Bulletin of the Royal Entomological Society Volume 45 (3) 2021

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Symposia. Nos 1-3 were published by the Society; Nos 4-10 by Blackwell Scientific Publications; Nos 11-17 by Academic Press; No. 18 by Chapman & Hall; No. 19 by Kluwer; Nos 20-23 by CABI.

CONTENTS

106 Editorial

107 Correspondence

109 Letter from the President

110 Research Spotlight – The Extended Lifespan of an Ant: Social Insects and the Fountain of Youth

117 Article – Understanding Butterfly Mimicry: Miriam Rothschild's Seminal Posthumous Contribution

122 Article – Host Plant Resistance to Insect Pests in Jute

128 Society News
- 128 – RES Strategy 2022–2025
- 128 – News from Council

129 Meetings
- 129 – Aphid Special Interest Group Meeting
- 134 – Insects as Food and Feed Special Interest Group Meeting
- 138 – Sustainable Agriculture Special Interest Group Meeting
- 141 – "Saving Swallowtails" – An Online Conference in Two Time Zones

Honorary Fellow Interviews
- 144 – Erica McAlister
- 147 – Laurence Mound

Journals and Library
- 148 – Rebeca Rosengaus

Competitions
- 149 – Early Career Entomologist Awards
- 150 – Student Essay Competition 2020

Schedule of New Fellows and Members
- 153 – As at 2nd June 2021 and as at 20th July 2021

154 Reviews

156 Obituary
- Professor Barbara Ekbom

Diary

COVER PICTURE

Banded demoiselle, *Calopteryx splendens*, on the Grand Union Canal near Horton Wharf, Buckinghamshire.
Photograph by Richard Harrington using a Panasonic Lumix DMC-FZ330.

Author Guidelines

Antenna's Author Guidelines are published in full online at www.royensoc.co.uk/antenna-author-guidelines

Submissions are made by email to *antenna@royensoc.co.uk* and reviewed by *Antenna's* editorial team. There are no page charges for publication in *Antenna*, where we encourage use of full colour figures and photographs to accompany text. Standard articles are normally 1,000–4,000 words in length and submitted with four to eight images (file should be original size of image taken and not reduced in size nor cropped heavily).

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Bulletin of the Royal Entomological Society

The Royal Entomological Society
The Mansion House,
Chiswell Green Lane, Chiswell Green,
St Albans, Hertfordshire AL2 3NS
***E-mail:* antenna@royensoc.co.uk**

Editors:
Dr David George
(Newcastle University)
Dr Richard Harrington

Editoral Assistant:
Dr Jennifer Banfield-Zanin

Consulting Editor:
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COPY DATES
For *Antenna* **45** (4) – 1st October 2021 (DG)
For *Antenna* **46** (1) – 1st January 2022 (RH)
Diary Copy date:
five days before *Antenna* copy date above.

The Royal Entomological Society
The Mansion House, Chiswell Green Lane,
Chiswell Green, St Albans, Hertfordshire AL2 3NS.
Tel: 01727 899387 • Fax: 01727 894797
E-mail: info@royensoc.co.uk

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The following are the subscription rates due on 1st March 2021: Fellows £68.00, Members £62.00, Students £20.00 (first year of membership free), Early career (2 years after studies end) £35.00, Discounted rate – over 65/ country/career break/unemployed/parental leave £45.00. The journals of the Society are available to individual Fellows and Members at preferential rates via the Subscriptions Department at The Mansion House. *Antenna* is supplied free of charge to Fellows and Members not in subscription arrears. **Cancellation of Journal subscriptions must be notified to Subscriptions Department before the 31st October in the year preceding cancellation.**

Printed by Andrew Smith Print Ltd
Chelmsford, Essex
email: andrew@asmithprint.co.uk

EDITORIAL

There's no such thing as a normal year or, in Orwellian-style prose, *no year is normal, but some are less normal than others*. This has to be one of those. A cold, wet spring led to nature lagging two or three weeks behind the recent average; in other words back to how it was thirty or so years ago, when May flowered in May and June Bugs flew in June. And yet I'm writing this on the hottest day of the year so far, and wildlife is catching up fast. That's the UK. Much of Western Europe, including London, has suffered devastating flooding, as has China. The west coast of Canada has suffered devastating heat waves. And so on. Is this, to employ a much-used phrase of late, the *new normal*? Let's keep our fingers crossed for COP26.

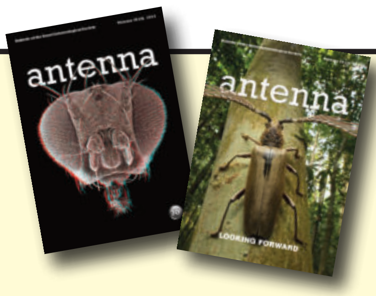
I am hoping that normality soon returns to our meetings programme and to other aspects of the Society's life and all of our lives. We've had some online corkers, as reported herein, but the overwhelming desire seems to be for hybrids which can be attended in person or online according to wishes and circumstances. This should increase attendance from around the world without increasing, and hopefully decreasing, our contribution to this turbulent weather.

None of us is getting any younger. Royals, though, live longer it seems. How does that work? Read Stuart Reynolds' latest fascinating Research Spotlight. One of our best-known and charismatic Presidents was Dame Miriam Rothschild. Philip Howse looks at her contribution to our understanding of mimicry in butterflies and the possible role of butterfly toxicity acquired from host plants. There has never been an article in *Antenna* on the insect pests of jute. I checked using the index – see below for how to do this and how to access back issues. This omission is corrected herein by Bhimashankar Gotyal, one of our three Early-Career Entomologist Award winners. The brilliant winning three contributions to the Student Essay Competition are also published. There were 52 superb entries, giving the judges an extraordinarily difficult task.

Two Honorary Fellows are celebrated, and two past Editors-in-Chief; one, very sadly, as an obituary. Peter Smithers stood down as *Antenna* Editor three years ago (it seems longer!). He kindly continued as Chief Reviewer and Hon. Fellow interviewer. He has decided that the time has come to relinquish the former and I would like to thank him for his huge contribution in that role.

Finally, our copy bank is back to levels such that good articles stand a good chance of being published in good time. So, please share your entomological knowledge and enthusiasm by telling us your stories.

Very many thanks to all contributors.
Richard Harrington



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Index and online copies

Index

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Correspondence

Controversial fossils and the first winged insects

Dear Editors,

I enjoyed Stuart Reynolds' two Research Spotlights on insect wings [*Antenna* 45(1) 6–12; *Antenna* 45(2) 58–65]. One point for your consideration: in the Devonian, *Rhyniognatha* is not an insect as suggested by Engel and Grimaldi (2004) but a millipede (Haug & Haug, 2017). (The head did look a bit odd, don't you think?) Therefore, could the apparent adaptive radiation of pterygotes in the Carboniferous be an artifact of under-collecting in the mid-Devonian to Early Pennsylvanian? Incidentally, there is tantalising evidence of pterygotes in the Early Pennsylvanian of County Clare, but I'm not sure that anyone is looking particularly hard as research results now apparently require advance knowledge to secure funding. The find (Fig. 1) was made on a student field trip, but to-date no fossil insect has been formally described and named from Ireland. The Mississippian of Scotland is another potential hunting ground for early winged insects, especially as they have been documented there from the Pennsylvanian. Disarticulated wings can be expected more often than complete specimens and may well resemble fern leaflets, especially if carbonized. Fossil larvae or nymphs should be expected as well as adults. Fine-grained, early-cemented deposits are more likely to preserve impressions which need not be very large – the pictured specimen is *c.* 2 cm long. In freshwater sediments, clam shrimps may be an associate and marine deposits should not be excluded from the search, as shown in Ireland. Trace fossils and coprolites are another resource. Repeat visits to suitable outcrops may well repay the time spent.

Ed Jarzembowski (Leverhulme Emeritus Fellow)

Figure 1. The oldest winged insect (paoliidan) found in the British Isles (Clare Shale Formation, Bashkirian) by Chris Nolan 30 years ago and dated at ~322 MYA. © Gerald Legg/Ed Jarzembowski.

Response from Stuart Reynolds

Ed Jarzembowski points out that Devonian fossil insects are controversial. In my article on the evolution of insect wings [*Antenna* 44(4) 155–60] I said that *Rhyniognatha hirsti* was "the earliest known obviously insect-like" fossil, but I failed to mention that not everyone agrees with this. Space was tight but I should have tried to indicate the extent of uncertainty better than I did.

It's generally accepted that apterygote Hexapoda were already present ~ 410 MY BP in the Devonian. Numerous well-preserved and relatively-complete fossils in the Rhynie Chert Lagerstätte show *Rhyniella praecursor* to have been a member of the wingless, entognathous Order Collembola (see e.g., Whalley and Jarzembowski, 1981 and earlier references therein). Discovered in the same material, a single contemporaneous fragmentary fossil of an obviously different arthropod, *Rhyniognatha hirsti*, was pronounced by Tillyard (1928) to be insect-like, but of unknown affiliation. The fossil preserves only fragments of the head, but Engel and Grimaldi (2004) asserted that its mandibles were characteristically ectognathous, and thus concluded that *Rhyniognatha* must have been (like all extant ectognathans) a proper insect. In their paper, they noted two other cases of late Devonian fossils from compressed shales that appeared to be wingless ectognathan insects, but even then, both of those cases were admitted to be contentious.

Following a careful re-examination of the same fossil material, Haug & Haug (2017) disagreed with Engel & Grimaldi's interpretation. In fact, they say, *Rhyniognatha* is not an insect at all but a myriapod, possibly a centipede. As I said in my article, since the fossil in question is fragmentary, we can know nothing about the thoracic appendages of *Rhyniognatha*; and even if it was an ectognathous hexapod as claimed by Engel and Grimaldi, it remains uncertain whether it had wings (two extant ectognathous Orders, Archaeognatha and Zygentoma, are wingless). Another claim that a better-preserved although still fragmentary Devonian fossil, *Strudiella devonica*, is that of a pterygote insect (Garrouste *et al.*, 2012) has also been strongly criticised as being over-interpreted (Hornschemeyer *et al.*, 2013). This fossil doesn't have wings either (the paper concludes it must have been a nymph) and, like *Rhyniognatha*, it must be considered uncertain that it was an insect at all.

So, when did insect wings first appear? The fossils of undoubted winged insects are common in the later Carboniferous (Pennsylvanian) Period (323.2 – 298.9 MY BP) and the implication is that their wings must have evolved earlier than this, either in the upper Devonian or the lower Carboniferous (Mississippian) Periods. It isn't an accident that insect flight evolved at that time; these two geological periods represent a time during which photosynthesis by land plants increased greatly and as a result atmospheric concentrations of oxygen rose and carbon dioxide fell steeply (Lenton *et al.*, 2018). Flight is metabolically demanding and the evolution of insect wings may have been the result of the increased availability of oxygen (Dudley, 2000). Nicholson *et al.* (2015) noted the first and last appearance of each described insect family in the fossil record and found a more or less regular increase in the number of described families of insects *versus* geological time that can be projected back to zero at ~ 320 MY BP, a date well after the end of the Devonian. This matches pretty well the earliest example of an unambiguously winged fossil insect, *Delitzschala bitterfeldensis* (Palaeodictypotera), from the Serpukhovian or lower Namurian (331 – 323 MY BP) (Brauckmann and Schneider, 1996), which although somewhat cockroach-like in appearance was apparently unable to fold its wings. A more recent claim that a slightly older fragmentary unnamed fossil from ~324 MY BP is the oldest known pterygote (Prokop *et al.*, 2005) now appears at best uncertain (Dvořák *et al.*, 2019).

So, it looks like the lower Carboniferous is a widely agreed crucial period for the origin of wings. But fossils of insects are mysteriously missing from the fossil record of exactly this period; this is the ~62 MY "Hexapod Gap" (385 – 325 MY BP). A similar though shorter hiatus ("Romer's Gap", 360 – 345 MY BP) afflicts the record of vertebrate fossils. These gaps could represent a real absence of both insects and vertebrates from the ecosystems of that period, perhaps reflecting a previous massive loss of terrestrial biodiversity due to intense UV(B) radiation at the Devonian–Carboniferous boundary (Marshall *et al.*, 2020). Alternatively, it's possible that the gaps simply reflect a shortage of suitable conditions for fossilization at the time; but (as Ed Jarzembowski points out) it is also possible that insufficient effort has been made to find fossils from this period. New material from the earliest period of the Mississippian, the Tournaisian (358.9 – 346.7 MY BP), is currently revealing many new arthropod and vertebrate fossils (Smithson *et al.*, 2012) but has not so far yielded the much sought-after pterygote missing link.

Ed is right to draw attention to this point; it's important because the age (410 MY BP) of the single specimen of *Rhyniognatha* has been used to calibrate the molecular clock by which Hexapod phylogeny is dated. If Haug and Haug (2017) are right in dismissing *Rhyniognatha* as an insect, then we have no reason to suppose that insect wings appeared before the first sign of their appearance in about 323 MY BP, a discrepancy of almost 90 MY. The uncertainty over these dates has led Klopfstein (2021) to argue in favour of minimum age molecular phylogenetic trees.

Let's hope that someone stumbles on the crucial fossil soon!

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The president recording her welcome to Insect Week. More on Insect Week in the next issue.

Letter from the President

Helen Roy

In early June there were some tantalising signs of summer in Oxfordshire, but by the time Insect Week arrived it was raining again! Some very damp walks around my neighbourhood demonstrated the resilience of insects. I was delighted to see the bumblebees making excellent use of the cow parsley umbels for shelter during the downpours. Meanwhile the umbels provided a plentiful supply of aphids for the 7-spot ladybird larvae which continued to forage despite the weather. Watching insects visiting flowers is always entertaining and enlightening. Many of us enjoy such observations of insects but it is wonderful to have Insect Week as an opportunity to share our excitement for the amazing world of entomology. I am delighted that Insect Week will be an annual event from this year onwards. There is so much to celebrate and it is inspiring to see all the activities highlighted through the Insect Week website. Thank you to everyone who ensures the success of the Royal Entomological Society's diverse and inclusive engagement programme – not least the Outreach Committee and the Society staff who share their expertise and enthusiasm so generously.

Of course there are many different ways in which we all promote the science of entomology. The diversity of communication approaches from social media to conference presentations and peer-reviewed publications is inspiring. The Society journals are going from strength to strength and the work of all those involved from editors to reviewers and authors is hugely valuable and appreciated. The hours of work that our editors and the committee chair devote to the task of ensuring the quality of our esteemed journals is incredible. Thank you all.

Collaboration is a theme that I have mentioned many times within *Antenna*. It has been wonderful to see the many and varied collaborations through Insect Week. "The Flea Circus: the smallest show on Earth" performed by Tim Cockerill FRES in collaboration with the British Ecological Society provides a fantastic example of the joy of insects and the reach that can be achieved.

My first year as President has come to an end and I have again been reflecting on the incredible contributions from so many people across the Society's committees and groups. Chris Thomas (past-President) has reached the end of his term as trustee of the Society and I wanted to express my immense appreciation for all that he has achieved on our behalf over the years. Words are insufficient to describe the extent of his contributions. The governance review has been pivotal in informing the Society's way forward for the benefit of everyone. Personally I have learnt so much from Chris and will miss his wise words but also the moments of laughter we have shared throughout our time together on Council. Indeed, when this letter is published we will know the outcomes of the trustee elections. I would like to thank all the trustees who have worked tirelessly over the last year – it has been an honour to work with this amazing team. I have approached each and every one of them on many occasions knowing that they would provide much-needed reflections and insights. I welcome all the new trustees and committee members – and encourage everyone to consider the ongoing opportunities to get involved with the Society.

It is wonderful to see the Society thriving through the work of the excellent staff team, dedicated trustees and committee members alongside the wider membership. It is exciting to reflect on all the activities of the last year while also thinking about future priorities and developments across the Society. The next year will see consolidation of the Grand Challenges, reporting from the membership survey and prioritisation of actions that come from these membership consultations. I look forward to meeting you all in the coming months at one of the many meetings planned – whether from behind the webcam in my home-working office or (hopefully) in person. Meanwhile my huge appreciation to you all for making the Society such a wonderful community.

RESEARCH SPOTLIGHT

The Extended Lifespan of an Ant: Social Insects and the Fountain of Youth

Stuart Reynolds

Department of Biology and Biochemistry, University of Bath

Our life's a clock, and every gasp of breath
Breathes forth a warning grief, till Time shall strike a death.
Francis Quarles (1592-1644), *Hieroglyphikes of the Life of Man* (1638)

Ageing and senescence

Many of us reflect ruefully upon growing inexorably older and less able-bodied. As the seventeenth century poet Francis Quarles sets out so mournfully, the clock is ticking while we metabolise, and with each hour our capacity to engage in life's activities diminishes a little. Quarles's lines imply that simply breathing is enough to bring on the decline. One popular scientific theory of ageing supposes that this is literally true, designating reactive molecules that are by-products of oxidative respiration (oxygen-derived "free radicals") as the single most important cause of ageing (Halliwell & Gutteridge, 2015; Lane, 2016). If so, then senescence inevitably accompanies the fire of life. But Quarles also implies that the passage of time alone may do the damage. If so, then our lives are literally programmed to end in death. Although most of us find it hard as humans to rationalise our individual mortality as being a personal benefit, it's evident that in the longer view of things, ageing and death are almost certainly evolution's optimal solutions to a biological problem that we haven't yet recognised.

Gerontology, the science of the evolution and mechanisms of ageing, is now a well-developed scientific subject (nicely reviewed by Flatt & Partridge, 2018) in which insects have played important roles as experimental subjects. As you might expect, the vinegar fly *Drosophila melanogaster* has been extensively used in research on the genetics of senescence (a recent typical paper is that of Parker *et al.* 2020). But it is a severe limitation of studies with model organisms that these species were originally selected for their short generation time; it doesn't seem sensible to study ageing only in animals with brief lives. And too often we don't know anything about the relevance of senescence to the lives of animals in their natural environment (Ricklefs, 2008).

The extraordinary effect on ageing of a parasite on an ant

This leads up to the theme of this article. The queens of eusocial Hymenoptera and both the kings and queens of termites (Isoptera) are exceptionally long-lived (in some cases up to 10-20 years), while the non-reproductive castes of the same species (workers and soldiers) die relatively young, perhaps after only months (Keller & Genoud, 1997; Keller, 1998; Tasaki *et al.*, 2021). These insects shine a very special light on senescence; although it is received wisdom among gerontologists that the optimum lifespan of an animal is determined by a trade-off between longevity and reproduction, in eusocial bees, ants, wasps and termites, there is no such trade-off, or if there is then it does not dominate the evolutionary outcome. In these insects, the lives that are extended are the same as those of the individuals who do all the reproducing. The very existence of long-lived eusocial insect reproductive castes shows that natural selection can act independently on reproduction and lifespan. This problem currently excites intense research interest (Korb & Heinze, 2021).

With this in mind, a new paper from the laboratory of Susanne Foitzik at the University of Mainz in Germany (Beros *et al.*, 2021) recently caught my eye. It concerns the tiny myrmicine ant, *Temnothorax nylanderi* (Figure 1A, B), whose colonies (typically a single queen with 100-200 workers) occupy hollow twigs or often the woody seeds (acorns) of oak trees (Varoudis *et al.*, 2018). Workers of this ant serve as intermediate hosts for a cestode (tapeworm) parasite, *Anomotaenia brevis* (Figure 1C) and parasitized workers are easily recognised because they are pale in colour (Figure 1D). Among the particular enemies of this ant are green woodpeckers (*Picus viridis*) (Figure 1E), specialist anteaters that break open nests and consume all the inhabitants; in doing so, the birds inadvertently consume the cysticercoid larvae of *A. brevis* that are contained within the ants, and so become the principal vertebrate hosts of the parasite.

Once within the ant, the parasite is able to control the host's behaviour so as to increase the probability of transmission to its next host. The more conspicuous lighter colouration of parasitized *T. nylanderi* workers, their increased tendency to stay within the nest, and their decreased tendency to emigrate on nest disturbance all render them more likely to be eaten by a woodpecker (Beros *et al.*, 2015; 2019). Importantly, Beros *et al.* (2019; 2021) have discovered that *A. brevis* also causes infected workers to live longer than usual. Fifty percent of workers in unparasitized colonies in Beros *et al.*'s (2021) study were dead after c. 230 days and all had died by the end of the three years for which the experiment continued, whereas c. 50 % of the parasitized workers from infected colonies were still alive at three years. This manipulation of host lifespan is to the parasite's advantage; if parasitized ants live longer, then they (and their parasite cysts) have an increased probability of being eaten by a woodpecker.

But surely, parasites are supposed to be bad for their hosts? We might hypothesize that parasitized ants live longer because once infected they rarely leave the nest. There is obviously a greater danger to active foragers of getting lost or being killed by predators while outside the nest, so that the lives of infected stay-at-homes would be expected to be longer. But in fact, parasitized workers live to a greater age than unparasitized ants even in the safe conditions of laboratory captivity, where foraging is not dangerous. Another way in which a parasite might cause its host to live longer would be by preventing reproduction, thus releasing resources that might otherwise go into making eggs, as seen in the life-extending effect of the rat tapeworm, *Hymenolepis diminuta*, on the beetle *Tenebrio molitor* (Hurd *et al.*, 2001). But in *T. nylanderi*, workers do not mature eggs either before or after parasitization unless the queen is removed; in that case, parasitized workers mature their ovaries to the same extent as do uninfected nurse workers also present in the nest, and indeed to a greater extent than unparasitized foragers from the same colony (Beros *et al.*, 2019).

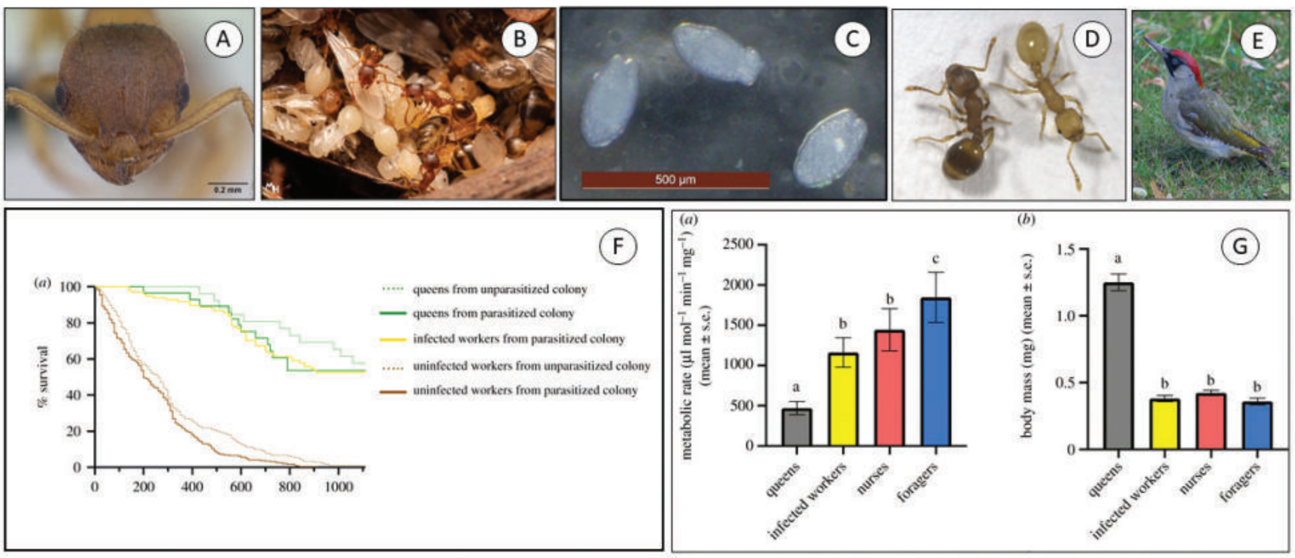

Figure 1: A. Head of worker, *Temnothorax nylanderi* (image: April Nobile / © AntWeb.org / CC-BY-SA-3.0); B. *T. nylanderi* workers and winged queens in nest (image: Matt Hamer / CC-BY-SA-3.0); C. The cestode parasite, *Anomotaenia brevis* (image: Susanne Foitzik, reproduced with permission); D. Unparasitized worker (left, with dark cuticle) and parasitized worker (right, with pale cuticle) of *T. nylanderi* (image: Susanne Foitzik, reproduced with permission); E. Green woodpecker, *Picus viridis* (image: ThG, from Pixabay); F. Survival curves of infected and uninfected *T. nylanderi*; G. (a) Metabolic rate and (b) Body mass of queens, infected workers, together with (uninfected) nurses and foragers of *T. nylanderi* (F and G both reproduced from Beros *et al.*, 2021, CC-BY-4.0).

Instead, it looks as though, from a survival point of view, the parasite converts its worker host into a pseudo-queen. The survival curve for infected workers is statistically indistinguishable from that of (uninfected) queens from infected colonies (Figure 1F). Infected workers don't reproduce like the real queen, because they don't lay eggs in her continued presence; but parasitized ants do change their behaviour so as to be more regal. Once infected, parasitized workers remain at home in the nest, staying close to the real queen, where they are fed by other workers as though they too were queens.

The negative effects of parasitism by *A. brevis* on *T. nylanderi* thus aren't felt at the level of the ants that are actually parasitized (Scharf *et al.*, 2012). Interestingly, however, Beros *et al.* (2021) find that the health of *un*infected workers in parasitized colonies is significantly worse than that of those in unparasitized colonies, their risk of dying being increased by a factor of 1.37 over the control level (Beros *et al.*, 2021). Presumably these unparasitized workers die sooner because they are exhausted by the unusually hard work of feeding the pseudo-queens. Why are uninfected workers fooled into behaving this way? Why do they not recognise that their idle nestmates are not real queens and eject them from the nest? To a human observer, real *T. nylanderi* queens are obviously visually different to workers, being larger and quite different in morphology. The sensory world of an ant is, however, one in which olfaction and taste are more important than vision, and their chemical communication system evidently fails to recognise that the infected workers aren't real queens but imposters. The extra attention that parasitized workers are given seems in part due to a change in the composition of their cuticular lipids, extracts of which elicited significantly greater attention from uninfected workers than did control extracts from unparasitized workers (Beros *et al.*, 2021). It isn't clear whether the chemical signal is altered by the parasite directly or indirectly.

This cost of parasitism also impacts upon the real queen. Beros *et al.* (2021) compared the survival curves of queens from infected and uninfected colonies; although the log-rank statistical test they used to interrogate the whole dataset found no significant differences, visual inspection strongly suggests that a gap between the survival trajectories of queens from infected and uninfected colonies opens up after around half of the total time of the experiment, with queens from parasitized nests surviving less well thereafter. This makes sense; queens from infected colonies would be expected to be less well-fed than those from uninfected colonies because some of their food supply is diverted to parasitized workers. On the other hand, the negative effect of the parasite on the productivity and survival of colonies in the field is not dramatic and sometimes can't be seen at all (Scharf *et al.*, 2012). Presumably this is because there are other natural dangers to wild ant colonies and the effect of the tapeworm is invisible in the statistical noise.

All this tells us that the parasite has evolved to take clever advantage of a phenomenon that has been a puzzle to gerontologists for many years. This is the fact that the reproductive castes of social insects have very long lives (up to hundreds of times longer) compared to conspecific workers who share the same genome in terms of gene content (Heinze & Schrempf, 2008; Korb, 2016). This extension of life associated with reproduction is true of queens (but not males) of eusocial Hymenoptera (ants, bees and wasps) and also of both the queens and kings of eusocial termites (Isoptera) (Korb & Heinze, 2021). By causing infected workers of *T. nylanderi* to masquerade as queens, the tapeworm improves its chances of completing its life cycle.

Ageing and the rate of living

To understand the effects of parasitization on *T. nylanderi* workers, we need to take an excursion into what is known of the mechanism of ageing. One theory of senescence is the "Rate of Living" hypothesis, originally put forward by Rubner (1908), and later elaborated by Pearl (1928). Briefly, the idea is that the higher the rate of metabolism, the shorter the lifespan. The theory is generally acknowledged to be simplistic; we know that some experimental treatments, like putting *Drosophila* on a restricted diet or interfering with the uptake of nutrients into cells through tinkering with insulin signalling, extend lifespan but don't interfere with the basal (resting) metabolic rate in the way expected from the Rate of Living theory (Hulbert *et al.*, 2004). It seems that in practice, life is usually terminated by an evolved developmental programme of self-imposed senescence (see below) rather than by metabolic exhaustion. Nevertheless, the Rate of Living theory is sufficiently successful in predicting the lifespan in many animals to persuade most gerontologists that metabolic collateral damage must indeed be an important aspect of age-related decline in performance (Speakman, 2005).

What is the mechanistic link between metabolism and ageing? Insects are overwhelmingly aerobic and the greater their mass-specific metabolic rate, the greater is the rate at which dioxygen (O_2) is used by the mitochondria in their cells. But oxygen-dependent metabolism is hazardous because, in the process, some of the respired O_2 is converted into highly reactive free radical intermediates such as superoxide ($^1O_2^-$), hydrogen peroxide (H_2O_2), hydroxide ions (OH^-), and hydroxyl radicals (^1OH). All these highly reactive molecules are likely to oxidise the first organic molecule that they encounter, and the cells' proteins (enzymes), lipid membranes, and nucleic acids (DNA and RNA) are all at risk of being structurally damaged. The greater the rate of metabolism, the greater the rate of production of free radicals, thus causing greater cellular damage and potentially shortened lifespan.

But these escaping free radicals can be trapped by reducing chemicals (often termed "antioxidants"), which effectively neutralize them by reacting with them, thus keeping them away from the rest of the cell. These defences against ageing are small organic molecules like ascorbic acid (vitamin C), glutathione and uric acid (Halliwell & Gutteridge, 2015). Because they are consumed by the free radicals, they must continually be replaced, which is a metabolic cost. Expenditure on protecting against collateral damage from the by-products of metabolism is not just about preventing cellular injury; resources are also spent on repairing free-radical induced damage once it has occurred. Thus, lipid peroxides and free radical-damaged proteins are destroyed and replaced, and (perhaps most importantly) damaged genes can be repaired (there's no need to go into the biochemistry of this here).

If the Rate of Living hypothesis is true, then genes affecting antioxidant defences should affect the natural lifespans of the animals that bear them. Studies on *Drosophila* and other model organisms have shown that mutations, allelic exchanges or knockouts of particular single genes, can indeed either extend or shorten lifespan; many of these genes are known to encode proteins that either enhance antioxidant defences or repair damage caused by free radicals (Piper & Partridge, 2018). Presumably, these are among the genes with which natural selection tinkers to optimise lifespan. Thus, life can theoretically be extended if more resources are spent on cellular defences, maintenance and repair. Here's a simplistic analogy: your car will last longer before it stops running if you spend more money on keeping it in good mechanical order. But if the total amount you can spend on the car is capped, then you may find that you can drive fewer miles per year during its lifetime, or that it must be scrapped sooner.

Now back to the parasitized workers of *Temnothorax nylanderi*, which appear to enjoy a life of ease. Is this imposed nest-rest the cause of their unnaturally long lives? Beros *et al.* (2021) set out to test the idea. We'd expect idle, parasitized workers to expend less energy and thus produce fewer damaging free radicals. They found that the mass-specific metabolic rate (measured as O_2 consumed mg^{-1}) of parasitized workers was indeed significantly lower (by about one third) than that of unparasitized foragers but higher than that of the queen (Figure 1G). Correcting these figures for the non-linear dependence of metabolic rate on size [according to Speakman (2005) it is proportional to $(mass)^{0.73}$] makes only a small difference, with parasitized workers still metabolising at about twice the rate of the queen.

According to the Rate of Living model of ageing, this relationship between size, parasitism and metabolic rate should extend the expected lifespans of both real queens and parasitized workers beyond that of unparasitized workers, but we'd still expect the lifespan of a parasitized worker to be only about 50% of that of a queen (instead of 33% of that of the queen in an unparasitized worker). It's a pity that the study of Beros *et al.* (2021) ended just a bit too soon; as it is, the true extent of the difference in life expectancy between parasitized workers and the queen can't be determined. Nevertheless, it is likely from the data that we have, that although the depression of the workers' metabolic rate by the parasite may account for some of its longer life, there is another major factor that we have to account for. What is it?

The evolution of programmed senescence

The answer almost certainly lies in a genetically-encoded programme of senescence. In an age dominated by Darwinian thinking, it's hard to argue that any phenotypic attribute is safe from natural selection, and so we must suppose that programmed senescence originally evolved as a trait that conferred an advantage. If a novel gene allele that promotes senescence (i.e., increases the probability of death) can spread within a population, it is self-evident that such an allele must confer increased fitness on those individuals bearing the gene; i.e., they have a greater lifetime contribution to the next generation than would have been the case had they possessed the original form of the gene.

What could that benefit be? It's a long-standing puzzle that is far from being solved, and anyway, maybe there isn't a single big benefit but many small ones. Nevertheless, theorists have not been idle and several explanations for the evolution of senescence have been proposed (classic papers are those of Fisher, 1930; Haldane, 1941; Medawar, 1952). The basic idea is that genes having positive effects on fitness in early life but negative effects on fitness in later life must be positively selected for programmed senescence to evolve. The three papers just cited each propose a slightly different way in which this might happen. It's a plausible idea; any degree of non-zero random mortality throughout life means that early reproduction must be valued more highly than late reproduction, since the former is more certain to come to fruition than the latter. Effectively this means that natural selection is less effective at removing mutations that adversely affect older animals. The fullest statement of this theory, usually called the Antagonistic Pleiotropy hypothesis, is due to Williams (1957). His mostly qualitative analysis was subsequently endorsed by Hamilton (1966) in a landmark mathematical paper that initially had little impact, but which has since become very influential (Rose *et al.*, 2007). In it, Hamilton showed that the "force of selection" (i.e., the consequence to fitness of any age-specific effect on mortality) inevitably declines in all organisms with increasing age. This confirmation of Williams's theory gave confidence that the original analysis was correct. Gaillard & Lemaitre (2017) have revisited the Antagonistic Pleiotropy hypothesis, finding that most of the predictions made by Williams about the conditions required for the evolution of senescence are well supported by more recent evidence.

It's at this point that we need to recruit yet another theory. This is the Disposable Soma theory proposed by Kirkwood (1977; 2005). Because the resources necessary for the expression of phenotypic traits (i.e., developmental, physiological and behavioural processes) are both costly and always limited in supply, each trait must be traded-off against the others in fitness terms. While some traits lead to increased production of progeny (i.e., they increase fitness), others are directed to somatic maintenance and repair and have no intrinsic fitness value other than assuring survival so that fitness can be enhanced at a later time. The Disposable Soma model is useful in that it specifically predicts that increased allocation of resources to reproduction will inevitably lead to diminished allocation to maintenance, and thus to a faster rate of ageing (shorter lifespan) due to accumulated damage (Maklakov & Chapman, 2019).

But Antagonistic Pleiotropy predicts that bodily maintenance gets increasingly expensive with age. Putting this together with Disposable Soma, we finish up with the prediction that there must come a point in life when it is no longer economically viable to allocate further resources to anti-ageing defences. It is better to allocate any remaining resources to reproduction and then to die. This is the rationale for the evolution of programmed senescence and death; like an old car that gets progressively more expensive to mend, there appears to be an active decision not to maintain the organism any longer. Although the vehicle may die, the genes that it contained (most pertinently, those that specified its senescence) live on in the organism's surviving close relatives.

Regulating the trade-off

The balance between investment in reproduction and somatic maintenance/survival in insects is known to be regulated through the TI–J–LiFe network (TOR/IIS–JH–Lifespan and Fecundity), in which three distinct hormonal and cellular signalling pathways interact (Toivonen & Partridge, 2009; Korb *et al.*, 2021). In this network, the IIS endocrine/growth factor pathway (a cascade of insulin-like peptide hormones and growth factors, PI3-kinase intracellular signalling, and induction of the transcription factors Akt and FOXO) interacts with the nutrient-sensing Target of Rapamycin (TOR) pathway, each negatively regulating the other. Both pathways also have downstream effects on circulating Juvenile Hormone (JH) levels. The negative feedbacks between the IIS, TOR and JH modules of the pathway make it act like an on-off switch that regulates reproduction and also limits expenditure on somatic maintenance. Once synthesis of yolk precursor proteins (YP; vitellogenins) begins, allowing ovarian maturation to go ahead, the YPs also feedback negatively to downregulate somatic maintenance, so that the switch stays flipped (Rodrigues & Flatt, 2016; Korb *et al.*, 2021).

But how does all this tie in with the genetic programming of ageing, senescence and death? The genes that actually regulate senescence at the level of the cell remain mostly unidentified, but such evidence as is available doesn't provide strong support for the inevitability of a trade-off between reproduction and somatic maintenance/survival. To take a single example, overexpression in *Drosophila* of FOXO, a transcription factor in the IIS signalling pathway that mediates oxidative-stress responses and extends life-span (Lehtinen *et al.*, 2006), is sufficient to prolong the life of adult flies, but doesn't affect fertility at all (this and other similar cases are discussed in Toivonen & Partridge, 2009). This result is sufficient to tell us that although we know that reproduction and somatic maintenance/survival are often traded-off in many insect life-histories, they don't have to be.

Genes and queens

But wait! How can natural selection act differentially on queens and workers when both are members of the same species, and both have the same genome? If, as is often argued, natural selection operates on social insects at the level of the colony as a superorganism rather than on the individual (Hölldobler & Wilson, 1990) then when we are thinking about the evolution of lifespan and senescence, we must consider not the longevity of individuals but that of the colony to be the decisive factor. This idea of selection operating at a higher level than the individual isn't an evolutionary novelty that applies only to social insect colonies. It is also true for the longevity of individual multicellular organisms; the lifespans of the various cell types that comprise the organism are a different matter from the lifespan of the whole animal. In humans for example, the lifespan of a red blood cell is about 120 days (Lindsell *et al.*, 2008), while that of the human in which the cells circulate is 81.25 years (Office for National Statistics UK, 2020), or 247 times as long.

Natural selection is thus capable of separately determining the optimum lifespan of the organism as a whole and its cellular components; we can say that the longevity of the whole and of its parts are "adaptively decoupled" as far as natural selection is concerned (in the sense of the term used by Moran, 1994). This is possible because the genetic control of senescence is hierarchically controlled by developmentally-compartmentalised and mutually-exclusive signalling pathways, allowing natural selection to tinker with senescence separately in the different compartments. Such adaptive decoupling also allows the separate control of ageing in the different castes of eusocial insect societies. In the case of queens and workers, the developmental compartments within which senescence is separately controlled are in fact whole animals, in the form of the different castes. Again, this isn't a novelty; a similar decoupling of developmental morphogenesis between the different life stages of insects is involved in the complete metamorphosis of holometabolous insects (Rolff *et al.*, 2019).

The control circuits that we are interested in here are gene regulatory networks of hierarchically-organised transcription factors (Levine & Davidson, 2005). Some candidate gene regulatory networks thought to be involved in programming senescence in a wide range of animals, including the TI–J–LiFe network mentioned above, are discussed in Fabian *et al.* (2021). What we are looking for is evidence that these gene regulatory networks are developmentally decoupled, i.e., they are differently driven by high-level transcription factors in different social insect castes.

Sure enough, when Negroni *et al.* (2021) sequenced mRNA from *T. nylanderi* workers that had become fertile because the queen had been removed from their nest, they found that numerous genes related to longevity, fecundity and stress adaptation were expressed to a greater extent ("upregulated") than in infertile ants from the same nests, while other genes in the same three categories that were downregulated were more common in infertile than fertile ants. The authors picked out five genes that were upregulated in the newly-fertile workers as candidates for extending lifespan; four are components of the TI–J–LiFe signalling network that is known to regulate the reproduction–longevity trade-off, while another is an autophagy gene involved in cellular defence. This looks like the rewiring of a gene regulatory network by altering the expression of its components. There doesn't appear, however, to be a "master gene" that regulates lifespan in a top-down fashion.

Korb *et al.* (2021) used a comparative approach to investigate whether this rewiring of the control of senescence between queens and workers involves similar changes in different social insect species. To do this they extracted mRNA from the insects and sequenced it, comparing the transcriptomes of different castes of several different hymenopteran and isopteran species. In brief, there appeared to be no common pattern used in all social insects to promote reproduction concomitantly with somatic maintenance. The most commonly observed longevity-related change seen in the TI–J–LiFe networks of the social insects relates to the role of yolk proteins (YP). These proteins play a central role in oocyte maturation, and in non-social insects also act as a negative feedback signal to shut down somatic maintenance (see above). In some (but not all) social Hymenoptera, expression of YP is positively correlated with both processes (Rodrigues & Flatt, 2016), suggesting that this changed role of YP may be one way in which longevity is controlled differently in social insect queens. It isn't currently understood how this works. YP have been claimed in a high-profile paper to have antioxidant properties, and the pattern of expression in honeybees supports the hypothesis that caste-specific differences in YP localisation may be involved in queen longevity (Corona *et al.*, 2007). But Korb *et al.* (2021) cautiously comment that "*a causal role for [YP] in affecting ageing and longevity in social insects still awaits experimental confirmation*".

The main conclusion available at present is thus that the gene regulatory networks controlling the reproduction–maintenance trade-off in social insects appear to have evolved in a number of different ways, convergently reaching the same end of allowing simultaneous reproduction and somatic maintenance. This makes sense; eusociality is thought to have evolved on at least four occasions in Hymenoptera (Peters *et al.*, 2017) and although it is uncertain whether eusociality in termites originated only once, it is certain that its emergence was much earlier and entirely separate from that in the Hymenoptera (Thorne, 1997).

There is, however, evidence that the developmental pathways followed by the presumptive queens and workers of at least some social insects differ in the pattern of epigenetic modification of the genome (particularly DNA methylation) and also in the roles of non-coding RNAs (reviewed by Oldroyd & Yagound, 2021; Sieber *et al.*, 2021). It is quite possible that the rewiring of the regulatory gene networks governing caste formation (and perhaps lifespan extension) is achieved by epigenetic means rather than by recruiting additional high-level transcription factors. If it does occur, then it remains to be seen whether such epigenetic regulation is similar or different in different species.

Parasites and queen genes

But now we must come back to those parasitized acorn ants. How does the tapeworm affect the lifespan of its worker host? Perhaps the parasite directly alters the expression patterns of one or more genes that directly regulate the ant's lifespan. Or perhaps it may affect host metabolic activity indirectly through some non-developmental effect. These are not mutually exclusive hypotheses. Two studies have appeared that address this question through a transcriptomic approach. Feldmeyer *et al.* (2016) compared mRNAs in the brains of parasitized and unparasitized *T. nylanderi*. Stoldt *et al.* (2021) compared transcripts in the abdomens of parasitized and unparasitized ants from the same species. Both studies are impressive in their power, but nevertheless disappointing in the sense that neither manages to give a strong pointer as to how the lifespan of a parasitized ant is extended. I won't give details of the results of these studies here, because it's clear that further work will be required to reveal the parasite's clever trick in converting infected workers into pseudo-queens. Stoldt *et al.* (2021) simply comment that "the results suggest that the lifespan extension of infected workers is not achieved *via* the expression of queen-specific genes". But I share the enthusiasm of the authors for this experimental system. Please persevere!

The British national anthem expresses the wish that the nation's monarch (incidentally, the Royal Entomological Society's patron) should enjoy a long life. And indeed, this is so; recent British kings and queens have lived longer than their subjects by about 30 years (Olshansky, 2021). We now know that this postponement of senescence is also true in general of social insect reproductive castes, and although there is evidence of the rewiring of the gene regulatory network that controls the trade-off between reproduction and somatic maintenance, we don't yet know in detail how the royal lives are prolonged. In particular, there is as yet no evidence of a controlling "master gene". Watch this space!

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Understanding Butterfly Mimicry: Miriam Rothschild's Seminal Posthumous Contribution

Philip E. Howse OBE, FRES

Professor Emeritus, School of Biological Sciences, University of Southampton.

(philipehowse@gmail.com)

Former Society President, The Hon. Miriam Rothschild, was imbued with the curiosity and drive that are the hallmarks of genius and which earned her eight honorary doctorates, a CBE and a Fellowship of the Royal Society. Her interest in the chemical ecology of Lepidoptera dated back to the early 1930s when, walking with a friend, she made a startling observation about brown butterflies:

> '*In the early 1930s an outbreak of anthrax occurred along the banks of the flooding River Nene close to Ashton Mill… … one of us (MR) had walked through the river meadows and had been deeply impressed by the magnificent population of Meadow Browns and Ringlets which occurred there, and a possible link with the anthrax outbreak suddenly occurred to her*'.

This led her to speculate that the butterflies might contain antibiotics, but it was not until over 60 years later that she saw the potential in this observation.

In 2001, when terrorist activities were at their height, there were serious concerns about the possible use of anthrax (*Bacillus anthracis*) spores in microbiological warfare. Anthrax has been used as a weapon around the world for over a century and, at this time, powdered anthrax spores were deliberately put into letters that were sent to well-known people through the U.S. postal system. Twenty-two people, including 12 mail handlers, got anthrax, and five of these 22 people died. The problem of growing resistance of bacteria to the antibiotic methicillin was then brought to the foreground. Around that time, in the UK, the numbers of death certificates mentioning MRSA was increasing sharply and doubled from 487 to 955 between 1999 and 2003. It was estimated that there were approximately 90,000 deaths a year in the USA due to resistance of *Staphylococcus aureus* to antibiotics.

This prompted Miriam to begin research into the suspected bactericide that allowed brown butterflies to survive. If this agent could be identified, she thought it might prevent thousands of deaths. Miriam's fascination with the chemical defences of butterflies and other animals began in the early 1990s, when she started a collaboration with a natural product chemist, Robert Nash, then a researcher at the Royal Botanical Gardens at Kew. She was interested in a beautiful lycaenid (blue) butterfly, *Eumaeus atala* (Fig.1), once thought to be extinct in Florida, but which had made a sudden comeback there. This butterfly has psychedelic blue and red colour-patterns and the caterpillar is bright orange and yellow. Miriam thought this must mean that it was toxic, and the colours were a warning to predators. This butterfly is very unusual in that its food plants are cycads, sometimes known as 'Sago Palms'. Analysis of extracts of the butterflies (Rothschild *et al.*, 1986) revealed the presence of cycasin, which was taken up by the caterpillars and sequestered in the adults, with the result that birds learn to avoid them.

The toxicity of cycads was highlighted in the study by the psychologist Oliver Sacks of the Chamorro people of Guam in Micronesia (Sacks, 1987). The islanders were prone to 'Guam disease', a chronic and often terminal brain disease also known as *amyotrophic lateral sclerosis-parkinsonism-dementia*. Sacks traced this illness to the Chamorro diet, which included flour made from cycad seeds. Cox *et al.* (2003) then found that the toxin is produced by symbiotic cyanobacteria in the roots of cycads. Flying foxes (fruit bats), a common food for the Chamorros, were found to feed on cycad seeds, and eating even a few bats was enough to induce neurotoxic symptoms (Cox & Sacks, 2002).

In a paper published in the same year, Schneider *et al.* (2002) found that certain present-day cycads, a group which preceded the evolution of flowering plants, are dependent upon a weevil, *Rhopalotria mollis*, for pollination, which

Figure 1: The Atala Hairstreak, *Eumaeus atala*, the largest and most iridescent hairstreak in southern Florida. Photo: A Sourakov ©, with permission.

Figure 2: Silver-washed Fritillary *Argynnis paphia* (top left), Dark Green Fritillary *Argynnis aglaja* (top right) (Photos: K. Dolbear, with permission of Stratford-on-Avon Butterfly Farm), High Brown Fritillary *Argynnis adippe* (bottom left) (Photo: P. Eeles, with permission), Pearl-bordered Fritillary *Boloria euphrosyne* (bottom right) (Photo: Bob Eade, with permission)

occurs when they pick up pollen while feeding on the cycad cones. The authors speculated that this mutualism may have existed since the Mesozoic period. Their paper was dedicated to Miriam Rothschild "*the grande dame of insect ecophysiology and chemical ecology, for her pioneering and untiring research*".

The results of the research on butterfly antibiotics were not published until 2017, twelve years after Miriam's death, but I had access to the initial drafts that were prepared by Miriam before she died, and decided to consult these because of my current interest in the evolution of fritillaries.

During June and July in the south of England you are likely to see the Silver-washed, Dark Green and Pearl-bordered fritillaries (Fig. 2) visiting bramble flowers on the outskirts of woods. The similarity between these species is striking but is not a phenomenon that is limited to British species.

There are over 40 species and 40 sub-species of larger fritillary in Europe, all with very similar wing patterns. Among the smaller fritillaries, the genus *Boloria* (which includes the Pearl-bordered Fritillary), has over 200 species and subspecies, with a circumpolar distribution, the majority occurring in Northern Europe and Asia (http://www.nic.funet.fi/pub/sci/bio/life/insecta/lepidoptera/ditrysia/papilionoidea/nymphalidae/heliconiinae/boloria/index.html). I puzzled over this for a long time – surely Darwinian theory says that closely-related species that fly together should evolve different colour-patterns to reduce the chances of interbreeding. So, have these butterflies all hit on a particular colour-pattern with magical properties?

In my book (Howse, 2014), I advanced the hypothesis that butterflies gain protection by mimicking features of birds of prey, which will frighten away insect-eating birds. Kestrels, for example, tend to sit around on the outskirts of woodland, sporting orange-brown breast plumage covered with dabs of black in a fritillary pattern – one that might arouse suspicion and alarm in most small birds. An alternative hypothesis is that all fritillaries are distasteful to predators and hence may be mimics. Such mutual resemblance is known as Müllerian mimicry, in which it is believed that a number of species that are toxic may share the same form and colour-pattern so that birds and other predators carry over their learning experiences from encounters with one species to others. At first, I could find no hint that fritillaries are distasteful to predators; indeed, the leaves of some violets, which are the food-plants of all the British fritillary species except the Marsh Fritillary, are said to be edible and are used to treat respiratory problems and as anti-cancer agents (which are also mostly human toxins). It was an exciting discovery, then, to find that the Silver-washed Fritillary had been among 23 species tested by Miriam's co-workers, and extracts of the butterflies had shown antibiotic activity.

In this research, Robert Nash and other chemists and microbiologists from the USA, Israel and Aberystwyth, with whom Miriam collaborated, began to identify antibiotic pyrrolizidine alkaloids (PAs), which they found in all but one of the butterflies tested. They tested the extracts against two gram-positive bacteria: *Bacillus anthracis* (the cause of anthrax), *Staphylococcus aureus*, and two other less pathogenic gram-negative bacteria: *Pseudomonas aeruginosa* and *Proteus mirabilis.* The butterfly species tested were all those found in the vicinity of Miriam's home in Ashton Wold, Peterborough, with the exception of the iconic Monarch butterfly (*Danaus plexippus*), which Miriam and her assistant Kate Garton were breeding at Clive Farrell's Butterfly House (then at Syon Park in Chiswick). There were fifteen nymphalids (including nine satyrines such as the Meadow Brown and Ringlet), two pierids (whites), two lycaenids (blues) and two hesperiids (skippers). The first results showed that extracts from all these species, except the Small Heath (a satyrine), killed the anthrax bacterium, and some were also toxic to *S. aureus*. None was effective against the less lethal *Pseudomonas* and *Proteus*.

Although various PAs derived from plants were known at this time (notably from the Monarch butterfly), they were toxic to humans. But it emerged that the newly discovered butterfly PAs, which proved to be derivatives of the alkaloid loline, had no human toxicity, and so were possible candidates for medicinal use.

After the first draft was completed in 2002 (but not submitted for publication), Robert Nash and Paul Wolferstan, along with three Oxford-based scientists, filed a patent in 2003, in the name of a company called Molecular Nature Ltd (MNL), for the use of the loline derivatives as antibacterial agents. The International Patent was granted in 2005, but MNL went into liquidation a year later and the patent was acquired first by Vastox Ltd., a drug development company, and subsequently by the Oxford-based company Summit Therapeutics Ltd.

Because of the focus on the commercial prospects for the newly-discovered antibiotics, Miriam's final draft was not completed until shortly before her death in 2005. She was nearly blind by this time, and asked her scientific helper and friend, Kate Garton, to submit the draft to *Nature*, the authors being herself, Robert Nash and Naomi Balaban, an Israeli microbiologist. *Nature* rejected the paper, possibly because of the lack of detailed scientific evidence for the identity of the PAs and proof of their origin.

By this time, Miriam, along with Robert Nash, Paul Wolferstan and others, had developed the hypothesis that the PAs were not synthesised by the grasses themselves but, in the case of satyrine and hesperiid butterflies, suspicion fell upon fungi that infested them. This was prompted, it appears, by a paper (Richardson, 2000) intriguingly entitled "Alkaloids of endophyte-infected grasses: defence chemicals or biological anomalies?".

A lot was known about the PAs occurring in the Monarch butterfly, where they act as deterrents to insect-eating predators and are held responsible for Batesian mimicry (i.e. mimicry in which a palatable insect gains protection by resemblance to a poisonous one) but it was always believed that this was a unique insect–plant relationship, or was at least restricted to other danaines and toxic plant species that contain PAs. It turns out, however, that this is not just a Monarch story but one involving all the grass-feeding butterflies that had been tested in her collaboration with Nash and others in relation to bactericides. So, no-one thought of looking at the toxicity of grasses – after all, these have been the basis of the human food chain for 10,000 years and, apart from the well-known case of creeping ryegrass, which can harbour the pathogenic fungus ergot, they could not possibly be poisonous or, surely, we would have learnt about that long ago? However, when the PA loline, which is the component found in rye grass that causes ergot poisoning, and derivatives of it, were identified in the butterfly extracts, suspicion fell upon fungi that were symbiotic with grasses. These included the fungus *Epichloë*.

PAs active against the anthrax bacterium and, in most cases, *Staphylococcus aureus*, were found in all the grass-feeding butterflies, and so Miriam appears to have been given to believe that all the butterflies tested contained pyrrolizidines. This was counterintuitive, particularly in the case of the Silver-washed Fritillary, which, like many fritillary species, feeds as a larva on supposedly edible violets. A possible answer to this paradox came into view when I discovered a report by Nishida (2017), that both males and females of the Indian Fritillary, *Argynnis hyperbius*, reared on the S.E. Asian wild violet, *Viola yedoensis*, or on cultivated pansies, also belonging to the Violaceae, contained substantial amounts of highly toxic cyanide-producing glycosides. As these cyanides were not detected in the host *Viola* plants, Nishida (2017) tentatively concluded that the Indian Fritillary is able to biosynthesise them from amino acids. This is not too surprising: it has been shown that the toxic neotropical Passion Vine Butterfly *Heliconius melpomene*, which feeds on *Passiflora* vines, obtains cyanogenic glycosides from the larval food-plant, but is also capable of biosynthesising them from precursors (Nahrstedt & Davis, 1983).

This unexpected finding signals the distinct possibility that all fritillaries are protected by alkaloids that are either obtained from their food plants or synthesised from precursors by the insects themselves. If that is so, my hypothesis that all fritillary species are Müllerian mimics seems to be confirmed. But I encountered another twist to the story. What I had not realised, in coming to this conclusion, was that since Miriam's death in 2005, there has been a steady stream of research results showing the presence of novel toxins in various plant families, including compounds with a strange cyclical molecular structure known as cyclotides. Cyclotides were first found over 30 years ago in a member of the Rubiaceae (coffee family). Since then, they have been identified in many flowering plants, including violets, and even in algae and soil bacteria. Every species of violet tested so far contains cyclotides, and one of the most toxic comes from violets.

Cyclotides are reported to be cytotoxic, herbicidal, insecticidal and nematocidal, and there is no reason to believe that they would not make butterflies with these substances in their bodies distasteful to vertebrate predators. They have been found now in the families *Cucurbitaceae*, *Fabaceae, Solanaceae* and *Apocynaceae* in addition to *Rubiaceae* and

Violaceae (Grüber, 2010). We can tentatively suggest, therefore, that fritillaries have a variety of options for sourcing toxins: either they can feed on violets, in which case they obtain cyclotides, or cyanogenic glycosides, or they can feed on Apocyanaceae to obtain pyrrolizidines. Failing that, they are able to synthesise toxins from precursors to which they are immune.

A paper by Rasooly *et al*. (2017) focussed on chemistry and microbiology but omitted biologically significant data, curiously not mentioning nine species that were named in Miriam's earlier drafts, namely, the Painted Lady, Comma, Small Tortoiseshell, Mountain Ringlet, Large Heath, Small Heath, Speckled Wood, Common Blue and Large Blue. Neither were the Latin names of the butterflies given, so it is only possible to identify "Skippers" in Table 2 of that paper by recourse to Miriam's early draft as either the Small Skipper (*Thymelicus sylvestris*) or the Large Skipper (*Ochlodes venata*). The reason for this information being left out now becomes clear. The biochemists may have failed to confirm that the species omitted contained pyrrolizidines, possibly realising that compounds such as cyclotides could be responsible for the antibacterial activity of the extracts of those species, which might then have interfered with a patent application.

It appears likely that what makes many butterflies distasteful includes a suite of antibiotics, rather than a single one. It is noteworthy that cyclotides have also been found in many Apocyanaceae, including milkweeds (asclepiads), opening up the question of whether pyrrolizidines are wholly responsible for the distastefulness of danaine butterflies. Likewise, one wonders whether the omission in the 2017 Rasooly *et al*. paper of the Small Heath, the Small Skipper and the Mountain Ringlet is related to the fact that, unlike the other grass-feeders, they all feed on *Poa* tufted hair grasses (Poaceae), in which cyclotides have been identified.

The hypothesis that mimicry is tied to allelochemicals (those used in defence against other species) in the food-plants of butterflies may apply also to the brown butterflies (Satyrinae), whites (Pieridae), swallowtails (Papilionidae) and blues (Lycaenidae). If we take the example of ringlets, it is remarkable that there are over 40 *Erebia* species in Europe, and over 50 sub-species. Many of these are almost indistinguishable from one another, and many overlap in their distribution. But all are grass-feeders, and Saikkonen *et al.* (2016), in a study of over 3,000 separate samples of 13 different grass species in Germany, found all were infected by *Epichloë* fungus at levels varying from 8 – 98% of samples tested.

We are left with the realisation that the different divisions of mimicry that have been erected are purely arbitrary, and based only on what and how much an insect has eaten during its growth period.

With Miriam Rothschild's death in 2005, no-one, it seems, seized on the importance of the findings about the toxicity of butterflies for the evolution of mimicry and for evolutionary theory in general. This raises the question of whether Miriam herself had seen the importance of the toxicity data for theories of mimicry, ecology and evolution before her life ended. I am certain that she had.

Acknowledgements

I am grateful to Clive Farrell Hon FRES, and Kate Garton for useful information and for making Miriam's unpublished drafts available to me, and to Prof Helmut van Emden for valuable comments on the manuscript.

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Figure 1.

Host Plant Resistance to Insect Pests in Jute

B. S. Gotyal[1*] and S. Satpathy[2]

[1] *Scientist, Division of Crop Protection, ICAR- Central Research Institute for Jute and Allied Fibres (CRIJAF), Barrackpore- Kolkata, West Bengal, India

[2] Principal Scientist and Head, Division of Crop Protection, ICAR- Central Research Institute for Jute and Allied Fibres (CRIJAF), Barrackpore- Kolkata, West Bengal, India

* Corresponding author E- mail: gotyalento@gmail.com

Introduction

Jute (Fig.1) is a commercially important bast fibre, rainfed, summer crop. Bast fibre is a strong woody fibre obtained chiefly from the phloem of the stem. Jute is considered the second most important natural fibre-producing crop in the world (Samira *et al.* 2010). The two cultivated species of jute, *Corchorus olitorius* (tossa jute) and *C. capsularis* (white jute), constitute the world's foremost bast fibre cash crops. They are mainly grown in South-east Asian countries including India, Bangladesh, China, Nepal, Indonesia, Thailand, Myanmar, and some South American countries. In India, jute is grown in the eastern region, covering 0.8 million hectares and producing 1.8 million tonnes of fibre per annum, including mesta fibre, of which the share of mesta is about 15% of the total fibre production in India. The jute crop grows well in high humidity (80-90%) and temperature (36-38°C) with annual rainfall of 1,500 mm or more with at least 250 mm of monthly precipitation during March, April and May to maintain appropriate soil moisture. The crop is harvested around 110-120 days after sowing. The fibre is mainly used for making sacks, bags, bundle cloths, wrappings, bedding foundations, bonded fabrics, and boot and shoe linings. It is also used for strings for all purposes, certain ropings, wall coverings, wool packs, etc. Jute is a labour-intensive crop and about 4,000,000 families derive their sustenance by cultivating jute in the country. Morever 250,000 people are employed in the organised jute industry, and over 2,500,000 people are engaged in jute-based ancillary and jute-diversified sectors. There is no doubt that the commercial and environmental importance of jute will be realised more in the future due to greater awareness of the adverse consequence of synthetic fibres in the environment as well as policy initiatives for restricting the synthetics in packaging and related ventures (Gotyal *et al.* 2019).

Insect pests are one of the bottlenecks responsible for low productivity and poor quality of jute fibre. More than 30 species of pest, including insects and mites, infest jute from the seedling stage to harvest and cause yield losses of up to 34%. Severe infestation of these pests affects fibre quality, causing loss in tensile strength, formation of knotty fibre and reduction in the length of fibre (Rahman and Khan, 2012). Among different pests of jute, indigo caterpillar, stem weevil, semilooper, hairy caterpillar and yellow mite are the most important. In addition, gram caterpillar (Selvaraj *et al.* 2013), green semilooper (Ramesh Babu *et al.* 2015a), leaf webber (Ramesh Babu *et al.* 2015b) and leaf miner (Selvaraj *et al.* 2014) have been reported to infest jute in the recent past. Among the sucking pests, intensity of damage caused by yellow mite has increased greatly. Changes in climatic conditions have led to increased frequency, intensity and outbreaks of cotton mealybug, which has emerged as a new pest causing significant damage (Satpathy *et al.* 2016). Few parasitoids and entomopathogens have been reported (Selvaraj *et al.* 2013; 2015) as effective biocontrol agents. Development of host plant resistance (HPR) against multiple insect pests is key to development of advanced integrated pest management (IPM) strategies.

Status of insect pests of jute

Considering the low input management strategy adopted in jute, the enhanced pest status and severity of the existing pests, and reports of new pests, hint at the role of various abiotic stresses. During the past few years, infestations of hairy caterpillar (Figs 2–4) have been more regular and severe and even raised to the status of outbreaks.

During the 110-120 days of crop growth, many sucking, foliage-feeding and borer pests cause damage to the crop at various growth stages. These insect and mite pests have been categorised into major, minor and new pests depending on their regularity of occurrence and severity of damage caused (Table 1).

Challenges of insect pest management in jute

An examination of weather conditions during the recent past showed an increase in maximum and minimum temperatures and a decrease in rainfall and number of rainy days. Such climatic conditions correlated with increased infestations of insect pests in the early growth stage (Satpathy *et al.* 2013). The crop is subject to varying levels of infestation (Pradhan, 1990-92) (Table 2).

Table 1. Status of insect and mite pests of jute.

Common name	Scientific name	Family	Order	Status
Hairy caterpillar	*Spilosoma obliqua*	Arctiidae	Lepidoptera	Major
Jute semilooper	*Anomis sabulifera*	Noctuidae	Lepidoptera	Major
Jute stem weevil	*Apion corchori*	Curculionidae	Coleoptera	Major
Yellow mite	*Polyphagotarsonemus latus*	Tarsonemidae	Acarina	Major
Mealybug	*Phenacoccus solenopsis*	Pseudococcidae	Hemiptera	Major
Grey weevil	*Myllocerus discolor*	Curculionidae	Coleoptera	Major
Indigo caterpillar	*Spodoptera litura*	Noctuidae	Lepidoptera	Major
Stem girdler	*Nupserha bicolor*	Lamiidae	Coleoptera	Minor
Termite	*Odontotermes obesus*	Termitidae	Isoptera	Minor
Red mite	*Tetranychus coffeae*	Tetranychidae	Acarina	Minor
Leaf miner	*Trachys pacifica*	Buprestidae	Coleoptera	New pest
Gram caterpillar	*Helicoverpa armigera*	Noctuidae	Lepidoptera	New pest
Safflower caterpillar	*Condica capensis*	Noctuidae	Lepidoptera	New pest
Green semilooper	*Amyna octa*	Noctuidae	Lepidoptera	New pest
Mesta hairy caterpillar	*Euproctis scintillans*	Lymantriidae	Lepidoptera	New pest
Tussock caterpillar	*Dasychira mendosa*	Lymantriidae	Lepidoptera	New pest
Leaf webber	*Homona* spp.	Tortricidae	Lepidoptera	New pest

Source: Gotyal *et al.*, 2019.

Table 2. Range of infestation (%) for three major insect pests in *olitorius* and *capsularis* jute germplasm.

Crops	Insect Pests	Range of infestation (%)
C. capsularis (white jute)	Yellow mite	6.2 – 17.0
	Semilooper	15.4 – 49.0
	Stem weevil	18.3 – 32.4
C. olitorius (tossa jute)	Yellow mite	5.4 – 63.7
	Semilooper	21.0 – 39.1
	Stem weevil	12.7 – 39.5

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Status of host plant resistance studies in jute

The development of pest-resistant varieties of jute has not been seriously attempted so far. The main reason is the lack of donor insect-resistance genes. Bast fibre crops are characterised by narrow genetic variability for adaptability not only to various agronomic environments but also fibre yield, quality, and susceptibility to diseases and insect pests, which makes it difficult for plant breeders to develop new varieties through conventional breeding (Kar *et al*. 2009). To circumvent these constraints, physical mutagens (X-rays, gamma-rays) have been applied extensively to obtain rapid genetic variation. Various aspects of both basic and applied mutagenesis in jute have been documented by Chattopadhyay *et al.* (1999), Kundu *et al.* (1961), Shaikh and Miah (1985) and Thakare *et al.* (1973).

Crop wild relatives, *Corchorus aestuans* (Fig. 5), provide a wide range of valuable attributes for traditional and molecular breeding. Most wild species of *Corchorus* are poor yielders, but potent sources of biotic and abiotic stress tolerance coupled with finest quality fibre (Mahapatra and Saha, 2008). Thus, jute breeders have become more aware of the need to maintain genetic diversity among varieties and improve the management of genetic resources through consideration of traditional landraces and germplasm (Kar *et al*. 2009).

Until the mid-1970s, only 300 accessions of jute were available. Concerted efforts in association with the National Bureau of Plant Genetic Resources (NBPGR), New Delhi, and the International Jute Organisation in the last two decades have resulted in an increase in the gene pool of jute and allied fibre crops to the tune of 4,723 accessions, which includes wild species and important breeding stocks (Sen, 2007). In Bangladesh, the largest gene bank of jute and allied fibre crops is being maintained at the Bangladesh Jute Research Institute, with 5,936 accessions comprising 15 species of *Corchorus*, 22 species of *Hibiscus* and 15 of allied genera yet to be characterised (Haque *et al*. 2007). In India from 1999 to 2004 a total of 655 accessions, including landraces and wild relatives, were collected from different agro-ecological regions. The Central Research Institute for Jute and Allied Fibre Crops (CRIJAF) is maintaining 939 accessions of *C. capsularis*, 1,647 accessions of *C. olitorius* and 313 accessions covering eight wild species (Mahapatra and Saha, 2008).

India has nine species (7 wild and 2 cultivated) of *Corchorus*, namely, *C. aestuans*, *C. depressus*, *C. fascicularis*, *C. pseudo-olitorius*, *C. tridens*, *C. trilocularis*, *C. urticifolius*, *C. capsularis* and *C. olitorius* (Mahapatra *et al*. 1998). Most of the studies in jute have been restricted to routine screening of germplasm on a limited scale without considering the basis of resistance mechanisms (Gotyal *et al*. 2014). A few accessions of wild jute species have been evaluated to find the source and mechanism of resistance to jute hairy caterpillar. Wild jute species adversely affected oviposition, larval feeding, larval survival, larval weight, pupation, pupal weight and adult emergence, clearly indicating antibiosis (Gotyal *et al*. 2013a). Among the wild species, *C. aestuans* and *C. tridens* caused significant non-preference for egg laying and larval feeding of jute hairy caterpillar. The remarkable variation in the biochemical parameters of the host plants significantly affected the biology of jute hairy caterpillar (Gotyal *et al*. 2015). The development of cultivars with resistance to jute hairy caterpillar is an urgent need because the cultivated varieties of jute show only moderate levels of resistance (Gotyal, 2013b).

Yellow mite is a very important pest where the nymphs and adults suck the cell sap from young leaves. Tossa jute suffers more than white jute due to yellow mite (Das, 1989). The development of suitable eco-friendly management strategies for this pest is an urgent need. Variation in host-plant traits, including food quality, presence of deterrents, and toxic chemicals are important factors in limiting pest populations. Understanding the variation in food quality among related host plants could have useful implications for the management of yellow mite. The yellow mite populations on cultivated jute species (*C. olitorius* and *C. capsularis*) varied significantly more than those on wild species, with the exception of population densities on *C. capsularis* being similar to those on the wild species, *C. aestuans*. It is evident that the biochemical content of jute leaves has an important role in the growth and build-up of mite pests in these crops. On the basis of relative resistance and susceptibility of the jute species, appropriate interspecific crosses may provide a platform for developing resistant varieties for yellow mite management (Mitra *et al*. 2015).

Identification and utilisation of sources of insect resistance

The potential of wild and weedy relatives of *Corchorus* has been assessed for biotic stress tolerance/resistance and fibre quality parameters. *Corchorus aestuans* has been found to be highly resistant to jute hairy caterpillar infestation (Gotyal *et al*. 2015). Wild species from East Africa are endowed with biotic stress tolerance as well as good fibre quality. The countries with an availability of trait-specific jute germplasm have been summarised in Table 3.

Sources and mechanisms of resistance in cultivated as well as wild jute species against jute hairy caterpillar were determined based on ‘no-choice’ and ‘multiple-choice’ tests. Larval duration, larval weight, larval survival, pupal weight, pupation rate and adult emergence were significantly impaired on the wild species, particularly *C. aestuans* (Gotyal *et al*. 2013b). This indicated antibiosis in the wild species against hairy caterpillar. The wild species, *C. aestuans*, also showed a

Table 3. Countries of availability for trait-specific germplasm of jute.

Jute Species	Traits	Availability of trait-specific germplasm by Country
C. capsularis	Quality fibre	S. Africa, Tanzania
C. olitorius	Waterlogging tolerant	Botswana, Senegal, Mozambique, N. Australia
C. angolensis	High yield and quality fibre	Angola, Namibia
C. kirki	Taller plant in wild condition	Botswana, Mozambique, S. Africa, Zimbabwe
C. merxmuelleri	High yield and quality fibre	Namibia
C. tridens	Fine fibre	Ghana, Nigeria, Angola
C. trilocularis	Fine fibre	Mozambique, Malawi, Sudan, Somalia, Zambia, Zimbabwe
C. asplinifolius	Drought tolerant	Zimbabwe, Mozambique, Botswana, Namibia
C. cinerrascens	Drought tolerant	Ethiopia, S. Africa, Somalia
C. depressus	Drought tolerant	Ethiopia, Sudan, Mauritania
C. erinoceus	Drought tolerant	Somalia, Sudan
C. erodiodes	Drought tolerant	Socotra
C. junodii	Biotic stress tolerant	Mozambique, S. Africa
C. pinnatipattitus	Biotic stress tolerant	Botswana, S. Africa
C. saxatilis	Biotic stress tolerant	Zaire, Zambia
C. gillettii	Biotic stress tolerant	Kenya
C. sulcatus	Colonise on shallow soil	Zambia, Zaire
C. hirtus	Colonise on shallow soil	S. America, Caribbean islands
C. siliquosus	Colonise on shallow soil	Central America

Source: Mahapatra and Saha, 2008

significant level of feeding deterrence to the larvae of hairy caterpillar. The adult of this insect exhibited a high degree of non-preference for oviposition on the wild species compared to the cultivated accessions. As C. *aestuans* is crossable with the cultivated species, C. *olitorius*, it is possible that this accession can be used for an insect-resistance breeding programme in tossa jute (Choudhary *et al*. 2015). Large-scale screening of jute germplasm at ICAR-CRIJAF multi-location network trials has resulted in the identification of several lines with reasonable levels of resistance to semilooper, yellow mite, hairy caterpillar and stem weevil. Sources of resistance to insects in jute have been used in the breeding programme, and many varieties with resistance to insect pests have been developed (Tables 4 and 5). However, resistance breeding programmes are underway for a few crop pests only. Slow progress in developing insect-resistant cultivars has mainly been due to the difficulties involved in ensuring adequate insect infestation for detecting resistance and screening in addition to low levels of resistance to certain insect species in the cultivated germplasm (Sharma and Ortiz, 2007).

Table 4. Germplasm identified to be resistant to insect pests in jute.

Insect Pests	Jute germplasm
Yellow mite	OIN-91, OIN-96, OIN-97, OIN-98, OIN-103, OIN-105, OIN-106, OIN-107, OIN-109, OIN-110, OIN-116, OIN-118, OIN-125, OIN-127, OIN-128, OIN-129, OIN-135, OIN-51, OIN-67, OIN-88, OIN-90, OIN-94, OIN-126, OIJ-06, JRO-524.
Jute hairy caterpillar	OIN-86, OIN-87, OIN-91, OIN-92, OIN-93, OIN-96, OIN-97, OIN-98, OIN-101, OIN-102, OIN-103, OIN-104,OIN-105,OIN-110, OIN-111,OIN-112,OIN-113, OIN-114, OIN-120, OIN-121, OIN-124, OIN-125, OIN-126, OIN-131, OIN-109.
Semilooper	OIN-87, OIN-88, OIN-89, OIN-92, OIN-94, OIN-96, OIN-97, OIN-101, OIN-104,OIN-106, OIN-107, OIN-109, OIN-112, OIN-114, OIL-116, OIL-118, OIL-119, OIN-127, OIN-132, OIN-204,OIN-02, OIN-04, OIN-12, OIN-26, OIN-39.
Stem weevil	OIN-95, OIN-114, OIN-121, OIN-100, OIN-110, OIN-117, OIN-122, OIN-126, OIN-127, OIN-130, OIN-131, OIN-133, OIN-134, OIN-135, OIN-94, JRO-524, JRO-204, OIN-96, OIN-103, OIN-109, OIN-111, OIN-112, OIN-116, OIN-123, OIN-36.

Source: ICAR- CRIJAF, AINP Annual Report, 2016-2017

Table 5. Jute varieties resistant to insect pests developed at ICAR- CRIJAF and State Agricultural Universities.

Insect Pests	Improved varieties less susceptible to insect pests
Stem weevil	Bidhan Pat-2, Bidhan Pat-3, NDC-2008 (Ankit), JBC-5 (Arpita), JRO-7835 (Basudev), JRO-524 (Navin), AAU OJ- 1(Tarun), CO-58 (Sourav), JBO-1 (Sudhangsu), JRO-2407 (Samapti), JRO- M1(Pradip)
Semilooper	Bidhan Pat-2, Bidhan Pat-3, NDC-2008 (Ankit), JBC- 5 (Arpita),AAU OJ- 1 (Tarun), JBO-1 (Sudhangsu), JRO- 2407 (Samapti), JROM-1 (Pradip)
Yellow mite	NDC-2008 (Ankit), JBC-5 (Arpita), JRCM-2 (Partho), JRO-7835 (Basudev), JRO-524 (Navin), CO-58 (Sourav), JRO-M1(Pradip)
Jute hairy caterpillar	JRCM- 2 (Partho)

Source: S. K. Pandey *et al.* 2015

Need for future research

- Standardisation of simple, robust, repetitive techniques for screening jute germplasm against different types of insects in the field and in glasshouses.
- Improvement of jute for both yield and fibre quality along with redesigning the insect-resistance breeding programme involving newer germplasm.
- Identification of insect-resistance traits in jute genotypes which can be incorporated in jute cultivars through a breeding programme.
- Search for genetic and biochemical bases of host plant resistance.
- Search for molecular markers responsible for resistance against yellow mite, mealybug and lepidopteran pest complexes for use in marker-assisted selection.
- Identification of multiple toxin genes for lepidopteran pest complexes for development of transgenic varieties with resistance to insect pests.

Conclusions

Exploitation of plant defences is already a component of IPM programmes. Unlike other crops, the existing varieties/ cultivars of cultivated species of jute substantially lack resistance against important insect pests. The HPR study revealed that considerable resistance in the wild species, C. *aestuans* and C. *tridens*, will help to redefine the resistance breeding programme and provide the basis for strategies in developing insect-resistant jute varieties. Importantly, HPR studies will facilitate the development of truly resistant varieties for making insect pests more manageable.

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Society News

RES Strategy 2022–2025

Since the beginning of May, we have been looking at what the Royal Entomological Society can do to best support its membership and increase its impact as a Learned Society. We are collaboratively developing a strategy that will focus our work between 2022 and 2025 with a clear Vision, Mission, and identification of some target areas. To do this, we have been holding workshops and interviews, and have been using the recent membership survey to inform these.

Running alongside this, we are working on our image. We are developing a brand that takes into account our history, whilst looking at how we will move forward as a learned society. We have been working with an agency, ThreeDoors, which has recently been through a similar process with the British Geological Survey.

As the strategy emerges, we will keep you informed. We are really excited to be engaging with our Fellows and Members as well as some of our key partners and the general public to achieve this. Related to this, there will be some great events planned for 2022 so please watch this space!

Simon Ward
Chief Executive Officer

News from Council

Meetings of Council

Council met on 3rd February, 7th April, 2nd June and 22nd July. Much time has been devoted to the membership consultation, strategy review and brand outlined by Simon above. The following is a summary of other main issues. Please note that this edition of *Antenna* went to press before the AGM and ENTO'21.

Bye-laws

Work has continued in collaboration with solicitors Taylor Vintners on changes to the bye-laws to be voted on at the AGM (25th August).

Trustee elections

All trustee positions from the date of the AGM have been put to election. Eighteen people applied for positions, including six for the new position of "early career trustee".

Auditors

After going to tender and carefully considering submissions, Knox Cropper (based in Hemel Hempstead) have been appointed as our new auditors.

Membership

A membership survey has been conducted, with more than 400 responses. Thirty of the respondents have been interviewed by telephone in order to expand on their views. The results are providing a major input into the strategy review.

Journals

The Society's journals continue to perform very well in terms of impact factors and income. Each journal has held a strategy meeting. Issues around the move from subscription-based to open-access income are being worked through with Wiley.

New-look Annual Review

The Annual Report has, in the past, been a set of A4 sheets stapled together and put on the chairs of those attending the AGM. As well as the statutory documentation for the Charity Commission, this year a colourful 24-page Annual Review has been produced, outlining the key features, committees and achievements of the Society. This will be available to all members via the website and may be passed on to any interested people. Some hard copies have been produced to promote the Society by handing out at events or at The Mansion House. If you would like a hard copy, or can't find the web version, please let HQ know.

Grand Challenges project

The analysis of the Grand Challenges questionnaire is almost complete with a two-day workshop (21-22 July) concluding the process. The outcomes will be presented at ENTO'21. This will help inform the Society's priorities in relation to journal content, meetings, library accessions, conservation strategy, outreach activities etc.

The Mansion House

Fire safety, asbestos and underground facilities audits have been commissioned as part of a drive to ensure compliance with relevant legislation. Plans for developing the garden are progressing.

Insect Week

The Outreach Committee organised the first annual Insect Week (missing the word "National"). Around 140 virtual events were run and much good publicity resulted. Insect Week will now be held every year.

Website

Our current website uses Drupal, and will not be supported beyond 2022. A replacement system is thus urgently required. After going to tender and seeking the advice of referees, Council approved hiring Headscape to develop our new website and integrated CRM (Customer Relationship Management – i.e., membership database) system.

Richard Harrington
Interim Honorary Secretary

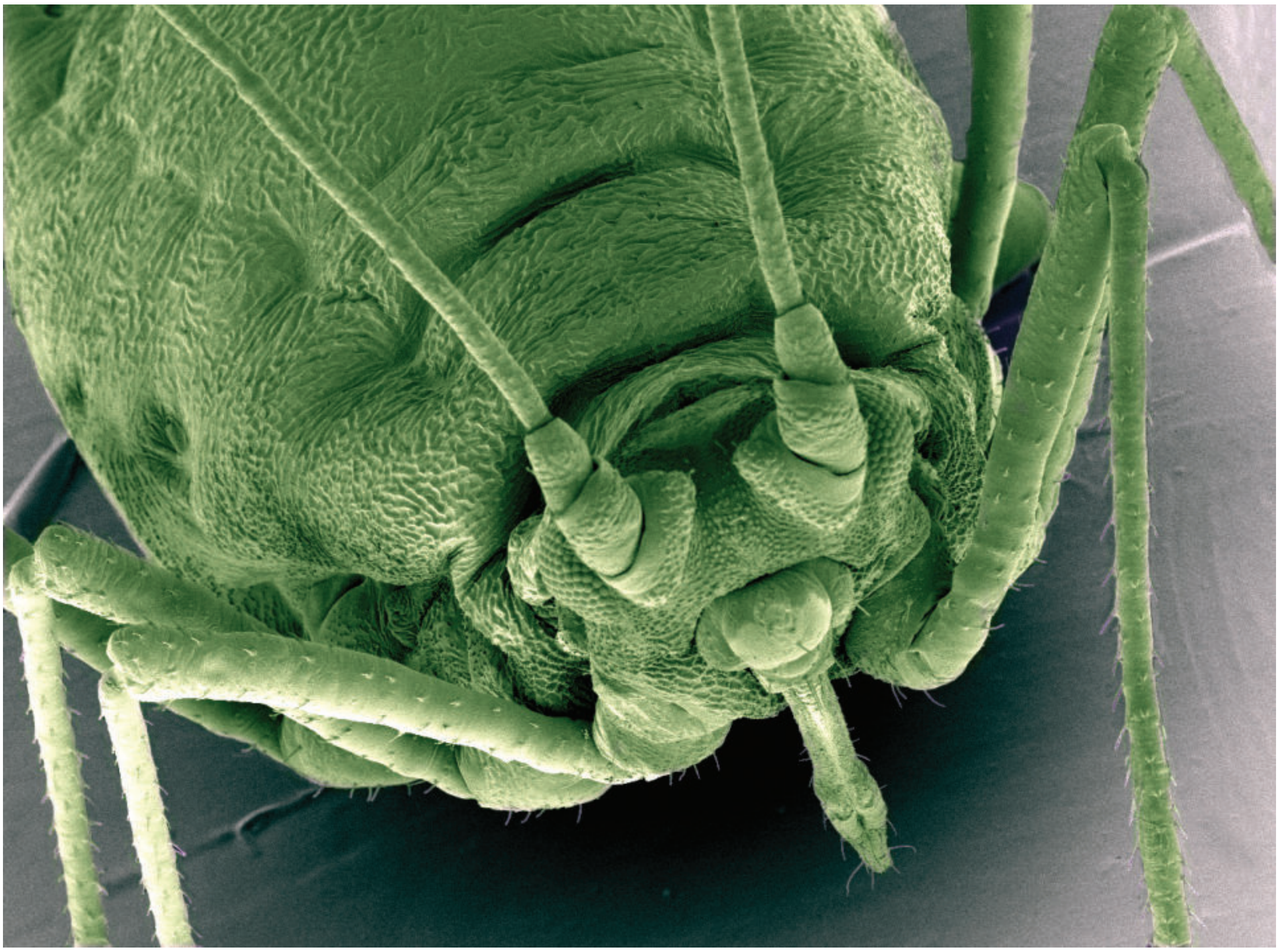
Meetings

Aphid Special Interest Group Meeting

Online Meeting, 15th–16th April 2021

Convenors: Gia Aradottir, Daniel Leybourne, Simon Leather and Francisca Sconce

Report by Richard Harrington



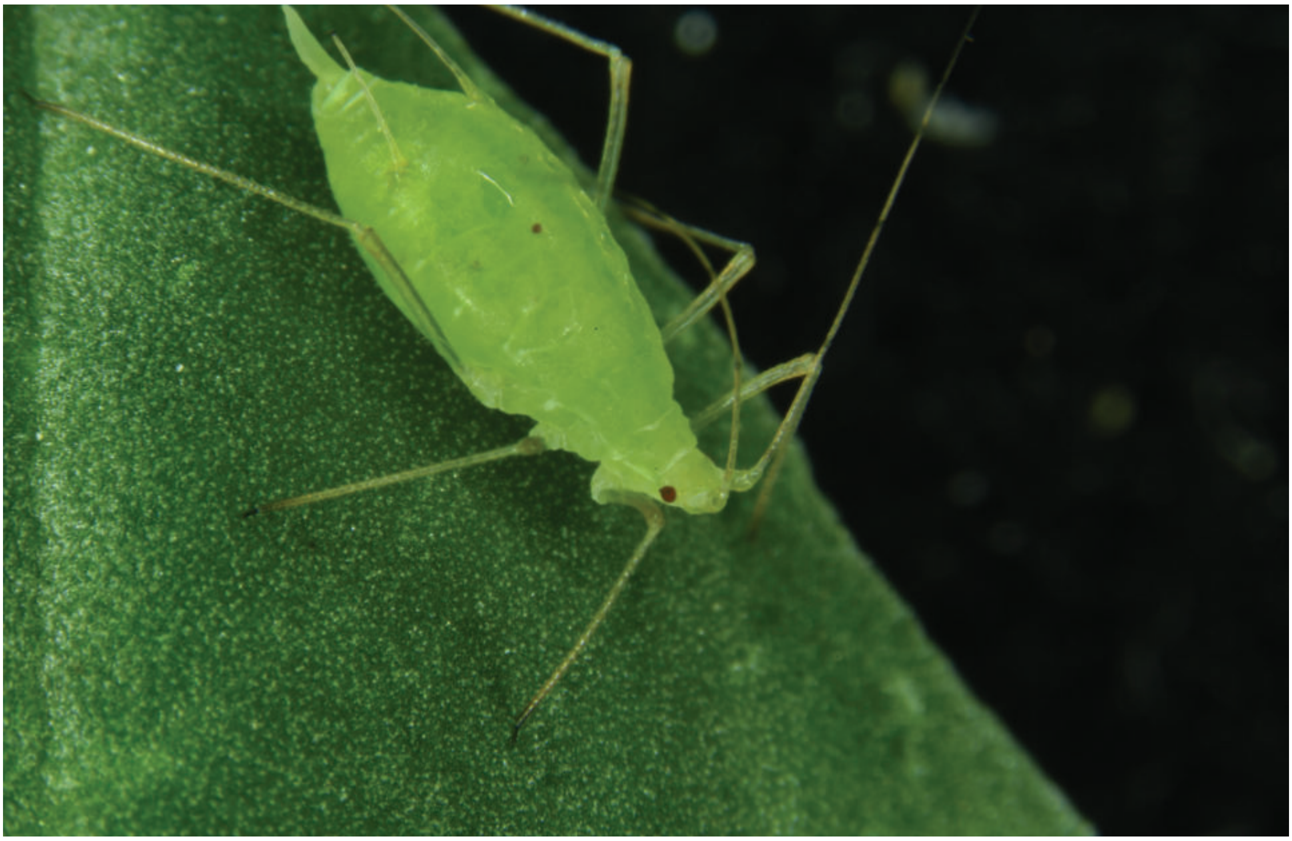
Scanning electron micrograph of *Myzus persicae* (Jean Devonshire, Rothamsted Research).

Introduction

When reporting a two-day meeting with 26 presentations, it is impossible to do justice to the speakers and their science within the space available. I have thus majored on the two keynotes and on an interview with an aphidologist whose work has been of huge significance to every speaker. I have summarised briefly the, nonetheless excellent, work of others.

Session 1
(Chaired by Joe Roberts, Harper Adams University)

The first keynote was given by Tom Mathers (John Innes Centre) on the evolutionary genomics of host range in aphids. How have some aphids managed to evolve to become polyphagous and cope with the defences of a wide range of plant species? To investigate this, Tom compared chromosome-scale whole-genome sequences of closely related pairs of aphids, one of which is highly polyphagous, one not. Cutting to the chase in a fascinating and complex investigation, he found that there have been multiple independent transitions from monophagy/oligophagy to polyphagy. In *Myzus persicae* (peach–potato aphid), 52 genes were found that might be described as "polyphagy genes". Grass specialisation has evolved multiple times in aphids and Tom wanted to find out to what extent hybridisation has shaped patterns of genetic diversity and whether there is a genetic basis to specialism on grasses. *Sitobion avenae* (English grain aphid, found mainly in Europe) and *S. miscanthi* (Indian grain aphid, found in Asia, Australasia and the Americas) both feed on Poales and are very closely related, perhaps synonymous. Chromosome-level assemblies were again used to compare a number of lineages of each species. Of six



Acyrthosiphon pisum (John Baker, University of Oxford).

Chinese lines of *S. miscanthi*, one was found to group with a UK *S. avenae* line. *Sitobion avenae* and *S. miscanthi* are likely to be part of a cryptic species complex. Hybridisation has played an important role in the evolution of *Sitobion* and is potentially the cause of very high diversity in some lineages. Even if sex is infrequent, it plays a significant role in shaping the adaptive potential of grain aphids.

In Scotland, *S. avenae* has been found to be more genetically diverse in the north than the south, probably because colder winters lead to a greater need for holocycly. Also, an insecticide-resistant clone which now dominates southern regions is less prevalent further north. Beth Moore (University of Aberdeen) is using experimental and genomic approaches to understand this clonal variation, with a particular focus on climate. She tested the hypothesis that the insecticide-resistant clone has a lower thermal tolerance than non-resistant clones, but found no evidence for this, although she acknowledges the need to examine aphids over a wider geographical range.

Acyrthosiphon pisum (pea aphid) diversification and radiation were thought to have occurred over the past 8,000 to 16,000 years in response to human agriculture. Varvara Fazalova (University of Oxford) used a mutation accumulation experiment with a genome-wide estimate of divergence between distantly-related *A. pisum* host races to re-examine this and found that radiation pre-dates human agriculture by several hundreds of thousands of years. This suggests the need for a re-assessment of the role of allopatric isolation during Pleistocene climatic oscillations in the divergence of *A. pisum* complexes. Chris Bass (University of Exeter) has developed a chromosome-scale genome assembly and living library of 110 fully-sequenced lines of *M. persicae* from around the world, which have been used to show a remarkable diversity of insecticide-resistance mutations. The distribution of these mutations is influenced by host-plant associations, and some have arisen independently multiple times. These resources offer opportunities for exciting new research on aphids. Mariska Beekman (Wageningen University) has found that a single clone of *M. persicae* dominates conventional, but not organic, bell pepper greenhouses in the Netherlands. It is likely that insecticide usage drives clonal selection in conventional greenhouses by selecting for insecticide-resistant genotypes. Jyoti Sharma (Punjab Agricultural University) is hoping to develop wheat varieties resistant to *Rhopalosiphum padi* (bird cherry–oat

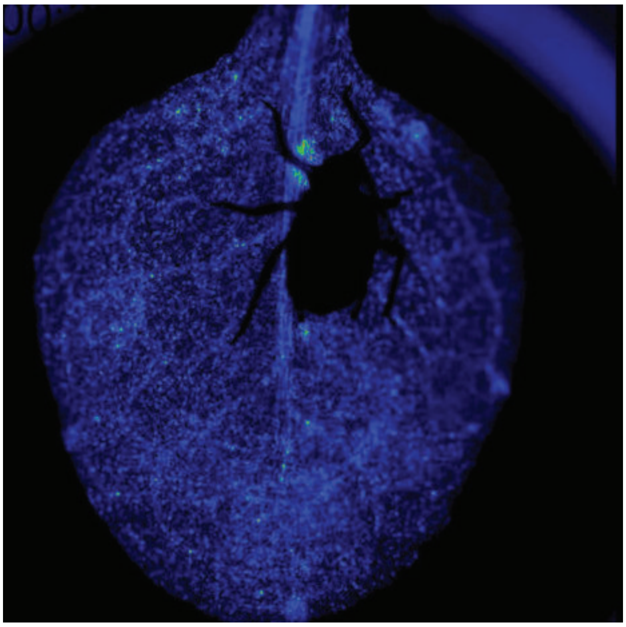
Phenotypic variation (colour) in living library of asexual lineages *Myzus persicae* (Jo Mackisack, University of Exeter).

aphid). Resistance has been found in the wild grass species *Aegilops tauschii*, a genome donor to cultivated wheat, and behavioural and developmental studies were done to investigate the mechanisms of this resistance. Antibiosis and antixenosis were identified as key mechanisms. Kennedy Zimba (Harper Adams University) is evaluating resistance to *Aphis fabae* (black bean aphid) in genotypes of common bean in Zambia. One accession showed slower nymphal development and is thus a promising parent line for developing resistant varieties.

Session 2
(Chaired by Gia Aradottir, NIAB)

The second keynote talk was given by Jenn Brisson (University of Rochester). Wing dimorphism in asexual female *A. pisum* is environmentally-induced (phenotypic plasticity) whilst male wing dimorphism is entirely genetically controlled, which Jenn found by QTL-mapping and association mapping to be at a single locus on the X chromosome (males are X0). In wingless males there is a 120kb insertion compared to winged males. The only gene that the insertion brought with it is a follistatin gene, Fs3, and it is expressed more in the early instars of winged males compared to later instars, matching expectations in relation to the time of determination of wing development. As discussed above, *A. pisum* biotypes diverged in the Pleistocene, and different biotypes have different frequencies of winged and wingless alleles. The ancestor was probably a monomorphic winged form prior to the insertion bringing dimorphism. Some biotypes are now moving back to having entirely winged or entirely wingless males. Three follistatin paralogs are known in pea aphids. Fs1 is expressed across development in both sexes and both wing morphs. Fs2 is expressed strongly in wingless early instars of asexual females and weakly in the early instars of winged asexual females, and Fs3 is not expressed in females. Thus, Fs3 is the male dimorphism gene and Fs2 is the asexual female dimorphism gene determining the degree to which environmental cues such as crowding and nutritional quality influence the proportion of winged to wingless asexual females in different biotypes. Follistatin is thus implicated in both dimorphisms. Analysing recorded descriptions of wing states in male aphids of a range of species in an evolutionary context, Omid Saleh Ziabari (University of Rochester) found the polymorphism to be evolutionarily transient, and polymorphic species to have an elevated speciation rate. He proposed a model of how wing polymorphisms have the potential to act as a precursor to speciation.

Jenna Shaw (Harper Adams University) is studying the ecology of hyperparasitoids, which have the potential to derail the beneficial effects of aphid parasitoids. In protected sweet peppers, *M. persicae* is parasitised by *Aphidius colemani* and *A. ervi* which, in turn, are parasitised by *Dendrocerus aphidium* and *Asaphes suspensus*. Jenna will be looking into the role of semiochemicals in host selection by hyperparasitoids in the hope of developing a synthetic lure to pull hyperparasitoids away from protected horticultural systems. *Myzus persicae* does well on senescent potato leaves as a result of phloem enrichment as metabolites move from source to sink. Agustin López Gialdi (Universidad Nacional de Salta) is studying the performance of *M. persicae* on plants with natural and induced senescence and trying to understand the mechanisms through analysing phloem composition and feeding behaviour. Jacob Pitt (Colorado



Rhopalosiphum padi-induced calcium signal being visualised using epifluorescence microscopy of *A. thaliana* expressing the GFP-based calcium reporter, GCaMP3 (Josh Joyce and the Hogenhout and Sanders/Miller labs, John Innes Centre).

State University) has identified *Phorodon cannabis* (cannabis aphid) as an efficient vector of potato virus Y (PVY) and found that, on hemp plants, viruliferous aphids spend less time ingesting phloem than aphids which are not carrying the virus. As the acreage of hemp (a known host of PVY) increases, *P. cannabis* could have an increasingly important impact on the health of potato crops. Sharon Zytynska (University of Liverpool) has identified a rhizobacterium, *Acidovorax radicans*, from barley that can both promote plant growth and reduce the growth rate of populations of *S. avenae*. The bacterium induces plant defence genes in response to aphid feeding. Inoculation with this bacterium has the potential to reduce aphid populations under a range of abiotic and biotic conditions, especially with an understanding of the molecular pathways underlying the effects. Amma Simon (University of Nottingham and Keele University) found that *Fusarium graminearum* that produced the mycotoxin nivalenol (NIV) in grain, induced volatile organic compounds (VOCs) that attracted *S. avenae* up to seven days after wheat inoculation, whereas *F. graminearum* that was unable to produce NIV did not. Fourteen days post-inoculation, aphids were repelled by these VOCs. Aphid fecundity was increased on wheat inoculated with NIV-producing fungi compared to wheat inoculated with non-NIV-producing fungi. Josh Joyce (John Innes Centre) is investigating how plants recognise aphid attacks. Wounding-induced glutamate elevation appears to trigger plant calcium signalling as part of a defence response to aphid attack. In *Arabidopsis thaliana*, this response is induced less strongly by *M. persicae*, which colonises the plant, than by *R. padi*, which doesn't, but the mechanism underlying this difference is unknown.

Session 3
(Chaired by Amma Simon, University of Nottingham and Keele University)

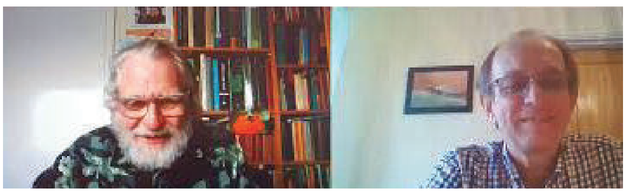
There have been many studies on the impacts of elevated CO_2 and its interaction with nitrogen levels on aphid populations with, as yet, no unified conclusions. Eva Carreras

Galls induced by *Tetraneura* aphids (Xin Tong, Hokkaido University).

(Agriculture Victoria and University of Melbourne) is continuing the quest, with *R. padi* on wheat as her model. She found that increasing nitrogen fertilizer application to mitigate lower protein content in grain under elevated CO_2 can backfire by increasing aphid infestation. Xin Tong (Hokkaido University) found that fighting for galling sites between fundatrices (clone foundresses) of *Tetraneura sorini* leads to larger females biasing their sex allocation towards females, contrary to the Travers-Willard hypothesis based on mammals. Xin Tong's talk took an unexpected turn at the end. Mermithid nematode parasitoids were found in sexuparae of the gall-forming aphids *Tetraneura radicicola* and *Erisoma harunire*. In my years in aphid biology, I have never heard of such, but I have previously discovered that the Akimoto lab in Hokkaido is full of interesting surprises! Maria Leandro (Harper Adams University) has just started a PhD on trap-cropping as part of an IPM strategy for managing barley yellow dwarf virus, using a heritage variety of wheat, Maris Huntsman, to encourage aphids to land away from commercial crops. Katharine Preedy (BIOSS) is modelling attacks of the parasitoid *A. colemani* on *R. padi* protected and not protected by the secondary symbiont *Hamiltonella defensa*. She predicts that stable coexistence of aphid clones is maintained as a result of parasitoids being more efficient at finding common clones, whilst experiencing a cost when switching to less-common clones. Stresses such as drought can cause destabilisation. Karina Wieczorek (University of Silesia) has found non-native aphids such as *M. persicae* and *Neomyzus circumflexus* (mottled arum aphid) on ornamental plants and agricultural products in the Svalbard archipelago. So far, this has been mainly indoors, but she is concerned over the potential threat to native species. Ken Newman (BIOSS) has been modelling aphid arrival in UK suction-traps in relation to the North Atlantic Oscillation (NAO) winter index, accumulated day degrees above 12°C during April and May, and latitude. He found earlier flights to be associated with a more positive NAO index, higher spring temperature and lower latitude, although the relationship varies with species. After these main effects, there remains a year effect; thus, increasingly early flights with year are due to additional factors. Paul Holloway (University College Cork) looked at the performance of machine-learning algorithms versus GAMs in predicting arrivals of aphids in suction-traps, machine-learning outperforming GAMs. There followed a discussion on automatic aphid identification, concluding that, whilst advances are continually being made, aphidologists will always be needed to refine techniques and interpret their outputs.

Roger Blackman interview

There can have been nobody at the meeting who hasn't heard of Roger Blackman and very few, if any, who haven't cited his work. He discovered that aphid parthenogenesis is apomictic (clonal); that spermatogenesis in aphids is achiasmate (no crossing over of chromosomes); that a translocation in *M. persicae* chromosomes is linked to resistance to organophosphate insecticides; andocycly, whereby the ability to be continuously parthenogenetic can be passed on through the sexual cycle via the males; and



Roger Blackman and Richard Harrington.

much more. On top of all that, he and the late and great Victor Eastop gave us the aphid bible, *Aphids on the World's Plants*, which Roger keeps updated online (http://www.aphidsonworldsplants.info/). I was immensely fortunate to do my PhD under his supervision at the Natural History Museum, and he continued to be a big influence throughout my career. It was thus a huge pleasure to be asked to interview him for the meeting. I've always known, but the younger generation may not, how modest he is about his achievements. Vic was the same and they were a perfect pairing. In a *Desert Island Discs*-style ending to the interview, Roger chose to take Louis Armstrong's *What a Wonderful World* and Sibelius's Violin Concerto. He would take *War and Peace* as his book and code-breaking puzzles as his luxury. I invited him to choose an aphid to keep him company, confidently expecting it to be *M. persicae*. But no, Roger chose *Aphis* (*Toxoptera*) *aurantii* (brown citrus aphid) because it is the only aphid known to make a sound, so he might be able to have a conversation with it! It also has a wide range of host-plants, so might find something suitable to eat. Roger is a past President and an Honorary Fellow of the RES and has contributed hugely to it in numerous ways. He said that his involvement has, likewise, contributed to his career, thus it is appropriate that the interview came at the start of the session on symbiosis. The interview can be viewed at https://www.youtube.com/watch?v=XVOPeU3LVyA. Incidentally, Gia was my PhD student, and Amma was Gia's, so we had four academic generations present at the meeting.

Session 4
(Chaired by Daniel Leybourne, ADAS)

The final session covered the fast-moving field of aphid associations with bacterial endosymbionts. Edward James (University of Miami) described his work with computer scientists to develop image segmentation and recognition software to determine the number of *Buchnera aphidicola* present in bacteriocytes viewed with confocal microscopy, and how this may facilitate analysis of responses of *Buchnera* population density to experimental manipulations. Catriona Anderson (Newcastle University) is characterising the transporter proteins involved in selective movement of sap-derived non-essential amino acids across membranes from aphids via the bacteriocyte to the symbionts, and essential amino acids back the other way. Hsiao-ling Lu (National Formosa University) is studying the molecular mechanisms regulating developmental integration of aphids and *Buchnera* and at what developmental point the bacteriome reaches maturity. She discovered that metabolic integration of *Buchnera* differs between embryonic and mature bacteriocytes. Uxue Rezola (University of Helsinki) is beginning a Master's thesis looking at whether, and how, aphid-associated bacteria interfere with plant-virus transmission, her hypothesis being that intraspecific genotypes which can infect plants have a different microbiome to those which cannot. Mariska Beekman stood in valiantly at the last moment for her fellow PhD student Helena Donner (Wageningen University), who is studying whether aphids of bell pepper and strawberries in greenhouses and in the field are protected from parasitoids by secondary symbionts in the Netherlands. No such symbionts were found in bell pepper glasshouses, so they do not explain the failure of parasitoids. In the field, 450 colonies of 104 aphid species were examined and half of them carried secondary endosymbionts, some of which are known to confer resistance to parasitisation, although there is still much to learn about interactions between aphids and their symbionts.

Acyrthosiphon pisum stage 18 embryo showing actin filaments (red), host and bacterial symbiont DNA (blue), germ cells (yellow), and autofluorescence (green). The developing embryonic bacteriome is located in the middle of the two sets of germ cell clusters. Images were acquired using a Leica TCS SP5 Confocal Spectral Microscope Imaging System under 40x magnification condition. (Hsiao-ling Lu, National Formosa University).

Conclusion

With new techniques complementing the old, our understanding of the workings of aphids from the molecular to the population level was shown in some of these talks to be advancing apace, and in others to being usefully tweaked. This is leading to some small victories in their control, but the war is far from won. Indeed, the adaptability of aphids will ensure that it never is, but we have to keep up the pressure. The meeting showed that we are. Many thanks to the organisers, Gia, Daniel and Simon, and to Fran for her usual masterful handling of the online technology. Thanks to the session chairs, all speakers and their co-authors and all 150 participants from around the world.

Insects as Food and Feed Special Interest Group Meeting

Online Meeting, 20th–22nd April 2021

Peter Smithers and Mark Ramsden

Introduction

The meeting attracted 350 registrations from 28 countries with up 127 people logging in at any one time. The first day provided insight into the legislation, research and policy developments in the UK, and offered a preview of the WWF roadmap for developing their UK strategy. The second day focused on insects for human consumption, highlighting the progress already made in understanding and overcoming people's initial hesitancy towards eating insects. On the third day, coinciding with Earth Day 2021, the focus was on insects as livestock feed, and the challenges and opportunities for insect-based feed to contribute to improving the sustainability of supply chains.

Day 1 Legislation, research and policy

Fera, its research and role in the Insect Bioconversion Forum
Andrew Swift, CEO of FERA

In 2012, Fera obtained funding from Innovate UK to explore the role of insects as animal feed. This grew into PROteINSECT, an EU-funded project with 15 partners. It had become clear that insects offer a rapid conversion of biomass residues to a product that is high in protein and fat. Furthermore, by adjusting the composition of the substrate that the insects feed on, the amino acid content of the insects themselves can be manipulated. This offers the possibility of tuning the substrate to achieve a predetermined protein profile. Insects were screened for over 1,000 contaminants and biological hazards, and no biological hazards were detected in any of the samples.

Fera also saw the potential of insects to deal with a range of environmental issues such as food waste, biomass accumulation and landfill, upcycling these waste streams to a more valorised product. It is currently investigating the insect conversion of sewerage sludge and animal slurries into a product that could be used in non-food applications such as biofuels.

The UK Biomass Conversion Forum comprises a wide range of participants from insect bioconversion start-up companies through retailers, feed producers, farm industry trade bodies and NGOs, plus government and regulatory bodies. To date it has produced two high-impact publications for government and investor communities, and formed part of the final recommendations to the UK Food and Drink Council. This ensured that insect protein was included in the UK national food strategy. It also brought regulators to the table to discuss changes required. Over three years it grew from a membership of 12 to 30, establishing both a trade association and a platform for national and international product and process assurance.

The post-Brexit legislative landscape
Freya Lemon, Michelmores

Following Brexit, EU-derived law is retained as domestic law in the UK. Some laws have been changed to replace European organisations and agencies with UK equivalents. The overriding principles informing food and feed law are still based around protection of human life and health. EU law does not differentiate between insects and other animal feeds, which limits the range of substrates that insects can be fed on, and also limits which animals insects can be fed to. Insect PAP (processed animal protein) is still not permitted as an animal feed under EU law, however it was approved as fish feed in 2017. EU novel food regulations apply to insect products, making pre-market authorisation a requirement. Twenty authorisations have been submitted to date, but only yellow mealworms (*Tenebrio militor*) have so far been approved. In the UK, the Food Standards Agency will take on the role of approving all applications for insect products as novel foods. The requirements remain the same as those in the EU. Post-Brexit, any EU changes do not apply in the UK, but the UK can respond to these changes by implementing its own laws. The ambition to facilitate continued trade between the UK and the EU implies continued compliance with EU law. Current funding for agriculture is linked to land-based farming, so at the moment the Common Agricultural Policy funding is not available to insect farmers.

Zero Waste Scotland, a progress report
William Clark, Zero Waste Scotland

Zero Waste Scotland's aim is to use products and resources more responsibly while working towards a circular economy. It works across the whole economy from regulators to consumers, facilitating a paradigm shift from individual enterprises working in isolation to a collective community moving the industry forward.

Scotland has 980,000 tonnes of pre-farm gate waste to dispose of and insects appear to offer a solution to removing and recycling this and other wastes. In 2019 Zero Waste Scotland hosted a stakeholder workshop which was attended by insect farmers, academics, government and industry. At this workshop the possible impact of insect farming on the Scottish ambition to attain a cyclical economy was explored. Since then, a conversation has developed around insects as food and feed but also the possible use of insect products in biotechnology.

There has been a huge increase in enquiries from communities, farmers and small business about the use of insects to valorise their waste streams. Many enquiries have also been received from households that want to process their domestic organic waste to produce mealworms. As a new industry, insects will have a vital part to play in the evolving Scottish economy.

Insects as feed: the development of a roadmap for the UK – Mollie Gupta and Piers Hart, WWF

The rearing of livestock utilises 77% of all agricultural land with just 23% being used to grow crops for direct human use. Currently, only a narrow range of crops is used to supply our vegetable-based nutrients. The banning of animal-based products from animal feeds following the BSE crisis had led to an increase in the demand for soya and the production of soya is now a big driver of deforestation and biodiversity loss. The Eating Better Alliance hopes to reduce meat consumption in the UK by 50% and move towards a situation where all feeds are sustainable. Soy production is predicted to double by 2050, so there is a need to explore alternatives. WWF has identified insect protein as a good replacement for soy and fish meal.

The development of a road map to scale insect protein in the UK
Charles Ffoulkes, ADAS

A survey of insect farming in the UK was conducted to examine perceived opportunities, possible reductions in environmental impact, the role of insect farming in the circular economy and increasing food security plus access to new markets. The main barriers identified were: the requirement to adhere to inappropriate legislation; a lack of substrate availability; a lack of investment; existing commitments to retail requirement; and a lack of knowledge of the risk of contaminants. The disposal of frass, low consumer acceptance and a lack of access to low-cost technologies were also identified as potential challenges. Currently-permitted substrates are: vegetable and fruit by-products; brewers' grains; dairy by-products; fats and oils; and bakers' surpluses containing no animal products. Substrates identified for potential use are: mixed food surpluses from domestic housing, catering or retail; abattoir and fishery by-products; animal manures; anaerobic digestive by-products; and water treatment solids and sludges. Ranking these substrates based on risk, acceptability, supply and suitability highlighted the following as priorities for further research and development: bakers' surpluses containing animal products; mixed food surplus from manufacturing and retail; fish trimmings; poultry manures; and anaerobic food-based digestate. By 2050 up to 1,300 tonnes of these substrates could potentially be processed per day, leading to up to 60 tonnes of insect protein per day.

The road map due to be published later in 2021 will model possible demands for insect protein by the feed industry and will examine the capital and operational costs for the production of various insect-related products and an evaluation of their predicted revenues.

What the roadmap means: a retailer's perspective
Laurence Webb, Tesco

Tesco supports the roadmap project and the need for sustainability in the supply chain. It has been supporting various start-ups by making its waste streams available for them to trial, and has persuaded some suppliers to trial insect-based feeds. It has been pushing for changes to the current legislation and has been raising the media profile of insects as feed. Tesco also plans to encourage all of its suppliers to use sustainable feeds and will be researching consumer acceptance of insect-based products.

Day 2 Insects as food

A European perspective from the International Platform for Insects as Food and Feed, IPIFF
Christophe Derrien, IPIFF

IPIFF is the voice of the European insect production industry and aims to engage in a dialogue with the EU and other public authorities, act as advocate for appropriate legislative frameworks, offer support for the implementation of legislation and promote and share best practice within the industry. The 75 member organisations are widely spread across Europe. Most of these are small to medium-scale enterprises that are working towards a fully-automated process with a view to upscaling to industrial production rates. The industry has attracted one billion euros of investment and has created over 1,000 new jobs. Seven species of insect are currently farmed, with black soldier fly (*Hermetia illucens*) and mealworms being the most common. Silkworm pupae are currently being assessed for authorisation.

Since its inception in 2012, IPIFF has influenced major changes in European legislation, produced the IPIFF guide to good hygiene practices and lobbied for the authorisation of the use of processed insect proteins as feed for poultry and pigs. It has also set standards for the production and use of insect frass as a fertiliser. There is a lengthy and costly process for submitting a dossier for approval of a new novel food. Over twenty new applications have been made to use insects as novel food. In January 2021 EFSA ruled that yellow mealworms were authorized, and in October 2020 the European Court of Justice ruled that whole edible insects are not novel foods – a judgment that will have wide-ranging ramifications for the industry.

"You'll never get kids to eat that!": introducing edible insects into Welsh School canteens
Verity Jones, University of the West of England

Only two studies have so far investigated consumer reaction to insect-based foods and none has involved children. Working with Sara Beynon and Andy Holcroft from Bugfarm Foods, local authorities were approached regarding the introduction of insect-based foods to the school dinner menu. Three schools and 187 pupils participated. All pupils filled in pre- and post-lunch questionnaires, and at a lesson prior to the first lunch the children raised three main questions: how are the insects produced, is it sustainable and will it make me ill?

Children did not want to see whole insects on their plates, so the meat substitute known as Vexo was created to look and taste like bolognese. The key to acceptance lies in the processing. 74% of the children liked the taste and 54% said it was better than they had expected. There was also a large shift in acceptance after the children had seen and tasted a Vexo lunch. Local authorities were willing to offer Vexo as a lunch option in schools, and catering staff were able to adapt to the new dish. All the children who took part in the trial were keen to learn more about sustainability in the food supply. They wanted to be able to choose the foods that supported action to combat climate change. Insect proteins appealed to some vegetarian families as a steppingstone towards a reduced meat diet for the wider population. Teachers were enthusiastic to embed the teaching of sustainable food systems into the curriculum. This research has now been published and sustainable food systems have been embedded into the teacher training courses at UWE. (For more details, see *Antenna* 44(2) 64–67)

The current state of the insect farming sector in the UK and beyond
Adam Banks, Instar farming

Adam received a Nuffield Farming Scholarship to tour insect farms around the world in order to gain an appreciation of the diversity of approaches to farming insects. When the financial crisis hit Thailand in the 1990s, the ability of many people in the northern areas to purchase traditional proteins was greatly reduced, so a program to encourage cricket farming was launched to redress this. This was very successful and cricket farming now supports over 20,000 people in the area. This proved that insects were a viable alternative to traditional farmed animals. This was one of the drivers of the first FAO report on the potential of insects as food. Three points became clear following this tour of international insect farms: i) scale and automation are the key to success; ii) the development of the business is a marathon not a sprint and iii) it's not just about sustainable protein – there are many other potential products and health benefits. Some problems were also encountered. There are no off-the-shelf solutions, and the end products vary enormously. The solution is more collaboration and the exploration of hub-and-spoke models for processing. The industry needs agreed standards, guaranteed pricing and group purchasing to reduce input costs.

Farming insects for food: a global perspective
Nick Rousseau, Woven Network

When Woven had its first stand at the Food Matters Live exhibition, there were just two companies supplying insect products as food. Two years later there were 25 companies offering insect-based products at the exhibition. As the industry matures and becomes more complex, Woven will endeavour to evolve into a professional body that will disseminate information and lobby on behalf of the industry. Woven is currently engaged in discussion with the Food Standards Agency in relation to novel food regulations and has also been compiling an A to Z of insect companies in the UK that will be available on its website.

IPIFF estimates that in 2019 500 tonnes of insect-based products were consumed by 9 million Europeans and there have been no reports of any adverse effects from consumers. This and other work, such as the PROteINSECT project, indicates that the risks to health are extremely low and that the potential benefits easily outweigh them.

The potential of palm weevil farming to deliver sustainable protein as part of a drive to circularise agricultural waste in West African palm farms
C. M. (Tilly) Collins and Vincent V. Savolainen, Imperial College London

Insect eating is an important component of ancestral diets; it has provided protein and micronutrients throughout human evolution. Wild-caught beetle and moth larvae are embedded in many tribal cultures. Two factors that contribute to its decline in Africa are a decrease in availability of these insects due to chemical pesticide use and habitat change, and the aspiration for a 'developed diet'.

The potential contribution of the consumption of insects to food security in Africa remains substantial and there is interest in tying this to circular and sustainable use of agricultural waste streams. Small-scale farming of the Akokono (a.k.a. Mpose) or palm weevils (*Rhynchophorus phoenicis* and *Rhynchophorus ferrugineus*), highly-prized and formerly common wild-catch species, has much potential. The cropping cycle of palms provides fodder for these and there is local small-scale commercial experience of farming weevils for consumption.

This project, with partners in Ghana, Côte d'Ivoire and South Africa, will develop information on farming and trading to promote flexible alternative livelihoods for migratory workers and land-poor rural communities.

Farming insects as part of a sustainable food and farming future in the UK
Vicky Hird, Sustain and Tilly Jarvis, Six Legs Farm

There are ethical challenges regarding insect sentience and the methods used to kill farmed insects. The health and welfare of the insects are important, and it is also important that the health, welfare and wages of the insect farm workers who will support this industry are properly considered. It is essential that farm supplies are obtained from sustainable sources to maintain credibility. While insects are recognised as a healthy source of nutrients, it is important that they are not made more marketable by the addition of unhealthy sugars and fats.

Bug Farm Foods: the story so far
Sarah Beynon and Andy Holcroft, Bug Farm Foods and Grub Kitchen

Insect-based dishes were trialled at a number of public events and received a positive response. One avenue to the acceptance was to offer various levels of insect inclusion, from an insect-based sauce served with a conventional meal to dishes that have insects as a major constituent. Another way was to use insects in a familiar dish such as a burger. Grub Kitchen now offers a wide range of insect dishes to tempt customers, ranging from crepes to cakes to scotch eggs. Grub Kitchen feeds 10-15,000 visitors a year, which is a relatively small number of people to share their insect-based foods with, so Bug Farm Foods was created to sell their products to a much wider audience. They began with the gift market, offering a range of cookies, and then offered insect ingredients in the form of whole insects and insect flours in an effort to persuade customers to experiment.

Day 3. Insects as feed

Nutritious mealworms produced using circular economy principles
Olivia Champion, Entec Nutrition

Biosystems technology was set up to produce wax moth (*Galleria mellonella*) larvae as test organisms to replace reliance on vertebrates. Having gained experience in the production of high-quality insects, an opportunity was recognised in the production of insect larvae for animal feed. Entec Nutrition was set up to explore these possibilities. Whilst farmed insects offer many nutritional and environmental benefits, there are problems in that the farms are mainly small scale, much of the processing is manual and there are high energy costs in maintaining the optimum environment. All of these combine to make the product expensive. There is also the risk of pathogen transmission within the farm and on to the customer. The solution is automation, which would reduce the price of the product. Entec has patented a design for such a system and is focused on producing yellow mealworm because of its superior nutritional values. Compared to black soldier fly, mealworm protein values are higher (dry content = 53%) and the ash content is lower. Yellow mealworms also contain easily-digestible fats which are high in mono- and polyunsaturated fatty acids including oleic, linoleic and alpha-linolenic acids. They are also high in essential amino-acids, important vitamins such as B1, B12 and C and in minerals such as magnesium. Spent brewers' grains are used as mealworm feed. Waste materials from mealworm production are being examined as a raw material for chitin production and fertiliser. Utilising waste products in this way will further reduce the environmental impact of feed production.

Insect Doctors: educating the next generation of insect pathologists to tackle infectious diseases in insect mass rearing
Helen Hesketh, Centre for Ecology & Hydrology

The successful mass rearing of insects relies on culturing healthy insect colonies in high-density monocultures under controlled environmental conditions. Emergent insect pathogens present a threat to mass-reared insects in such circumstances, as pathogenic infections may be easily triggered. Currently there is only a limited number of specialised insect pathologists located in dedicated research laboratories across Europe and it is widely acknowledged that there is a dearth of knowledge specifically on pathogens that threaten mass-reared insects. This led to the creation of the INSECT DOCTORS programme, the first European joint doctoral programme, which will educate 15 PhD students and develop their skills to diagnose and manage disease problems in commercial insect-production systems. The programme, funded in the 2020 Marie Skłodowska-Curie ITN framework, will deliver research over three science themes: i) host–pathogen interactions; ii) mechanisms behind covert pathogen infections and disease outbreaks; and iii) increasing insect resistance to pathogens. All students will have research projects built around the central concept of understanding biological interactions between insects and their pathogens and how these interactions are influenced by other biological and environmental factors, including genetic background, microbiota or rearing conditions.

Entocycle
Kieran Whitaker, Entocycle

The current production of animal feeds is based on fish or soy meal which are now widely recognised as unsustainable. It has been estimated that by 2025 there will be a global protein shortage of approximately 60 million tonnes. Barclays and Rabo banks have identified insects as part of the solution to this problem and have identified the industry as an investment opportunity.

Currently there are no industrial-scale insect production units in Europe, but three will be coming online in the near future. Entocycle plans to use food wastes to generate black soldier fly as pet and animal feed, with their frass being sold as a soil fertiliser. Entocycle has patented a process that automates the rearing and harvesting of black soldier fly. This will produce a constant and predictable product. In 2020 Entocycle won government funding of £10 million to develop their process, build Ento Farm 1 and bring together the entire value chain.

Black soldier fly larvae in British livestock farming: options, opportunities and outlook
Miha Pipan, Better Origin

Black soldier fly larvae have a voracious appetite for a broad range of biomass feedstocks, and show great potential for upcycling of lost nutrient sources, such as agricultural and food wastes, converting them into a range of valued products. One of these is the use of live insects as feed, which has been shown to offer the additional benefit of encouraging more natural feeding behaviours.

Better Origins is trialing its X1 units, which are self-contained insect farms housed in a shipping container. These can be operated at the source of supply to generate live insects for feeding to vertebrate livestock. Better Origins is working with the poultry industry and has found that feeding live insects to hens increases their overall welfare and egg production. Having an X1 unit on site means that waste can be processed at source and the larvae produced only travel within the farm.

Once a network of the X1 units has been established, there is the opportunity for farmers to form cooperatives to process the insects at a centralised plant that will be run by Better Origins in order to generate protein flours, oils and chitin. The units are not limited to the production of feed products but could also be used to process waste streams that would be undesirable in the food chain but which could be converted into biofuels or resources for biotech companies.

Concluding remarks

The number of delegates attending the meeting trebled that of previous years, and the global distribution clearly indicates that an online element is an essential component of any future meeting. The three days of talks demonstrated an industry that is transitioning from small start-ups exploring possibilities, to major production units that will generate the volumes of protein required to feed a growing human population. Insects were promoted not just as a source of protein, but also for a wider range of associated products, from frass as fertilisers to chitin as a raw material for biotech companies. It was also clearly shown that it is not just the range of end products that insects offer but also the process of bioconversion which can transform waste materials that would have to be disposed of at a cost into products that have a value. Until recently, insects have been unappreciated as a resource, but increasingly they will become an integral element of the circular economy that we aspire to.

Sustainable Agriculture Special Interest Group Meeting

Online Meeting, 12th May 2021

Convenor: John Holland

Report by Richard Harrington

Fig. 1. Devil's-bit scabious at The Bug Farm (Copyright Andy Holcroft Photography)

Farmland provides important habitat for insects and insects provide important services to farmland. Some, of course, are pests, but this meeting concentrated on beneficials. Meeting organiser, John Holland (Game & Wildlife Conservation Trust; GWCT) introduced some of the issues. There are many long-term challenges to insect conservation, such as climate change, cheap and reliable insecticides, lack of strong evidence for the economic effectiveness of biocontrol in field crops, insufficient pressure on farmers to change, and the dynamic complexity of farmland, making it difficult to provide general rules and to influence favourably one aspect without disturbing others. Insect declines are a concern. In the GWCT's Sussex Study, in which 64 ha of downland has been monitored for 50 years, invertebrates have declined by 37%, and the subset of predators by 70%. There are many opportunities to turn around such declines within and around fields, including increasing public interest in the plight of insects and in sustainable agriculture and, the subject of the first talk by Catherine Jones (Buglife), changes to agri-environment schemes.

Catherine briefly outlined Buglife's *No Insectinction* (https://www.buglife.org.uk/campaigns/no-insectinction/) and *B-Lines*, a network of wildflower-rich "insect superhighways" (https://www.buglife.org.uk/our-work/b-lines/) campaigns before concentrating on Defra's post-Brexit Environmental Land Management Scheme (ELMS). Defra's vision is to reward public goods with public money and to achieve a thriving, self-reliant and resilient farming sector. Buglife's involvement is through its *Landscapes for Wild Pollinators* project, which calculated the cost to ELMS of creating and managing an additional 10% of wildflower-rich habitat within the *B-Lines* to be an average of £97 million per year over the period 2023 to 2048 (£750 per hectare per annum for creation and £450 for ongoing management).

Niamh McHugh (GWCT) and John Holland aimed to identify how management of cultivated margins and floristically-enhanced grass margins influences botanic composition and the presence of a range of invertebrate groups, monitored using vacuum sampling and pitfall traps. They concluded that cultivated margins established using minimum tillage support a broader range of beneficial invertebrates than those established by ploughing, probably because ploughing reduces overwintering success in the soil, but that ploughing reduces grass weeds and encourages annual plant species which, in some situations, may be more appropriate. Floristically-enhanced margins should be established by natural regeneration rather than by sowing, in order to achieve high vegetation coverage. In all cases it is essential to consider why a habitat has been put in place before finalising management regimes. For example, if rare arable plants are present, then management for these should be a priority.

Dr Beynon's Bug Farm has featured in two successive Special Interest Group meetings. This time, Sarah Beynon and Hannah Kerr looked at the possibility of bringing back the Marsh fritillary butterfly (*Euphydryas aurinia*) to their land on the St David's Peninsula, from where it went extinct in 2013. The farm is situated between two SAC (Special Area of Conservation) sites. The plan was to improve habitat to restore the larval host-plant, Devil's-bit scabious (*Succisa pratensis*) (Fig. 1), to levels that will support the butterfly's short-term survival (50 ha estimated to be needed) and long-term survival (76–104 ha). This was attempted by using 0.3 Welsh black cattle per hectare to keep scrub height suitable and then testing the suitability of three establishment methods involving combinations of strimming, sowing seeds and planting out. An 89% improvement in suitability for Marsh fritillary has been achieved and it is hoped that it will be possible to reintroduce the butterfly under licence. Sarah concluded that farmers should be proud of efforts made to conserve rare species and should not be financially penalised through, for example, subsequent restrictions aimed at maintaining the species. For more information and a video see www.thebugfarm.co.uk/research-farm/marsh-fritillary-project.

Climate change is predicted to impact trophic interactions and cause phenological mismatches. Laura Reeves (University of Reading) is looking at its impacts on interactions between pear trees, the Pear sucker (*Cacopsylla pyricola*) (Fig. 2) and its natural enemies, which comprise mainly spiders in winter and anthocorids in spring. She found that flowering phenology was advanced by an average of 12 days in 1990 to 2019 compared to 1960 to 1989, with January to April temperatures being most strongly associated with flowering time. There was significantly earlier Pear sucker nymph emergence when temperatures were above average. There was, however, no significant relationship between date of peak natural enemy abundance and temperature, and natural enemy abundance was lower at higher summer temperatures. There is thus potential mismatch between peak Pear sucker abundance and the migration of natural enemies.

Aphids are important pests and disease vectors of barley. Sharon Zytynska (University of Liverpool) is finding out whether the presence of flowers (Buckwheat, Red clover, Broad bean), as strips or by intercropping, leads to a reduction in aphid numbers by recruiting and establishing a natural enemy community. Using field-based pot experiments, she found that a mixture of all three flowers reduced aphid numbers by increasing natural enemy

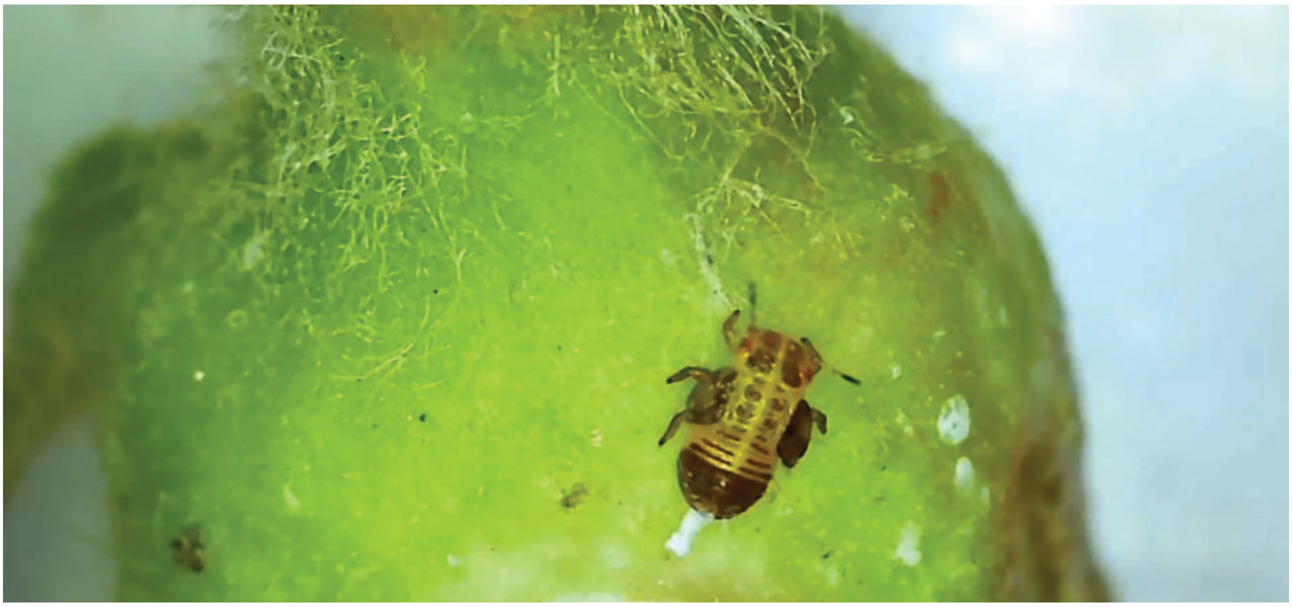


Fig. 2. Pear sucker (*Cacopsylla pyricola*) (Copyright Laura Reeves, University of Reading)

Fig. 3. Silvopasture in Colombia (Copyright Lois Kinneen, University of Reading)

diversity, and that different flower species hosted different non-crop aphids which in turn recruited different natural enemies. Aphid control is a result of numerous weak interactions rather than a few dominant ones, facilitating effective control over a wide range of environmental conditions. Work is needed to see if this translates into increased yields at field scale.

The BioSmart project focusses on silvopasture in the Colombian Amazon. An interdisciplinary project involving ecology (entomology and botany), behavioural economics and cultural geography, it examines the social and environmental impacts of a pasture–tree system. Lois Kinneen (University of Reading) is involved in the entomology side of the project and is examining the effects of silvopasture systems (Fig. 3) on invertebrate communities. Colombia is the second most biodiverse country in the world and home to 10% of the Amazon rainforest. Five farms were sampled in 2018 and 16 in 2020 using Malaise traps and sweep-net transects. In 2018, 2,932 individuals from 15 orders were collected in Malaise traps, and 6,967 individuals from 14 orders were collected using sweep nets (Fig. 4). The greatest difference in abundance and community structure of invertebrates was detected between forest and pasture, with the difference between silvopasture and pasture being greater than the difference between silvopasture and forest. Identification of the specimens collected in 2020 is ongoing and Lois plans to increase the taxonomic resolution in order to explore whether different functional roles are affected by the adoption of silvopasture and to associate diversity and abundance with a range of explanatory variables.

Fig. 4. Processing sweep samples (Copyright Lois Kinneen, University of Reading)

The SUPER-Farm project is exploring opportunities to move away from agriculturally intensive pest management (chemical inputs) to ecologically intensive interventions (biocontrol and other ecosystem services) in rice fields at sites in northern and southern India. Yellow stem borer (*Scirpophaga incertulas*) is the target species and Bryony Willcox (University of Reading) is examining the abundance of this pest along with the natural enemy communities that could potentially regulate it (Fig. 5). Several experimental factors were compared including sites under high *vs* low agrochemical inputs and floral interventions being present or absent, as well as a density gradient of seminatural vegetation surrounding each site. Across the Southern Indian sites treatments had no effect on natural enemies, however pest abundance was much greater in low-input systems when no additional floral resources were planted compared to high-input systems (with and without floral interventions) and the low-input system with floral interventions. There was also no influence of seminatural vegetation on either pest or natural enemy communities across sites.

Fig. 5. Sampling for the SUPER-Farm project in India (Copyright Bryony Willcox, University of Reading)

The Monarch butterfly (*Danaus plexippus*), as well as being iconic for its size and extraordinary migration and roosting behaviours, is an important pollinator and crucial to ecosystems and agriculture, but is in decline for various reasons such as climate change, deforestation, drought, herbicide use and habitat loss. Thomas Chen (Academy for Mathematics, Science and Engineering, Rockaway, New Jersey) has developed an artificial-intelligence-based computer-vision system (MONARCHNET) that allows citizen scientists to distinguish it from morphologically-similar species such as the Viceroy (*Limenitis archippus*), Queen (*Danaus gilippus*) and Soldier (*Danaus eresimus*) with reasonable accuracy and hence help to monitor its fortunes. It is based on analysis of more than 400,000 images. Automated methods such as this help to inform conservation strategies in a targeted way.

Many thanks to John for organising an excellent meeting, and to the speakers, their co-authors and all delegates for making it so. Thanks of course to Fran Sconce who, yet again, handled the technology and minor incidents with great professionalism.

Sometimes it seems as though progress in farmland conservation is slow and that the same loops are being travelled repeatedly, but every piece of evidence is crucial to the big picture and, as John said at the outset, there is an ever-growing body of opinion that less-intensive agricultural systems are key to no less than the long-term survival of humankind.

"Saving Swallowtails" – An Online Conference in Two Time Zones

Swallowtail and Birdwing Butterfly Trust (SBBT) with the Conservation Special Interest Group

N. Mark Collins

Troides andromache andromache. Photo: Murphy Ng

Introduction

Swallowtail butterflies remain the only family of insects that has been assessed in its global entirety for conservation purposes and action planning (Collins and Morris, 1985; New and Collins, 1991). Some reassessments have recently been made by IUCN, notably of the birdwings, but progress on the ground is limited. The main challenge is that drivers of threats to swallowtails have outstripped conservation action, but the situation is not helped by global conservation reports such as the *Global Biodiversity Outlook 5* that fail to communicate quantitative data from the insect world (Secretariat of the Convention on Biological Diversity, 2020 – see Diversity, 2020, page 88).

Despite these headwinds, committed groups are finding new ways to achieve lasting conservation through project methods that could be applied more widely. The SBBT decided to bring practitioners together, electing to hold two recorded conference sessions online on World Swallowtail Day, 12 June 2021, each with seven papers and a live discussion. One session began at 08:00 UTC for Europe and Africa across to Fiji, and the other at 17:00 UTC for the Caribbean and Americas. There were 150 registrants and all presentations were published on YouTube where views quickly exceeded 1,000 (SBBT, 2021).

Eastern Time Zone

The first two papers, by Matt Cecil of the Richmond Birdwing Conservation Network and Ian Gynther of the Dept of Environment and Science, Queensland Government, explained that habitat fragmentation in eastern Australia since the 1870s has severely impacted the Richmond Birdwing *Ornithoptera richmondia*. The species suffered "inbreeding depression" as a result and was further hampered by the female laying on invasive species of *Aristolochia* that poisoned emerging larvae. Habitat corridor development, coupled with enrichment using nursery-grown foodplants, removal of invasives and release of captive-bred stock has turned the situation around. The campaign inspired local communities to engage through education, fieldwork and financial support, resulting in major improvements to the butterfly's viability.

Fabien Condamine, CNRS Institut des Sciences de l'Evolution, explained that Queen Alexandra's Birdwing *Ornithoptera alexandrae* is confined to two separate populations in Papua New Guinea. A captive breeding programme is under development but the conservation strategy depends upon whether the populations are different taxa. Genetic analysis of two adults and two larvae sacrificed under licence from each site concluded that, despite a lack of geneflow between the populations, they are the same taxon and a regional strategy should therefore be pursued.

Sabah's Stephen Sutton introduced the Borneo Birdwing *Troides andromache*, found only in cloud forest at 1500-2000m elevation on Mt Kinabalu. Lowland competitors prevent downward range expansion, while climate change is gradually shifting suitable montane zones to smaller areas. Through research, education and communication, the lifecycle and foodplant have been discovered and local

Queen Alexandra's Birdwing. Photo: Charles Harbottle

people are engaged in rearing and stewardship. The Borneo Birdwing is now an icon of the Mt Kinabalu World Heritage Site and its future is more assured.

SBBT's Martin Partridge presented an assessment of the 36 species of birdwing found from India to the Solomon Islands. Twelve are threatened, one each from the Philippines, Malaysia, PNG and Australia and eight from Indonesia. With the exception of Rothschild's Birdwing *Ornithoptera rothschildii* and the Borneo Birdwing, these are lowland species vulnerable to deforestation. Mapping demonstrated that current protection systems are inadequate. Research is needed on life histories and foodplants, and engagement with local landowners and communities is a necessary precursor to successful projects.

Richard Markham of KokoMana Pte Ltd, Nunia Thomas-Moko of NatureFiji-MareqetiViti and Clive Huggins, Associate of the Natural History Museum, presented the Natewa Swallowtail *Papilio natewa*, discovered on Vanua Levu in 2017. The unusual ebony tree foodplant has now been found but not formally identified. Threats include illegal trade and land clearance for kava production, leading to erosion and land degradation. Captive breeding facilities have been built and agroforestry, ecotourism and carbon credits explored as alternatives for the local communities. Protected areas and control of trade are urgently required.

Anuj Jain of the Nature Society described how Singapore's 478 species of butterfly (nine extirpated) lost 90% of their forest in the twentieth century but now have 40% secondary forest cover. Of the eighteen extant swallowtails, conservation effort is focused on the Common Rose *Pachliopta aristolochiae*, recently adopted as Singapore's national butterfly and the Common Birdwing *Troides helena*, both of which now depend on non-native foodplants. Community-based butterfly trails and other initiatives are raising awareness, setting the scene for a detailed conservation strategy.

Natewa Swallowtail. Photo: Greg Kerr

Western Time Zone

Eric Garraway of the University of West Indies, supported by John Parnell, formerly of UWI, described the phenology and habits of the western hemisphere's largest butterfly, the Homerus Swallowtail *Papilio (Pterourus) homerus* of Jamaica. The two populations of this rare butterfly are widely separated but attempts at genetic analysis for conservation planning have proved inconclusive. Early success in promoting the species as a national treasure, building community support and establishing a protected area have suffered setbacks in the face of a declining economy, rising unemployment and threats from bauxite mining. Ecotourism has not been a success and ways to reward local community stewardship are needed.

Tom Turner of the McGuire Centre for Lepidoptera and Biodiversity, University of Florida and Vaughan Turland, an Associate of the Windsor Research Centre, explained the lifecycle of the Blue Swallowtail *Protographium marcellinus*, which is found in just five sites where its foodplant Black Lancewood *Oxandra lanceolata* grows in low rainfall limestone habitats. The tree is over-exploited for poles to support yam vines, and nurseries are needed. The butterfly should be classified as critically endangered and protected through engagement with landowners and training of wardens.

Jaret Daniels, also of the McGuire Centre, introduced the only butterfly federally listed as endangered in the USA, Schaus' Swallowtail *Papilio (Heraclides) aristodemus ponceanus*. Populations fluctuate dangerously in Florida's few remaining tropical hardwood hammocks where the rutaceous foodplants Torchwood *Amyris emelifera* and Wild Lime *Zanthoxylum fagara* are found. Captive breeding with hand-pairing has succeeded and, with wild releases exceeding 1,500 individuals since 2014 and additional support for habitat restoration, the future of the subspecies is brighter.

SBBT's Mark Collins explained that the British Swallowtail *Papilio machaon britannicus*, confined to seventeen reedbed sites together with its Vulnerable foodplant Milk-parsley *Thysselinum palustre*, is threatened by sea-level rise and an invading subspecies. Sea-level rise would change large areas of reedbed to saltmarsh and the currently well-protected sites may not survive such inundation. Climate warming encourages European mainland *P.m. gorganus* to migrate to the UK, where it has been recorded breeding on the south coast. A strong flier able to breed on many common species of Apiaceae, *P.m. gorganus* may eventually out-compete its reedbed cousin. Transfer of *P.m. britannicus* and its foodplant to newly restored wetlands further inland is a possibility.

Simona Bonelli, University of Turin, said that the Southern Swallowtail *Papilio alexanor* suffers from habitat loss and illegal collecting on calcareous slopes of Italy's Maritime Alps. The larvae feed on Apiaceae and modelling has identified twelve areas suitable for population enhancement and habitat restoration, including in quarries. To be sustainable, such measures require greater awareness in local people, landowners and tourists, with butterfly trails and information panels made available.

British Swallowtail. Photo: Mark Collins

Richard Bennett of Mida Butterfly Farm on Kenya's coast described how 500 community butterfly farms in the region supply 100,000 captive-bred pupae per year to exhibits in the UK, USA and Europe. Several years' research and training are needed to prepare for export. Fifty species are currently made available, including eight swallowtails. Breeding cages are designed to provide near-natural conditions. The Emperor Swallowtail *Papilio ophidocephalus* requires a 5m circular cage to carefully control shade, humidity, predation and parasitism. The industry helps community development and builds respect for the natural environment.

Andre Freitas and Augusto Rosa of the University of Campinas explained that Brazil's Action Plan for Lepidoptera includes 71 elements, twelve of them for swallowtails. Of Brazil's 67 swallowtails ten taxa in eight species are threatened. Two subspecies of *Papilio (Heraclides) himeros* have disappeared from haunts around Rio de Janeiro, as has the highly endangered *Parides ascanius* and the *Parides* mimics *Mimoides lysithous harrisianus* and *M.l. sebastianus*. *Parides klagesi* is scarce in the Amazon basin; *Parides tros danunciae* is a rarity of the Atlantic forests; in riparian forests *Parides panthonus castilhoi* is local while CITES-listed *Parides burchellanus* is endangered and the poorly known *Parides bunichus chamissonia* has few remaining colonies. More information as needed on localities, populations, behaviour and foodplants of Brazil's rich swallowtail fauna.

Conclusions

In the live discussions, a number of themes common to the swallowtail conservation effort arose.

- Information on the natural history and conservation status of many species remains inadequate, particularly in South America, Africa and Southeast Asia.
- Where there are known to be threats, the protected areas system is all too often inadequate, with little or no regard paid to swallowtails or, indeed, to any other insects.
- Total habitat loss through agriculture, deforestation and other impacts is a major concern, but gradual degradation of habitat through overuse and climate change is also a problem.
- Climate change is impacting swallowtails through sea-level rise, ecosystem shifts and the encouragement of invasive species.
- Unsustainable collecting and trade require greater controls but a change in public attitude towards enjoyment of living butterflies will have greater impact.
- Engagement with local communities to enhance a sense of stewardship and encourage sustainable use, such as ecotourism and captive breeding, will show clear dividends.
- Successful conservation will require a good understanding of sociology and the local economy in addition to an appreciation of the natural history of swallowtails.
- Swallowtail butterflies are worldwide, well-studied compared to many insects and attractive to the general public. They have great potential as conservation icons.

Acknowledgements

The Royal Entomological Society and several individuals contributed generously to the cost of the conference. Field projects reported from Australia, PNG, Fiji, Jamaica, Sabah and the UK benefited from SBBT grants. SBBT Trustees organised the conference voluntarily.

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Honorary Fellow Interviews

Erica McAlister

Time's fun when you're having flies!

by Peter Smithers

A storm has been sweeping across the country: a high-energy system that leaves a trail of devastated prejudices in its wake; a one-woman crusade that has set out to change the British perception of the much-despised fly; a storm of untamed enthusiasm that is waving the flag for our dipteran friends and shifting the public perspective to a more tolerant and appreciative view. This storm is, of course, Erica McAlister, curator of Diptera (and Siphonaptera) at the Natural History Museum, London and author of both *The Secret Life of Flies* and *The Inside Out of Flies*. I have attended several of her public talks and been swept away by the unbounded enthusiasm of her presentations, which are always entertainingly informative and seriously irreverent. Audiences love every moment. I had been looking forward to talking to her at the NHM but the pandemic intervened once more and we had to revert to Zoom. So, I met Erica digitally in her shed/office/lab (her "shoffice") that sits in her garden to discuss her life in entomology.

Early years

"Nature has always been a huge influence on my life. As a child we had limited access to TV as I was lucky enough to have parents who took reading seriously. Whenever we had a question, we were told to look it up in a book, so we did, and books became an important part of my childhood. I was also an outdoor kid but, being small and clumsy, I fell over a lot and also fell out of many trees. As a result of these falls, I spent a lot of time just staring at the ground. I would just sit and stare at the insects in the garden for ages. I remember watching ants for hours and I was lucky that my father acquired a microscope for me. So, as all kids do, I began to look at fleas from the cat or the remains of the small mammals that they would bring in – there was definitely a dark side to having a microscope.

Despite this, I grew up not knowing that anyone could be an entomologist. The only 'green' organisations I was aware of were the *World Wildlife Fund* and *Greenpeace*, which both seemed to look at big mammals, which are fabulous but did not float my boat. I knew I wanted to work in ecology and was becoming more and more interested in insects but, at this point, I was like a rudderless ship. I did my fourth-year school work placement with the National Trust and had great fun scrub bashing but realised, gosh, it was very physical and mostly just that. Then in sixth form I worked with the Surrey County Wardens which gave me a really good understanding of a range of habitats and their management."

University *etc.*

"I went on to read Environmental Biology at Manchester University, where the legend that is Dick Askew fired my kindling interest in entomology. I remember vividly being on our first-year field course at his place in France, where he just scooped up a pile of insects and talked through them, describing who ate who and in which way. It was brilliant, I just loved it – the graphic descriptions of their interactions had me hooked. How insects interact with each other is one of the fascinating things about them, and these interactions are so available for us to see if we choose. In the comfort of your garden, you can watch thousands of invertebrate interactions at close range which, to my mind, makes these little postage stamps of nature comparable to the wilds of the African savannahs.

During my degree, I underwent a placement year, starting with the then Institute of Terrestrial Ecology (now the UK Centre for Ecology & Hydrology) where I was chasing heather beetles around Studland Heath, looking at their impact on the heathers. We were also breeding them at a range of temperatures and CO_2 concentrations and looking at their parasites to see if we could use these as biological control agents. I remember trying to video one of these parasites emerging from a beetle. It happened over lunch time so, there I was, with my sandwiches, watching and waiting, and a maggot crawled out, waggled around for a bit, and then went back into the beetle. I was amazed. But that's what I loved – making personal observations of these behaviours and asking, 'What are you up to, you crazy little creatures?'.

The second half of my placement year was in Australia, where I worked at the University of Adelaide on ants. After identifying 330,000+ individual ants, I decided this was not for me. This was also my first flight ever and, to while away the journey, I read aloud, to the friend who went with me,

Erica at 21 downunder.

extracts from a book on the deadliest animals on the continent. It was such a contrast from home in Surrey, where the most dangerous thing was a car driver, to be arriving in a land where it seemed just about everything could kill me. It was also a massive temperature change, as I left the UK in January where the temperature was -5°C to arrive at our destination in South Australia where it was 46°C.

In the team I was working with, I would often be the only entomologist; I would go out with a geologist and a botanist, so I was having to learn how to design experiments on the hoof and how to adapt when having very limited resources. It was a baptism of fire, but it was also a life-changing experience. I was very lucky; we went to so many places that most people never see and I realised that I loved fieldwork."

PhD

"I found a PhD advertised in the back of *New Scientist* for a position at the London Wetland Centre (WWT) and I was surprised to find that the Centre was actually in the middle of London. I applied and got the studentship. The PhD was looking at the invertebrate communities of areas of wetland sown with different grass seed mixes. It was ecological entomology and, as well as many hours in the field, I was often in the lab ten hours a day identifying insects. My supervisors were Dr Peter Shaw, who worked on soil biodiversity, and Dr Claire Ozanne (now Prof.) who worked on canopy arthropods, and there I was studying aquatic invertebrates in wetlands. So, they suggested I talk to people

Aquatic sampling at the London Wetland Centre.

at the NHM about identifying the aquatic invertebrates. At that time, I had no idea about the research that went on behind the scenes, but a colleague recommended that I email Dr Steve Brooks and ask for help with the chironomids I was finding. He was amazing – he went through keys with me and followed up with advice and guidance. I then wanted help with water beetles, so I talked to Max Barclay and, following our conversations, I began volunteering at the Museum. Later, as I was writing up my PhD, I was also volunteering at the NHM, but at the same time I was managing a restaurant in the evening and part-time lecturing at Roehampton. I had no hours left in the day but I really can't complain about these experiences – I learnt so much and gained a lot of practical experience.

The combination of the PhD and volunteering at the NHM was a great introduction to UK invertebrate diversity. We are not a mega-diverse country, but we know so much about our fauna. I was able to name the inverts I encountered easily as I had a range of experts on hand to help. As we have such a well-known fauna, we can get past the sometimes-laborious process of naming the invertebrates and start looking at their interactions, which is when it starts to be fun and we can begin to figure out what they are actually doing. I can look at an invertebrate and think 'I know your name and I know what you do, so now I can look at how you do it'. It's at this point that I feel totally connected with nature."

The NHM

"There had been lots of Diptera to identify in my PhD but I also worked on Diptera from the tropics when I was volunteering at the NHM. As well as this, I was going through unit trays and just sorting beetles to family level but also sorting Malaise trap samples, which took weeks for each sample. At this point, I was also undertaking field work in Costa Rica a couple of times a year, thanks to some Roehampton funding.

Pitfall sampling in Costa Rica.

Sampling flies from Titum Aram in Kew.

Whilst volunteering, a job in the Diptera section came up as cover for maternity leave – I applied and got the job. Luckily, a full-time post came along in Diptera and I was exceptionally happy to be successful in that application as well. Once I realised just how diverse and interesting the Diptera were, I felt totally at home. I had found my soul mates in the flies. They look amazing, they are morphologically diverse, they display bonkers behaviours. You name it, they have done it. They are also ecologically diverse; they have a tarsus in every ecological niche imaginable.

At the Museum, I have worked with Dr Ralph Harbach on mosquitoes, conducting field work in Indonesia, Malaysia, Thailand and Vietnam. I also worked in Tajikistan, where we were involved in the training of local research scientists so they could develop a malaria control program. They were wonderful people in extraordinary habitats; massive mountains that sat on vast plains. I've worked on Australian robber flies with an external collaborator, Dr Bob Lavigne, and also internally with Dr Sandy Knapp, 'the queen of potatoes'. We went back to the birth place of potatoes and tomatoes in Peru to find their pollinators and herbivores. We were sampling at 5,000 m asl, so trying to poot up flies was hard work – with our feeble attempts the flies would turn and look at us then just walk away.

I have spent the last five years working in Dominica in collaboration with Operation Wallacea, collecting insects and teaching 15–18-year-olds, mostly from the UK, who all arrive wanting to work with primates or turtles. Each day I have a new group of students and I have 24 hours to persuade them that insects are cool and interesting. This is often not hard, as once the students start looking and they see how incredible they are, they are amazed; the phrase that I hear over and over again is 'I had no idea'.

When the students return home, they have the opportunity to come to the Museum and see the flies that they collected in the collections. I explain to them that some of the flies that they collected may be new to science, and their excitement is palpable. Not only do they understand why the field work is so important but they themselves have contributed to scientific research."

Books and the media

"Back in 2012, The Museum was asked to supply a member of staff to appear on the radio program *The Museum of Curiosity* and they asked me to go along. Each guest donates something to the Museum, so I donated a pile of dung and talked about the many interactions within it. Thus began my path on science outreach in a big way, including many in-house talks on flies. I was approached at one such event to write a book. I relayed this back to the Museum and it was suggested that I write a book on flies. This is not something I would ever have thought of doing as I am hopeless with written words (my PhD supervisor thought I was dyslexic and my spelling is terrible). But once I started, I was carried away and really enjoyed the process (although many mistakes were made!). I think that science communication is still under-utilised – we need the public to understand what and why we study to ensure that the funding and commitment to these projects are there."

Museums in the future

"The only limits to what can be done with museum collections are imagination and money. In the past, collections were made in order to describe species, but technological advances have allowed us to realise their full potential. They are now seen as a data set which can be mined in many ways. Individual museums possess large data sets, but combine these across the country and the world, and the data sets are vast.

With advances in imaging, collections are now being digitised. We can photograph specimens, scan the internal structures and analyse their gut contents. We can look at the pollen on individual insects and work out which plants they visited when they were alive. We can also look at historic DNA and using this we can work out when insecticide resistance appeared, work which myself and a team from The Sanger Institute, led by Dr Mara Lawniczak, undertook recently on some of the mosquito collection. The collections are no longer just dead specimens, they are very much alive with information."

Erica's desire to make flies acceptable in polite conversation and persuade the public that they are interesting, useful, even essential, and that we should all learn to love them, is probably unprecedented. Her talks and her books are densely informative but are delivered with an informality and self-effacing humour that leaves even sceptics with a warm glow about flies. Her desire to understand not only what invertebrates are doing but why, reveals her innate inquisitiveness – an observer who wants to understand the world around her; observations that build into stories that Erica then tells as if it were a chat over a cup of coffee. But these observations are based on a lengthy taxonomic apprenticeship, hard-won skills that allow her to say "I know what you are" and allow her to study the interactions that fascinate her. We hope she will continue to collect and tell these dipteran stories and continue to ask "What are you up to, you crazy little creatures?"

Laurence Mound

by Peter Cranston

Editor's introduction

It is usually a while between receiving an Honorary Fellowship and getting a call from Peter Smithers requesting an interview for these pages. This time, Peter Cranston has taken the pleasure from Peter Smithers by offering a biography of a man who has only just been admitted to the Honorary Fellowship.

Laurence Mound's professional interests in entomology started in the country of his birth, England, burgeoning in postgraduate studies at the British Museum of Natural History (BMNH), now The Natural History Museum. As with many entomologists of his generation, employment in the 'colonies' followed awards by Her Majesty's Colonial Office to study agricultural entomology; he was awarded the Diploma of Imperial College, London, in Economic Entomology in 1958 and the Diploma of Tropical Agriculture from the Imperial College in Tropical Agriculture in Trinidad in 1959. A posting to the Nigerian Federal Department of Agricultural Research in Ibadan allowed him to study whitefly vectors of crop virus diseases, especially noting host-crop-induced natural variation. The following years, 1961 to 1964, saw Laurence in the Sudan where he studied the effects of whiteflies on cotton lint for the Empire Cotton Growing Corporation. His work in Sudan revealed environmental influences on insect behaviour and encouraged his understanding of the application of taxonomy in the widest context. Laurence took these insights with him back to London where he was made responsible for the whitefly and thrips collections at the BMNH. There his research turned more towards the thrips, where it has remained for the past 50 years. Laurence progressed within administration, becoming Deputy Keeper in 1975 (the year in which he was awarded a DSc by the University of London), and Keeper (head) of Entomology in 1981. All the while Laurence made the time to continue and expand his globally-based insights into thrips taxonomy, behaviour and evolution with a prolific publication record. His profile as a major player in international entomology led to positions on the organising committee of the ICE from 1976–1992 and many invitations to speak on the role and future of the discipline, addressing gatherings from clusters of agronomists to the hoards at international congresses of entomology. These contributions were always stimulating, challenging the status quo in demanding that entomology be placed in a rigorous scientific context while justifying the allocation of taxpayer dollars. Laurence retired from the Museum in 1992, one of many victims of the Thatcher-government-driven cuts to science, but Britain's loss became Australia's gain.

From the earliest days of his professional involvement in entomology, Laurence has always been actively engaged with professional societies in our discipline. He was a very active Fellow in the Royal Entomological Society, increasingly so when located 'across the road' from the Queen's Gate HQ. With the benefits of hindsight, his role as journals' editor should be seen as very significant and most transformative. Under his guidance, the worthy but dull Proceedings A and B were reworked into modern scientific journals (and the portfolio has expanded dramatically since) under professional management and bringing substantial income to the Society. As Keeper of Entomology at the BMNH, Laurence encouraged his senior staff to contribute their expertise to the RES in management, journal matters, publication of handbooks and also in the organisation of RES events and expeditions. Under Laurence's guidance, these roles were considered to be part of the 'outreach' side of our prestigious public service employment in entomology. Furthermore, as the BMNH moved into education outreach in training students in systematics with linkages to the University of London (Imperial College, Birkbeck, Queen Mary, Royal Holloway and the London School of Hygiene & Tropical Medicine) and Reading University, Laurence encouraged these students to join, participate in and deliver PhD summaries to the monthly meetings of the Society.

Following his relocation 'down under' he encouraged his colleagues to communicate their studies more widely including into the RES journals. He played an important role as editor for *Myrmecia* from 1999 to 2004, expanding the contributions from regional laboratories, and caring very much for the issues of layout and coherence of contributions.

Laurence has now been in Australia for more than two decades, working initially with Canadian Bernie Crespi in seminal studies on social acacia thrips. An Australian thrips catalogue followed, with funding from Australian Biological Resources Study. Subsequently a 12-month CSIRO McMaster Fellowship was obtained, preceding his Honorary Research Fellowship based in what was then the Division of Entomology, on the Black Mountain site.

Laurence continues his field-based research, covering all points of Australia, from wettest to most arid, and including offshore islands such as Lord Howe, Kangaroo, Flinders and

Norfolk Island in relation to potential quarantine issues if trade were to increase.

Laurence has retained an international perspective, with annual overseas travel to work with others, notably revisiting the UK, and collaboration with Kiwi exile in California, Mark Hoddle. The 'Thrips Room', Laurence's home base, hosts a continuous stream of visitors from everywhere on the globe, each receiving individual advice on projects and training in thrips identification, with strong emphasis on the significance of thrips biology; all the while Laurence publishes numerous papers with co-authors from a wide spectrum of students and collaborators. As subject editor for thrips and whitefly for the international journal *Zootaxa*, Laurence has been influential in maintaining publication standards on these groups.

In keeping with his urge to train others, Laurence has hosted many workshops in Australia for quarantine and agriculture personnel, and also in Malaysia over several years, involving Indonesians, Malaysians, Vietnamese and Californians. Thai and Singaporean students and biosecurity workers have received his wisdom. In recent years he has formally aided students from Australia, Japan, Indonesia, Malaysia, China and Brazil. Laurence is no luddite in his training techniques, having been involved from early days in interactive keys with numerous montaged photographs. The LuCID developers have benefitted much from his pilot keys and continuing testing of software, as in the 'Thrips ID: Pest Thrips of the World: an Interactive Identification and Information System' with Gerard Moritz.

Laurence has been recognised recently by the award of Honorary Fellowship of the Society in a richly deserved reward for a lifetime dedicated to serving entomology and entomologists. Congratulations!

Journals and Library

Rebeca Rosengaus

Francis Gilbert, Bernie Roitberg, Sheena Cotter, Rosa Menendez Martinez

We, the co-Editors-in-Chief for *Ecological Entomology*, wish to acknowledge the recent retirement of the senior EIC, Rebeca Rosengaus, from our journal, and to thank her for the many important contributions she has made to *Ecological Entomology* and to the Royal Entomological Society in general.

Becky joined the journal as an Associate Editor in 2008, and stepped up to Editor-in-Chief in 2011, joining Jane Hill and Adam Hart. When Jane retired in 2017, Becky became the senior editor of the team along with Francis Gilbert and Bernie Roitberg. Thus she has been an editor for thirteen years (handling 117 papers) and an Editor-in-Chief for ten years (handling 1,856 papers), acting as senior EIC for the past four years during which time she was responsible for most of the communications from our group. She was organised, efficient and sensitive to the needs of authors and editors. She kept us on our toes in a gentle, supportive manner.

Aside from the day-to-day activities, Becky has been deeply involved in particular projects that we launched. For example, starting three years ago, Becky proposed and then organised our novel apprenticeship programme (see *Antenna* 43(2) 97-99) that included defining the roles, liaising with the Society, assembling the rules of engagement, communicating with candidates and developing methods for assessing the programme. A large part of its success is due to Becky's dedication and perseverance.

We also note Becky's long-held desire to ensure that all members of our Society, scientific and otherwise, are treated fairly and equitably. She has been a champion for strong ethics, engagement and encouragement of all groups to share in our passion for entomology. She brings that same strong passion to issues regarding the study of biodiversity, conservation, and the role of scientists in safeguarding our planet.

We would be remiss not to mention the humour, style and candour that Becky brought to her position. Be it with a smile, a laugh or an anecdote, she always seemed to be having fun, and her infectious enthusiasm kept the rest of us smiling through the good and the not-so-good.

It is with a deep sense of gratitude that we thank Becky for all she has done for *Ecological Entomology* and we wish her the very best moving forward.

Competitions

Early Career Entomologist Awards

Richard Harrington

I must admit that, being at the other end of the spectrum, the very existence of these awards had passed me by until I, along with other Council members, was sent the nominations to review. These were all hugely impressive and very diverse. So much so, that Council decided to confer the award on three people.

Dr Bheemanna Gotyal from the Indian Council of Agricultural Research's Central Research Institute for Jute and Allied Fibres, West Bengal, India, has made a huge practical impact on jute production through his work on identification, biology, ecology and control of insect pests and exploration of their natural enemies. He has also identified the insect-resistant wild jute source which paved the way for breeding of insect-resistant varieties. He has developed a farmer-friendly mobile app "JAF-Safe" for the identification, description, biology, nature of damage, and management of jute pests. "It is an honour to receive this award under the umbrella of the Royal Entomological Society", he said. You can read more about his work on pages 122 to 127.

Iranian entomologist, Dr Maryam Yazdani, works on IPM methodologies. On winning an International Postgraduate Research Scholarship, she moved to Adelaide in 2011 to study for her PhD and has remained in Australia since, lecturing on biosecurity and pest management, and researching citrus gall wasp (University of Adelaide) and Queensland fruit fly (Macquarie University) with a view to improved monitoring and control. She has recently joined CSIRO (Commonwealth Scientific and Industrial Research Organisation). Her passion is to facilitate the transition from "great idea" to commercial product. Maryam said "Winning this award to me is just absolutely phenomenal. I didn't expect it! There's a lot of hard work, days and years away from family that get put into delivering the research projects and studying. This is a great inspiration to keep me going on the road I've been heading down, especially in my new role at CSIRO".

Dr Juliano Morimoto, from Brazil, has studied in Brazil, Italy, UK and Australia, and is currently at the University of Aberdeen. His research includes work on the impacts of nutrition on infection, immunity, development and fitness; the role of sexual selection and the microbiota on fruit fly reproduction and behaviour; the suitability of policies in protecting insect biodiversity; and the role of insect ecosystem services on the sustainable future of our societies. Said Dr Morimoto: "Winning the award was emotional to me due to the challenges I had to overcome during my career. I am very thankful to the Royal Entomological Society and every person who has helped me along the way".

Each of these three winners has a publication record belying their years, and each has demonstrated a depth and versality to their commitment to science, teaching and outreach, which sets an example to all. They are richly deserving of this award.

Nominations for the next award close on 31st December. See https://www.royensoc.co.uk/res-award-early-career-entomologist for details.

Student Essay Competition 2020

1st Prize

Fighting on a miniature front

Zeke W. Rowe

University of Bristol, UK

As war is declared, you are swept up by the terrifying excitement which this entails. You begin to wonder, what will it cost to win? How many people will be lost? Are the insects on your side?

Alright… maybe not the last one. However, this could be the difference between victory and defeat, survival and death; changing the course of human history. No, I'm not talking about the insects gathering in a committee and discussing which side they ally with, that would be ridiculous. I'm talking about how these minibeasts have shaped human history, both by being weaponised by humans, and by passively weakening armies just by their biology.

The most obvious way these brilliant bugs could be used in war is by throwing the naturally weaponised ones at your enemies… easy, right? Entomological history is full of examples of projectile bees being used as warheads. The Tiv people of Nigeria developed an ingenious device, where bees were loaded into large horns and, once nice and angry, pointed in the direction of the enemy and unleashed! The Romans were the most impassioned users of the fling-and-sting technique, having catapulted so many hives that it has been suggested that the reduction in bee hives in the late Roman era may have been due to how many they chucked at their foes (I wonder if they shouted "Bombus away" when launching them). Not only were these harmful Hymenoptera used on the offensive, they were also used defensively. This involved the laborious task of lugging these hives, sometimes weighing over 100 pounds, to the scene of the battle, so why not place the hives in areas for dual-use? In the UK so-called 'bee bores' were placed into the south-facing walls of the castle, providing a defensive and honey-producing permanent resident.

Defeat is often simply a case of being in the wrong place at the wrong time. Alexander the Great, the Emperor of Macedonia, was on a perfect battle record of 20-0 when his campaigns finally halted on the banks of the Beas River in India. After growing his empire through Turkmenistan, Uzbekistan, Tajikistan, Afghanistan and Pakistan, why did he stop just short of such vast riches? Having traversed and camped among the swamps and rivers well into the summer mosquito season, his soldiers were riddled with diseases such as malaria, spread by these pesky bloodsuckers. With his once-formidable army reduced to a skeleton of its former self, it is no surprise that the campaign was abandoned and the trajectory of East Asian history was altered. This is not the only great leader who has been defeated by the humble insect. Napoleon Bonaparte was often outwitted by such six-legged soldiers. For example, during a three-day murderous spree of revenge in Jaffa, the flea caused a great plague to strike his soldiers with a massive 92% mortality, some committing suicide rather than succumbing to illness. He lost his chance to incite rebellion against the Ottoman Empire and to weaken the British influence in India by losing this strategically vital clash.

As the world grew, so did the entomological arsenal. During the Second World War, Japan's Biological Warfare Unit 731, led by Lt General Shirō Ishii, used these unwitting bugs to attack mainland China to devastating effect. Yagi bombs, comprising two compartments (one filled with houseflies, and one with a bacterial slurry which coated the flies just before release) were developed. Once released, they would spread this disease amongst the populous of China. It was declared in 2002 that Japanese entomological warfare in China was responsible for the staggering deaths of 440,000! The Japanese also planned to attack San Diego in a similar manner by dropping plague-infected fleas onto the populous in the cheerfully named 'Operation Cherry Blossoms at Night'; thankfully the surrender of Japan preceded this.

We have looked over how our ancestors have weaponised these tiny warriors, how chance can play its part and how in more recent conflicts they have been utilised for domestic attack, but what does the future hold for these insects of war, and should we be worried? Bioterrorism is a real threat we could face, with insects being used to intentionally spread diseases as they are easily gathered and their eggs easily transportable without detection. US intelligence officials have suggested that insects could be genetically engineered to produce 'killer mosquitoes' or super-effective plagues which could attack staple crops. Although these ideas seem well into the realms of science fiction, they could be closer than one might imagine. Therefore, we must all hope and work together to make sure the power of insects doesn't fall into the wrong hands.

2nd Prize

Bug business

Jennifer Newell

Harper Adams University, UK

***Opening sequence fades into ANNOUNCER…

ANNOUNCER: Welcome to this week's episode of "bug business". Today we'll be looking at one of the most striking insects in the freshwater ecosystem; the dragonfly. Hovering just above the pond surface, the iridescent kaleidoscopic carapace of the nimble dragonfly might be mistaken for the shimmering reflection of water. Don't let their mesmerising morphology fool you though; these flying fancies are the apex predators of the wetland world. Interviewer Richard Cheshire meets Odonata expert Professor David Brooks to find out more...

***Camera pans across grassy wetlands. A large lake stretches behind the announcer, framed with rushes and waterfowl. Wind rustles through the reeds and there is the distinctive rustling/tearing noise of dragonfly wings.

INTERVIEWER: We're down here today in the New Forest National Park on the south coast of England, and I'm joined by Professor David Brooks. Professor, can you tell us a little bit about the area and its appeal for dragonflies?

EXPERT: Sure; the aquatic-terrestrial ecosystem here in the New Forest is perfect for the varied needs of different stages in the dragonfly lifecycle. Dragonflies actually spend a good portion of their life underwater. Females deposit fertilised eggs in the water, the eggs hatch and nymphs remain underwater for a few more months feeding on aquatic invertebrates and moulting through several growth-stages. They will then emerge from the water, often on a plant stem like this, where the exoskeleton will split and the young adult will emerge.

INTERVIEWER: I can see several different species on this rock. First, I have to say, look at those wings! They're like stained-glass windows; the sun's even reflecting that amber colouration onto the rock below…

EXPERT: That's *Sympetrum flaveolum*, a female yellow-winged darter, and those wings aren't just for decoration. Some dragonflies, like the hawkers, can reach flight speeds of up to 30mph. Watch those huge greenish-blue *Anax imperator*, or emperor dragonflies, patrol the pond surface near the centre of the lake. The males are quite territorial and if you watch them for a few minutes, you'll see them hover, turn abruptly mid-air, and very speedily chase intruders. See how the wings are spaced on the body? They're directly connected to large flight muscles in the thorax that allow them to use each pair of wings independently. They're incredibly agile.

INTERVIEWER: I imagine that makes them a pretty formidable predator!

EXPERT: Absolutely. They're voracious carnivores with a predation-success rate of up to 95%. In the aquatic nymph stages, they actively seek out prey with incredible speed and deadly accuracy. There might be some zipping around in these reeds here… Yes! See this one chasing mosquito larvae? That quick burst of speed is fuelled by releasing a jet of water from its anus…

INTERVIEWER: …like jet-propulsion?!...

EXPERT: Exactly. As for the airborne adults, very few insects can match their predation efficiency, and a single adult can eat hundreds of flying insects a day! The powerful wings are a huge asset here, but they also have incredible eyesight.

INTERVIEWER: Hmm, I wasn't sure if that bulbous head was all eyes; they seem almost cartoonishly out-of-proportion…

EXPERT: They are indeed all eyes and, like the wings, they aren't just for show. Take this common darter, *Sympetrum striolatum*. If we ignore the colouration, you can see the two large compound eyes that occupy most of the head. These produce almost 360° vision, with just a single blind spot behind their head – typical of an effective predator. They're made up of 30,000 simple lenses, with up to 33 opsins, or proteins, that dramatically increase their colour and light perception. As a comparison, you and I only have 3 opsins. If that weren't enough, there are also three ocelli, more eyes, there on the nose or 'vertex'. These simple eyes resolve basic images and detect light, which allows the dragonflies to orient themselves in flight.

INTERVIEWER: Incredible! So their vision is like UltraHD on super-fast broadband!

EXPERT: At the very least! They obviously have excellent mid-air prey-detection skills. Their aerial agility and tough grip then allow them to catch and consume prey mid-air with deadly proficiency.

***The pair pause to gaze over the buzzing lake.

INTERVIEWER: I'm glad their size means they don't pose a threat to us. I can't imagine I'd last long against a predator like that.

EXPERT: They're small now; but if you were around about 325 million years ago, you'd meet the protodonatan, *Meganeuropsis*, prehistoric dragonflies with a wing span of around 1m. Today, the largest the UK can offer are the emperor dragonflies with a wing span of about 10 cm.

INTERVIEWER: Fun, but terrifying fact to end on! Thank you again, Professor Brooks, for the fascinating foray into the world of dragonflies. Tune in next week for the spell-binding story of stick insects!

***Fade out to credits.

3rd Prize

Work smarter, not harder: the parasitic plan of the cuckoo bumblebee queen

Robin Hutchinson

University of Reading, UK

A far cry from the bumbling, flower-loving species we know and love, some bumblebees have given up collecting pollen in favour of a more devious method of parental care. But whether this helps or hinders them in the long run remains to be seen.

A queen's work is never done

Being a bumblebee is hard work, especially if you are a queen. A queen spends the winter alone, hidden away underground, trying to survive the cold. Should she make it through to spring, the hungry queen will have an even more daunting task ahead of her - founding her own colony. First, she must find enough pollen and nectar to regain the energy stores she lost over the long winter. Then, she will need to set out to find a nest site. As keen recyclers, bumblebees like to repurpose the nests of birds or mice from previous years. She may have to travel hundreds of kilometres to find a prime location, as human-altered habitats simply do not have enough suitable spots. When she has decided, our queen will need to repair any damage from the winter, create a bed of nectar and pollen, and hope that the previous tenants do not come back. And still a queen's work is not done! Until she rears enough worker bees, she will be responsible for laying eggs, sitting on them to keep them warm, and of course flying backwards and forwards collecting food for her young. With over 50% of colonies dying before the first workers hatch, it's not surprising that some bumblebee queens like to cheat.

A smarter strategy

At first glance, the cuckoo bumblebee queen appears very similar to other bumblebee queens, even mimicking their distinctive stripes. But look closer, and her body is purpose-built for a very different objective. Larger than her colony-building cousins, the cuckoo queen has a much tougher exoskeleton and a powerful sting, ready for a fight. Whilst the more honest queens are braving the chill to build their nests, a cuckoo queen will enjoy a bit of a lie-in. Once things start to warm up a little, the cuckoo queen will wander out of her hiding place and mill about nearby flowers. Eventually, she might wander a little further afield, on the hunt for a colony ripe for the taking. She cannot pick a very young colony, as there will not be enough workers to rear her young. If she picks a colony that is too old, there will be too many workers and the cuckoo queen will be forced out, or even killed. She needs to find something just right. With her target acquired, the cuckoo queen will storm into the nest, defending herself against the host workers' attacks using her armoured exoskeleton as she fights her way towards the queen. Even up against a queen determined to defend her nest, the cuckoo queen has the upper hand. With her big, strong jaws and mighty sting, she will subdue or even kill her rival. She will then compel the remaining host workers to accept her into their nest through mimicking both the appearance and smell of her new nestmates. Of course, by eating the host eggs, the cuckoo queen will give the workers very little choice in the matter. The intimidated host worker bumblebees, at a loss for what to do, will set about caring for the next generation of cuckoo queens.

Not quite so smart after all

Unfortunately for cuckoo bumblebees, cutting corners comes with its own set of problems. Cuckoo bumblebees are now completely dependent on other bumblebees for reproduction. With five of the six cuckoo bumblebee species in the UK in decline alongside their hosts, it seems that the cuckoo queen's underhand tactics might be her own downfall. Cuckoo bumblebees need a minimum number of suitable nests in an area in order to maintain their own population; when host bumblebee numbers dip below this number in an area, the cuckoos will disappear. And even if there are enough host nests available, rising temperatures could alter the spring behaviour of cuckoo bumblebees, leading them to emerge at the wrong time. If this happens, the cuckoo queens will miss their window of opportunity when the host nests are the perfect size, and be unable to reproduce. In addition, the cuckoo queens are now trapped in an arms race, constantly having to evolve new ways to thwart the host bumblebees' defences. Failing to keep up would also spell extinction. With all of these threats to contend with, perhaps working harder is the smarter strategy after all.

New publication announcement

Handbooks for the Identification of British Insects
Vol 10 Part 16
Blow flies (Diptera: Calliphoridae, Polleniidae, Rhiniidae)

By Olga Sivell

This stunning new full-colour handbook takes a different approach, using high-quality diagnostic photographs in the keys, providing a reliable aid to identification for both the amateur and professional entomologist. The book covers the Calliphoridae, Polleniidae and Rhiniidae, collectively known as Blow flies. These flies are an important group of pollinators and decomposers, also parasites – some of veterinary, economic and medical importance. They are also known for their use in forensic science.

RRP £40 - Early bird offer £35
plus postage and packaging;
Members/Fellows receive 30% discount.
www.royensoc.co.uk/publications/handbooks

SCHEDULE OF NEW FELLOWS AND MEMBERS

as at 2nd June 2021

New Fellows (1st Announcement)
Prof. Duane McKenna
Dr Huaxi Liu
Dr Corrie Saux Moreau
Dr Manjulakumari Doddamane
Dr Mathukumalli Srinivas Rao

New Fellows (2nd Announcement and Election)
Dr Aidan O'Hanlon
Prof. T.V.K. Singh
Prof. Rosana Tidon

New Members Admitted
Miss Susmita Aown
Dr Kumar Saurabh Singh
Mr James Haselman
Dr Francesco Poggi
Dr Peter Mitchell Ridland
Dr Janet Cole

New Student Members Admitted
Miss Alison George
Miss Rebecca McGowan
Miss Jennifer Sudworth
Miss Andrada Denisa Opris
Mr Lawrence David Collins
Miss Astrid De Jaham
Ms Maria Elisa Damascena de Almeida Leandro
Ms Gail Ashton
Mr Hayden Tempest

Reinstatements To Fellowship
Dr Marcio Roberto Pie

Reinstatements To Membership
Dr Frazer Hamilton Sinclair

Deaths
Prof. Stephen Tobe, 1974, Canada

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as at 20th July 2021

New Fellows (1st Announcement)
Dr Trevor John Hawkeswood
Dr Arran James Folly

New Fellows (2nd Announcement and Election)
Prof. Duane Mckenna
Dr Huaxi Liu
Dr Corrie Saux Moreau
Dr Manjulakumari Doddamane
Dr Mathukumalli Srinivas Rao

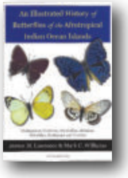
New Members Admitted
Mr Zachary Stavrou-Dowd
Dr Pratheesh Mathew
Dr Clair Rose
Mr Benjamin Fowle
Dr John Howard
Mr Sebastian Hemer
Dr Hadura Abu Hasan
Mr Kelvin Francis Campbell Murray
Dr Diane Hird

New Student Members Admitted
Mr Connor Russell
Mr Venkatesh Vemulapati
Miss Elysha Duke
Mr Gino Brignoli
Mr Sabir Hussain
Mr William Bayfield-Farrell
Mr Aravindhan Ag
Miss Molly Richardson

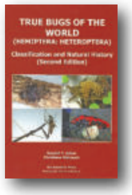
Deaths
Mr Antony William Davies, 1965, UK

Reviews

The following reviews have been added to the *Antenna* website:
www.royensoc.co.uk/publications/reviews

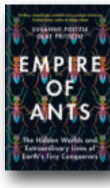


An Illustrated History of Butterflies of the Afrotropical Indian Ocean Islands
James M. Lawrence & Mark C. Williams
Siri Scientific Press. ISBN 978-1-8381528-3-3. £29.99
Reviewed by Dmitri V. Logunov



True Bugs of the World (Hemiptera: Heteroptera) Classification and Natural History (2nd edition)
Randall T. Schuh & Christiane Weirauch
Siri Scientific Press. ISBN 978-0-9957496-9-6. £129.99
Reviewed by Dmitri V. Logunov

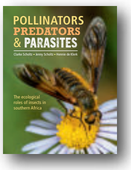
A Natural History of Insects in 100 Limericks
Richard A Jones, illustrated by Calvin Ure-Jones
Published by Pelagic Publishing
ISBN 978-1-78427-250-0. £9.99
Reviewed by Peter Smithers



Empire of Ants
Susanne Foitzik & Olaf Fritsche
Published by Gaia Books
ISBN 978-1-856-75459-0. £16.99
Reviewed by Adam Hart

Butterflies of the Levant. Vol.II: Papilionidae, Pieridae, Hesperiidae
Dubi Benyamini and Eddie John
Published by 4D Microrobotics
ISBN 978-965-92822-0-3. £115.00
Reviewed by Arthur M. Shapiro

Mosquitoes of the World
Richard C. Wilkerson, Yvonne-Marie Linton & Daniel Strickman
Published by Johns Hopkins University Press
ISBN 978-1-421-43814-6 (hardcover); 978-1-421-43815-3 (ebook)
$195.00 (hardback); $185.25 (ebook)
Reviewed by Graham White



Pollinators, Predators & Parasites: the ecological roles of insects in southern Africa
Clarke Scholtz, Jenny Scholtz & Hennie de Klerk
Published by Struik Nature
ISBN 978-1-775-84555-3 (hardback); 978-1-775-84632-1 (e-book)
£26.50 (hardback); £12.99 (e-book)
Reviewed by Malcolm Scoble

Mosquitoes of the World

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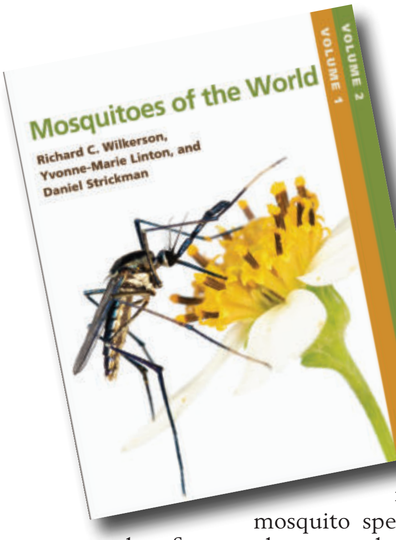

This monumental pair of volumes, boldly entitled *Mosquitoes of the World*, cover almost everything known about mosquitoes plus what they mean to science and humanity. The narrative text is lucid, replete with precious inferences supported by >6,000 references, expounding wider principles of biosystematics, ecology, evolution, insect behaviour and physiology, while comprehensively reviewing mosquitology. Augmenting the internet resources that evolve daily, this solid monograph (weight >5kg) summarizes and expertly interprets information on every recognized species of mosquito for anyone to understand, enjoy and evaluate. Volume 1, Part 1 Biology chapters explain mosquito evolution, nomenclature, classification, identification (without keys), distributions, development, dormancy, movements (of eggs, larvae, pupae, adult males and females), feeding and nutrition (of larvae and adults), excretion and reproduction (copulation, insemination, egg development and oviposition), pest and vector roles but not mosquito control. Part 2 defines 41 mosquito genera and gives profiles of 128 important species (each portrayed on a double-page spread with synoptic text, beautiful illustrations and distribution map) comprising bionomics, diagnostic morphological characters with annotated pictures to facilitate identification of each species and group, citations of exemplar genomes and DNA barcodes; also specifying pathogens of medical interest (arboviruses, filarias, malarias) associated with and potentially transmitted by each mosquito species. Following an essential glossary of >300 morphological structures used for mosquito identification, the main subject index of ~7000 terms completes Vol. 1 (x + 599 pages).

The bigger Volume 2 (pages 600-1308) contains the updated global 'Taxonomic Catalog of Culicidae' comprising 3,570 named species and 130 subspecies of mosquito (Family Culicidae in the insect Order Diptera), formally classified into 41 genera and 187 subgenera with informally ranked Tribes, Series, Sections, Groups/subgroups of species, plus complexes of sibling species, many pending formal description and naming under the Rules of Zoological Nomenclature. Guided by the systematic accounts and supporting references in this book, all these taxa can be identified, investigated, understood and classified phylogenetically. Earlier catalogues of the global mosquito fauna were published by Theobald (1905), Edwards (1932), Horsfall (1955 bionomics), Stone *et al.* (1959) and Knight & Stone (1977) plus the *Culicipedia* by Harbach (2018 CABI) whose online Mosquito Taxonomic Inventory (MTI) http://mosquito-taxonomic-inventory.info/ already includes newly described mosquito species (>1/month) since this book went to press. Due to the so-called 'taxonomic impediment' (Coleman, 2015: *J. Crust. Biol.* 35: 729-740) many newly-recognized species of mosquito lack Linnean names and are omitted from the MTI, whereas this comprehensive book covers those reported until mid 2020. *MoW* authors Wilkerson, Linton & Strickman have all served as managers of the Walter Reed Biosystematics Unit at the Smithsonian Institution (www.wrbu.si.edu) which ostensibly maintains the Mosquito Catalogue online http://mosquitocatalog.org, although it has lapsed since 2016 and the website refers enquiries to Vol. 2 of this book instead. Mosquito scientific names are indexed separately for each Volume. Literature references are cited for each species, genus and tribe in their catalogue entry (Vol. 2), but omitted from their synoptic profile page (Vol. 1), so the reader may be tantalized by cross-checking. Innumerable figures are mostly original diagrams (~200) and colour images (~170), each worth at least a thousand words.

Tabulated lists of valuable details bolster the narrative text, summarizing topics such as the 'timeline of events in culicid history' – 'mosquito fossils in chronological order' – 46 'substances in mosquito saliva that affect host responses' and 308 'viruses detected in various mosquito genera'. The most intriguing Table 2.6 proposes 'common names for genera of mosquitoes' (with linguistic explanations) including Nail Mosquito for *Anopheles*, Pointy Mosquito for *Aedes*, Typical Mosquito for *Culex*, Submarine Mosquito for *Mansonia* and Gang Mosquito for *Psorophora*. Hence the catalogue entry for every species gives it an informal English name of 4 or 5 words, intending to provoke more interest in mosquito speciation! Among the more familiar species, *Aedes albopictus* remains the Asian Tiger Mosquito, whereas *Aedes aegypti* is awkwardly called the 'Yellow Fever Malaysian Pointy Mosquito'; *Culex pipiens* and *Cx. quinquefasciatus* usually known as northern and southern house mosquitoes are called the 'Piping Swedish Typical Mosquito' and the 'Five-banded American Typical Mosquito' respectively. Among the many erudite examples, *Mansonia indiana* is called 'Yawadvipa Indonesian Submarine Mosquito' since its type-locality in Java, Indonesia, was previously in the Hindu kingdom of Yawadvipa (~2,220 years ago), although this species prevails more across the Indian subcontinent. Hopefully these peculiar names will remain follies of this publication. Who would want to use them instead of latinized names for such infamous vectors as the *Anopheles gambiae* complex of sibling species – for which the proposed informal English names are: Amharic Ethiopian Nail Mosquito (NM) for *An. amharicus*; Arab Yemeni NM for *An. arabiensis*; Bwamba Ugandan NM for *An. bwambae*; Coluzzi Malian NM for *An. coluzzii* [ignoring forms GOUNDRY and TENGRELA (Tennessen *et al.*, 2021: *Mol. Ecol.* 30:775-790)]; Fontenille Gabonian NM for *An. fontenillei* (rejected by MTI for being published only electronically); Malaria Gambian NM for *An. gambiae* itself; Black Gambian NM for *An. melas* [ignoring allopatric divergences (Deitz *et al.*, 2016: *G3* 6: 2867-79)]; Unadulterated (misinterpretation of seaside) Tanzanian NM for *An. merus*, and Four-ringed South African Nail Mosquito for *An. quadriannulatus*? Conversely this book glosses over controversies and instability with conventional nomenclature and systematics of anopheline and aedine genera/subgenera that have confused mosquito literature recently.

The quality of this truly *magnum opus* gains much from its robust and flawless printing by JHU Press, at reasonable price. Despite avoiding the applied field of mosquito control and minimizing the veterinary roles of mosquitoes while emphasizing their medical importance, which is why they are so exhaustively studied and understood biologically, this indispensable book should boost the value of mosquitoes in ecological, evolutionary and other fields of investigation, while standing as a landmark publication in mainstream entomology.

Graham White

Obituary

Professor Barbara Ekbom

6th October 1950 – 7th February 2021

Riccardo Bommarco
Professor of Agricultural Entomology
Swedish University of Agricultural Sciences, Uppsala

Barbara Ekbom, Professor of agricultural entomology at the Swedish University of Agricultural Sciences in Uppsala, Sweden, passed away at the age of 70 in February 2021. She is missed by her daughter Moa and son Emil and their families, and by her many friends and colleagues all over the world.

Barbara's extensive contribution to her fellow human beings, society and academia is impossible to convey in a few words, but I will make a valiant effort. Barbara was born in California, moved to Sweden in the 1970s, defended her dissertation in 1981 in plant pathology and became a professor of agricultural entomology in 2006.

Her research on plant protection in agriculture has laid the foundation for Sweden today leading in the field. It is largely to her credit that there is a general and widespread understanding in Swedish agriculture of the fundamental importance of biological regulation of pests for our food supply. Throughout her career, Barbara had an extensive international involvement with researchers and students, mainly in East Africa.

As part of her many endeavours in academia, Barbara supported the Society as a senior editor of *Agricultural and Forest Entomology* for over ten years. She led efforts to ensure a better gender balance on the Editorial Board and helped make the journal a truly international one. Those who worked on the journal with Barbara remember, in particular, her efficiency and the respect she showed for the efforts of the many entomologists who strive to get their work published.

She always cared with great generosity about young researchers, leaving freedom and providing resources for students and junior researchers around her to develop their own ideas. Many of us received her support and mentorship and had the joy of evolving our capacities in our collaborations with her.

Barbara accomplished much in her career. She combined successful research and esteemed teaching with taking on several key positions of trust such as research funding board member, head of department, dean and a wide range of other assignments. She often took the leadership role in difficult situations and steered conflict-filled situations. She strategically built an academic environment that remains permeated by her zeal for science of the highest quality and relevance, and for equal opportunities within academia.

Barbara is missed by many friends and colleagues. She was a woman of action who always put the people around her and the quality of science foremost. Barbara was a very modest person who, according to us who were close to her, could have promoted herself much more given her accomplishments. Personally, I had the great fortune to have Barbara as mentor, and it is a great honour for me to have inherited her professorial chair, from where I hope to continue to build on her achievements. Her passing leaves a huge void. At the same time, Barbara has given us and academia a rich legacy and she remains with us in many ways.

Diary

Details of the meetings programme can be viewed on the Society website (www.royensoc.co.uk/events) and include a registration form, which usually must be completed in advance.

Offers to convene meetings on an entomological topic are very welcome and can be discussed with the Honorary Secretary.

MEETINGS OF THE ROYAL ENTOMOLOGICAL SOCIETY

Forest Insects Special Interest Group (online)
21 October, 2021

Orthoptera Special Interest Group meeting
3 November, 2021

2022 Verrall Lecture
2 March, 2022

Pollinators in Agriculture meeting in collaboration with the AAB & BES
6–8 September, 2022

For full details on all RES meetings please visit
www.royensoc.co.uk/events

RES STUDENT AWARD 2021

Write an entomological article and WIN!

REQUIREMENT
Write an article about any Entomological topic that would be of interest to the general public. The article must be easy to read and written in a popular style. It should be no more than 800 words in length.

WHO CAN ENTER?
The competition is open to all undergraduates and postgraduates, on both full and part-time study.

PRIZES
First Prize: A £400 cheque and your article submitted for inclusion in *Antenna*.

Second Prize: A £300 cheque and your article submitted for inclusion in *Antenna*.

Third Prize: A £200 cheque and your article submitted for inclusion in *Antenna*.

ENTRIES
You can send electronically via e-mail to info@royensoc.co.uk

For further information telephone 01727 899387

Please include:

- Your name and address (including postcode)
- Your e-mail address
- The name and address (including postcode) of your academic institution
- Evidence of your student status e.g. scan of student I.D. card

THE JUDGES
The judging panel will be made up of three Fellows of the Royal Entomological Society. The judges' decision is final.

CLOSING DATE
The closing date for entries is 31 December 2021. The winner will be announced in the Spring 2022 edition of *Antenna* and on our website.

ROYAL ENTOMOLOGICAL SOCIETY - FOUNDED 1833 -

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