches and leaves of trees. The Herminiinae (and Gelechioidea such as Lecithoceridae) are general feeders on leaf litter and other vegetable detritrus, and the Boletobiini are fungus-feeders. Perhaps these pabula are deficient in carbohydrates, requiring some sugar intake by the adults. The aggregation of herminiines on the *Boletus* fruiting body in Fig 2 is also of great interest, and further observations of such behaviour might prompt attempts to find out what substances could be involved.

Most other groups with a strong presence at the baits do not appear to have a marked larval host preference apart from the Calpinae where the tropical taxa feed mainly on vines of the family Menispermaceae and the *Anomis* group of the Scoliopteryginae where there is a concentration of records in the Malvaceae. By contrast, in the Erebinae, many genera appear to be polyphagous, but there is also specialism on Acanthaceae, Combretaceae, Euphorbiaceae, Fagaceae, Gramineae, Leguminosae, Sapindaceae and Smilacaceae, though the hosts of many genera are yet to be discovered (sources here are Robinson et al. (2001) and the Moths of Borneo series, and references therein). The Spilomelinae recorded above as eye-frequenters provide a similar eclectic mix of polyphagy and apparent specialism on Acanthaceae, Bombacaceae, Gramineae, Moraceae, Rhamnaceae, and Verbenaceae. Possible influence of larval diet is also assessed in the next section.

Adult lifespan. — Beck (2007, 2008) investigated the correlation of adult lifespan with nutrient intake by that stage in butterflies, and established that, in Borneo, fruit-feeding taxa lived longer than those solely taking nectar, and that mud-puddling behaviour is associated with a short life. However, he found no independent relationship of lifespan with larval diet. Amongst mud-puddling butterflies, degree of amino acid intake showed correlation with longer lifespan (Beck, 2007).

In a more global survey, Beck & Fiedler (2009) also found only weak influence of various aspects of larval diet on adult butterfly longevity, apart from a stronger correlation of long lifespan with plant growth form, particularly with regard to lianas, though this did not appear to have any chemical basis. They noted that the main liana-feeders were the papilionid Troidini and the nymphalid Danainae and Heliconiini. They

Fig 2. Herminiine Erebidae assembled to feed on a sliced *Boletus* fungus in Sabah, mostly *Bocana manifestalis* but also *B. silenusalis* (bottom and right, with a white spot), *Adrapsa thermesia* (right and left, brown with a paler rectangle at the forewing apex) and *A. geometroides* (lower left, with an array of white flecks). (Photograph by: Peter Bruce-Jones).

also detected a lifespan correlation with adult feeding, this decreasing, again with the pollen-feeding Heliconiini at the long-living end of the spectrum already identified by Beck (2008). One might therefore predict from the moth data that tropical Calpinae, feeding on lianes in the family Menispermaceae as larvae and on fruit as adults, would also show longevity, though the reversal to blood-sucking noted for this group earlier might complicate this.

Biotope characteristics. — It was suggested earlier that the groups recorded at prawn bait in the Tortricoidea (Olethreutinae) and Pyraloidea (Spilomelinae) were those that were particularly adapted to disturbed, open or ephemeral successional habitats, and characterised by mobility as indicated by their high proportion of geographically widespread taxa. This perhaps also holds for the Thyrididae, Hesperiidae, Pieridae, Satyrinae, Macroglossinae, Sphinginae, Calpinae, Scoliopteryginae and Erebinae, is neutral for the Geometridae where this trend is not strongly represented, but fails when the Noctuidae are considered. Records for the family are few and, though two Plusiinae in a basal group are of this nature (Zahiri et al., 2013b) are represented singly at prawn bait, and *Condica illecta* (Condicinae) was taken in small numbers at banana, the bulk of the taxa in the major component of the family termed the ‘Pest Clade’ is unrecorded, though many are known to be abundant at the Genting locality (Barlow, unpublished): the genus *Spodoptera* and the Leucaniini have already been mentioned in this context, and no records have been made of genera in the Noctuinae such as *Athetis* (Caradrinini), *Sasunaga* (Dipterygiini) and *Agrotis* (Noctuini).

Assessment of diversity with baits. — The Noctuidae were recorded at only low levels at bait in our study, but in temperate latitudes, the Noctuinae make up almost all the diversity and abundance of Macroheterocera that come to sugaring or fruit baits, Furthermore, these come in numbers sufficient to provide data for diversity analysis as illustrated by a study undertaken in Bavaria in central Europe by Süssenbach & Fiedler (1999) using two ‘sweet’ bait types: sugar or banana in red wine. Application of richness estimators, including Chao1, suggested that, for Noctuinae at least, regular sampling over a full spring to autumn season could capture a percentage of the fauna susceptible to bait approximating to that for the Satyrinae in the Genting study. However, the species taken by Süssenbach & Fiedler (2000) included only two Herminiinae, one Hypeninae and one Erebinae from the Erebidae in addition to the predominant Noctuidae amongst the Noctuoidea, though that might be expected from their relative proportions in the local fauna. Similarly, Larentiinae predominated amongst the Geometridae, with small numbers of Sterrhinae and Ennominae also sampled, the Sterrhini predominant in the former subfamily and the Boarmiini in the latter. The only other families recorded were Sphingidae with one macroglossine, and Drepanidae, represented by five Thyatirinae but no Drepaninae.

Life history traits of big moths. — Mention was made earlier in this paper of the work of Janzen (1984) on the general life strategies adopted by big moths, particularly Bombycoidea, in the tropics, and applied to South-east Asian members of these groups by Holloway (1987). Janzen recognised two categories: moths that do not feed as adults, are short-lived, the male searching for a static female that is calling with a pheromone, showing marked sexual dimorphism, ovipositing in masses, usually in tree crowns, the larvae aposematic or cryptic, often urticating, feeding on foliage often low in nutrients, high in phenolics; moths with both sexes feeding, highly active, often streamlined (the high energy demand moths referred to by Scoble (1992)), long-lived, with sexual dimorphism weak or absent, ovipositing singly on small plants, saplings, shrubs, vines or tree crowns, the larvae cryptic, with a high rate of nutrient assimilation from more nutrient-rich foliage that may also contain toxic alkaloids, but being low in phenolics. Both strategies are found in the Erebidae, with the Lymantriinae falling into the first category and the Erebinae, Calpinae and Scoliopteryginae falling into the latter. The Calpinae and Erebinae generally contain most of the really large moths in Southeast Asia outside the Bombycoidea and Lasiocampoidea. In the Bombycoidea, non-feeding would appear to be the ancestral condition, with the second strategy evolving within two lineages of the Sphingidae. In the Noctuoidea, the feeding strategy is the ancestral condition, with the non-feeding strategy evolving within one relatively basal group of the Erebidae: the Lymantriinae.

Amino acid and salt requirement. — Bänziger (2007) began to explore the distribution of protease production amongst generally savoury-feeding Lepidoptera, finding them lacking in blood-sucking *Calyptra* species; these mostly (85–95%) sequestered sodium chloride from the blood ingested. As mentioned earlier with reference to the Nolidae, he found proteases in both sexes of *Lobocraspis* and *Arcyophora*, lachrymal feeders obtaining both salt and protein. Lachrymal feeding in other groups is restricted to the males, as in most of the exclusively prawn-feeding groups in this study, the only obvious exception being *Tetragonus catamitus* in the Callidulinae. The study mentioned earlier of Beck (2007) on the varying importance for adult butterflies of amino acids may provide a starting point for investigating presence of proteases in that group.

Rotting prawn is obviously a potential source of protein as well as salt, and so the results presented here offer a basis for deriving a strategy for sampling for presence or absence of proteases more widely amongst the male only groups, and those such as within the Nymphalidae and Erebidae where both bait types are exploited by both sexes. Bänziger (2007) tested some geometrids and crambids for proteases and obtained positive results in the genus *Hypochrosis* of the former, and *Paliga* and *Thliptoceras* of the latter, but got negative results from the geometrids *Chiasmia*, *Ascotis*, *Ctenognophos*, *Hyperythra*, and *Metapercna*. He also obtained positive results from the thyatirines *Chaeopsestis* and *Neotogaria*. The function of both salts and proteins when ingested by male Lepidoptera is also still not entirely clear, such as whether they are essential dietary supplements for high levels of activity such as mate-searching, hill-topping and migration where the male sex may predominate, or whether these substances are sequestered in the spermatophore as what Bänziger (2007) termed 'male dowry' for the female at mating to enhance oviposition, a phenomenon reviewed also by Beck et al. (1999).

CONCLUSIONS

The results of this essentially pilot study are likely to have posed more questions than they have answered, because there is obviously a lot more that could be done to elucidate the role and nature of adult feeding in the Lepidoptera. A more effective way of estimating the importance of nectaring in nocturnal groups is needed. In the absence of information on this, savoury feeding appears to be more widely distributed in the Order than is the obtaining of sugars from non-floral sources, but this latter has developed in several lineages of the Obtectomera, particularly in the Nymphalidae of the Papilionoidea and in the Erebidae of the Noctuoidea. In the former, as with the Noctuidae in Bavaria, bait-trapping offers an effective and perhaps the only means of estimating diversity of the family in the tropics and is seen to be doing this in the studies referred to earlier and others. Light-trapping is not an option for butterflies and the structure of tropical forest makes it difficult to quantify diversity in other butterfly families (but see Basset et al., 2013); the numbers of Lycaenidae and Hesperiidae coming to prawn bait would not appear to offer this quantification except by a much more intensive programme of trapping.

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