Bulletin of the Royal Entomological Society Volume 44 (4) 2020

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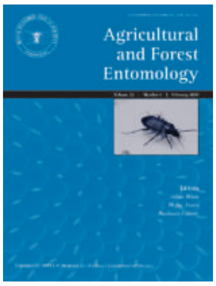

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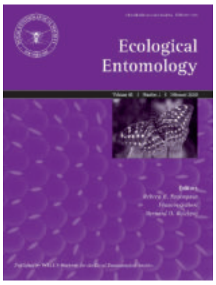

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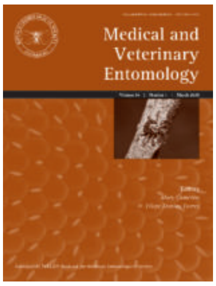

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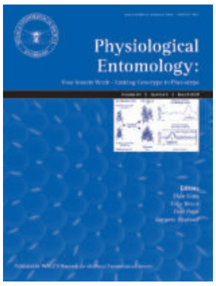

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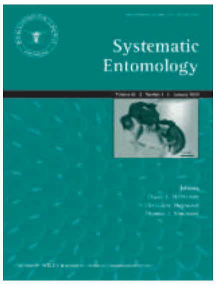

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COVER PICTURE

Fly orchids have returned to the Royal Entomological Society's Daneway Banks nature reserve after an absence of 15 years. Pollination is by a male digger wasp, *Argogorytes mystaceus*, which is attracted by a mimetic pseudo-pheromone secreted by the orchid.
© Anna Pugh, Daneway, May 2019

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Bulletin of the
Royal Entomological Society

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EDITORIAL

Hello and welcome to *Antenna* 44(4). Preparing this Editorial in early October, I can't help but feel a sense of déjà vu; the last being written in April as we adjusted to Round 1 of lockdown in the UK, and this contribution being penned just as we're re-entering the ring for Round 2! While none of us will have been immune to the chaos caused by COVID-19, it's been heartening to see how the entomological community has adapted to what's become the 'new normal' over the last nine months. Whilst I greatly missed seeing the *Antenna* team 'in the flesh' at our Annual Meeting in September, for example, the alternative online format adopted prompted record attendance and afforded all present a carbon-neutral glimpse at one another's home decor! As usual, this was a hugely enjoyable meeting, with many great ideas tabled and approved to improve *Antenna* over the coming year. Thanks, as always, to all those involved. If you have any ideas of your own, we'd welcome these to be shared at 'antenna@royensoc.co.uk'; there should also be the opportunity to comment on *Antenna* in the RES Membership Survey.

As evidenced in this issue's Society News, the *Antenna* Annual Meeting wasn't the only recent RES gathering to 'go virtual'. Both the Behaviour and Infection & Immunity SIGs took to 'the cloud' with resounding success, as did judging for the 2019 Wallace Award, where Jesamine Bartlett quite literally 'Zoomed' to first place. Whilst some of our regular Society News items have had to be benched for now – including Richard's EnTeam – we're delighted to still be able to bring you Peter's latest Hon Fellow Interview with Jane Hill, plus an enthralling update on Daneway Banks Nature Reserve. We're equally pleased to feature a 'Letter from the President' in 44(4), courtesy of Helen Roy. Helen has kindly offered to make this a regular feature during her term, setting a standard we hope other president's might follow in the future. We also have three Letters to the Editors to get the Issue underway, with a response from David Hubble to Mike Edward's correspondence concerning insect hotels and introduced species.

As Richard reported in his Editorial for 44(3), we've been hugely humbled by the response to our call for articles early in the pandemic, with your entomological efforts here bolstering our copy bank to help fill *Antenna* cover-to-cover through COVID-19. This issue features no fewer than six fantastic and varied submissions, with Stuart Reynolds opening our articles section with a 'Spotlight' on when, why and how insects got their wings. Other subjects covered include the north black bog ant, insect fossils, the entomology of non-native plants, and mating in the speckled bush cricket. Given this deliciously diverse line-up, the only common theme that comes to mind is 'unpredictability'; apt then that Helmut van Emden closes this section with his 'Tales of the Unexpected'.

Please do keep the submissions coming in – on any and all entomologically-interesting topics – your input here is greatly appreciated and all accepted articles will be published, even it takes an issue or two to get them into print. For those wanting to check our author and image guidelines, these will shortly be available online via the *Antenna* website, freeing up even more pages to feature your continuing contributions! You'll find our Book Reviews published on the website already, with four new entries appearing online since the last issue; from Peter Brown on *Ladybird Beetles of the Australo-Pacific Region*, John Walters on the *Atlas of Water Beetles of Britain and Ireland* and Peter Smithers on both the *Dictionary of Natural History of the British Isles* and *Britain's Butterflies (4th Ed)*.

Wishing you all a safe and happy seasonal break.

Dave

Guidelines for submitting photographs

To maintain a high quality we suggest that submissions for *Antenna* be presented via e-mail or on CD. Files must be in a PC-compatible format, preferably in MS Word.

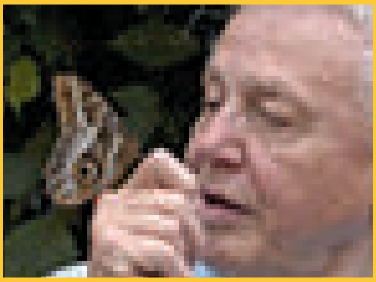
Electronic images can be embedded in the Word document but we will also require separate electronic images. These should be the full size image (.jpg or .tiff) from the camera even after the author has edited the file.

Please do not submit images that have been printed from a computer on a domestic inkjet or laser printer. Even if the camera is a good one and photo-quality paper is used, the graininess is very hard to deal with. If plain paper is used, the prints are virtually unusable.

If an image is intended for the front cover then the photograph should be in ***portrait format*** and again should be the full size image from the camera even after the author has edited the file.

To give an idea as to what happens when the image is not of sufficient size, take a look at these two photographs. One is 300dpi and the other is 72dpi.

300dpi



72dpi

Correspondence

Guaranteeing the Uniqueness of a Species Name Using 3NF

Dear Editor,

I am a software engineer who has been examining causes of errors in the Linnaean taxonomic system and would welcome any comments from readers.

The scientist and mathematician E.F. Codd established a series of rules for the design of complex data storage systems, with the goal of ensuring logical consistency. His design rules now form the basis of all relational databases across all disciplines, as well as data recording in spreadsheets. These rules are typically referred to as the rules of data normalisation, which are then grouped into sets of rules known as normal forms (NF).

Whilst there are now several normal forms, for this purpose we need only consider Third Normal Form (3NF). A system can be considered to be in 3NF if every unique object/idea has a unique identifier, such as a name. The benefits of being in 3NF are many, though the particular interest for this study is the 'guarantee of uniqueness'. This means that, once a system is in 3NF, every reference to a unique identifier is permanently guaranteed to be correct.

The Linnaean taxonomic system is an almost 300-year old system for the classification of life, designed to provide the scientists of the time with a framework to unify disparate nomenclature in an era where communications could take weeks. This taxonomic system can be regarded as one of the oldest relational data systems in existence. The term 'relational' refers to the notion that each entry to the system relates to other entries in the system, for example the link between a species and genus, or genus and family. As such, it is possible to apply Codd's design rules to the Linnaean taxonomic system. Applying these rules will enable us to ensure 3NF, providing the much sought-after guarantee of uniqueness. In taxonomic terms the guarantee of uniqueness ensures that, outside of human error in determination, any reference to a type is, and will always be, correct.

To illustrate, consider the species *Nomada integra* (Brullé 1832). This species has apparently been recorded 97 times on the NBN Atlas at the time of writing, been assessed for the GB Red List by Falk, and features in many collections. There's just one problem: none of these references to *N. integra* refer solely to material which matches the type of *N. integra* as defined by Brullé in 1932. This is because, in 2017, Notton & Norman published material showing that what had been considered *N. integra* in Great Britain (and possibly Ireland) was comprised of both *N. integra* and *N. facilis*. Consequently, these materials referring to *N. integra* are in fact referring to an aggregate of *N. integra* and *N. facilis*.

This statement immediately raises a conflict between the requirements of the Linnaean taxonomic system: *the name* N. integra *should refer only to specimens which are considered the same as the type specimen of* N. integra, and the requirements for our guarantee of uniqueness: *There should be one and only one occurrence of an identifier.*

Viewing this in a table starts to provide the answers:

Used name	Intended type(s)
Nomada integra	*Nomada integra*
Nomada integra	*Nomada integra* **or** *facilis*

This table is a classic demonstration of another of Codd's normal forms: Second Normal Form (2NF). 2NF happens when an identifier is not unique, and is typically solved by the addition of another 'translational' aspect to make the system 3NF again. This additional aspect is, by definition, not currently independently defined within the Linnaean taxonomic system, though taxonomists frequently use it. The solution is already presented in the above table and indeed implicitly throughout the Linnaean taxonomic system: that there is a difference between the type specimen and other specimens considered to be the same as the type. This is evident in the ruling that a type specimen may not be replaced without considerable effort, as the type is the ultimate point of reference. Evidence of attempts to upgrade the Linnaean taxonomic system to 3NF are already present in the '*sensu stricto* and *sensu lato*' epithets:

Used name	Intended type(s)
Nomada integra sensu stricto	*Nomada integra*
Nomada integra sensu lato	*Nomada integra* **or** *facilis*

Here we can see that each 'used name' is unique and corresponds to a unique 'intended type(s)' entry. However, the *sensu* system has a serious flaw which results in a return to 2NF. The flaw arises from the idea that the type name is the 'correct' method of identification, without any *sensu* epithet. In other words, the *sensu* system is considered a temporary diversion which should eventually be reverted to drop the *sensu* epithet. This leads to the following:

Time period	Used name	Intended type(s) at writing	Final understanding
Initial	*Nomada integra*	*Nomada integra*	*Nomada integra* **or** *facilis*
Post split	*Nomada integra sensu stricto*	*Nomada integra*	*Nomada integra*
	Nomada integra sensu latu	*Nomada integra* **or** *facilis*	*Nomada integra* **or** *facilis*
Post split ++	*Nomada integra*	*Nomada integra*	*Nomada integra*

The first and fourth entries demonstrate the problem. When these are extracted, they look as follows:

Used name	**Intended type(s)**
Nomada integra	*Nomada integra* **or** *facilis*
Nomada integra	*Nomada integra*

This is the exact problem that the *sensu* system attempts to fix. Once again, the system is back in 2NF. It is therefore impossible to remove a *sensu* epithet once one has been used without also reverting to 2NF, meaning that the *sensu* system is not a solution.

Until the Linnaean taxonomic system is placed into 3NF, attempts to create solutions which rely on a 3NF system will continue to fail. This includes solutions which aim to address taxonomic confusion, and any solution which attempts to aggregate taxonomic knowledge in search of a 'universal' checklist. Codd's rules of normalisation provide guidelines to resolve the difference between the assumed 3NF manner in which the Linnaean taxonomic system is used, and the 2NF state that the system is currently in.

Rowan Edwards

Nectar feeding in the carnivorous bush cricket, *Saga pedo* (Orthoptera, Tettigoniidae)

Dear Editor,

Four years ago, close to my home on the Triestine karst in northern Italy (and as reported in *Antenna*), I was fortunate enough to observe and photograph an unusual sequence of events – an adult *Saga pedo* bush cricket preying on a female praying mantis (McGrath, 2018).

Since then, I have learnt that *S. pedo* has been recorded taking *Mantis religiosa* before, at least under captive rearing conditions (Krištín and Kaňuch, 2007). Indeed, a number of reports, many based on captive rearing experiences, confirm that *S. pedo* is entirely carnivorous (Fontana *et al.*, 2002; Schall, 2002).

Nevertheless, on 10 June 2020, I observed a nymph of *S. pedo* imbibing nectar from the flowers of rue plants (*Ruta divaricata*), having climbed up to the inflorescences that were standing above the level of the surrounding grasses. Here it paused to place its mouthparts at the base of a flower's ovary where it meets the petals – and where the nectaries are located – and conspicuously imbibed whatever was there, presumably nectar (see photo). It then moved forward a few centimetres and repeated the behaviour at another flower, continuing for several minutes.

Despite *S. pedo* being considered (till now) entirely carnivorous, many other species of bush crickets (Tettigoniidae) are omnivorous to greater or lesser extents (Benton, 2012). Two endemic Australian subfamilies of the Tettigoniidae, however – the Phasmodinae and Zaprochilinae – are nectar and pollen feeders (Mugleston *et al.*, 2018). Interestingly, Mugleston *et al.* (2018) show that the Saginae (the subfamily to which the genus *Saga* belongs) diverged early from, but is a sister lineage to, the Phasmodinae and Zaprochilinae, as well as a third Australian endemic subfamily, the Tympanophorinae.

Schall (2002) confirmed that the *S. pedo* he reared for some ten years did not eat vegetables or fruit, but would drink water, especially if the terraria in which they were being reared had not been misted for a few days. He also noted that Matthey (1941) had recorded *S. pedo* taking a bite from a cherry, but it is considered that this was also an effort to obtain liquid. An internet search in multiple languages for observations of *S. pedo* imbibing nectar proved negative. I believe, therefore, that what is documented here is truly an unusual behaviour for this fascinating insect, a behaviour unrecorded until now.

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Disclaimer: The ideas and opinions expressed in this letter are those of the author (Peter F. McGrath) and do not necessarily represent the view of the author's employer, UNESCO.

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Entomological record hunting in the pages of *Antenna*

Dear Editor,

Reading David Hubble's article on Lockdown Entomology in the last issue of *Antenna* (44:3), my eye was taken to the image of *Osmia bicornis* on page 110. It is actually a male of *Osmia cornuta*, as is the image of one disappearing into the bee hotel on page 112. This photo of the male shows the white 'beard' below the antennae, which in *O. bicornis* is dirty brown/white. The red of the metasoma is also more intense, and the mesosoma black, so that the whole insect is more contrasting in colours in *O. cornuta*, this also being true of females. Structural and size differences also exist between the two species, though these are not distinguishable in the photo.

Osmia bicornis female closing her nest with mud. Photo: Mike Edwards.

Osmia cornuta female. Photo: Greg Mabbett, supplied by Tom Mabbett (Naturetrek).

Osmia cornuta is a continental species which is not frequent on the Channel coasts, but more southern and continental. At BWARS we suspect that this species has been introduced along with 'stocked bee hotels' offered commercially. We are currently aware of populations of this bee around London, the first in 2014 in Greenwich, the most recent in Guildford in 2020. Most of these have come to our notice through photos of '*Osmia bicornis*' and this is another one. I wonder if lockdown might provide more records.

The presence of the bee fly *Anthrax anthrax*, another continental species and a cleptoparasite of aculeates, using cavity nests (collections of which is what 'bee hotels' are) in Cambridgeshire further suggests this mode of colonisation; although this species has become frequent around bee hotels in the Netherlands and could, conceivably, have got here on its own.

Even within GB, the popularity of 'bee hotels' has resulted in what look like long-distance and sudden distributional shifts in *Osmia bicornis*, which was suddenly found nesting in bee hotels in Midlothian, Fife and Perthshire during the early part of this century.

This provides an interesting conundrum, given the sort of reactions of fellow allotment holders noted by David: does it matter? Importing a 'species not normally present' is an offence under the Wildlife and Countryside Act – as long as it is done 'knowingly'. As both species have a colloquial name of 'Red Mason Bee' it could be a genuine case of 'not understanding' – scientific names are there for a very good reason.

I must question the wisdom of encouraging any deliberate long-distance movement of live insects without very careful scientific consideration of the issues involved, whatever the 'help our bees' message, which is clearly a factor in this case. Actually, just providing empty nesting tubes of a sensible diameter (many of the commercial ones are completely hopeless) in a garden will attract a reasonable range of cavity-nesting bees and wasps, especially if the holes are of varied diameters. Cut lengths of bamboo, placed within a short piece of drainpipe, are both cheaper and more effective than most of the commercial nests which are advertised, even by 'conservation' charities!

Mike Edwards

Response from David Hubble

Thanks for the correction – interesting to know. The bees in question were found in my garden in Hampshire, using home-made 'insect hotels'. If they have indeed come in with stocked bee hotels I imagine they are widespread. Given they are not mentioned in Falk & Lewington (2015) nor in Benton (2017), I wonder if they are under-recorded by general recorders (including myself in this case as I specialise in beetles) due to unfamiliarity?

Letter from the President

Helen Roy

There is no doubt that the past summer was unusual. It was a worrying time for many people and there has been no respite from COVID-19 through the winter months. Throughout the summer, I took the opportunity to spend a little more time observing and recording insects in my garden and the surrounding countryside.

At the start of lockdown, I began moth trapping. I had been meaning to do so for many years and this seemed the perfect time. Every night I put the light on in the trap and every morning I enjoyed the delights, with a cup of coffee in the garden. Utterly captivating. All of the many species were exquisite but I confess to having a few favourites: the pale tussock, *Calliteara pudibunda*, elephant hawk-moth, *Deilephila elpenor*, and spectacle, *Abrostola tripartita*.

I also spent ten minutes whenever I could taking part in the UK Pollinator Monitoring Scheme Flower-Insect Timed Counts. Sometimes I had no insects landing on the flowers within my small quadrat and other times there would be a flurry of activity. Whatever the count, it was an incredibly relaxing lunchtime activity.

I hope that you also had many enjoyable insect moments throughout the year.

As the temperatures fell and the light began to fade earlier and earlier each day, I thought of the months ahead when many insects become dormant and mostly hidden away. I definitely miss the chance garden encounters with various insect species and get very excited when I see a winter-active bumblebee. However, there has been lots to keep me busy.

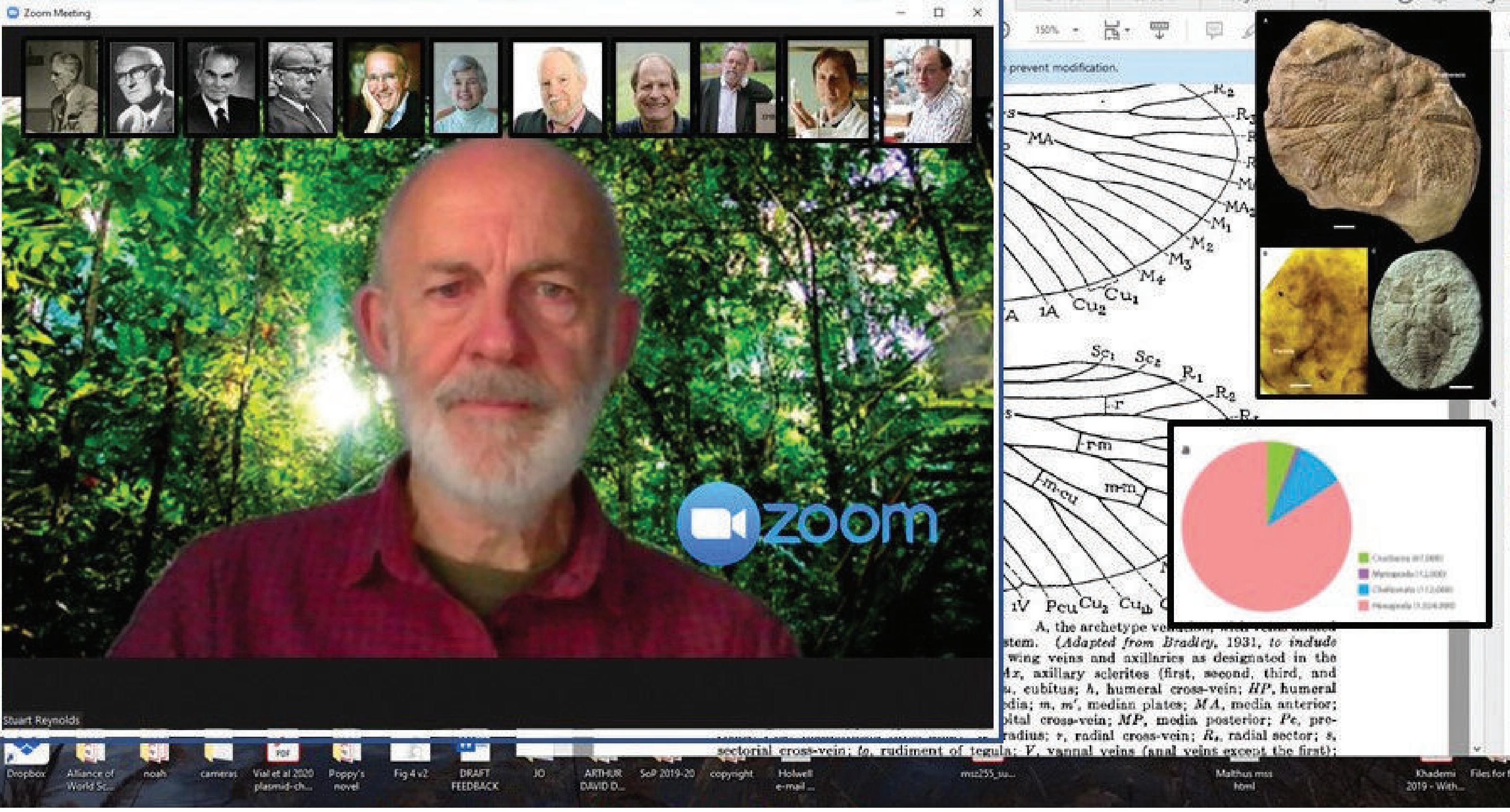
The ways in which the Society ensured that the Special Interest Group meetings continued, despite the restrictions, was inspiring. The commitment and enthusiasm from the organisers and participants was wonderful to see. I am enjoying the ongoing programme of meetings and thank everyone involved for providing these opportunities for sharing the excitement of entomology far and wide.

These are exciting times for the Royal Entomological Society, as we launch the Grand Challenges project and invite you all to get involved with sharing your ideas on priorities for entomology in the coming years. I am also looking forward to working with you all more and more as we launch the members' survey. We all have an opportunity to inform and shape the future of our Society.

A number of colleagues have stepped down from their positions within the Royal Entomological Society over the summer. All have given in many and varied ways over many years and I thank them for their commitment to entomology and the Society. Kirsty Whiteford decided to move on to pursue new opportunities. I would like to thank Kirsty for her dedication to the Society and wish her well with her new endeavours.

I am so privileged to work with such an amazing team of staff and trustees. They have all worked so hard to make progress in implementing some of the actions from the recent governance review. I hope you will consider joining us. Please do get in contact with me if you have any questions about the roles available.

I hope that you all stay well and enjoy entomology throughout the winter months. I am looking forward to another wonderful edition of *Antenna* to entertain me on the winter evenings. Thank you to the amazing production team for ensuring that our Society magazine is something we can all look forward too.



RESEARCH SPOTLIGHT

Success! When, why and how insects got their wings

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The astonishing evolutionary success of insects

Nine years ago, writing for *Antenna*, I reviewed the extraordinary evolutionary success of insects. Reviewing some then contemporary discussions about the number of extant insect species, I plumped for a figure of about 3.6 million (Reynolds, 2011). Since then there have been new attempts to estimate the diversity of insects. In a careful accounting exercise Stork (2018) has now revised the probable total count up to about 5.5 million species. Most recently, García-Robledo *et al.* (2020) have reflected still further on the problem, upping the possible number of species to *c.* 8.8 million while making it clear that they consider that the true figure could be much larger. It's clear that the total estimated number of insect species considerably outnumbers the sum of all other animal kinds. This certainly seems like an evolutionary triumph.

Insects are evolutionarily successful because they have wings

Why are insects so successful? I suggest that the answer is so obvious that it stares us in the face every time we look at an adult insect. Insects have hyperproliferated *because they have wings*. Because only insects could fly at the time their wings first evolved, they were the only animals able to get to where the surface area of the environment is largest, i.e. the surfaces of land plants. In addition, and as was suggested by Robert May in 1988, smaller species of animal will be most numerous just because more of them can be fitted into the space that's available.

Put simply, when insect wings first evolved around 400 million years ago, being able to fly enabled their owners to exploit a much larger volume of environmental space than their competitors. Whereas their apterygote relatives were limited to a thin layer just above and just below the land surface, winged insects were able to fly to the tops of tall plants and there exploit the huge, fractal surface area of all the aerial leaves of the plants that were at that time demonstrating their success at turning carbon dioxide into biomass. The species:area curve has been described as the nearest thing that ecology has to a general rule (Lomolino, 2001), but when you can fly, you live in three dimensions not two. In this way, wings opened new evolutionary horizons for insects.

Being able to fly enables insects to disperse to new locations during their lifespan, whether they are looking for a new host plant if they are herbivorous, seeking new prey items if they are predators, escaping from predators if they are not, finding a mate to have sex with, or locating a suitable egg laying location. Dispersal by flight leads to increased reproductive success and (within limits set by the physical environment) also a bigger geographic range. These factors enhance persistence in evolutionary time and space, and thus in the long run provide greater opportunity for speciation through adaptation to different niches. It's no surprise that dispersion ability is correlated with species richness (Irmler *et al.*, 2010). Wigglesworth (1973) was insistent that the adaptive advantage in having wings is that it facilitates dispersal. Its hard to disagree with that conclusion.

But there are probably other advantages. Another factor in the evolutionary success of insects is their unparalleled ability to exploit plants as food. During the Devonian geological period, when insect wings first evolved (see below), the ancestors of insects were just one of a number of animal groups that had recently colonised the land, pursuing the opportunity presented by the proliferation of vascular plants in this new habitat. But it was the winged clade of insects that succeeded most spectacularly as herbivores. This was a great evolutionary opportunity. The biomass of available plants on land must have been very great; as an indication of this, over a period of about 60 MY at that time, photosynthetic fixation of atmospheric CO_2 pumped down CO_2 concentration in the air from *c.* 2000 ppm to 1000 ppm (Foster *et al.*, 2017). We don't know much about plant diversity at that time, but it seems safe to presume that then, as now, herbivory required the ability to avoid plant defences, and therefore to move from site to site to find the most suitable plants to eat; wings must have been essential to such mobility. Even today insects are by far the most important consumers of green plants (Futuyma & Agrawal, 2009), and the trophic interaction between insects and plants is mostly one in which specialists consume highly defended resources. Although communities of insects on trees are complex (Brändle & Brandl, 2001), most insects are specialists and monophagy is by far the most common trophic habit among insect consumers of plants (Forister *et al.* 2015). It couldn't be like this without the mobility that wings give to adult insects, enabling them to find their own special food even when it is patchily distributed.

You can't be a specialist unless you can detect and then move towards the object of your specialist interest. Thus, possession of wings also drove other adaptations. The evolutionary innovation of flight likely required the simultaneous development of sophisticated sensory systems that are used to orient to relevant features of the environment, and highly organised nervous systems that can process this information to organise complex behaviours. And moving in three dimensions is more complex than just two; in the same way that the cockpit of a jumbo jet has a lot more instruments than a juggernaut, the brain of a flying insect needs to be a lot bigger with more inputs than that of a non-flying apterygote. Increased brain power, directly required by the possession of wings, provided insects with evolutionary opportunities that would not have been available without flight.

One such opportunity was the chance to co-evolve with angiosperms as pollinators; the fantastic modern variety of flowers has developed through competition among flowering plants to attract insect pollinators (Hu *et al.*, 2008), and without the ability of flying insects to orient to flowers according to their species, pollination would not have evolved as it has. Another evolutionary open goal waiting for winged insects to score was the chance for highly mobile flying insects to co-evolve as parasites with other insects as hosts. Hymenoptera is one of the largest hexapod orders, in which it is probable that the majority of species are parasitoids. A parasitoid's way of life is only possible for insects that are highly mobile and well equipped, with sufficient sense organs and neural processing power to locate and successfully parasitise hosts. Predictably, trophic networks involving parasitoids indicate a high degree of specificity, and this has in turn driven growth of hymenopteran diversity (Forbes *et al.*, 2018). None of this would have been possible without the mobility conferred by the possession of wings.

When and in what kind of arthropod did insect wings first appear?

Obviously, the ancestors of insects had to leave the sea and colonise the land before they could evolve wings and take to the air. Insects are members of the Phylum Arthropoda, paraphyletic to the Crustacea. The generally accepted closest relatives of the Hexapoda (the class-level grouping that includes both winged insects and the ancestrally wingless Apterygota) are Remipedia, an obscure and tiny class of blind, venomous crustaceans, which today live only in caves connecting freshwater aquifers to the sea (Schwentner *et al.*, 2017). Genomic comparisons indicate that Remipedia diverged from the line that led to hexapods at some time in the Palaeozoic, more than 444 MY BP.

What would the first terrestrial insect-like organisms have looked like? There is a group of modern insect relatives that don't have wings. Although Remipedia have lots of appendages, modern apterygotes all have six legs, so that we can call them Hexapoda. They include Protura (coneheads), Collembola (springtails), Diplura (two-pronged bristletails), Archaeognatha (jumping bristletails), and Zygentoma (silverfish). Just how closely related to insects these various groups are is the subject of continuing debate. It's difficult to be sure because it all happened such a long time ago, and perhaps in the context of thinking about the origin of wings, it doesn't really matter. The hexapodan phylogenetic tree proposed in a very influential paper by Misof *et al.* (2014) has the wingless Zygentoma as closest relatives of insects proper, diverging from them *c.* 420 MY BP. Other apterygotes are generally agreed to be less closely related to insects, and their lines of descent separate at increasingly remote times up to c 480 MY BP. The date proposed by Misof *et al.* for the ancestral divergence from silverfish has recently been backed up by new genomic evidence from Manni *et al.* (2019). But phylogenetic divergence is one thing; the possession of actual wings is another, and there are various opinions as to when the first winged insect could have been captured by an imaginary prehistoric sweep net.

To see actual wings, we had better look at the fossil record. Fossils of insect-like creatures from the Early Devonian period are all wingless and resemble modern apterygote groups, but by the Early Carboniferous, winged insect fossils are abundant, placing the origin of insect wings no later than 360 MY BP. The earliest known obviously insect-like fossil is from the Scottish Rhynie (Pragian), *c.* 396–407 MY BP (Engel & Grimaldi, 2004). This creature had jaw articulations that unambiguously show it to be a member of the Hexapoda; it is very similar to today's Zygentoma (silverfish) but it isn't clear if it had wings. But after this splendid fossil, there is nothing, and a 62-million-year period (the 'Hexapod Gap') now follows in the fossil record in which no insect fossils have yet been found. Not until the Pennsylvanian, *c.* 323–299 MY BP, are insect fossils found again, and by this time we find that winged insects very like modern Palaeoptera and Neoptera are already abundant and diverse, with holometabolous insects (i.e. those undergoing a complete metamorphosis with a pupal stage) appearing shortly thereafter.

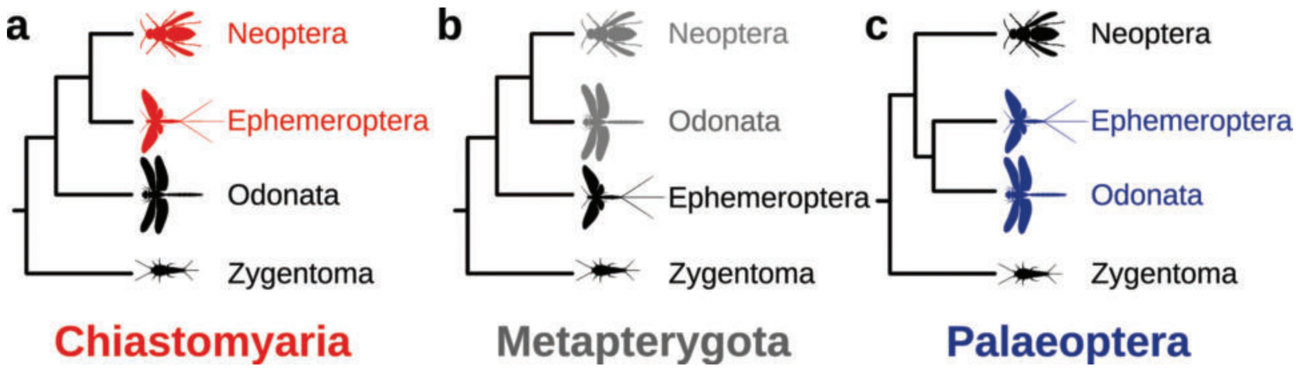

Figure 1. Three hypotheses for the early branching events within pterygote evolution: **a.** Chiastomyaria (Ephemeroptera + Neoptera) in red, **b.** Metapterygota (Odonata + Neoptera) in grey, and **c.** Palaeoptera (Ephemeroptera + Odonata) in blue. Reproduced with permission from Simon *et al.* (2018).

The reason for this long gap (>50 million years) in the fossil record is not clear. It was originally suggested that the absence of insects (and also of other animal groups) from rocks of this age may have been due to low levels of atmospheric oxygen, which (it was supposed) would have made flight (known to require high rates of metabolism) impractical (Ward *et al.*, 2006). Unfortunately for this idea, Schachat *et al.* (2018) have now shown that O_2 levels during the gap were not low, and so hypoxia cannot have caused the apparent absence of fossil insects. Instead, these authors plausibly suggest that it simply took a long time for insects to become sufficiently numerous to be fossilised in any quantity. We are thus no nearer to locating the exact moment at which the first flying insect took to the air. But surely fossils from this period must exist somewhere? That would indeed be a great opportunity, and we can only hope that a geologist's hammer will find the missing link in the Upper Devonian.

Did insect wings evolve only once?

This seems likely but it isn't certain. Two major taxonomic divisions of winged insects, Palaeoptera (Odonata and Ephemeroptera, both unable to fold their wings over the abdomen) and Neoptera (all other extant insect orders, which can fold their wings in this way) are usually recognised. In fact, however, the status of Palaeoptera is uncertain. Although the maximum likelihood phylogeny presented in Misof *et al.* (2014) strongly indicates (bootstrap support >95%) a monophyletic origin of the insects as a whole (i.e. it suggests the paraphyletic status of insects and silverfish), the subsequent divergence of Palaeoptera and Neoptera illustrated therein is in fact not strongly supported (<75%); moreover, the node at which Ephemeroptera and Odonata diverge is also not well supported. On the other hand, Misof *et al.* (2014) did find strong support for the monophyletic origin of Neoptera. Most readers of this very well-known paper probably don't notice the text's note of caution, in which it is said "additional evidence… will be necessary to corroborate" the status of the Palaeoptera.

Lack of certainty on this important point is a well-recognised problem in the guild of insect phylogeneticists; three different possible branching sequences are possible; alternative groupings to the Palaeoptera being designated Metapterygota (early divergence of Ephemeroptera) and Chiastomyaria (early divergence of Odonata) (see Fig. 1). A recent re-examination by Simon *et al.* (2018) using transcript sequences from a larger sample of species has unfortunately failed to resolve the question. Although Simon *et al.*'s analysis gave strong confirmation (bootstrap support 100%) in favour of Palaeoptera, and convincingly failed to give significant support to Metapterygota, the alternative grouping of Chiastomyaria could not be dismissed. Resolution of this question is not helped by the fact that Odonata and Ephemeroptera themselves diverged a very long time ago, at the Devonian–Carboniferous transition, the deepest node within the hexapodan clade, occurring *c.* 360 MY BP. In the authors' words "the Palaeoptera problem has to be considered an unsettled issue of insect systematics". It will doubtless continue to give useful employment to molecular insect phylogeneticsts for some time. Meanwhile, it remains possible that the divergences preceding the origin of the palaeopteran groupings might represent multiple origins for insect wings. Whatever the manner in which Ephemeroptera and Odonata diverged from the neopteran lineage, we can't be sure that these events took place at a time when the ancestors in question actually had wings.

Implications of having wings for metamorphosis

Both in a journal article (Bellés, 2019) and in his recent excellent book on *Insect Metamorphosis* [reviewed in *Antenna* **43** (3), 143-145], Xavier Bellés has emphasised that the evolution of the winged condition almost certainly necessitated the adoption of metamorphosis among insects. All arthropods are encased in a chitin-protein exoskeleton ("cuticle") that must periodically be moulted to allow for increase in body size. In preparing to moult, a new larger, folded cuticle is produced within the old one; when the new cuticle is ready, the old one is largely destroyed and its material content reabsorbed for recycling. Moulting arthropods undertake an impressive feat of escapology in which the body, now encased in its new exoskeleton, is extracted from the old skin. Although great feats of moulting agility are used to extract long appendages with complicated shapes from the old cuticle sheath, there are limits to what can be achieved. In particular, moulting of fully functional, flat and fragile wings is likely to be very difficult, and thus adult insects do not moult.

Actually, there is an exception to this; adult mayflies (Ephemeroptera) are a special case in entering a short pre-adult stage (the subimago) that already has fully inflated wings and is capable of flight, which is rapidly followed by a moult to the final adult stage (Edmunds & McCafferty, 1988). It's not clear why Ephemeroptera differ from all other insects in undertaking an additional post-nymphal moult. It seems likely that this is in fact a special adaptation to the mayfly lifestyle; all insects in this order are fully aquatic as nymphs, and most emerge from the last larval skin whilst still in the water. It may be that the abundant cuticular microtrichia of the subimago confer special hydrofuge properties on this stage's body surface, and this may be beneficial during escape from the water surface, while the adult's aerial reproductive life would perhaps be easier once the subimaginal skin has been shed. There is no agreement as to whether the subimago corresponds to a second adult stage, a terminal nymphal stage or even a pupa-like condition.

Thus, because it is so difficult for an insect to moult once it is in possession of fully functional wings, moulting ceases in the adult stage of almost all insects. This is achieved in many cases by the apparently desperate measure of destroying the prothoracic glands, the structures that produce ecdysone, the steroid hormone that initiates moulting in all arthropods. This sets the scene for other large scale developmental and physiological changes associated with the terminal moult, which achieves what we call metamorphosis.

This in turn poses a life history strategy problem for insects. Because the evolutionary innovation of wings results in the cessation of moulting, there is a drastic change in reproductive allocation of resources. Instead of continuing to moult in the reproductively mature (i.e. adult) condition, which allows the adult animal to continue growing and undergo multiple rounds of reproductive activity, perhaps surviving for years in this condition (this happens in all apterygotes, including Zygentoma, the taxon most closely related to insects), winged insects must cease both growing and moulting when they become adults, thus limiting their remaining life span. Instead, they adopt a "big bang" reproductive strategy that maximises reproductive output in a short period of time. Although some adult insects (like cockroaches) can undergo multiple rounds of egg laying over months to years, a high proportion of insects adopt an approach in which they mobilise all their stored reserves in favour of a single round of capital reproduction, as would be expected in an organism with an uncertain future (Houston *et al.*, 2006).

From what pre-existing structures did wings develop?

When inventing new traits, evolution generally tinkers with existing structures and functions, rather than creating new ones from scratch (Jacob, 1977), and wings appear to be no exception to this rule. Two principal competing theories of wing formation exist, both of which assume that wings are modifications of previously existing structures. First, and perhaps most consistently popular, the *paranotal hypothesis* was built on the observation that winged fossil insects from the cockroach-like order Palaeodictyoptera not only possess quite conventional-looking wings on the meso- and metathoracic segments, but also have smaller lateral extensions (*paranota*) from the notum (dorsal surface) of the prothoracic segment. Guy C. Crampton (1916), supported by R.E. Snodgrass (1935), suggested that present-day insect wings are derived from these ancestral structures (see Figure 2).

This idea is attractive because it enables us to see the innovation of wings as resulting from tinkering with previously existing structures. In line with this, Kukalová-Peck (1978) found that paranotal structures were also present, although smaller, in preadult stages (nymphs) of Paleodictyoptera, where they appear similar to the wing pads on late stage nymphs of modern hemimetabolous insects like cockroaches and grasshoppers. It is supposed that differential growth of the T2 and T3 paranota would have occurred during maturation, exactly as takes place in these modern groups, leading to the formation of wings.

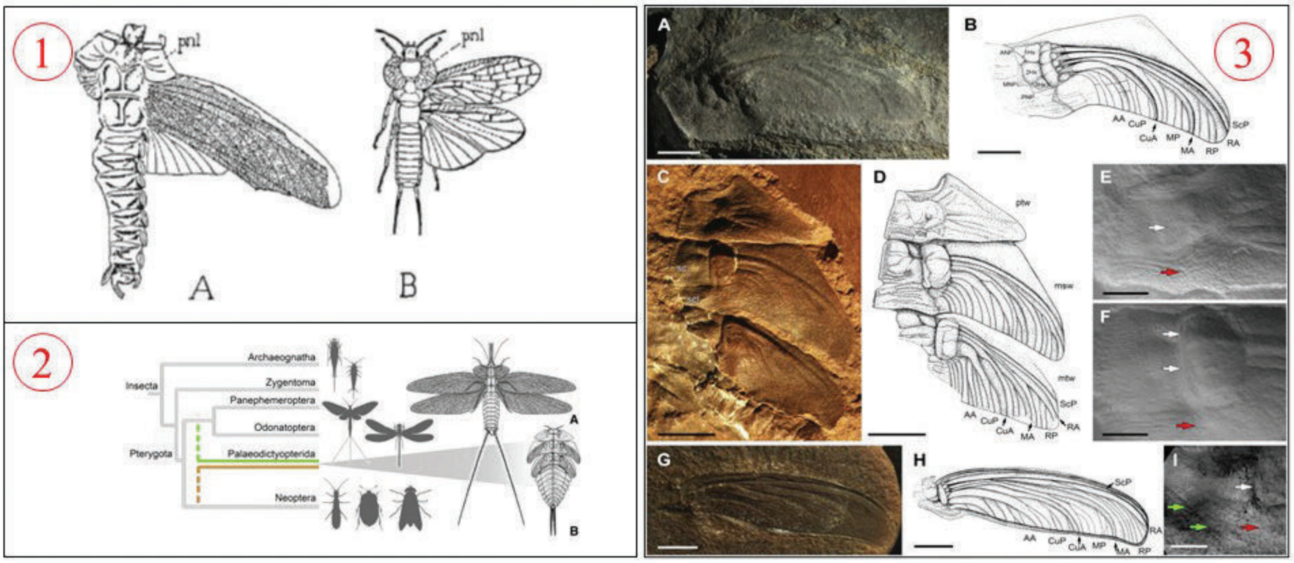

Figure 2.

Left panels: (1) Examples of fossil Dictyoptera; *A. Stenodictya lobata* (from Brongart, 1890); *B. Lemmatophora typica* (from Tillyard, 1928). Both insects are adults with meso- and metathoracic wings, but they also display smaller paranotal lobes on the prothorax. Illustration reproduced from Snodgrass, 1935. (2) Alternative phylogenies for Paleodictyptera, as sister group of Palaeoptera (green) or as sister group of Neoptera (orange). (A) *Stenodictya lobata*, adult male, late Carboniferous, Gzhelian, Commentry, France. (B) *Rochdalia parkeri*, nymph, Late Carboniferous, Bashkirian, Rochdale, Lancashire, UK. See the original paper for more detail. Reproduced with permission from Prokop *et al.* (2017).

Right panel: (3) *Top*: Wing pad, *Idoptilus* sp., Late Carboniferous, Moscovian, Mazon Creek Lagerstätte, Illinois, USA. (A) Photo of wing pad; (B) Reconstruction of wing pad to show articulated joint. *Middle*: Palaeodictyoptera family, Late Carboniferous, Bashkirian, Upper Silesian Coal Basin, Sosnowiec–Klimontów, Poland. (C) Photo: Thoracic part of exuvial cuticle including wing pads; (D) Reconstruction of original exoskeleton and wing pad tracheation; (E and F) Micrographs of basal parts of prothoracic and mesothoracic wing pads. *Bottom*: *Lycodemas cf. adolescens*, FM PE31983, Late Carboniferous, Moscovian, Mazon Creek Lagerstätte, Illinois, USA. (G) Photograph of wing pad; (H) Reconstruction of wing pad including articulated joint; (I) Micrograph of basal part of wing pad. Scale bars represent: (A)–(D) 3 mm; (E),(F),(I) 1 mm; (G),(H) 5 mm. Reproduced with permission from Prokop *et al.* (2017).

Various suggestions for the original adaptive role ("purpose") of paranota have been made that include facilitating gliding flight, sail-like propulsion while floating on water, and thermoregulation. Wigglesworth (1973) considers some of these possible roles. For a wing to function in flapping flight, as is the case in insects today, the paranotal extensions would need to be articulated and suitable muscles would need to be present in thoracic segments. We can't see inside these fossils, but a paper by Prokop *et al.* (2017) has revealed evidence of clearly discernible articulations at the base of all three pairs of wing pads. Although the articulation of prothoracic paranota is less well-developed than those on segment T2 and T3, that it is there at all suggests that paranota of all three thoracic segments are homologous. This doesn't necessarily mean that prothoracic paranotal pads were used in flight. Even though less mobile than the proper wings of T2 and T3, they could, for example, have been sufficiently mobile to be useful solar collectors, being orientable by muscular action to regulate heat gain from sunlight.

The other major theory for the origin of wings, the ancestral gill, or exite hypothesis, was also first raised in the 19th century. It was revived by Wigglesworth (1973) who credited Sir John Lubbock (1873), and C.W. Woodworth (1903 – citation in Wigglesworth's paper) as among his predecessors. The basic idea is that the developmentally very versatile branched segmental limbs of crustacea, which in some species form gills, are the origin of insect wings. These were supposed to derive specifically from the subcoxal region of limbs, the more distal parts of which had subsequently been lost. This idea was taken up by Kukalová-Peck (1978; 1983) and was given a significant boost when Averoff & Cohen (1997) isolated gene homologues expressed during wing development in *Drosophila* from the crustacean *Artemia franciscana*, and found that they were expressed during the shrimp's development in the distal epipodites of the thoracic legs, exactly as predicted by the gill/exite theory.

More recently, these two hypotheses have been reconciled by a number of studies showing that both are correct. Insect wings are in fact formed through the respecification of tissue that is located in two different places in less derived arthropods, the most proximal region of the meso- and metathoracic legs, and the lateral (i.e. paranotal) region of

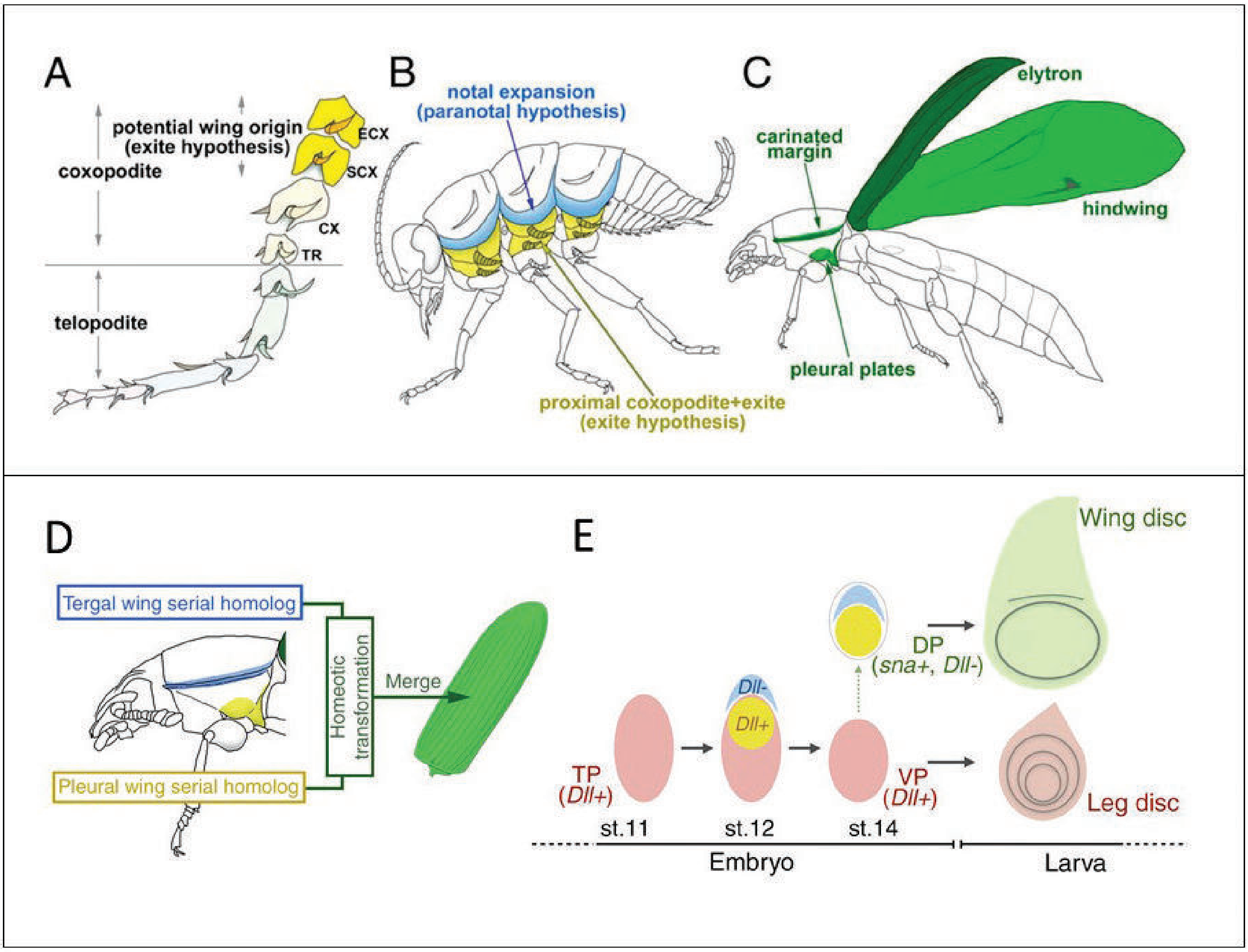

Figure 3. Top (A-C): Two classic competing wing origin hypotheses and the newer combinational (dual) model for the origin of insect wings. (A) Arthropod leg ground plan. The proximal coxopodites (ECX and/or SCX) and their exites are proposed as possible wing origins in the gill/exite hypothesis. CX, coxa; ECX, epicoxa; SCX, subcoxa; TR, trochanter. (B) The locations of two proposed wing origins (blue and yellow) in ancestral insect ground plan. Blue, notal expansions; yellow, proximal coxopodites (pleural plates in extant insects) with their exites. (C) Wing serial homologs in *Tribolium* (green). The two wing serial homologs in the prothoracic segment (T1) appear to be homologous to two proposed wing origins (blue and yellow tissues in B). The merger of these two tissues in *Tribolium* produces ectopic elytra in homeotic transformation, consistent with the combinational wing origin model. Reproduced with permission from Clark-Hachtel *et al.* (2013).

Bottom (D-E): Two distinct sets of cell populations contribute to the formation of insect wings. (D) Two distinct sets of wing serial homologs in the first thoracic segment (T1) of *Tribolium*. Upon homeotic transformation, the tergal (blue) and pleural (yellow) wing serial homologs merge to form a complete wing (green). (E) Wing disc development in *Drosophila*. The dorsal primordium (DP) is composed of two separate groups of cells (yellow and blue). TP: thoracic primordium, VP: ventral primordium.

the dorsal tergites. This is called by Clark-Hachtel & Tomoyasu (2020) the combinational (dual) model. The essentials of the scheme are illustrated in Figure 3. There seems little doubt that studies of this kind are closing in on the part of the body from which evolution has crafted one of its most famous inventions, the insect wing. A number of genes involved in wing development have been investigated, including *vestigial*, *apterous*, *nubbin*, and *optomotor-blind*. These genes are all expressed in both the subcoxal and tergal regions and knocking down their expression with RNAi in either place has the expected result of preventing wing formation, just as predicted by the dual model.

But the crucial task now will be to find the transcription factor networks that we must presume have driven the patterns of expression whose operation differs between basal insects and their apterygote relatives. It is these genes that exert high level control over the recruitment of the genes that actually *make* the wing. To identify these genes we need to compare the genomes of actual insects with insect-like creatures that don't have wings. A paper by Manni *et al.* (2019), which describes the genome of the modern bristletail (dipluran) *Campodea augens*, is thus a step in the right direction. The paper emphasises that many of the functional and morphological innovations of the Class Hexapoda first appear in this organism, the closest living outgroup to proper insects. But a research programme like this is indeed very ambitious. The hexapods that we would really like to investigate lived almost 400 million years ago. Only if we are lucky will we find that their evolutionary trajectory has left identifiable traces in the genomes of organisms still alive today.

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Grey dagger (*Acronicta psi*) larva. (Photo by Malcolm Storey) – see Figure 5.

Non-native plants in Britain & Ireland – how much do we know about their insect fauna?

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Introduction

Many plant species have been introduced to the UK, both deliberately and accidentally. Stace & Crawley (2015), in their compendious book *Alien Plants*, estimate that, in Britain and Ireland, a staggering 2,068 alien or non-native vascular plant species[1] have been recorded since 1987, amounting to around 60% of the British flora. Up to 2,000 more non-native species have been recorded prior to that date. Of the former, around 63% are naturalised, with the remainder generally unable to form self-sustaining populations without continual re-introduction.

It is well known, from a plethora of agronomic and ecological studies, that introduced plants rapidly recruit a suite of insect herbivores. The mechanisms have been well-researched, although there remains much to understand (Padovani *et al.* (2020) and references therein). In the British Isles, the Database of British Insects and their Foodplants (DBIF) (CEH, BRC, 2016) has data on the herbivorous insect fauna of plants including non-native species. This is discussed in more detail later.

The purpose of this article is to raise the profile of this topic, its potential significance for biodiversity and hopefully to stimulate further systematic recording and research.

What are the key issues for biodiversity?

To date, only a small number of introduced non-native plant species have established and caused detrimental impacts on biodiversity in Britain and Ireland. These include rhododendron *Rhododendron ponticum*, Indian balsam *Impatiens glandulifera* and several aquatic plants, including New Zealand pigmyweed *Crassula helmsii*. The 'tens rule' suggests that 10% of non-natives imported into a region appear in the wild, 10% of these establish, and 10% of the establishing species, i.e. 0.1% of imported species, are invasive. This rule of thumb holds in Britain and Ireland for flowering plants (Williamson, 1996). However, it seems that is not possible to arrive at any general conclusions about links between plant species' attributes and their invasive ability (Manchester & Bullock, 2000). Thus, it is a major challenge to identify, at an early stage, plants that may prove problematic for biodiversity in the future. The most likely source of such species is ornamental plants – either those already established in parks and gardens or novel species entering the horticultural market. However, certain introduced plants may provide conservation benefits. Schlaepfer *et al.* (2011) argue that they may provide habitat or food resources for rare species, serve as functional substitutes for extinct taxa, and provide desirable

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[1] Includes **Neophytes** – alien plants that have been recorded in the wild since 1500 and **neonatives** – plants originating in the area without direct human involvement, but have arisen as the result of hybridisation between a native and alien taxon or between two alien taxa, or as a result of evolution from an alien or neonative taxon. This number excludes the 197 species of **archaeophytes** – these are alien plants that have been present in an area in a wild state before 1500.

ecosystem functions. They speculate that non-native species might contribute to achieving conservation goals in the future because they may be more likely than native species to persist and provide ecosystem services in areas where climate and land use are changing rapidly and because they may evolve into new and endemic taxa.

A review by Bodsworth *et al*. (2005) concluded that there are several examples of invertebrates of conservation concern using non-native plant species. This includes larvae and adults feeding on the vegetative parts of the plant, as in the case of some moths and beetles, as well as adult insects visiting the flowers to collect nectar and pollen, as in the case of several species of fly, bee and wasp.

Alexander *et al*. (2006) also make the point that certain introduced species of tree may provide other aspects of wildlife value, such as habitats for epiphytic bryophytes and lichens, fungi, and for fauna associated with dead wood or feeding on pollen, nectar or fruit.

Certain naturalised, non-native species may harbour lower numbers of foliar-feeding insect species but support a high biomass of insects, which may provide a valuable food resource for other species. Sycamore (*Acer pseudoplatanus*) is an example, generally hosting fewer species compared to native trees with a similar geographical range and architecture (Kennedy & Southwood, 1984), but with a large herbivorous insect biomass, including the common sycamore aphid *Drepanosiphum platanoidis*, one of two dominant aphid species feeding on the tree.

Research into the flora and fauna of domestic gardens in the UK has led to increasing recognition of their wildlife value in the widest sense (Smith *et al*., 2006). More specifically, Smith *et al*. highlight the utilisation of the large variety of alien plants by herbivorous insects.

Another aspect is the existence of novel plant communities consisting of single or mixed non-native plants, with or without the presence of some native species such as *Buddleia davidii* and *Conyza* spp. scrub (after Stace & Crawley, 2015) occurring along railways, in disused quarries, and on urban wasteland. The latter areas may consist of often diverse assemblages of native and alien species that are unlike semi-natural vegetation in their species composition. Recent studies have shown that such 'brownfield' sites can harbour high insect and other invertebrate species diversity, including several scarce species (Bodsworth *et al*., 2005).

Novel plant communities can thus provide a valuable additional resource for a range of fauna. It could be argued that, provided they are not supplanting or adversely affecting existing semi-natural vegetation of high conservation value or causing other negative impacts, they make a valuable contribution to British biodiversity.

Fig. 1. The introduced species greater periwinkle (*Vinca major*) – one of the top 52 most abundant British neophytes by number of hectads, here growing with native species including dog's mercury, ground ivy, bramble and ivy on the edge of ancient woodland in Lincolnshire. The species belongs to the Periwinkle family (Apocynaceae), which does not have any native species in the British flora. The recorded insect fauna is rather small, which might be predicted given its taxonomic isolation.

What is known of their insect fauna?

Our knowledge of the herbivorous insect fauna of British non-native plants appears to be somewhat inadequate, perhaps apart from those species that have major commercial importance, such as certain crop (including forestry) species, although not all of these have become naturalised.

The main source for information on the herbivorous insects of non-native plants is the DBIF. This is a very useful resource but it is acknowledged that it is still work in progress (Smith & Roy, 2008). Despite this, host plants have not been sampled systematically with variation in recorder effort. DBIF thus either lacks, or has incomplete entries for, some non-native plants, possibly for around 10% (Smith & Roy, 2008; Padovani *et al.*, 2020), and data for scarcer native plants are also deficient.

Stace & Crawley (2015) listed the top 52 most abundant neophytes in Britain and Ireland based on the occupancy of hectads (10 x 10 km squares). Of their top 52, nine 'species' (17%) do not have entries in the DBIF. Admittedly, of these, one is a hybrid (hybrid bluebell *Hyacinthoides* x *massartiana*) and another is a distinctive garden subspecies of a native woodland herb – variegated yellow archangel *Lamiastrum galeobdomon* ssp. *argentatum*.

There are few specific published studies on the insect fauna of non-native plants. Those that the author is aware of include for *Buddleia davidii* (Owen & Whiteway, 1980) and the Lepidoptera of *Nothofagus procera* and *N. obliqua* (Welch & Greatorex-Davies, 1993), sweet chestnut *Castanea sativa* (Parsons & Greatorex-Davies, 2006) and alien cypresses (Agassiz, 2004).

Where are species recruited from and what are the key factors?

There are three main sources of insects that have colonised novel non-native plants. Many will have switched from native plants, usually, but not always, taxonomically-related to the non-native species (though in many cases the species may still maintain populations on its existing native host). Some will have been accidently imported with the host plant and a small number have been deliberately introduced, while other more mobile species may have colonised from the continent. An example of the latter is the rapid range expansion of the horse chestnut leaf miner *Cameraria ohridella* (Lepidoptera: Gracillariidae) across Europe (Pocock & Evans, 2014). This species attacks horse chestnut *Aesculus hippocastanum*, introduced to Britain and Ireland in the late 16th century and the commonest of the three species of introduced horse-chestnuts.

There is a large evidence base on the topic of the mechanisms of recruitment of insect herbivores, with research generally commencing from the late 1970s to the present. It is beyond the scope of this article to cover this in any depth. In summary, the probability of an introduced plant species being colonised by native insects depends on many different factors, including the plant's physical, chemical and phenological traits, as well as the phylogenetic or taxonomic isolation of the species, the size of the native family/genus species pool to which it is related, its abundance or distribution in the introduced range, the habitat it exploits and the time since it was introduced (Padovani *et al.*, 2020). Although apparently not much researched, the context of the habitat or plant community the non-native species is growing in, especially the abiotic environment and associated plants and plant communities' species diversity, may also have an influence.

Fig. 2. The introduced neophyte, common fiddleneck *Amsinckia micrantha* (Borage family (Boraginaceae)). An example of a species with no entry in the DBIF. Now widespread in arable land especially in eastern England and Scotland. Probably introduced from North America in grain/agricultural seed and wool shoddy. First recorded in the wild in the early 20th century. (Photo by R.G. Jefferson)

Fig 3. Mullein moth *Cucullia verbasci* larva. Now established on *Buddleia davidii*. (Photo by R.S. Key)

Fig. 4. The flowers of horse chestnut *Aesculus hippocastanum* – a 16th century introduction to Britain & Ireland. (Photo by R.G. Jefferson)

Table 1: Three examples of introduced plants and their insect fauna.

Plant	History	Relatedness category	Number of insect/mite species recorded in DBIF	Notes
Cotoneaster horizontalis (wall cotoneaster)	The most widespread of the naturalised cotoneaster species. 82 species have been introduced for ornamental purposes. Species originate from China & Asia. Wall cotoneaster has been recorded from 1316 hectads in Britain & Ireland (34%).	There is a single native species in the genus – *Cotoneaster cambricus* – but its native status is much debated. The genus is part of the Rose family (Rosaceae). The latter has the highest number of herbivorous insects of any British plant family (Ward & Spalding, 1993).	10 (34)[1]	The insect species found on *Cotoneaster* spp. consist of species feeding on a wide range of herbaceous and woody shrubs/trees, plus a few that are otherwise confined to native members of the Rosaceae.
Buddleia davidii (butterfly-bush)	First introduced from China in 1896. First recorded in the wild in 1922. Recorded from 1974 hectads (51%).	A member of the family Scrophulariaceae with no native members of the genus but with three native genera in the family including *Verbascum* and *Scrophularia.*	34	Associated insects are mostly polyphagous or generalist [2] moth species apparently feeding on a wide range of other herbaceous and woody plants but with a few species that feed on native Scrophulariaceae (*Verbascum* & *Scrophularia* spp.), including the weevil *Cionus scrophularia* (Coleoptera: Curculionidae), the mullein *Cucullia verbasci* (Lepidoptera: Noctuidae) (Fig. 3) and the leaf-miner *Amauromyza verbasci* (Diptera: Agromyzidae).
Juglans regia (walnut)	Possibly native in Greece & the Balkans. A Roman introduction from SE Europe to Britain (Archaeophyte). Widely planted and naturalised, most commonly in England. Recorded from 684 hectads (21%).	No native members of the family (Juglandiaceae) occur in Britain & Ireland.	14 (9)[3]	Two aphid species (Homoptera: Callaphididae) (Figs 6 & 7) are only known from walnut [4]. The aphids are presumed to have colonised either by long-distance dispersal or were introduced with the tree (or both).

[1] It is probable that individual species of *Cotoneaster* suffer from under-recording of their herbivorous insects so the figure for the genus as a whole is given in parentheses. [2] Note the caution about the accuracy of statements about diet breadth in the empirical literature (Loxdale & Harvey, 2016). [3] The figure is inflated by non-native species and probable 'tourist' species (*sensu* Moran & Southwood, 1982) not feeding on the plant – the likely number is nearer the figure in parentheses. [4] There are also two species of herbivorous mites that are exclusive to walnut.

Fig. 5. Grey dagger (*Acronicta psi*) larva. This species feeds on a wide range of broadleaved trees and shrubs including species of *Cotoneaster.* (Photo by Malcolm Storey)

Table 1 provides examples of introduced species that cover three different situations – firstly, an introduced species where there is a British native species in the same genus (*Cotoneaster*); secondly, one where there is no native species in the genus but there are some in the same family (*Buddleia* – Scrophulariaceae); and thirdly, a species that does not have any native species of the family (*Juglans* – Juglandiaceae).

The complexity of the factors influencing the accumulation of herbivorous insects is illustrated by the fauna of turkey oak (*Quercus cerris*). This species was introduced to Britain and Ireland in the early 18th century as an ornamental tree and originates from southern and eastern Europe. It has become widely naturalised in Britain and Ireland and has been recorded from 1,293 hectads, around 34% of the total (Stace & Crawley, 2015). Its close native relatives, the pedunculate oak *Quercus robur* and sessile oak *Quercus petraea*, have a very large number of associated herbivorous insects, collectively having more species than any other tree in Britain apart from the willows (*Salix* spp.) (Kennedy & Southwood, 1984). The genus *Quercus* has the highest number of galls (around 50 species) of any plant genus (Redfern, 2011).

The fauna of turkey oak has a species richness somewhat less than that of the native oaks – around half the number that feed on pedunculate oak. However, the specificity of this fauna to oaks is not significantly different to that of the fauna on the native oaks, according to Southwood *et al.* (2004). Thus, a significant proportion of the species pool of oak insects is present on turkey oak, but these herbivorous species are not as abundant as on native oaks. Southwood *et al.* (2004) concluded that leaf miners and gall makers (which are more intimately associated with the leaf), are scarcer on turkey oak. The introduction of turkey oak to Britain, Ireland and other countries has enabled several heteroecious species of gall wasps (Hymenoptera: Cynipidae) to expand their European range over time, previously being restricted to south-eastern Europe (Redfern, 2011). These are species which require turkey oak for the sexual generation and pedunculate or sessile oak for the agamic generation and are found where the two species of oak co-occur. In Britain, eight of these gall wasps are species in the genus *Andricus* and, all bar *Andricus aries*, have sexual galls on turkey oak. Species of two other genera have recently been found – *Aphelonyx cerricola* with an asexual gall on turkey oak with the sexual generation host being unknown, and *Neuroterus saliens* with both generations on turkey oak.

Range expansion into Britain and Ireland has occurred by natural colonisation and by accidental introduction, although *Andricus kollari* was a deliberate introduction as its marble gall is used for tanning leather, dyeing cloth and ink-making due to its high tannin content.

Redfern (2011) states that more species may arrive in the future and existing colonists are still spreading, with the rate of invasion varying between species.

Why is a better knowledge important?

Fundamentally, knowledge of the insect fauna of introduced species is important basic biological information. Padovani *et al.* (2020) call for more systematic and controlled sampling to be carried out at a broader geographical scale. They go on to make the case for a better understanding of the processes underlying insect accumulation on non-native plants. This may give useful insight into the accumulation of species in novel anthropogenic habitats in general.

As mentioned earlier, non-native plants may act as hosts for desirable or rare insect species and other wildlife, including as important sources of pollen and nectar. There is

Fig. 6. *Panaphis juglandis* (male alata) on walnut.
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Fig. 7. *Chromaphis juglandicola* (alata) on walnut.
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Fig. 8. Gall of *Andricus grossulariae f. agamic* on pedunculate oak. (Photo by Malcolm Storey)

evidence that some non-native plants and their habitats also play host to a unique and distinctive fauna. For example, Padovani *et al*. (2020) report that around 10% of DBIF insect taxa have only been sampled from non-native plants.

Perhaps there may be scope for harnessing the skills of the entomological recording community in order to start filling the gaps in our knowledge?

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Fig. 1. *Formica picea* workers

The Black Bog Ant (*Formica picea*): a species under threat

Ray North

Introduction

The Black Bog Ant, *Formica picea* (Nylander, 1846), is restricted to bogs, valley mires and wet lowland heath, mainly in southern England and Wales. It can be distinguished from most bog-inhabiting ant species by its shiny black appearance and large size, approximating 6-8mm in length (Fig. 1). It was listed as a priority species in 2007; now the risk is even greater because of accelerating habitat fragmentation and climate change.

Distribution of *Formica picea*

I was commissioned to carry out surveys of the New Forest and Dorset for *F. picea* during 1998-2003 (Table1). The species was already known to occur in large colonies at Rhossili Down and Cors Goch, Llanwch in Carmarthenshire, South Wales and was thought to be confined to the southern counties of England and Wales. However, in the last 15 years or so, it appears to have been present much further north. In 2007 two nests were confirmed in the Gwaun Valley, Pembrokeshire, South Wales (Hudson, 2008). In the same year it was recorded in West Yorkshire, north of Leeds, (http://sifolinia.blogspot.com/2007/12/death-of-monarch.html) and in 2013 it was found near Colebrook in Northern Ireland (National Biodiversity Network Atlas; nbnatlas.org). These records might indicate a gradual movement of *F. picea* northwards, perhaps to avoid increasing temperatures and drier conditions in the south. Migration northwards would nevertheless be hampered by habitat fragmentation. Bogs and mires could be considered to be insular ecosystems, and without the ability to adapt to a rapidly-changing climate, many bog species may soon disappear (Cartwright, 2019).

Habitat preference of *Formica picea*

Much of the information on the distribution and habitat preferences of *F. picea* is based on observations from unpublished data collected from surveys. The principle vegetation community in which nests were found is valley mire, which includes *Erica tetralix*, *Calluna vulgaris*, *Myrica gale*, rushes (*Juncus* spp.) and grasses where *Molinia caerulea* is dominant with a sub-community of *E. tetralix*, *C. vulgaris* and *Eriophorum angustifolium*; this vegetation type is found in acidic soil with low levels of nutrients. The ants construct nests mostly in tussocks of *Molinia*, although other plant species such as *Erica* or *Calluna* may be present within the tussock. The leaves or stems of the vegetation support a pile of plant fragments, or solaria, where the brood are maintained at the optimal temperature and humidity (Fig. 2). Although constructed in bogs, nests are never near open water, but *Molinia* tussocks may be surrounded by deep runnels filled with water from small streams (Fig. 3). At several sites, the valley mire plant community, particularly on peat seepage slopes, consisted of *E. tetralix*, *Sphagnum compactum* and other *Sphagnum* species in the open and wet areas. On drier parts of mires and bogs, *M. caerulea* occurred in variable amounts with *C. vulgaris* and *M. gale*. *Formica picea* workers were often discovered in cushions of *Sphagnum* moss (Fig. 4) and other cushion-forming mosses like *Polytrichum*. Single nests were sometimes found in drier humid heath, but were never found in areas

Table 1. Known sites and nest numbers for *Formica picea* in the UK..

	Period			
Site and Grid Ref (where available)	**Pre-1997**	**1997-2000**	**2000-2011**	**2011-2019**
Foulford Bottom - SU190058	3	5	0	-
Ridley Bottom - SU199061	-	2	-	-
Ridlley Plain (on hill) - SU211066	-	21	3	7
Ridley Plain (in valley) - SU217072	-	-	8	7
Slufters Bog - SU222095	2	3	-	-
Buckherd Bottom - SU215084	-	23	4	5
Harvest Slade Bottom - SU216070	0	2	0	-
Backley Bottom - SU223086	-	9	-	1
Vales Moor (Broad Bottom) - SU1904	-	1	0	-
Cranes Moor - SU194024, SU196023	-	3	1	-
Kingston Great Common NNR - SU185023	-	2	-	-
Holmsely Bog - SU225013	13	3	-	-
Wivelery Bog West (Avon Water) - SZ245999	8	8	-	-
Penny Moor (Denny Bog) - SU352050	0	0	1	-
Roydon Wood - SU313001	28	37	-	1
Dibden Bottom - SU394063	-	2	0	-
Rakes Brakes Bottom - SU222125	-	3	0	-
Dogwood Bottom - SU217063	2	1	-	-
Ferny Crofts - SU373055	-	1	-	-
Ackercomb Bottom - SU198075	-	3	-	-
Acres Down - SU267087	-	1	-	-
Duckhole Bog - SU258030	-	1	2	-
Blackgutter Bottom - SU206166	-	-	1	-
Milkham Bottom - SU218099	-	-	5	-
Crabtree Bog - SU226027	present	0	-	-
Matley Bog - SU333072	>20	0	-	-
Red Hill Bog - SU2601	present	0	-	-
Shatterford Bottom - SU342062	present	0	0	-
Common Moor (Burley) - SU205047	6	0	-	-
Dur Hill Down - SU202013	1	-	-	-
Colony Bog - SU930592	-	-	present	-
Pirbright Ranges - SU921595	-	-	present	-
Hartland Moor NNR - SY943852, SY946856	>100	18	1	-
Morden Bog NNR - SY913923	5	2	1	-
Parley Heath - SZ0998	1	0	-	-
Cor Goch, Llanllwch NNR - SN3618	111	148	-	-
Rhossili Down - SS426901	12	74	-	-
Gwaun Valley, Pembrokeshire	-	-	2	-
Chevin Forest Park - SE207444	-	-	present	-
Colebrook, N. Ireland	-	-	-	present

Key: present = known to occur, but data not available for nos. of nests; - = no data available. Data summarised from the author's own records, personal communications (with Pinchen), the NBN Atlas (and entries therein by Baldock, Collins and Jarmen) and, in chronological order: Lucas (1997), Else (1998), Orledge *et al.* (1998), Pinchen (2001), Pontin (2005), Hudson (2008) and Sifolinia (2008).

where there was a uniform diversity of valley mire vegetation, such as the *Narthecium ossifragum – Sphagnum papillosum* communities of Shatterford Bog in the New Forest. Nests are never found in wooded areas or Carr (a type of waterlogged wooded terrain that, typically, represents a succession stage between the original reedy marsh and forest).

I have recorded *F. picea* from about 24 sites in the New Forest and three in Dorset. It is evident from the survey data (Table 1) that *F. picea* was local in the New Forest at the time of the surveys. Cranes Moor, Harvest Slade Bottom, Denny Bog and Holmsley Bog held early records but surveys in 1997 failed to find any nests. However, nests were rediscovered at these sites in 1998 and 2002. Furthermore, in 2003 a single nest was discovered at Penny Moor (Denny Bog), where *F. picea* was thought to have been extinct since about 1970. Several new sites where *F. picea* had not been previously recorded have now been added to the list (Table 1). Populations were thought to have declined on Hartland Moor, as a detailed survey carried out in September 1998 found only two nests, but a further 16 nests were found in September 1999. Colonies have been found on the Surrey heaths but the size of the population is not known. Two sites in South Wales, Cor Goch and Rhossili Down in Carmarthenshire, have the largest populations, with between 100 and 200 nests.

In July 2019 I returned to the New Forest and found that the largest *F. picea* populations occurred at sites on Ridley

Fig. 2. *Formica picea* nest in a tussock of *Molinia*.

plain, Buckherd Bottom, Backley Bottom and Roydon Wood. On Ridley plain, where water levels are maintained from peat seepages, *F. picea* populations are still thriving. At Buckherd Bottom and Backley Bottom, there appears to have been a decline in nest numbers since the 1997-2003 surveys. The most obvious decline was at the Roydon Wood site where only one nest was found after two hours of searching. At these sites, the water table was very low and much of the bog had been invaded by bracken. Backley Bottom was also found to be very dry, mainly consisting of mud rather than water-filled runnels, as in the past. This is likely to be the consequence of a very hot and dry summer. The decline of bog habitat at these sites, and possibly other sites, may be the direct result of higher ambient temperatures and a low water table, producing change in vegetation and loss of diversity – *Sphagnum* in particular. This is evidenced by the amount of bracken now invading many of the New Forest bogs and mires.

Importance of Vegetation structure

Formica picea is restricted to peat bogs in temperate zones and southern boreal regions (Spitzer and Danks, 2006). Surveys suggest that *F. picea* flourishes where water emerges from seepages in the peat and circulates in deep runnels between tussocks of vegetation. This gives rise to the unique vegetation characteristic of lowland mires and bogs. Though *F. picea* is also found in drier conditions of humid heaths, populations here may be small, usually only one or two isolated nests.

Soil moisture is the primary determinant of botanical composition. Mires damaged by drainage lack clear vegetation zones (North *et al*., 2003). What seems to be important to *F. picea* is proximity to a vegetation mosaic where most stages of the plant communities or zones are present together. This was certainly the case with some of the large sites such as Buckherd Bottom, Ridley Plain and Roydon Wood in the New Forest, and in South Wales. Where the mosaic of vegetation is very poor, sites have only one or two nests, or *F. picea* may be absent altogether.

Vegetation structure may be an important factor determining locations of nests. Orledge *et al.* (1998) suggested that the most favoured nest sites are those where the vegetation is relatively short. Fieldwork carried out at Roydon Wood in 2000 showed that nests were found both in grazed and ungrazed areas. Vegetation in parts of bogs supporting the largest concentration of nests/solaria had a mean maximum height of 70cm. Cutting back the vegetation to simulate grazing may be detrimental to *F. picea*, resulting in colonies vacating the solaria after about 6 weeks, perhaps due to exposure to excessive solar heat. These conditions appeared to favour *Lasius* spp., which were found to invade experimental plots (North, 1998). These effects were more pronounced after about a year, when further movements of *F. picea*, *Lasius* and *Myrmica* nests were more evident (North, 1998, 2000).

Formica picea appears not to depend on any species of plant as a food, although they have been seen to collect nectar from the flowers of ericoid species during the summer. The workers have been observed carrying tiny Diptera, but very few workers were seen to climb small birch trees to reach sucrose baits, although large numbers were foraging in a *Molinia* sward below the trees (North, 1998). It is likely that *F. picea* harvests secretions from homopterous insects, such as aphids found on roots and stems of vegetation growing through the nest and solaria (Fowles and Hurford, 1996).

Hydrology

The wetland sites described in the New Forest and elsewhere depend on a high water table to create the ideal vegetation community for *F. picea*; the most viable populations are found in the valley mires, where water filters through the peaty soils from rain runoff or ground water. Since hydrology determines the plant communities, seeping water may be important for stability of populations because it gives rise to mosaic vegetation types. It also has a cooling effect, keeping internal temperature and humidity of solaria optimal for development of the brood. In the New Forest, the largest populations of *F. picea* were found where the water table was relatively high (Tubbs, 1986).

Optimal microclimate conditions

The optimal conditions required by *F. picea* were investigated at Cors Goch, South Wales (North, 1998). Nests were most numerous where relative humidity at the surface of peat exceeded 80%. The humid conditions created by peat and vegetation were most likely responsible for stabilizing the internal temperature and humidity of the nests, even when the ambient temperature was in excess of 25°C and the humidity around 49%. Over 90% of solaria which had an internal relative humidity of 75-80% and temperature of 17-18°C were found to contain brood**.** This could be the optimal microclimate for the development of brood.

Field observations showed that *F. picea* nests and solaria often moved to different locations, possibly because the colonies were selecting optimal microclimatic conditions. Strimming vegetation in field plots around nests stimulated relocation, possibly due to exposure to direct solar radiation and drying of the soil and vegetation. However, workers continued to forage in the vegetation until the ambient temperature reached around 27°C, before returning to the nest.

Tolerance to low temperature and waterlogging

Generally, ants tend to avoid flooded or waterlogged conditions (Sendoya *et al*., 2014), but some ant species are able to survive complete inundation by water (Nielsen, 1997) and these have evolved various mechanisms to achieve this (Philpott *et al*., 2010). Bogs and mires are subject to flooding and to freezing temperatures in winter. In spring, they may be subjected to flooding after heavy and prolonged rain. Building nests in tussocks of vegetation above the water table would provide some protection against the nest becoming waterlogged. *Formica picea* appears remarkably resilient to waterlogged conditions and low temperature. However, North (2001) demonstrated that hibernating colonies tend to be exposed to lower temperatures near the top of a tussock, possibly as a trade-off to avoid getting wet at the base of the tussock. A temperature gradient was found inside vegetation tussocks; a difference of almost 2.5°C between the top and bottom, the bottom being the warmest. In a nest found in winter, workers were clustered in the top 10cm of the tussock, presumably to avoid the saturated soil at the bottom. The temperature inside the nest galleries, which contained hibernating workers, was between 0.3 and 0.5°C.

Formica picea workers, when completely submerged in water, are highly active for several minutes, appearing to walk beneath the surface, after which they become still and fold their legs beneath the thorax. In one study, when two groups of workers were submerged in water at 20°C and 4°C for 3 days, both groups showed 66% mortality. The survivors demonstrated apparently normal locomotor activity after being removed from the water (North, unpublished report). It therefore appears that *F. picea* may be able to survive inundation for several days. Another mechanism for survival may involve taking advantage of air trapped in the nest galleries during periods of flooding (Nielsen, 1997).

Why does *Formica picea* favour certain bogs?

Generally, bogs and mires should present ideal conditions for survival, but the species is present in only a select few. Its ability to disperse is extremely poor, so it would be unable to migrate to new areas and establish new colonies because of habitat fragmentation (Mabelis and Chardon, 2005; Mabelis and Korczynska, 2012). Another possibility is that *F. picea* is unable to compete with more aggressive generalist ant species living in bogs, especially *Lasius platythorax*. However, there may be several reasons why *F. picea* colonies are limited in their distribution, such as microclimate, intraspecific competition and habitat fragmentation.

Microclimate

It may be that *F. picea* is confined to bogs due to its preference for cooler microclimatic conditions. Owing to the high specific heat of water, peaty soils with a high water table resist rapid warming. Consequently, mire and bog microclimates are highly heterogeneous. The hummocks, hollows and slopes provide a variety of microclimatic conditions due to a variable vertical thermal regime, and exhibit diurnal variations in the surface temperature compared to the deeper layer of peat (van der Molen and Wijmstra, 1994). The thermal regime creates a habitat that is unique and is exploited by invertebrate bog specialists, which would find it very difficult to survive elsewhere. *Boloria aquilonaris* and *Boloria eunomia* are peat bog butterflies considered to be glacial relicts. The heterogeneity of bog habitats provides a refuge for these species. Turlure *et al*. (2010) showed the survival rates of the caterpillars were greater in the early vegetation succession zones (*Sphagnum* communities) of bogs, where humidity is highest. The *Sphagnum* hummocks provide humid and cool conditions, optimal for the survival of the caterpillars. *Boloria eunomia* prefers the somewhat darker, colder and wetter microenvironment created by the *Molinia* tussocks of bogs (Turlure *et al*., 2011). This suggests that *F. picea* might be

Fig. 3. Example bog habitat on Ridley Plain, New Forest, where *Formica picea* is present. The vegetation consists mostly of *Molinia* tussocks with *Erica*, *Calluna* and *Myrica*. The *Molinia* tussocks are surrounded by water-filled runnels.

Fig. 4. Nest of *Formica picea* in *Sphagnum* Moss, with brood.

confined to bogs because of its thermal ecology and selection of optimal microclimatic conditions for brood development. Bogs and mires have good temperature-buffering capacity, creating regions of varying climatic conditions; temperature at the centre may be 5-8° C lower than temperatures outside the bog (Spitzer and Danks, 2006). Maybe *F. picea* is a cold-adapted species originating from cold temperate or boreal regions of the Northern Hemisphere. The bogs and mires in the south of England may have provided a refuge in the past for cool-adapted species to flourish, when the climate began to warm during the post-glacial period (Sommer *et al.*, 2015).

Intraspecific competition

Formica picea colonies coexist with several ant species and therefore compete for resources. From biological surveys conducted in the New Forest (North *et al.*, 2003), the genus *Myrmica* was widespread. *Myrmica ruginodis* was the most common species in wet habitat, followed by *Myrmica scabrinodis*. *Lasius platythorax* was present in nearly all mires and bogs surveyed, preferring to make nests in rotting wood. *Lasius niger*, however, is not abundant in the New Forest bogs, probably because it avoids waterlogged conditions (Seifert, 1991). Most species of *Lasius* and *Myrmica*, with the exception of *M. scabrinodis*, are generalists and may be least affected by habitat change (Vepsäläinen *et al.*, 2000).

It has been suggested that *F. picea* is restricted to bogs because it would be out-competed by other species of ant such as *L. platythorax* in drier habitats (Punttila *et al.*, 2016). *Lasius* spp. build solaria which resemble those of *F. picea* and there is some evidence that *L. platythorax* aggressively evicts *F. picea* from its nest. This may, however, be circumstantial; it is likely that *F. picea* nests are vacated because the thermal conditions are no longer optimal, and are later occupied by *L. platythorax*.

In earlier studies, feeding stations were set up in strimmed vegetation to observe behavioural interactions between *F. picea* and other ant species in ericoid-dominated vegetation (North, 2000). By the end of the experimental period *Lasius* spp. had taken over nearly all of the feeding stations. If workers of both species came into contact, *Lasius* would attack *F. picea* and drive it away. Very little actual contact occurred between these species; *F. picea* workers seemed to be aware of *Lasius* at the feeding stations and kept a distance of 1-2 cm from *Lasius* workers. Nevertheless, feeding stations occupied by large numbers of *F. picea* workers were not foraged by *Lasius* and, furthermore, there were no observations of *Lasius* actually invading *F. picea* nests and attacking the occupants. This suggests that *Lasius* may take over *F. picea* nests only when they vacate and move to a new site. *Myrmica rubra* also shares resources with *F. picea*. Both species were seen to occupy the same feeding station where *F. picea* workers were attacking *M. rubra*. *Myrmica rubra* is less aggressive than *Lasius* and exists in smaller populations, so is probably not a serious threat to *F. picea*.

Behavioural interactions between different species of ant may be a function of ambient temperature. Those species which are behaviourally dominant (e.g. *L. platythorax)* tend to forage in a narrow window of warm temperatures, while subordinate species (*F. picea*) forage at low temperatures, within a wider thermal window (Lessard *et al.*, 2009). Species of ant having foragers with low-temperature tolerance generally have a longer foraging season, and brood develops at a low critical maximum temperature, as with *F. picea*; the converse is true for species with a higher-temperature tolerance (Penick *et al.*, 2017). *Formica picea* has been observed to forage in late October/November and may thus avoid ant species which forage at higher ambient temperatures.

Habitat fragmentation

Fig. 5 maps the distribution of *F. picea* populations in relation to habitat types and highlights the importance of habitat connectivity to aid the dispersal of alate queens. The model from which the figure is derived assumes that queens cannot fly more than 3km and cannot traverse unsuitable habitat (Mabelis and Chardon, 2005). The *F. picea* population could be considered a metapopulation with smaller populations being separated by unsuitable habitat. The largest populations at the Ridley Plain/Buckherd Bottom sites (7-15 nests) probably represent the core patch near the centre of the forest, which replenishes the surrounding sites by emigration within the 3km buffer zones. No nests were found outside the buffer zones, even where the habitat may be suitable. The white areas are unsuitable habitat (mostly woodland and agricultural or urban areas). The three small sites to the east have become isolated and there is a high probability that these cannot be reached by winged queens from the reservoir population due to fragmentation of bog habitat.

Rees *et al.* (2010) demonstrated the existence of three distinct *F. picea* populations: (i) Cors Goch, (ii) Rhossili Down and (iii) Harland Moor-Ridley Plain. Roydon Wood, in the south, is interesting because the local population was once very large and just outside the 3km zones, surrounded by unsuitable habitat. The Roydon Wood population might have been a distinct population, like those of Pembrokeshire and Surrey.

Those nests in close proximity on Ridley Plain are likely to be polygynous and reproduce by colony budding, as genetic relatedness is low (Rees *et al.*, 2010). On Ridley Plain, there is good connectivity with suitable habitat, where genetic material could be exchanged by sexuals from nearby colonies (Mabelis and Chardon, 2005). At sites outside the 3km flight radius, populations may become isolated, so are likely to exhibit low genetic diversity and go extinct. Significant inbreeding was found at Cors Goch, but none was evident at the Hartland Moor or Ridley Plain sites (Rees *et al.*, 2010).

Conserving *Formica picea* populations

In the New Forest National Park, several projects are underway to restore the mires and maintain the water levels, and hopefully ensure the survival of established *F. picea* populations. *Formica picea* may be a good candidate for translocation to new sites of suitable habitat. Migration northwards may be evident in the Welsh populations. If the optimal conditions are to be tracked successfully by invertebrates then corridors of suitable habitat should be restored.

Careful management of the bog/mire habitat to maintain water levels might ensure the survival of established *F. picea* populations with climate change, especially at Ridley Plain, which appears to be the reservoir population. The species could be a good indicator of the changing condition of valley mires resulting from climate change. It is also worth noting that other bog-specialist invertebrate species are likely to be affected. I recommend further surveys for the *F. picea* in Dorset and Hampshire and suitable habitats much further north.

Acknowledgement

I would like to thank the Hampshire Biodiversity Information Centre for supplying the broad habitat data used in the GIS model.

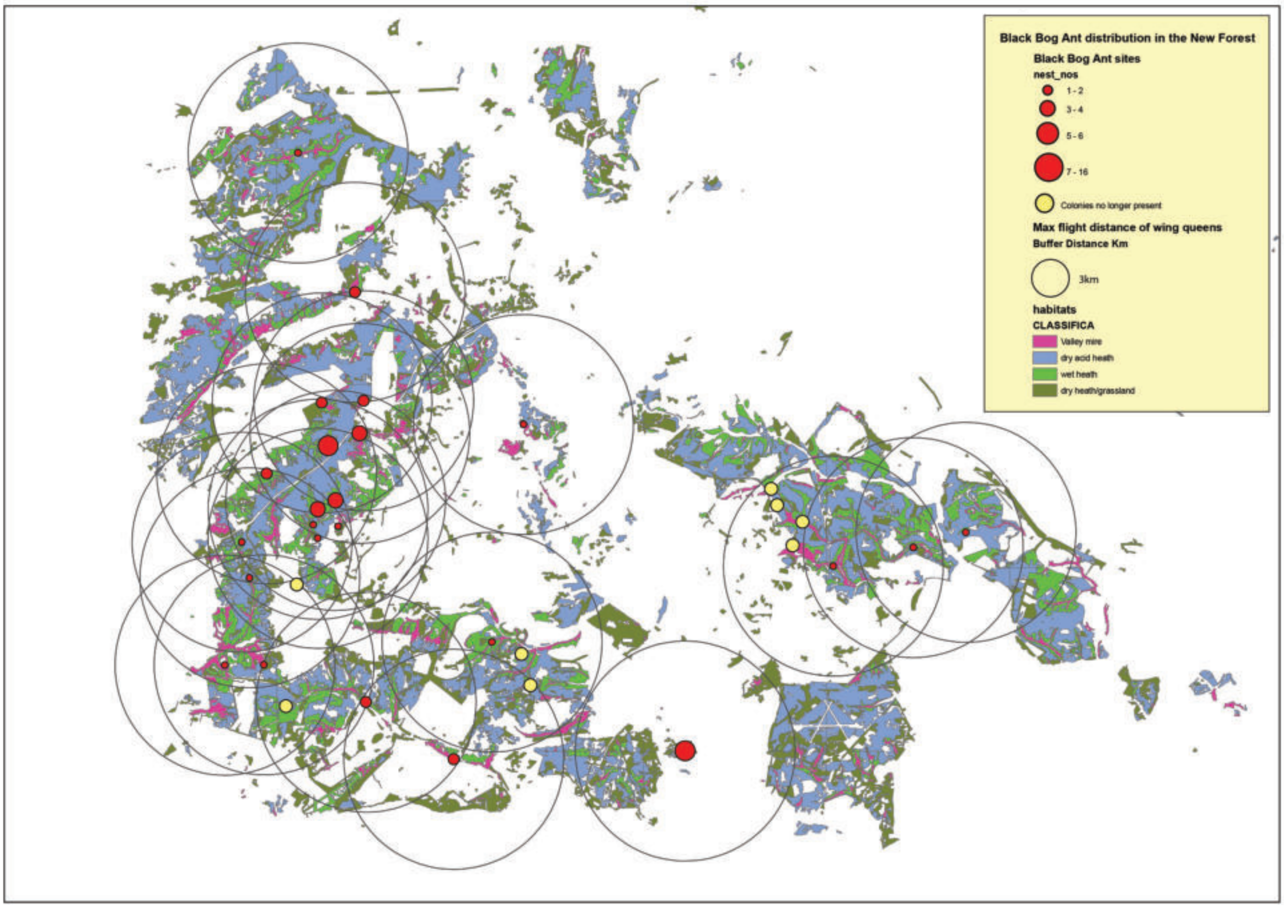

Fig. 5. The importance of habitat connectivity for the distribution of *Formica picea* populations in the New Forest. The figure shows suitable habitat types and realistic flight distance 3km (black circles) of winged *Formica picea* queens. The largest populations are found in an area of Ridley Plain (to the left of the figure) and considered to be a reservoir of fertile queens. Those habitats outside the flight range have not been colonised, even where suitable habitat exists.

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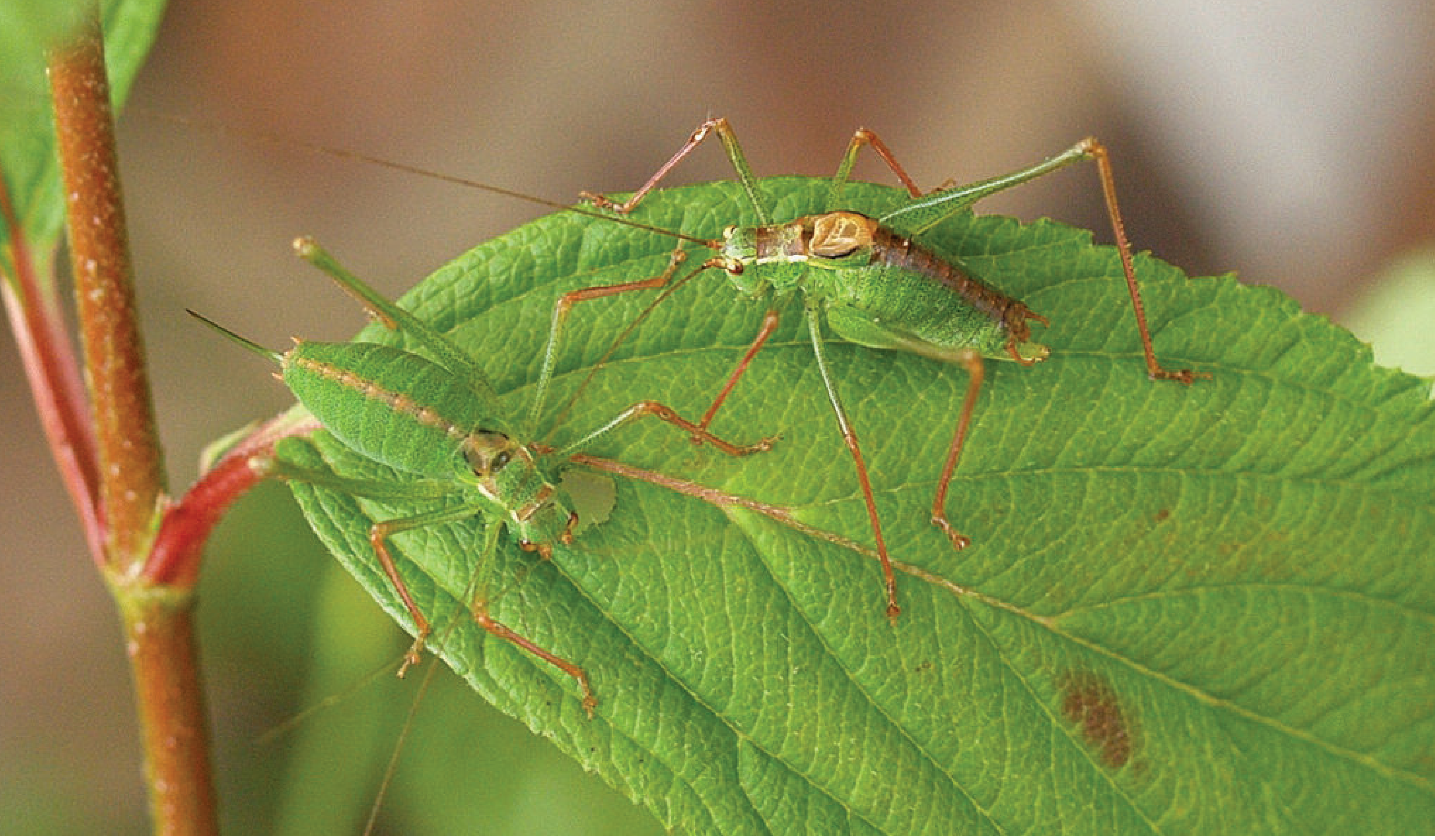

Mating in the speckled bush-cricket, *Leptophyes punctatissima*

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Leptophyes punctatissima is a flightless, medium-sized bush-cricket from the Orthopteran family Tettigoniidae, sub-family Phaneropterinae. It was first studied in detail by Duncan (1960) who observed its life cycle in the field and its reproductive behaviour in the lab and gave a brief description of copulation.

We have been working on various aspects of *L. punctatissima* behaviour and acoustics for several decades and have observed its behaviour in over 500 matings both in the lab and in the field. Since we have found very few full accounts of copulation in bush-crickets in the literature (though see Rentz (1972) for shield-backed katydids from the genus *Idiostatus* and Samietz *et al.* (2014) for *Phaneroptera falcata*), one of the main aims of this article is to provide a comprehensive description of copulation behaviour in *L. punctatissima*, based on a synthesis of our various observations.

Leptophyes punctatissima is common throughout Europe. In the UK its distribution is mainly in southern England, though over the last 30 years it has considerably extended its range northwards, and with more populations now established across the Scottish border (NBN Atlas, 2020). It is usually found patchily distributed in mixed vegetation close to trees or tall shrubs. The nymphs are usually found in low vegetation but the adults may move high up into the trees.

Overwintered eggs hatch from early May and the nymphs go through six instars before reaching sexual maturity around early August. Adult females are larger than males (males: mean body length 13.7mm, SD±0.9mm, *N*=79; females: mean body length 15.8mm, SD±1.2mm, *N*=85; recorded from a population reared in the laboratory from about instar 4). Mating tails off after the end of August and most adults are dead by the end of October.

Mating system and calling behaviour

Some bush-crickets have a duetting mating system, especially common among the phaneropterines, in which the male calls and the female responds, though which sex then approaches the other varies (Robinson & Hall, 2002). *Leptophyes punctatissima* is, however, the only UK species where both male and female call in this way. Males call both during the day and at night, with three peaks of calling in the field occurring from midnight to 04.00, from 09.00 to 11.00 and from 14.00-19.00.

Both male and female calls are ultrasonic (~40 kHz) and extremely brief (Robinson *et al.*, 1986; Figure 1). If the female's response falls within a particular time window (Figure 2), the male approaches the stationary female, finding her by orienting to her call (phonotaxis), with the pair continuing to duet throughout his approach (Zimmermann *et al.*, 1989).

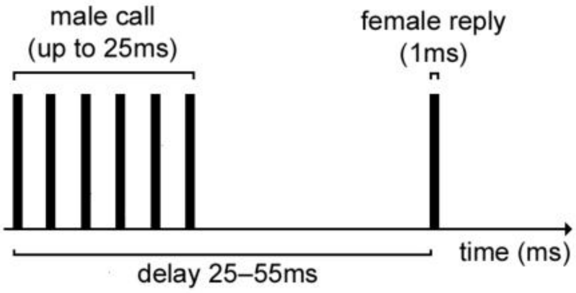

Figure 1. Diagrammatic representation of the timing of the duet. The male call is a brief click consisting of 5-8 syllables and lasting up to 25ms in total. The female call is even briefer with 1-2 syllables, lasting 1-2ms.

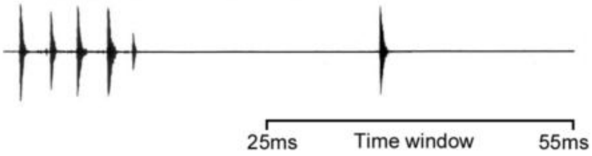

Figure 2. Oscillogram of the male call and the female response and the time window during which the female must respond if the male is to approach her to mate.

Figure 3. Mating in *L. punctatissima* 1 – the male has approached close to the female but is not oriented straight towards her.

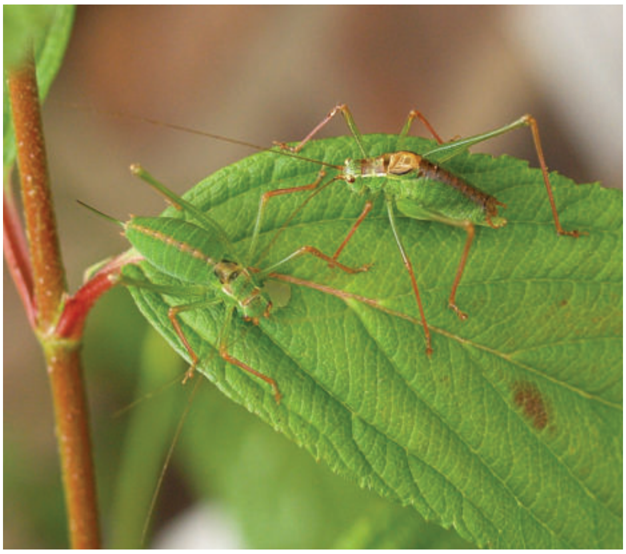

Figure 4. Mating in *L. punctatissima* 2 – the male antennates the female.

Figure 5. Mating in *L. punctatissima* 3 – the male moves in front of the female and backs towards her.

Figure 6. Mating in *L. punctatissima* 4 – the male pushes underneath the female, arching his body, and the female begins to palpate and mouth his back.

Figure 7. Mating in *L. punctatissima* 5 – the female moves up the back of the male as she continues to palpate and mouth him.

When the male has approached within a few centimetres of the female, often his approach becomes less direct and he appears to be moving more hesitantly, sweeping his antennae around as if trying to find her (Figure 3). We believe that at close proximity phonotaxis may be hampered, with the male possibly having to rely more on cues such as smell or vibration.

Behaviours associated with copulation

Copulation can take place at any time of day in the field and, since we have observed males performing phonotaxis at night, we assume it also takes place at night. When the male finds the female, they explore each other with their antennae (Figure 4). Similar antennation has been widely observed in Orthopteran mating and Ryan & Sakaluk (2009) showed that it is important in sex recognition in decorated crickets, *Gryllodes sigillatus*. Next the male moves in front of the female and backs towards her (Figure 5). He pushes his abdomen underneath her, arching his body, and the female begins to palpate and mouth his back (Figure 6). She gradually moves forward, up the back of the male, as she continues to palpate and mouth him (Figure 7).

If nothing else during this stage, the female must be receiving chemical stimuli from the male. But it is also possible that she is ingesting secretions produced by the male from glands situated on his dorsal tergites that specifically encourage the female to copulate (Gwynne, 2001; Vahed, 1998).

When the female has moved far enough forward so that she is fully mounted over the male, she stops palpating and mouthing his back and bends her abdomen downwards. The male probes the female's genitalia with the tip of his abdomen until he and the female lock genitalia (Figure 8). This is achieved by means of the male's cerci, each of which has an apical tooth that hooks over the lamella and engages with a pit situated on the lateral surface of the base of the female's ovipositor (Vahed *et al.*, 2014). The copulation position shown in Figure 8 has been the same in every mating we have observed. Duncan (1960) described mating taking place with the male and female facing in different directions, but it is unclear how many copulations he actually observed.

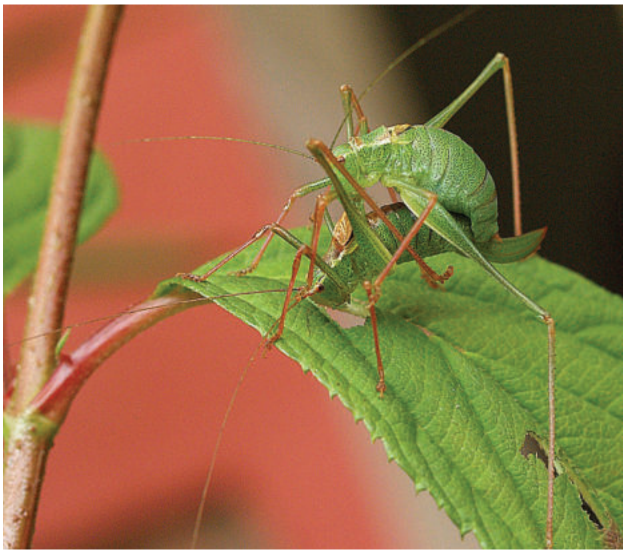

Figure 8. Mating in *L. punctatissima* 6 – the male and female lock genitalia.

At any time up to the point where they lock genitalia, either the male or female may reject their potential mate, either by simply moving away from them or by kicking with the hind legs to push them off. Females are significantly more likely to reject their partner than males are (binomial test, $p<0.0001$). In 249 attempted matings, observed in the lab, where we recorded whether or not rejections took place, successful copulation took place in 173 (69.5%), the female rejected the male in 57 (22.9%) and the male rejected the female in 19 (7.6%). This difference is not because the refractory period (length of time after mating until the individual is willing to mate again) is longer for females than it is for males; we have observed females mating again immediately after they have finished mating, whereas males will not mate again for at least 24 hours.

Like all tettigoniids, *L. punctatissima* produces a nuptial gift in the form of a large, edible spermatophore in which a sperm sac, or ampulla, is surrounded by a spermatophylax consisting of a mass of edible, sperm-free material. In some species, such as *Uromenus stalii*, the spermatophore can be up to 40% of the male's body weight (Gwynne, 2001), but *L. punctatissima* provides a more modest gift averaging only 6.6% in measurements in our lab (SD±2.6%, $N=110$). The main function of the spermatophyllax is to act as a sperm-protection device, allowing sperm to transfer from the ampulla to the female's spermatheca before she eats the ampulla. In many species of Orthoptera, the spermatophore has very little value as food, but in others it has a parental investment function, providing important nutrients that contribute towards the female's egg production or the survival of her offspring (Gwynne, 2001). In *L. punctatissima* there is, so far, no evidence that the spermatophore has any paternal investment function (Vahed, 2003).

Spermatophore size is largest in the male's first mating (mean 0.013mg, SD±0.004mg, $N=37$) and gradually decreases in subsequent matings. There is a significant difference between the weight of the spermatophore produced by a male at his first mating compared with his third mating (mean 0.009mg, SD±0.006mg; paired samples t-test, $t=-2.323$, $N=16$, $p<0.05$), with no correlation between male size and spermatophore weight. In some other bush-crickets, spermatophore size is related to body condition (e.g. Lehmann & Lehmann, 2009). We measured condition using a slope-adjusted ratio index between overall body length and weight, where this index is independent of size (Jakob *et al.*, 1996). Across the first three matings, combined for all males, the weight of spermatophore produced is significantly correlated with condition just before mating (Spearman rank correlation=0.224, $N=100$, $p<0.05$), but not with condition just after mating. Nor is there any correlation between condition and the relative size of the spermatophore, i.e. weight of spermatophore as a percentage of body weight. This suggests that spermatophore size is independent of male size and condition, with the correlation with condition pre-mating being due mainly to the effect of the weight of the spermatophore itself on the condition index. Spermatophore weight could depend more on factors such as the length of time since the male's last mating.

The male transfers the spermatophore 2-3 minutes after locking genitalia (Figure 9) and very soon after transfer is complete, the female dismounts from the male by moving forward over him (Figure 10). We recorded the duration of copulation (time from locking genitalia to female dismount) in 169 matings. Copulation lasted from 1min 48s to 5min

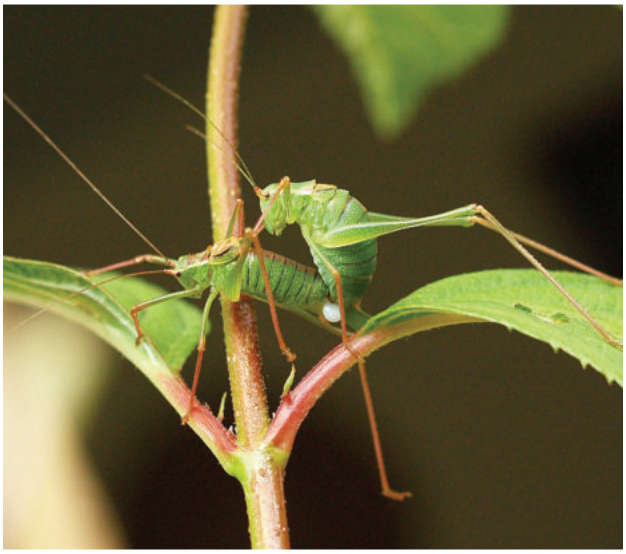

Figure 9. Mating in *L. punctatissima* 7 – the male transfers a spermatophore to the female.

Figure 11. Mating in *L. punctatissima* 9 – after the female dismounts, the male and female gradually move away from each other.

22s (mean 3min 27s, SD±45s). This is very similar to the durations reported for several other bush-cricket species (Samietz *et al.*, 2014; Vahed *et al.*, 2011).

Once the pair have separated they usually wander away from each other (Figure 11), though the female tends to move farther than the male. We have never observed any behaviour that could be interpreted as mate guarding by the male, i.e. behaviour intended to prevent other males trying to mate with the female.

Between 1 and 11 minutes after the pair separate (mean 4.7min, SD±2.0min, *N*=57), and usually close to where the mating took place, the male normally tremulates. In this behaviour, the male performs a series of rhythmic 'push-ups', raising his body and then flexing his legs repeatedly so his body moves up and down quickly several times without actually touching the substrate. He then pauses for at least a few seconds before performing another bout of push-ups. This post-mating tremulation can last for several minutes. It is often performed in the absence of the female and has no effect that we can observe on any other individuals which happen to be nearby at the time. Its function is therefore unclear. Nevertheless, in 68 matings by 17 males where we recorded whether the male tremulated or not, tremulation took place in 89.7% of cases, with all of the males tremulating for at least some of their matings. Tremulation was only observed in males after copulation and was never observed in females. The only other bush-cricket species we know of where the male usually tremulates after mating is *Leptophyes laticauda* (Vahed, 1994). In other bush-crickets that tremulate, the behaviour seems to have a pre-copulatory function, either to attract females for mating or as part of courtship (Gwynne, 2001). De Luca & Morris (1998), for example, showed that pre-copulation tremulation in meadow katydids provides a reliable indicator of male size and that females prefer larger males. Apart from the two *Leptophyes* species, the only evidence we have found of post-copulatory tremulation in bush-crickets, is for *Copiphora vigorosa*, though it was only observed once (Sarria-S *et al.*, 2016). This species is unusual, however, in that vibration rather than calling is its preferred communication channel, with both males and females tremulating. Male post-copulatory tremulation has, however, been observed as the norm in other Orthoptera (e.g. Brown, 2016; Stritih & Cokl, 2012).

Figure 10. Mating in *L. punctatissima* 8 – when spermatophore transfer is complete, the female dismounts.

Usually about 20 minutes after the female dismounts (mean 19min 5s, SD±7min 46s, range 6min 16s-45min 10s, *N*=158), she starts to eat the spermatophore. She bends her whole body ventrally so that she can reach the spermatophore with her mouth parts, biting it and pulling strings of it away (Figure 12). Then she slowly consumes the lump she has pulled away before taking another bite (Figure 13). It can take her up to two hours to finish eating the spermatophore (mean 38min 34s, SD±14min 40s, range 12min to 1h 57min, *N*=145).

In 31 cases, we observed males long enough after they mated to record when they started to call again. Even though they do not mate again until at least 24 hours after mating, males may start to call again very quickly. Eighteen males started calling again within an hour of mating and one started only nine minutes after. Males calling soon after mating reject any attempts by females to mate with them. It is unclear why males call when they cannot mate, unless it has some function in male–male competition. However, though we have not studied this systematically, we have not observed nearby males being affected in any obvious way by the calls of a male; they do not appear to move away from him, for example.

Although we have observed only 10 or so copulations in the field, we have never noticed any differences between the

Figure 12. Mating in *L. punctatissima* 10 – the female bends to bite the spermatophore and pull away pieces.

Figure 13. Mating in *L. punctatissima* 11 – the female eats a piece of the spermatophore.

behaviours observed in the lab and those seen in the wild. Most of the behavioural elements associated with copulation described here for *L. punctatissima* have also been observed in other tettigoniids (e.g. Dorkova *et al.*, 2019) or other Orthoptera (e.g. Field & Jarman, 2001). The only unusual behaviour in *L. punctatissima* is possibly tremulation occurring as the norm after copulation. This may be limited to the genus *Leptophyes*. We would therefore be interested to hear if anyone has observed it in another bush-cricket genus, or another species of *Leptophyes*.

Acknowledgements

We would like to thank Ian Kilduff for data collection, Roger Lowry for a huge contribution to insect collection and maintenance, Martin Kincaid from The Parks Trust Milton Keynes for additional assistance with insect collection, Mike Manley from Railtrack PLC (as it was at the time) for arranging vehicle access to the Folkstone Warren, and the Open University and the British Council for their financial support.

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Figure 1: *Aptenoperissus etius* Rasnitsyn & Öhm-Kühnle, 2018.

Meet the Dracula wasp – how a musicologist came to collect insect fossils

Christoph Öhm-Kühnle

Christoph Öhm-Kühnle (Photo: Copyright Christoph Öhm-Kühnle)

I am not a professional biologist or palaeontologist. I am a trained musicologist and pianist – but I like to continually learn and discover. My areas of interest are quite broad: musicology and music, bird watching, historic novel writing, vintage watches, art collecting, and collecting and studying insect fossils (in particular, wasps).

I have collected fossils since my childhood. As a kid, we went every other weekend with the whole family to the Swabian Jura (which gave its name to the Jurassic), near my hometown in South Germany. Soon I had gained a thorough knowledge of the Earth's geological history. Also, I collected amber pieces which I found on the beach during my vacations by the North Sea in Germany. A great advantage in my collecting hobbies was that I had the privilege to grow up in a large house (where I still live today) with plenty of space. It is located on a hillside and our garden borders a nature park. Among the first insects I observed in our garden were butterflies (including the beautiful swallowtail; *Papilio machaon*) and a large colony of antlions (*Euroleon nostras*) –

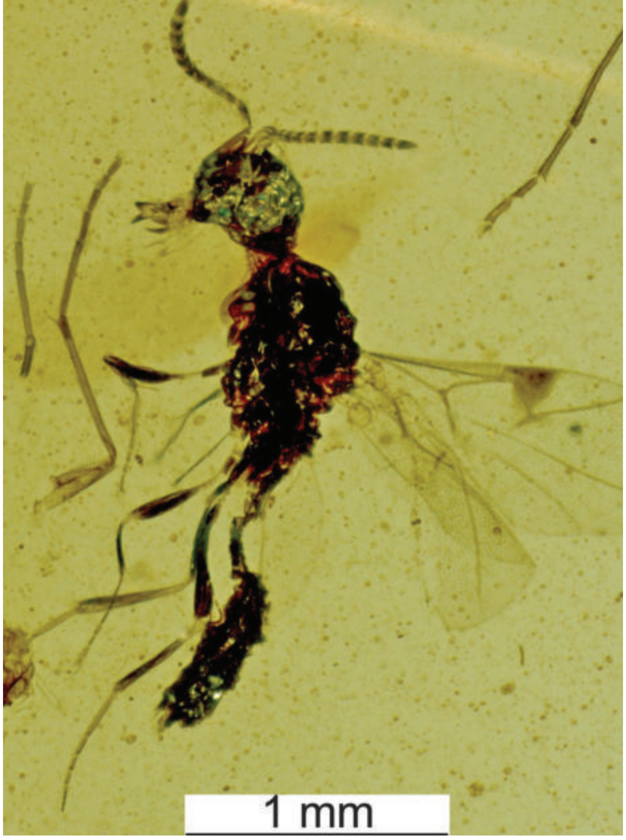

Figure 2: *Supraserphites draculi* Rasnitsyn & Öhm-Kühnle, 2018.

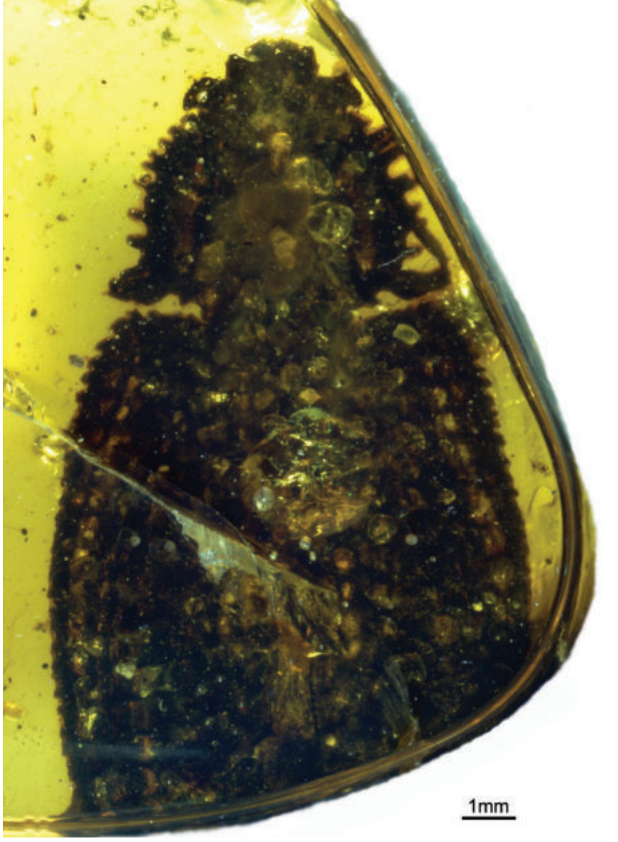

Figure 3: *Echinocups ohmkuhnlei* Jarzembowski, Wang & Zheng, 2020.

the latter are still there today, but swallowtails have sadly disappeared.

Some years ago, I read about the amazing treasure of unknown insects buried in amber, which more and more come into the focus of science because of the remarkable quality of their 3-D preservation, and the importance of these fossils for understanding insect evolution. I began studying entomology thoroughly by myself: I dived into books and articles on insects and, to get a better understanding, I began collecting insects. Somehow, I became most fascinated by parasitoid wasps, maybe because there are so many grotesque-looking species among them. Most important for me, however, was to learn more about the evolution of Hymenoptera. Owning insect fossils was never important to me, but I enjoy sharing and discussing my finds with others. So, it did not make sense to gather the specimens at home, but rather to deposit them in public institutions, or to donate them to experts on particular insect families.

The first article on insect fossils which I published involved a new species of the enigmatic Cretaceous aptenoperissid wasps, in approximately 99 million-year-old amber (Figure 1). When I first saw the amber piece containing this wasp inclusion in the seller's catalogue (offered as "unknown insect inclusion"), I was startled: the insect looked like nothing else I had ever seen: it had no wings, but showed a thick sting, long antennae, a bug-like body without a wasp waist, and strong hind legs for jumping. This odd morphology was the reason that I chose to name the species after the quite similar looking movie character E.T. (*etius*).

Among the researchers I contacted about my *Aptenoperissus* was Prof. Alexandr P. Rasnitsyn, who was the first to describe this family (together with co-authors George Poinar and Alex Brown). He right away proposed publication of this wasp together with me, which was most kind, considering that I am not college-educated in biology, but self-taught.

The cooperation for this first article of mine worked out well and, as an expression of my gratitude for Alexandr Rasnitsyn's kindness to publish this wasp (and two other species which I soon after acquired) with me, and in order to make these fossils publicly accessible, I decided that the ambers published in our article should stay at the Academy of Sciences in Moscow, at the Palaeontological Institute which Alexandr Rasnitsyn directs and which already houses a famous fossil collection. This was the starting point for my collection at the Academy, which soon grew significantly (although transportation of the newly acquired specimens can sometimes be difficult). Under Prof. Rasnitsyn's guidance, my own interest for general taxonomic issues grew, and we have co-authored several articles since concerning the taxonomy of proctotrupomorph wasps. However, our description of a new subfamily in Serphitidae, Supraserphitinae, with its rather grotesque-looking species *Supraserphites draculi* (Figure 2) earned more notice by the press than some of our other, possibly more important, articles. The reason for this public interest might have been that we named this species after Count Dracula, due to the wasp's nicely visible mandibles and 'teeth', and its demonic appearance.

Through donations of other insect fossils of undescribed taxa, which I had the privilege to acquire, I got in touch with other wonderful entomologists all over the globe. Some "ohmkuhnlei" patronyms (most studies are still in preparation) document these gifts, my appreciation of the work of these wonderful scholars, and my aim to help to better understand insect evolution (Figure 3).

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Tales of the Unexpected

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It is now many years ago since I received the response to a grant proposal that the sponsors were minded to award, but were not happy that the work of the third year would depend on the results obtained so far. I am ashamed to admit that I cracked, and asked to withdraw the proposal as I appeared to be mistaken in thinking it was a 'research' grant. My irritated reaction produced no response for several weeks, until I was simply informed that I had been awarded the grant!

If the progress of research can be predicted, it is hardly likely to do more than nibble away at the known frontiers of science. All my PhD students started with an initial idea to progress. However, I also advised them that they should hope to spot something unexpected; then they could translate to a truly original investigation. This article tells the story of some of the lucky ones, as well as of a more recent unexpected event since my retirement.

Very soon after I started in Reading, the Cyanamid company was marketing chlormequat chloride (CCC) to shorten the straw of cereals in order to reduce lodging. I was able to show that cabbage aphid (*Brevicoryne brassicae*) population growth was retarded on CCC-treated Brussels sprout plants (van Emden, 1964). During this work, I read a paper (Carlisle *et al.*, 1963) showing that topical application of the plant growth accelerator gibberellin shortened the instar lengths of locusts. Thus, starting a PhD on reciprocal effects of plant growth regulators on plants and insects was hardly an original idea, however previously unexplored. We used black bean aphid (*Aphis fabae*), but none of the different plant growth regulators we collected affected aphid population growth. But something totally unexpected did occur – a plant growth accelerator, ethylene bisnitrourethane (EBNU), under development at ICI, produced white black bean aphids. Figure 1 shows the results of transfer experiments which gave us white or black adults and offspring in all combinations (Honeyborne and van Emden, 1976). We were even able to advise ICI on the likely mode of action of their candidate compound. Melanisation is an oxidation process, suggesting that EBNU is an oxidase inhibitor. Plant growth involves the natural accelerator indole acetic acid (IAA), with its titre regulated by the enzyme IAA oxidase. An oxidase inhibitor would allow IAA to accumulate and continue to promote plant growth.

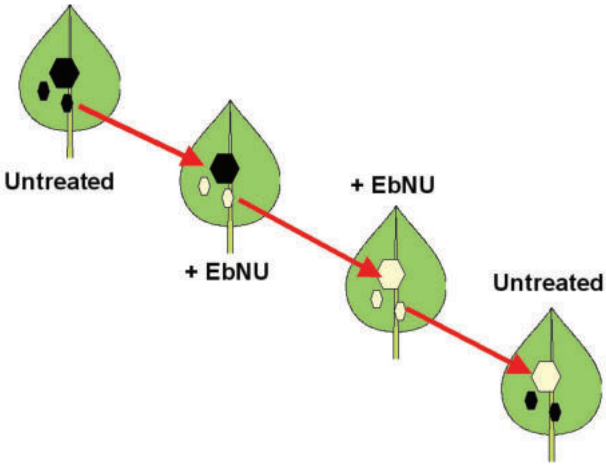

Figure 1. Diagrammatic representation of the results of transferring young black bean aphids between plants untreated and treated with the plant growth accelerator EBNU. Note that aphids retain their coloration after transfer, but the colour of their offspring is affected by the transfer.

In the late 1970s, reports started coming from New Zealand that the use of synthetic pyrethroids in apple orchards was causing outbreaks of red spider mite. The explanation proposed

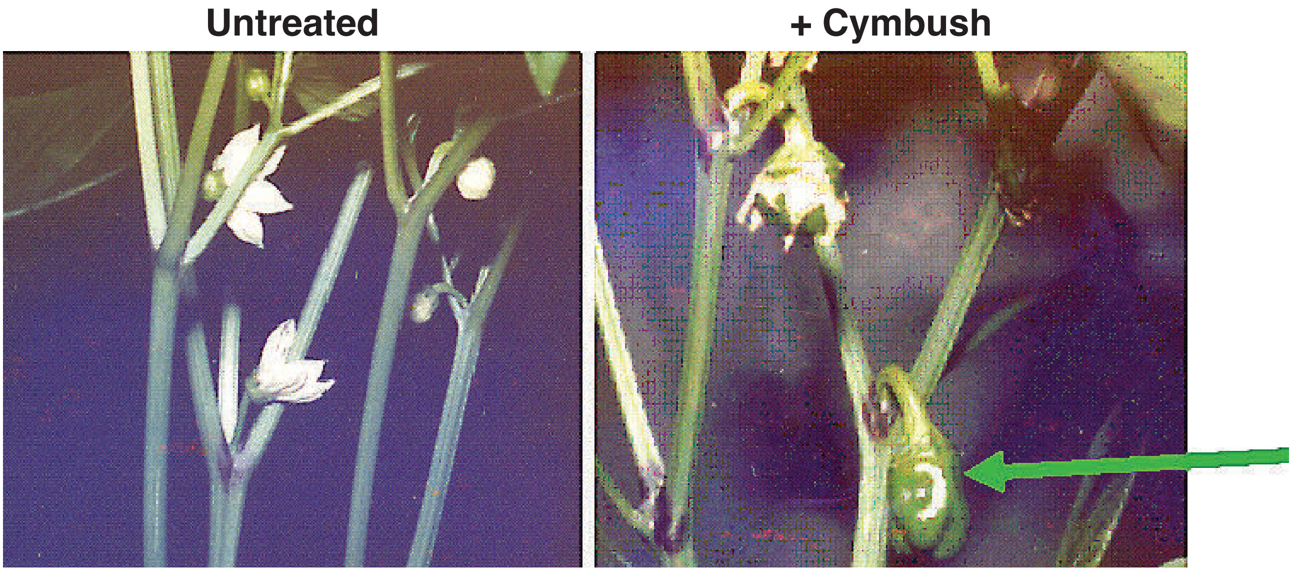

Figure 2. Pepper plants untreated and treated with the synthetic pyrethroid cypermethrin (as 'Cymbush'). The untreated plants have just started to flower, whereas the flowers on the Cymbush-treated plants are over and pods (arrowed) are beginning to form.

was that the insecticides were highly toxic to the mite's insect natural enemies. I thought an obvious alternative explanation was that the pyrethroids were changing the physiology of the plant to the mite's benefit, so again it was not that original an idea to launch a PhD study on whether synthetic pyrethroids stimulate aphid populations. My student was in a hurry, and set off with black bean aphid and cypermethrin (in the form of Zeneca's Cymbush^{TM}) -treated broad bean plants. This appeared to be a mistake, since the fast growth rate of beans resulted in plants having flowered and podded (as also with peppers, Figure 2) while the insecticide residues were still at aphid-lethal levels; but only the treated beans had accelerated growth. This was completely unexpected, and the project switched from entomology to a plant growth study.

The obvious next step was to check whether the culprit was indeed cypermethrin, so we asked Zeneca for the active ingredient-free blank formulation. They were happy to supply this provided we switched the work to cowpeas. The blank formulation produced the same effect as Cymbush, but so did just one of the several formulation components, the non-ionic emulsifier. This, like the blank formulation of Cymbush, increased plant aerial fresh weight of cowpea plants by some 20%, and so could be identified as the component of Cymbush that accelerated plant growth (Hutt *et al.*, 1994).

Why do other insecticides formulated as emulsifiable concentrates with the same emulsifiers not show the same plant growth stimulation? I think the answer lies in the cancelling-out of any growth stimulation by some phytotoxicity of these other insecticides. There is very little toxic effect, if any, of pyrethroids on plants.

Back to entomology – we finally showed that on broad beans the non-ionic emulsifier also gave a 3-fold increase in black bean aphids after seven days.

Following the introduction in the 1970s of the fungicide benomyl, rumours started circulating that it was also controlling aphids. It was suggested that the fungicide changed the nutritional quality of the host plant, but strangely no one appeared to have done a simple bioassay of the fungicide as an aphicide. Cue for another PhD study, which quickly showed that direct topical application killed bird cherry–oat aphids (*Rhopalosiphum padi*) and electronmicrography showed that the fungicide disrupted the mycetomes with bacterial endosymbionts (Figure 3B). The loss of these symbionts would kill the aphids, but of course death of the aphids from any cause would in turn lead to the death of the symbionts. So, we killed aphids with the carbamate insecticide pirimicarb, and this firmly established that the mycetomes in freshly-poisoned aphids were still intact (Figure 3C) and just like those of normal aphids (Figure 3A). Bingo! In less than two years of a PhD study, we had established that benomyl directly killed the obligate symbiotic bacteria essential for the aphid. I suspect we would have had no problem about publishing this conclusion in an entomological journal. However, unexpectedly we were saved from making this mistake by a microbiologist colleague who explained that benomyl was not toxic to bacteria. It was specifically a fungicide acting by the single mode of action of inhibiting the assembly of microtubules in the cytoskeleton of fungi, structures only found in eukaryotic cells. So there was, after all, work to do in the third year. Eventually we did

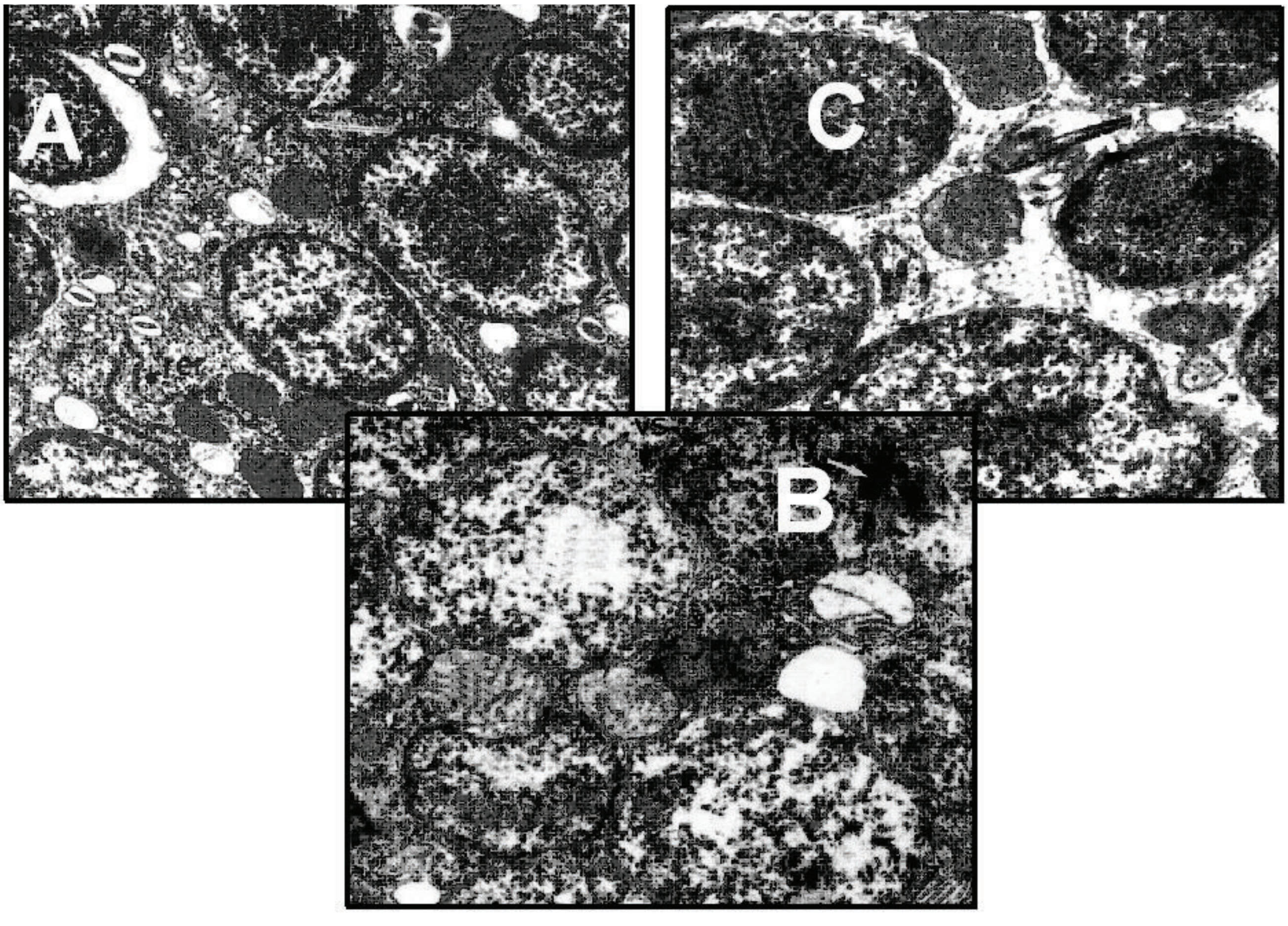

Figure 3. Electronmicrographs of the mycetomes of normal bird cherry–oat aphids (A), aphids killed with the fungicide benomyl (B), or with the insecticide pirimicarb (C).

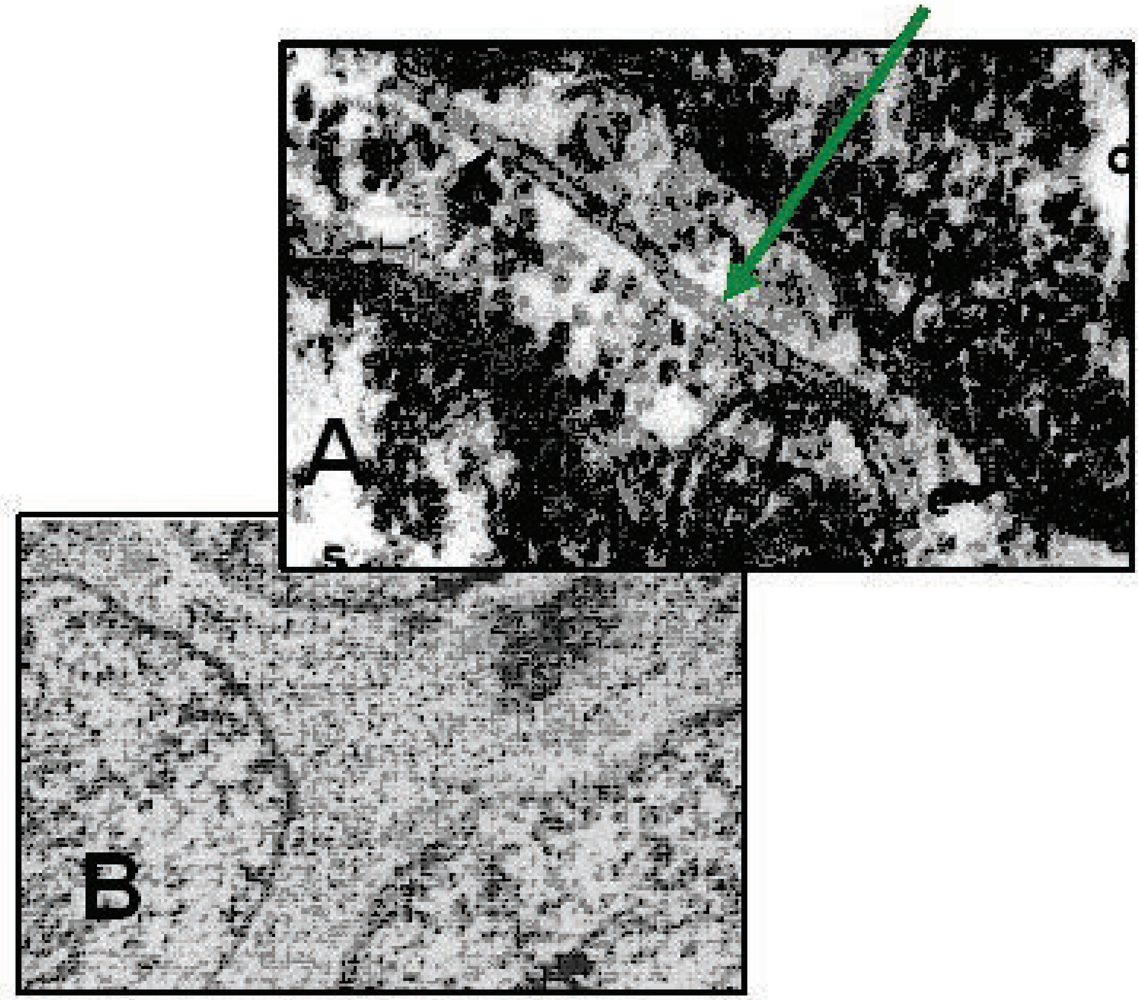

Figure 4. A microtubule (arrowed) present in the mycetome cytoplasm in a normal bird cherry–oat aphid (A), and absent in an aphid killed with benomyl (B).

find the microtubules targeted by the fungicide. They were present in the cytoplasm of the mycetocytes (Figure 4A), and we could show that they were absent in aphids treated with benomyl (Figure 4B). Thus, benomyl disrupted the interface through which nutrients pass from the aphid to sustain the symbiotic bacteria, which died but not as a result of direct toxicity of benomyl (Akhtar and van Emden, 1996). Our microbiologist colleague's advice that these microtubules must be fungal DNA implies its acquisition by horizontal transfer (Xiong and Eikbush, 1990).

For many years, my laboratory at Reading studied partial plant resistance to cabbage aphid by comparing reproductive performance of the aphid on two Brussels sprout cultivars, Bedford Winter Harvest (BWH) and the less susceptible Early Half Tall (EHT). At the end of one project we had a fair number of plants of the two cultivars with aphids left over, and we bunged them in a large cage as a reserve aphid culture. After some six weeks, we were somewhat surprised to see far more aphids on the supposedly less susceptible EHT than on BWH. The parasitoid *Diaeretiella rapae* had got into the cage, and a closer look showed many more mummies on BWH than on EHT. A proper experiment comparing aphid population growth on the two cultivars, with and without parasitoids, showed that a faster growing but heavily parasitised aphid population on BWH was eventually overtaken by a slower growing but less parasitised population on EHT (Figure 5). We also showed that the difference arose from the positive reaction of *D. rapae* to mustard oil volatiles (allylisothocyanates), which were twice as concentrated (as per cent dry weight) in the leaves of BWH as in EHT leaves (van Emden, 1978).

This reversal of plant resistance ranking in the presence of a natural enemy was the exact opposite of what I had been proposing and showing experimentally for this interaction ever since 1965 (van Emden and Wearing, 1965). We explored this phenomenon further in a whole series of projects and publications, soon switching the aphid and parasitoid species respectively to *Myzus persicae* and *Aphidius colemani*, as neither had any innate predilection for allylisothiocyanates. In

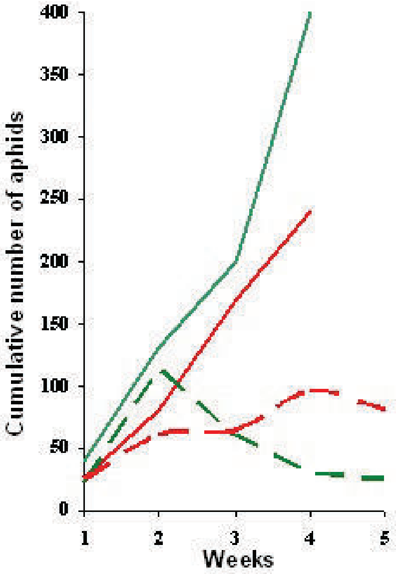

Figure 5. Population growth of cabbage aphid on the Brussels sprout cultivars Bedford Winter Harvest (green) and Early Half Tall (red) with (broken lines) and without (solid lines) the parasitoid *Diaeretiella rapae*.

this way we discovered the now well-established 'maternal influence' (Douloumpaka and van Emden, 2003), that a female *A. colemani* provides its offspring (in or on the egg) with the chemical spectrum to the level of cultivar specificity (van Emden *et al.*, 2019) of the host plant on which she developed. This is perhaps my favourite research conclusion of my career – and it only came about by accident.

The last research surprise I will describe came relatively recently. I used to spend some time in every summer vacation trying out an idea or two to see whether they showed enough promise to be the start of a student research project. So it was that some time in the early 1980s it occurred to me that aphids might need components that were not in my artificial diet for purposes other than growth and reproduction. Alarm pheromone came to mind, and a quick 'look-see' suggested that artificial diet-reared aphids did indeed not produce this pheromone. A student project in the next academic year confirmed this result with a proper experiment. End of story – for a while.

It was in 2012, well after my retirement and after I had stopped artificial diet work, that I reported this result at an Aphid Special Interest Group of the Society held at Rothamsted. After my talk, Professor John Pickett expressed surprise that the aphids could not synthesise the pheromone from my diet recipe, but suggested I could try adding acetate to get the metabolic pathway started. I made up some diet and added some sodium acetate. Eureka – there was an immediate response of plant-reared aphids to cornicle secretion of diet-reared ones. Not a surprise, perhaps, though it did transpire that aphids reared on diet without acetate were already synthesising the pheromone, and other aphids did respond if it was released as a larger pulse by puncturing diet-reared aphids with a pin.

I had already reared *M. persicae* on the diet for over 30 years, and adults had remained stubbornly much smaller than their plant-reared equivalents. Now I had stopped diet work we had discovered the magic bullet, sodium acetate, by pure accident. Too late in my career, I could now produce aphids on diet just as large as plant-reared ones (van Emden *et al.*, 2014). How irritating? You've no idea! I could have done with this discovery a good quarter of a century earlier.

With the first two projects, we set out on what was to us very familiar territory – measuring the reproductive rate of aphids. But much more exciting were, respectively, white black bean aphids and the plant growth promoting properties of a formulation component in an insecticide. We thought our hypothesis that a fungicide was killing the bacterial symbionts of an aphid was pretty novel stuff, but the demolition of this hypothesis by a colleague led to the even more unpredictable discovery of what is likely to be fungal tubulin in the aphid mycetome. The unwanted invasion of aphid cultures by a parasitoid opened up a new fascinating research area for us, providing rich pickings for eleven students and two overseas visitors. And could anyone have come up with the idea of adding sodium acetate to artificial diet in order to increase the body size of aphids? No, it was only discovered because we were doing something else with the compound.

We allowed the biological material to dictate the direction of our research. This is in contrast to quite a number of the several hundred research theses and dissertations I have examined at many different universities. I have not infrequently found that exciting leads were ignored because the insects were deemed to be 'getting it wrong'. Every statistical trick in the book was then tried to avoid rejecting the hypothesis being tested; I've encountered unwarranted log transformation, even double log, ignoring replicate variation by resorting to regression on treatment means, and increasing residual degrees of freedom by combining within and between plot variation.

It is no coincidence that none of the work I have described was grant funded. Research grant proposals tend to involve a three-year road map with 'milestones' to a predicted destination. There is a danger that these 'milestones' become 'millstones'. The outcome has to be identified in advance, since grant-awarding bodies want reassurance that the research will bring tangible benefits, such as contributing to greater profit or sustainability. This seems only reasonable in relation to publicly-funded research institutions. Sadly, universities now compete for funds for the same kind of research, when for much of my career they had a clearly defined different role of being curiosity driven rather than outcome-led. I think we've lost something.

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Society News

Fig. 1. Harebell, Wild Basil, Marjoram, St John's Wort, Cat's Ears and Birds-foot Trefoil bloom profusely on Daneway in July, providing nectar for an abundance of insects © Jeremy Thomas 2020

Daneway Banks SSSI in 2019-20: return of Duke of Burgundy and Pearl-bordered fritillary butterflies to the Society's Cotswolds nature reserve

Jeremy Thomas, David Simcox, Sarah Meredith, Alan Sumnall

In two recent articles in *Antenna*, we described the Royal Entomological Society's (RES) purchase of Daneway Banks Site of Special Scientific Interest in a 50:50 partnership with the Gloucestershire Wildlife Trust (GWT), and some specialities of this nationally important limestone grassland. The first (Thomas 2017) described the main entomological and botanical interests of the 42 acre Cotswolds reserve. It also reviewed the RES's history of pioneering the science, practice and UK policies of insect conservation during the 100 years since Charles and Walter Rothschild's Presidencies of 1915-22, and described the formal opening of Daneway as a nature reserve by HRH the Prince of Wales. The second (Thomas *et al.* 2019) described progress in 2017-18 – the third and fourth years of RES co-ownership – including the discovery of two further rare and exciting species breeding on it: the Downland Robber fly *Machimus rusticus* and one of the largest UK populations of the Rugged Oil Beetle *Meloe rugosus*, with new observations of the life-cycle and probable hosts of this fascinating kleptoparasite of sweat bees. In this article we focus more on the rarer butterfly and plant populations of Daneway Banks, as well as other target species that prospered in 2019-20 under the varied management of the Society's beautiful downland and its few acres of scrub and ancient woodland.

Flora

Let us start with flowers. The common – but nowadays all too local – species of unimproved calcareous grasslands were exceptionally abundant on Daneway, from the first Cowslips and Green-winged orchids of spring to the massed banks of Marjoram and St John's wort in high summer (Fig. 1). Several rarer plants for which Daneway is famed also had record populations in 2019-20, with the exception of Frog orchids which reached peak numbers three years earlier. Thus, among the numerous entomologists watching Large blue butterflies *Maculinea arion* and other insects during June and early July, was a smaller, equally enthusiastic, band of botanists seeking two Endangered plants: Cut-leaved self-heal *Prunella laciniata* (Fig. 2a) and Slender bedstraw *Galium pumilum*. Both plants flourish in warm, well-drained, early successional stages of calcareous grassland – in other words, the optimum habitat of the ant *Myrmica sabuleti* plus its symbionts and famous brood parasite: it is no coincidence that three of the *c.* 30 UK colonies of *P. laciniata* also support the Large blue.

Fig. 2. Nationally scarce plants on Daneway. (a) Cut-leaved self-heal occurs on *c.* 30 other UK sites. (b) Clustered bell-flower blooms throughout the grassland in high summer. (c) Cut-leaved germander provides nectar for, and is being pollinated by, the Common Carder bee *Bombus pascuorum*. © Jeremy Thomas, Daneway, 2019-20.

The white flowers and jagged leaves of this lovely self-heal can reliably be seen along the western stretch of the upper footpath. *G. pumilum* is less conspicuous, but flowered in record numbers below Adder Bank and in other patches of skeletal soil on this, its only known site in the Cotswolds (it occurs on about 40 other calcareous sites in southern England).

From mid-July onwards, Clustered bell-flowers *Campanula glomerata* (Fig. 2b) provide a showy source of nectar across the entire sward, but for botanists the real prize is the Cut-leaved germander *Teucrium botrysi* (Fig. 2c). Recorded from only six UK sites, this handsome biennial was historically known from just one or two (but often no) flowering specimens on Daneway. Its niche, again, is warm, early successional calcareous soil, especially where bare patches occur after disturbance, fire or drought. A record fifteen or so appeared following the recent excavation of the dew pond, and we predicted many more after the summer drought of 2018, based on numerous seedlings found once rain revived certain severely scorched patches overlying skeletal soils, mostly around and east of the dew pond (Thomas *et al.* 2019). These duly developed into 278 flowering plants in 2019 – an unprecedented number for this extreme rarity – providing a favourite nectar source for insects with sufficiently long proboscises, such as the Common carder bee *Bombus pascuorum* (Fig. 2c). Although flowering specimens were few in 2020, numerous seedlings germinated in July-August, again in drought-affected spots: another fine show of flowering plants is expected in 2021.

Orchids fascinate many entomologists, especially the mimetic *Ophrys* species. Bee orchids, *O. apifera*, are frequent across Daneway, but it has been a particular pleasure that the Fly orchid, *O. insectifera*, reappeared in 2015 under our new grazing regimes after an absence of about 15 years. Numbers are tiny still, but have increased each year in three compartments to reach 11 flowering plants by 2020. In the UK and northern Europe, Bee orchids self-pollinate due to the absence of *Eucera pulveraceae*, the Long-horned bee whose specific female sex-pheromone they mimic (Fenster & Marten-Rodrıguez 2007). Not so the Fly, as our cover image shows – photographed on Daneway by Anna Pugh on May 19th 2019. Although, to human eyes, the flowers resemble a dipteran – and while visual and tactile lures on the labellum are important for initial deception – the release by the same flowers of a volatile cocktail of aliphatic hydrocarbons, methyl esters and monoterpene and aliphatic alcohols that mimic the species-specific sex pheromone of a female hymenopteran is the primary signal that tricks males into attempting to mate (pseudocopulate) with it, thus transferring the pollinia (seen between the false 'antennae' on the top flower of the cover) from one orchid to the next, having first attached themselves to the wasp's head (Agren & Borg-Karlson 1984; Vereecken & Schiestl 2008). Although morphologically almost identical, the allomones of different subspecies of Fly orchid imitate and dupe very different species of bee or wasp in different parts of their range. In southern France, *O. insectifera* spp. *aymoninii* mimics and is pollinated by the mining bee *Andrena combinata*. Yet our UK subspecies, ssp.*insectifera*, has evolved to attract one of two species of digger wasp (Borg-Karlson *et al.* 1993): *Argogorytes mystaceus* in our image on Daneway. It is indeed enchanting to know that this complex interaction, like those of the Rugged oil beetle and Large blue butterfly, is once again being acted out each spring on Daneway.

Butterflies

We have previously described the history of the globally Endangered Large blue on Daneway (Fig. 3a), including its reintroduction in 2010 after successful trials in 1999-2005, and its use there of both Wild thyme and Marjoram as an initial larval foodplant, thereby doubling the number of *Myrmica sabuleti* ant nests available for older larvae to exploit (Thomas 2017; Thomas, Simcox & Meredith 2019). In 2019, a record emergence of approximately 10,000 adults laid an estimated 257,446 eggs (Fig. 3b), the largest population of any in the UK that year, or indeed so far as is known in Europe or the world. This however was a freak emergence – rather to be enjoyed while it lasted – resulting from a combination of optimum habitat management and ideal weather in the preceding 12 months. It was unsustainable because few *M. sabuleti* nests contain sufficient grubs to feed more than a single caterpillar to adulthood, even though a depleted colony will often desert, leaving the caterpillar – which has a remarkable ability to fast – waiting for up to three weeks in the vacant nest site for a neighbouring colony to bud in, carrying a fresh supply of ant brood (Thomas & Wardlaw 1992). Thus our models predicted a correction in 2020 back to around 3000-6000 adults, the densities in 2016-18. Numbers duly fell by 45% this year, a shade below that on Somerset Wildlife Trust's Green Down reserve, yet still one of the two largest known populations in Europe. It was safe, therefore, for us to take roughly 0.5% of Daneway's eggs in both years as the main source for four further introductions to newly restored former sites for this

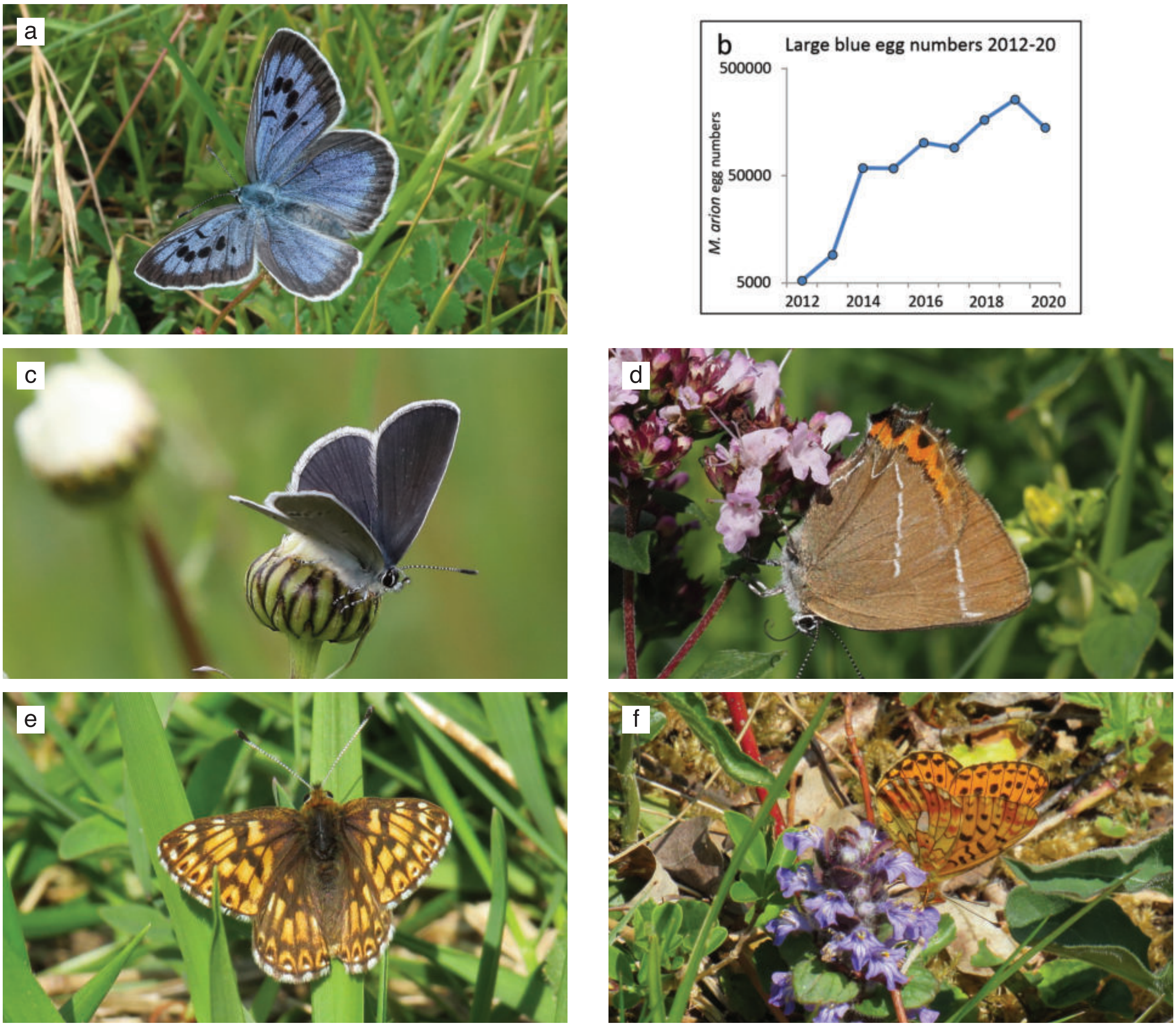

Fig. 3. 'Critically Endangered', 'Endangered' and 'Near-Threatened' butterflies breeding of Daneway. (a) Large blue ©David Simcox; (b) Large blue egg numbers since 2012; (c) Small blue ©Jeremy Thomas; (d) White-letter hairstreak ©Sarah Meredith; (e) Duke of Burgundy ©Alan Sumnall; (f) Pearl-bordered fritillary ©Alan Sumnall. All except Small blue were photographed on Daneway in 2020.

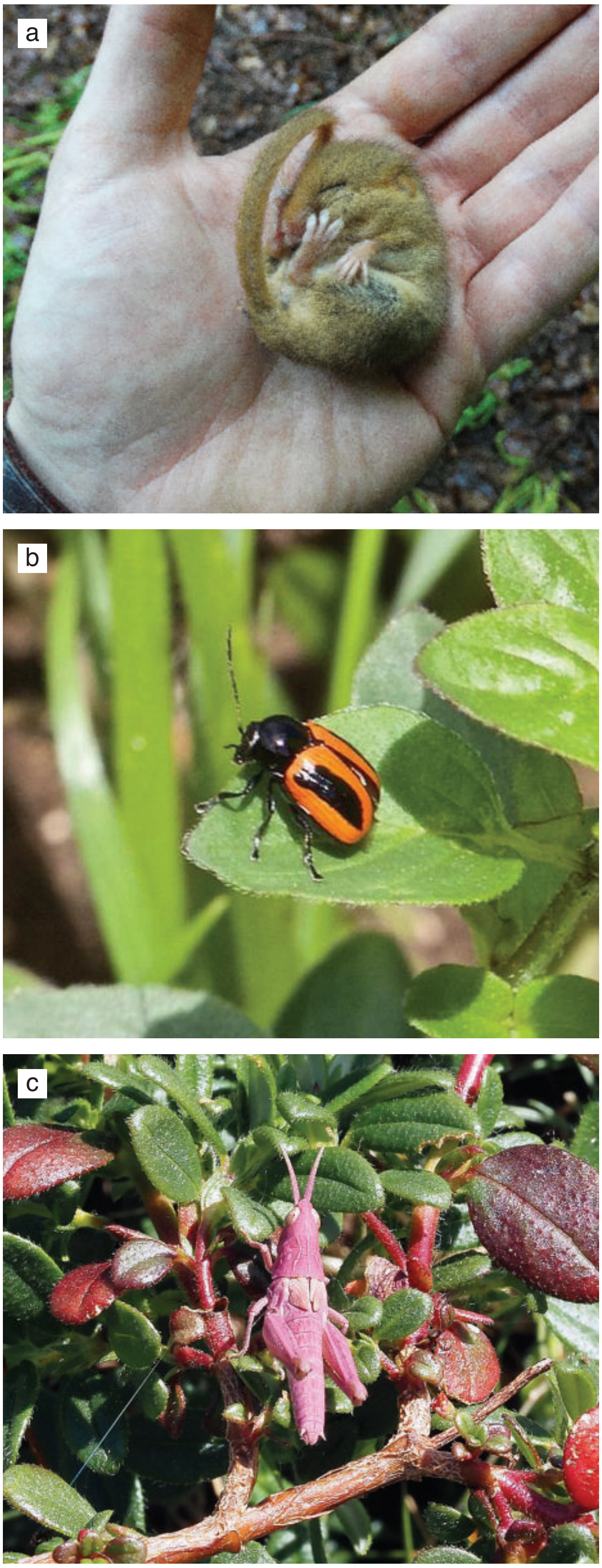

Fig. 4. Notable species newly recorded and photographed on Daneway.

(a) Dormice have spread from Siccaridge Wood to breed in similar densities in regenerating scrub on Daneway Banks in 2019-20 © Alan Sumnall, 2019 (AS is licensed to monitor and hold dormice).

(b) *Cryptocephalus bipunctatus,* a rare (UK Notable B) leaf or 'pot' beetle, probably associated with the regenerating shrubs and saplings © Nigel Gardner, 2020.

(c) A rare pink form of the female nymph of *Chorthippus parallelus*, the Meadow grasshopper © Sarah Meredith, 2020.

butterfly in the Cotswolds, all too distant for natural colonisation to be probable before 2060. Following a well-tried procedure, David Simcox and Sarah Meredith reared eggs and young larvae to their final moult, and released them at low densities at peak foraging times for *M. sabuleti* to adopt (Thomas, Simcox & Meredith 2019). The RES and GWT are proud to have played a key role is these restorations. Although premature to be sure of long-term success, the 2019 introductions resulted in a fine emergence of adults on Rodborough Common in 2020, which already match anecdotal reports from 1870, the last year of abundance (or presence) on this classic mid-19th century locality, now owned and restored (to our specifications) by the National Trust.

Daneway is a '*Helianthemum*-' rather than a '*Hippocrepis*-site' and so has no colony of Chalkhill blue, *Lysandra coridon*, or Adonis blue, *L. bellargus*. It does, however, support an exceptionally large population of Small blue, *Cupido minimus* (Fig. 3c), the UK's second rarest blue butterfly after the Large, for which the surviving fragments of unimproved Cotswold grasslands are a national stronghold. Under current grazing regimes, the larval foodplant, Kidney vetch *Anthyllis vulneraria*, grows and blooms in considerable (and increasing) abundance across all parts of Daneway, including on the thicker-soiled lower slope above the pub. Eggs and young larvae are also easy to find between the florets in late May and June, followed in most years by a smaller second brood in mid-summer. Another notable lycaenid is the White-letter hairstreak *Satyrium w-album* (Fig. 3c), seen every year especially where the west edge is overhung by the Wych Elms of Siccaridge Wood.

Two large fritillaries flew and drank nectar commonly across Daneway in 2019-20: the Silver-washed, *Argynnis paphia*, from a major colony breeding mostly in Siccaridge Wood, and the Dark Green, *Speyeria aglaja*, breeding on *Viola hirta* and *V. riviniana* throughout Daneway's grasslands. Pride of place, however, goes to the re-appearance of the Pearl-bordered fritillary, *Boloria euphrosyne*, now alas an endangered species across northern Europe. We deliberately restored, and will further extend, its specialised habitat within new areas of coppicing and rotational scrub cutting introduced by Alan Sumnall to the woodier sectors of Daneway (Thomas *et al.* 2019). We were thrilled to make six sightings of adults across several days in 2019; despite much-reduced monitoring due to COVID-19, this doubled to 12 sightings in 2020, with clear evidence that a small breeding population has established within the reserve. Equally exciting was the recolonization of Daneway by another target species, the Duke of Burgundy, *Hamearis lucina*. In 2019 we spotted one female laying eggs on Cowslips; by 2020 this increased to 10 sightings and an egg found, again despite little surveying being possible. We trust this heralds the foundation of a larger, permanent colony of the Duke. But for now, it is pleasing to know that Daneway Banks supports populations of four of the UK's ten 'Critically Endangered' or 'Endangered' butterfly species (Large blue, Pearl-bordered fritillary, Duke of Burgundy, White-letter hairstreak), as well as four 'Vulnerable' or 'Near Threatened' Red Data Book species (Dingy and Grizzled skippers, Small blue, Small heath) (Fox *et al.* 2011).

Dormice and other reports

One non-entomological aim of Sumnall's scrub management on Daneway was to entice the enchanting Hazel dormouse *Muscardinus avellanarius* across from a population in Siccaridge Wood (Thomas *et al.* 2019). So it was thrilling to discover a single pioneer in 2019 (Fig. 4a), followed by unequivocal evidence in 2020 of breeding in three of twenty-seven nest boxes erected for monitoring on Daneway. This already approaches a similar density, albeit over a smaller area, to that in Siccaridge Wood. Returning to entomology, 2020 saw two noteworthy additions to Daneway's list. The first, made on July 6th by GWT volunteer Nigel Gardener, was of the Scarce pot beetle *Cryptocephalus bipunctatus* (Fig. 4b), classed as 'Nationally Notable B' in the UK. The second, by Sarah Meredith, is more an oddity: a rare pink form of the female nymph of the Meadow grasshopper, *Chorthippus parallelus* (Fig. 4c).

People and Outreach

As in previous years, large numbers of entomologists and naturalists visited Daneway from across the UK and mainland Europe in 2019, especially during June and early July to see, photograph or film adult Large blues. In May, it was a particular pleasure to host a meeting of the Entomological Club (Fig. 5), which includes three former RES Presidents, current President Helen Roy and five Hon. FRES among its eight members. Some were visiting Daneway for the first time; all were highly appreciative.

Due to the COVID-19 lockdown, visitors were more locally sourced, though still plentiful, during the first months of 2020, when the Large blue emergence started exceptionally early, on May 29th. Nonetheless, Daneway was much in the news. In early June it starred in BBC's *Springwatch*, when GWT President (and *Countryfile* presenter) Ellie Harrison delivered a report about the Large blue from the site. Then in July, Daneway was cited as the main source of Large blue larvae introduced to Rodborough Common in a press release led by the National Trust and Butterfly Conservation. This resulted in considerable publicity for the RES, which was 'mentioned in dispatches' in numerous articles in the local and national media, including on the websites of BBC, ITV, Sky and CNN news, and internationally in China, Europe and the USA.

Acknowledgements

We thank Mike Edwards for identifying *A. mystaceus*; also Anna Pugh and Mark Greaves for their painstaking monitoring of species in 2019, and – with Nigel Gardner – for permission to reproduce photographs. They and many other dedicated volunteers provide invaluable help throughout the year not only in monitoring but also in practical conservation, including scrub management during autumn and winter, and with welcoming and informing our many visitors during spring and summer.

Fig. 5. Meeting of the Entomological Club and guests on Daneway Banks, May 2019: four Club members are visible. Foreground: RES President Helen Roy and Simon Leather; background, left to right: Richard Lane, Sarah Meredith, Mark Greaves, Clive Farrell, Alan Sumnall, David Simcox. ©David Roy

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Meetings

Behaviour Special Interest Group

On-Line Meeting On Chemical Ecology

8th September 2020

Richard Harrington

Blackcurrant sawfly, *Nematus olfaciens*

- Hymenoptera: Tenthredinae
- Common and pest of blackcurrant
- Infestation is sporadic and localised, and damage can occur rapidly
- No practical, systematic sampling methods or attendant crop damage thresholds have been developed

UNIVERSITY of GREENWICH

New look. Professor David Hall (Natural Resources Institute, University of Greenwich) giving the Society's first ever on-line-only conference presentation.

A little bit of RES history was made on this occasion, it being the first ever on-line-only scientific meeting of the Society. There are many pros and many cons of such. The former include ease and cheapness of access, lack of need for room hire and refreshments, and environmental considerations. The latter are mostly centred on the absence of social interaction, which engenders collaboration and plays an important part in making the scientific world go round. The meeting was to have been held at East Malling in Kent and was organised by NIAB EMR's Michelle Fountain and Rothamsted's Jozsef Vuts, with vital technical support from Christina Conroy and Cindaniah Godfrey from NIAB EMR, and Fran Sconce and Kirsty Whiteford from the Society. Sixty-one delegates attended, including some from the USA, Canada, Brazil and Argentina, for whom it began at an unearthly hour, and some from India and Australia, who must have had a very long day. Christina outlined the technical instructions and I introduced delegates to the benefits of belonging to the RES. Had the meeting begun five minutes earlier, there might have been an interruption or an expletive, as my house shook rather worryingly for a couple of seconds as a result of a magnitude 3.3 earthquake centred on Leighton Buzzard, less than five miles away. That was another first for me!

The on-line nature of the meeting made it possible to invite more keynote speakers than usual, without worrying about the cost of bringing them from overseas. The first, though, came from the Natural Resources Institute at the University of Greenwich, just down the road from East

Malling. David Hall spoke about insect cuticular hydrocarbons (CHCs) as volatile semiochemicals. CHCs are typically long-chain, involatile alkanes and alkenes that provide waterproofing for the cuticle, but they have been shown in many insects to have evolved secondary roles as low-volatility (hence short-range or contact) semiochemicals. Now it seems they can also synergise the effect of more-volatile compounds that have roles in sex pheromones. CHCs do not invoke clear electroantennographic responses and are hence difficult to detect, but can greatly enhance the effectiveness of pheromone-based field lures. It is possible that they are detected by receptors on, for example, the palps or tarsi, rather than the antennae. Interestingly, CHC semiochemicals have been found to be relatively conserved in structure across a wide range of insects, so it is difficult to understand how they add to the information in a pheromone blend. David suggested that pheromones which don't appear to elicit responses when synthesised, should be reinvestigated in case the problem can be resolved by addition of appropriate CHCs.

Esther Ngumbi (University of Illinois) is studying the potential of soil microbes in pest management. Plant growth-promoting rhizobacteria (PGPR) and mycorrhizal fungi can induce systemic resistance to insect herbivores. Esther is examining the effects of PGPR on inducible indirect defences (production of volatile organic compounds (VOCs)), and direct defences, against insect pests of corn and cotton. When plants are inoculated with PGPR, the plant VOC signature changes dramatically, both qualitatively and quantitatively. The changes can repel herbivores, reduce larval feeding, reduce pupal size, increase mortality and attract natural enemies. Certain PGPR strains are entomopathogenic, and these have the potential for use in foliar sprays. Esther's work has resulted in three US patents using PGPR to control chewing insects. She is interested in factors shaping the outcomes of soil microbe–plant–insect interactions, and has found that maize genotype significantly affects VOC composition, and overwhelms the effects of the composition of the microbiome. This suggests the need to breed crop varieties that can take advantage of the broad range of beneficial soil microbes. Esther's long list of pertinent questions for future research should keep her occupied for many years, and she is especially keen to see practical application of her work for smallholders in areas of Africa suffering most from low-productivity agriculture.

Time and space play crucial roles in influencing the outcome of interactions between insects and plants. Toby Bruce (Keele University) pointed out that host-seeking behaviour of insects has taken 400 million years to evolve, yet the interactions happen in a split second. Many odours impinge on insects' sensory systems, and to distinguish those that are relevant at a particular moment from those that are not requires sharp spatiotemporal deciphering of odour cues. In many cases, blends of odours are important. For example, many electroantennograph-active compounds in bean leaves repel *Aphis fabae* (black bean aphid) when presented individually, but attract it when presented as a blend. This makes sense, as the insects are unlikely ever to encounter the chemicals individually. A dilemma faced by plants is the need to attract pollinators whilst not attracting herbivores. Complex interactions and trade-offs are at play in this regard. Plants that are attacked by insects can warn neighbouring, insect-free, plants which are linked via mycorrhizae. These plants then become repellent. Similarly, the aphid parasitoid, *Aphidius ervi*, is attracted to un-infested plants linked to infested plants via mycorrhizae. The extent to which cues are innate or learned is an interesting question requiring further research. It seems likely that an ability to adapt to changing environmental conditions is needed. In answer to a question, Toby said that, in order to ease the transfer of such findings into practice, registration procedures should be streamlined for environmentally-friendly methods.

The fourth keynote was given by Zoltan Imrei (Plant Protection Institute, Budapest). He described a novel trap for monitoring *Agrilus* jewel beetles, some of which have become major pests of oak, ash and cypress throughout Europe. The trap is light green and a multi-funnel design, and has the advantage of cheapness, lightness, ease of hoisting up a tree, no fluid needed, and a non-sticky nature, making sifting of samples much easier than with sticky traps. Indeed, insects can be caught alive. More details can be found at https://onlinelibrary.wiley.com/doi/full/10.1111/jen.12727.

Drosophila suzukii (spotted-wing *Drosophila*; SWD), a recent arrival in the UK, is a pest of many soft fruits and stone fruits. Its wide host range and damage potential arise from its serrated ovipositor, unique to the *Drosophila* of Europe, and its ability to produce up to 16 generations per year. It was the subject of two talks and a poster from students at NIAB EMR. Control currently relies on frequent insecticide usage, but Trisna Tungadi is studying how oviposition is deterred dramatically if *Drosophila melanogaster* has laid first, and is hoping to find an oviposition-deterrent compound which can be synthesised and used to reduce damage by SWD. Trisna has discovered that effective deterrence only occurs if a substrate is pre-exposed to both male and female *D. melanogaster*. It is possible that the deterrence arises from eggs or larvae rather than adults, and this is being investigated. Rory Jones is exploiting SWD's penchant for yeasts and investigating their use as traps and as phagostimulatory baits to attract SWD to pesticides. All five single yeast species tested, and most combinations (either singly-fermented then combined, or co-fermented) were attractive to both winter and summer morphs, but to varying extents. Work is underway to investigate which yeast formulations will be most effective when combined with insecticides. Christina Conroy is developing a "push–pull" strategy to repel SWD from crops and attract them to traps, although the "pull" phase is beyond the scope of her PhD. SWD has distinct morphs in winter, which they spend in woodland, and summer, which they spend in the crop. Reducing the influx of winter morphs to the crop could lead to season-long reduction in damage. Electroantennography and behavioural trials were used to test a panel of potential repellents on winter morphs (tested in autumn) and summer morphs (tested in spring). Three of these were found to reduce the numbers of both winter and summer morphs in traps, and eggs on sentinel raspberry fruits in polytunnel trials.

Staying with "push–pull", Marla Hassemer (University of Brasilia, and Embrapa), is attempting to manage *Alphitobius diaperinus* (lesser mealworm), the most important insect pest of poultry worldwide because of its role in transmitting a range of bacterial, fungal and viral diseases. Brazil is the biggest exporter of broilers, and the industry accounts for 1.5% of the country's GDP. Marla has evaluated the combination of the recently-identified alarm and aggregation pheromones as a repellent and attractant, respectively. More *A. diaperinus* were captured in aggregation pheromonebaited traps where the alarm pheromone was being used to "push", compared to use of the aggregation pheromone alone. This in important, because the alarm pheromone appears to displace *A. diaperinus* from places that cannot be reached by insecticides. Impacts on poultry health have not yet been measured.

Diego Segura (INTA and CONICET, Argentina) described work looking at how VOCs produced by guava fruit affect the calling behaviour, chemical signalling and mating success of male *Anastrepha fraterculus* (South American fruit fly). Exposed mature males had an increased signalling rate, produced more sex pheromone, achieved significantly more matings and mated for longer, than mature males that had not been exposed to guava VOCs, in both laboratory and field trials. Females mated with guava-exposed males had a higher fecundity than those mated with non-exposed males. No contact with the plant was needed to induce these effects, and guava essential oil had the same effect as whole fruits. The effect does not appear to be mediated by a change in the aroma of the male cuticle or an accelerated sexual maturation.

Sándor Koczor (Plant Protection Institute, Budapest) is studying the chemical ecology of Central European populations of *Adelphocoris lineolatus* (alfalfa plant bug). A sex-pheromone blend of three chemicals, identical to those of East Asian populations, was identified, but another chemical, 1-hexanol, also elicited electroantennographic activity. When tested in combination with the pheromone blend, 1-hexanol significantly decreased attraction of males. Prospects for application of 1-hexanol as a sex-pheromone antagonist are under investigation. It is unclear as to whether its origin is the insect or the host plant.

Anthonomus grandis (cotton boll weevil) is the target of the work of Diego Magalhães (Embrapa). It is the main pest of cotton crops in the Neotropical region. Kairomones which attract *A. grandis* were identified from cotton plants and explored in laboratory and field experiments aimed at optimising trapping efficiency. The combination of a sex pheromone and the plant kairomone gave far stronger attraction than either component alone.

Richard Merrill (Ludwig Maximilian University of Munich and Smithsonian Tropical Research Institute) has identified candidate genes responsible for shifts in visual mate-preference behaviours in *Heliconius* butterflies. These candidates suggest that shifts in behaviour involve changes in integration or processing, allowing the evolution of preference without altering the perception of the wider environment. Emerging data also suggest that behavioural alleles may be acquired through introgression, allowing reassembly of existing genetic variation into new combinations, further facilitating the rapid evolution of novel behavioural phenotypes.

Behavioural experiments need to be reproducible, and this requires carefully-controlled experimental conditions. Bill Budenberg (Zantiks) described the Zantiks MWP Unit, an automated and controlled environmental set-up permitting standardisation of animal behaviour experiments. He demonstrated it by testing the "startle response" of *Culex* adults and larvae to light and vibration.

This was an excellent and varied selection of presentations. One unfortunate feature of an on-line conference is that the presenters can't hear the delegates clap so, at the end, the presenters and organisers were unmuted for a communal clap. Hopefully the other delegates joined in, albeit unheard. All the presenters had co-authors, to whom credit and thanks are also due.

The on-line platform included a poll facility, which was used to get an idea of the demographic of attendees. 40% were students, 66% were male and 34% female, 62% were members of the Society. Routine collection of such information will be very useful in helping to ensure that the Society is appealing to a diverse audience.

Infection & Immunity and Symbiont Special Interest Groups

Online Conference 24th – 25th September 2020

Alexandre Leitão
(ac2016@cam.ac.uk)
and Francis Jiggins
(fmj1001@cam.ac.uk)
(Convenors)

Department Of Genetics, University Of Cambridge

In April 2019, a very successful conference was organized at the University of Nottingham that combined the SIGs now called "Symbionts" and "Infection and Immunity". To keep pace with recent discoveries in both fields of research, we planned to repeat the formula in 2020, by organizing a conference of both SIGs at the University of Cambridge. However, as in any other area of society, we had to adapt to the restrictions caused by the COVID-19 pandemic and decided to organize a shorter version of the conference online, with the programme spanning two afternoons.

Scientists working in these fields, and interested amateurs, responded very positively to the conference changes. In total we had 139 participants signing up for the conference, from all around the world. We had peak audiences of 90 participants on both days.

The first day started with the theme of endosymbiosis. *Wolbachia*, the most common endosymbiont in insects, has been the subject of intensive research in the past decade. This is especially driven by concerted efforts to introduce *Wolbachia* into mosquito populations to control human

Figure 1. *Sitophilus oryzae*. © M. Ferrarina.

pathogens, like dengue. The work presented by Luís Teixeira (Instituto Gulbenkian de Ciência, Portugal) elucidated how a region of the *Wolbachia* genome, termed Octomom, is responsible for controlling its proliferation in the vinegar fly, *Drosophila melanogaster. Wolbachia* strains with multiple copies of the Octomom region over-proliferate in the host, causing premature death. Surprisingly, deletion of this region causes the same shorter-lifespan phenotype. This work demonstrates that it is possible to study the genetics of endosymbionts that are, so far, genetically intractable.

Daniel Leybourne (University of Dundee) continued to explore the interaction between endosymbionts and hosts. As in other insects, the presence of the endosymbiont *Hamiltonella defensa* confers resistance to parasitoid wasp infections in the bird cherry–oat aphid, *Rhopalosiphum padi*, but the fitness effects resulting from the interaction between host and endosymbiont are complex. For example, aphids with endosymbionts have a faster feeding behaviour and higher chances of feeding on the phloem of barley. However, this phenotype is reversed when feeding on wild barley varieties with partial resistance to aphids, where aphids without the endosymbiont feed faster.

The coevolution of hosts and endosymbionts leads, in some cases, to the evolution of specialized organs to contain the endosymbiont in the host. The work of Mariana Galvão Ferrani (University of Lyon) explores the development of such structures in the cereal weevil, *Sitophilus oryzae* (Fig. 1), which has an established relationship with the endosymbiont *Sodalis pierantonius*, in specialized cells called bacteriocytes that form a bacteriome. To comprehend the developmental changes observed in these organs from larva to adulthood, it was necessary to quantify the genes expressed at different life stages by the bacteria and the host. Combined with cellular imaging, Mariana and collaborators have shown that bacteriomes migrate along the midgut during metamorphosis to clusters of stem cells. This migration coincides with a change in expression of genes related to cell motility and adhesion in bacteriocytes. At the same time, endosymbionts start to express genes related with virulence factors. This work suggests that a molecular cross talk between host and endosymbiont is necessary to develop these organs.

Although arthropods do not possess an adaptive immune system, parasite infections can result in higher immune resistance to a second exposure, a phenomenon termed immune priming. Several factors can affect immune priming. The work of Cybèle Prigot-Maurice (University of Poitiers) explores how age, gender and the endosymbiont *Wolbachia* affect it. Although priming is observed in both young and old animals, it is reduced in old females. The effect is very different in *Wolbachia*-infected animals, where priming is only observed in old animals. This highlights how important it is to consider several factors when studying these ecological interactions.

The first day of the conference ended with a talk by Esteban Beckwith (Imperial College), which explored the interaction between the immune and nervous systems. Infection by pathogenic and non-pathogenic bacteria causes sleep disruption in *D. melanogaster*. Interestingly, in animals that cannot produce the immune signalling molecule Spätzle, the disruption of sleep caused by infection is not observed. This phenotype is observed when Spätzle is inhibited just in the fat body, an immune-responsive organ in insects. Interestingly, when two genes in the immune pathway downstream of Spätzle, *Dif* and *Myd88*, are inhibited in neurones, infected animals also show no disruption of sleep. This work suggests that a communication between the fat body and the brain exists to control behaviour after infection.

The theme of interplay between nervous and immune systems continued on the second day of the conference. Previously, the laboratory of Julien Royet (University Aix-

Figure 2. *Ips typographus*. © A. Ceballos-Escalera.

Marseille) has shown that bacterial-derived peptidoglycans reduce female oviposition in flies. Recent work now identifies the dopaminergic neurones in the brain that express genes from the immune pathway NF-κB, responsible for the detection of peptidoglycans. Upon sensing of the peptidoglycans, activity of a single pair of neurones in the brain transiently reduces egg lay in females, showing how rapidly animals can adapt their physiology upon infection.

Crystal Vincent (Imperial College) explored the differences in infection pathology between sexes. In flies, females show a higher tolerance than males for the negative effects of infection. This difference can be attributed to a different regulation of the NF-κB immune pathway in females upon infection.

The work of Arunkumar Ramesh explored how different selective pressures from parasites can affect the evolution of inducible immune responses. In *D. melanogaster*, one characteristic inducible immune response is the production of specialized immune cells upon parasitism. Using populations of *D. melanogaster* under artificial selection with constant infection by the parasitoid wasp *Leptopilina boulardi*, this work shows that production of specialized immune cells can evolve to become a constitutive immune response.

The conference included works describing the parasitic communities of important insect hosts. Juliana Nicolas Armache (University Minas Gerais, Brazil) used public sequence libraries from the honeybee, *Apis melifera*, to reveal the level of infection by known virus species like *Varroa destructor* virus and Deformed wing virus. In the process, potentially new virus species were discovered that need further characterization. Angelina Ceballos-Escalera Fernández (Natural History Museum, London) studies the community of fungi associated with a recent pest species found in the UK, the bark beetle, *Ips typographus* (Fig. 2). The work shows that with the beetle, fungal species were also introduced. These are in close association with the species but, in locations where it encounters closely-related species, it is possible that these fungi can cross-contaminate other species.

The conference ended with a talk by Alice Laciny (Konrad Lorenz Institute, Germany), that reminded us of the importance of always considering parasites in any study that bridges ecology with development and evolution. Using a thorough review of the literature, Alice described how infections by nematodes of the family Mermithidae can affect the development of ants, blurring the phenotypic differences between castes (Fig. 3).

The change from in-person to online conference affects how the participants interact. There is a long way for us to go to adapt this format to make the most of it. Nevertheless, the reactions from participants were very positive and show that the conference reached its most important aim, to inspire future research in insects.

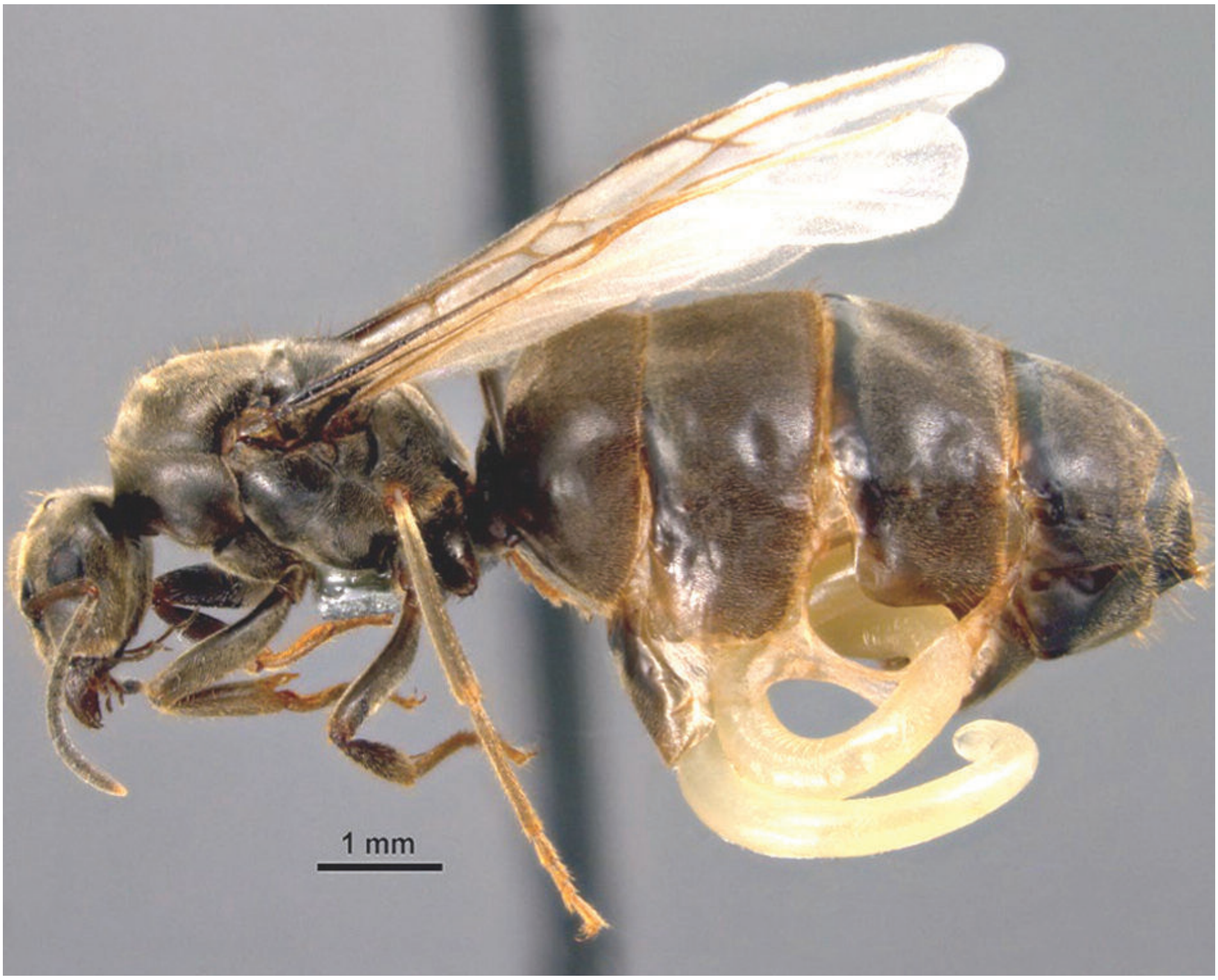


Figure 3. Gyne of *Lasius niger* from Austria, with a mermithid nematode erupting from the gaster, and shortened wings. © A. Laciny

Honorary Fellow Interviews

Jane Hill

A Life with Butterflies

by Peter Smithers

I first met Jane over a meal of sweet and sour fish at the Danum Valley field station on the island of Borneo. I was there running a student field trip and, as students tend to avoid staff at dinner, my colleagues and I would gravitate towards any other adults in the dining room. Jane's party was always very sociable so we would often meet over the evening meal and discuss her research on butterflies, our students and the curious insects that we had encountered in the forest that day. These conversations stayed with me, so when I began this series of interviews, Jane was high on my list. Nevertheless, Jane proved to be a difficult lady to pin down. While the current lockdown has had few positive aspects, it has meant that Jane was at home and available to talk. So, as has become the current norm, we connected via Zoom and discussed her life in entomology.

Early life

"When I was doing my PhD I was rearing caterpillars in Kilner jars; each time I replaced the leaves I would get wafts of a really evocative smell and I realised this was a smell from my childhood. When I was at primary school I was given emperor moth caterpillars to rear. These were just amazing and at that time I was sure they were exotic tropical insects. Each year I would release the adults into my garden but it was not until I was a teenager that I felt very guilty that I had released tropical moths into my parents' garden only to die. It was some years before I realised that these beautiful moths were native to the UK.

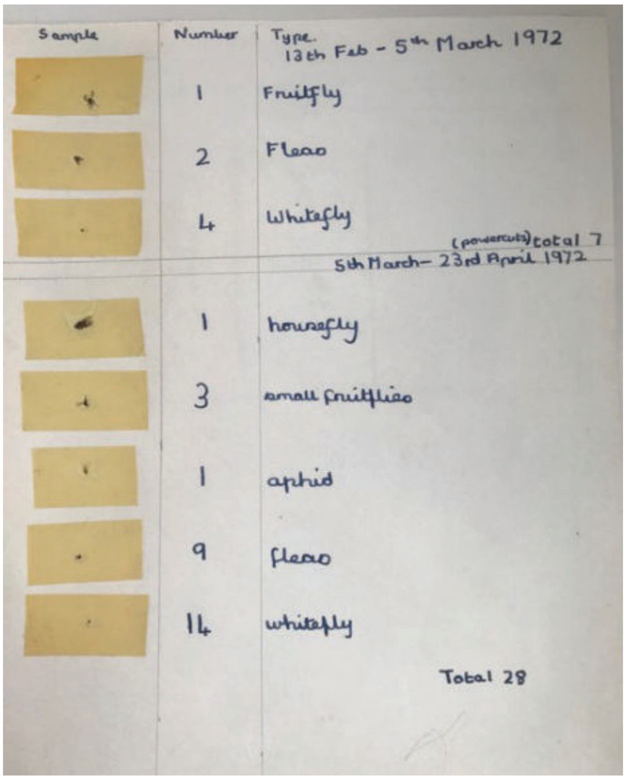
At home in London we had a fluorescent strip light in our kitchen and each month my father would take off the cover and empty it and we would sort and identify the contents, sticking them in a book with labels such as big fly, small fly, green fly and white fly. I still have the book with all the flies stuck down with Sellotape. I also recorded when the power cuts happened, which were common at that time in the 1970s strikes, so even then I was thinking about confounding variables!

When I first started my post doc I was amazed to come across people who knew all about British butterflies, the flight periods and food plants and where to find them, but I had never known that sort of detail."

School and University

"My father is a scientist, so at school I was always interested in science and really enjoyed biology. I attended an all-girls school, so I had no perception that science might not be a subject for girls, or that women couldn't hold positions of authority. So, when I arrived at university, I was surprised to find so few female lecturers, but I thought that was just University.

When it came to choosing a university, everyone in my family had gone to Manchester. My father had gone there



Sample	Number	Type.
		13th Feb - 5th March 1972
	1	Fruitfly
	2	Fleas
	4	Whitefly
		(powercuts) total 7
		5th March – 23rd April 1972
	1	housefly
	3	small fruitflies
	1	aphid
	9	fleas
	14	whitefly
		Total 28

Fly count from home in London.

and met my mother, and my sister was there at that time, so it seemed like an obvious choice. I went for a visit and everyone was so friendly that this convinced me that Manchester was the place for me. When I arrived I was surprised to find that many of my fellow students knew all about the course and what we were going to study, whereas I had chosen Manchester as it seemed like a great city to live in, and it was. I had also wanted to make sure I was far enough away from home that my parents could not visit unannounced, but near enough that I could get home for the weekend if the need arose.

My first tutorials were with Derek Yalden on biodiversity in the Peak District; he was just brilliant and these were a wonderful introduction to vertebrate ecology. I also did a project with Gordon Blower, an expert on millipedes, and really enjoyed that. I graduated in the 1980s when there were no jobs due to the recession, so I enrolled on a PGCE course as teaching was one of the few areas where there were still jobs available. I quickly became aware that being a school teacher was not for me when I realised that the bits of the course I enjoyed most were on the history of education, rather than facing a class full of children, although I now find teaching university students very rewarding.

I then took a masters' course where I was supervised by Dick Askew; I had enjoyed his undergraduate entomology lectures and he was happy to take me on to undertake a project on the leaf miners of Scots pine in the arboretum at Jodrell Bank. Back then we could sign on the dole and continue studying, which meant I could afford to remain in Manchester."

Life after University

"While I was writing up my master's thesis in Manchester, Robin Baker came into my lab and told me there was a PhD on offer with Gavin Gatehouse at Bangor University on migratory moths. So I applied, got the job, and was fortunate to spend four years in such a beautiful place.

Gavin was interested in insect migration and crop damage, and although most of his work was in sub-saharan Africa, my project was on a UK migrant moth, the Silver Y. Gavin was interested in the control of migration by genetic and environmental factors, which meant I conducted lots of rearing and selection experiments under different environmental conditions to see which ones produced migrants.

The challenge of rearing pests is that as soon as you bring them into the lab they die of some disease! As a result I had to make regular trips to Morocco and Sweden to collect fresh material to work with. These were fantastic trips. Gavin had put me in touch with research institutes in both countries to help me hunt for moths. I tried light traps, but these caught very few moths and I ended up just wandering around the crop fields with a net. I recall on one trip I worked out that each captured moth cost me the equivalent of £50, but the 15 females were very well looked after and produced exciting data.

In Scandinavia I stayed at a university field station where I collected in the day in a clover field. I spent all day walking up and down the rows of clover and saw on average one moth per hour. There was probably a 50/ 50 chance of me catching it, then a 50/50 chance of it being a female. It was slow going, but it eventually proved successful. As a PhD project there were lots of different aspects to the study which made it really interesting and enjoyable, and it was great when Ian Woiwod invited me to work on Silver Ys again several years later."

The Tropics

"While doing my PhD I spent time with friends from Manchester University studying biodiversity in Indonesia. We went to the island of Sumba in the Lesser Sunda Islands on one trip, and on another trip to Buru in the Maluku Islands, also known as the Spice Islands, which had been a penal colony until relatively recently before our visit, so most of the island was still covered in forest at that time. These trips to tropical rainforest made a huge impression on me, and were a great opportunity to get away from the UK in winter when there are no insects around. Since then I have continued to study tropical ecosystems and have returned to SE Asia almost every year, but I would love to go back to Buru and see what it is like now."

Post Docs

"I obtained a post doc at Liverpool John Moores University with Ian Hodkinson, which was my first research into climate change, studying psyllids along elevational transects in the mountains east of Bergen in Norway. We looked at psyllid phenology in relation to temperature and elevation.

Back then I would be presenting papers at conferences about climate change and insects while many of the other talks were discussing whether or not climate change was actually happening. Times have certainly changed. While at Liverpool I attended a conference and presented the butterfly work from Indonesia. A rather enthusiastic person approached me about a post doc they had coming up, and asked if would I like to apply. This was Chris Thomas and fortunately I got the job. The project was on meta populations of Silver-studded blues and Silver-spotted skippers, continuing a long-term study that Chris repeated every nine years.

It was increasingly evident to me, from both tropical and UK work, that butterflies were a great group for tackling lots of important ecological questions about the impacts of habitat and climate change. I don't think anybody has ever challenged why we work on butterflies; it's taken for granted that they are a worthwhile and important group to study.

While I was working with Chris, my husband Keith Hamer was at Durham University and introduced me to Brian Huntley who was working on climate change. It became clear that linking the work that Brian and Chris were doing would be really interesting, exploring the links between climate change and habitat fragmentation. We got a short NERC grant to start the project, and I have been working on these questions in UK Lepidoptera ever since."

Return to the Tropics

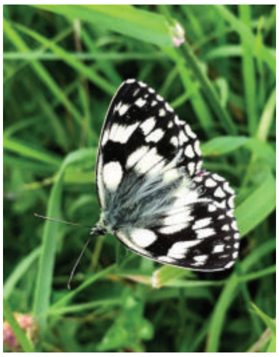
"While I was a post doc in Leeds I met John Willet, who was working with Stephen Sutton on the moths of Borneo, and I was complaining to him about problems of carrying out research in Indonesia due to their bureaucracy. John had just returned from the Danum Valley in Malaysian Borneo and recommended it as a place with much less paperwork, but equally amazing tropical forest. So, in 1997 I went out to see what it was like and realised what a great place it was to work; I've been back most years since then, either to collect data, or, more recently, to supervise students.

When I first went to Danum Valley I was working on the effects of logging on biodiversity. At that time, although there was good knowledge about how to log sustainably, the timber volumes that were extracted were so high that the remaining forest would have taken too long to recover to provide financial returns; so when oil palm came along it just took off and replaced much of the heavily logged degraded forest. It's both amazing and sad to think that the forests I first visited as a post doc are now palm oil plantations, and that humans can change landscapes so quickly. But the livelihoods of local communities have improved hugely too. When I first arrived everyone was on bicycles or motor cycles but now it's cars, new roads and traffic jams. I recall as a post doc there was a great outcry about the harm that logging was having on biodiversity, but in hindsight it was so much better than conversion to palm oil. In the back of my mind I worry what might be the next bad thing that will be even worse than palm oil."

Has Danum Valley changed over the 20 years of your visits?

"In some ways it has not changed that much; there is a wonderful group of researchers who use the centre, which gives it a great sense of community, and it has been a privilege to collaborate with local scientists. Sabah has become very popular with tourists, which is good for the conservation of the forest as it gives the forest value. The primary forest at Danum is an amazing ecosystem; it's wonderful to experience the sheer size of the trees, the darkness and humidity once you enter the forest, plus the noise at night is incredible. It is also amazing to think that you can get there so quickly. In just 24 hours I can travel from my office in York to the dining room at Danum Valley."

Borneo fieldwork; inset: Oil palm on peatland.




Mt Kinabalu

"While working at Danum I met with Stephen Sutton who introduced me to another moth person, Henry Barlow. Coincidentally, I had just read one of the 'Moths of Borneo' books and had also recently walked up Mount Kinabalu. This was just at the time when people studying the ecological impacts of climate change realised the value of re-surveying historical data sets to assess the changes in relation to climate change. Henry and Jeremy Holloway (who was at the Natural History Museum in London) had conducted an altitudinal transect using light traps on Mt Kinabalu back in the 1960s, while they were students at Cambridge. They had taken extremely careful records of the transect, and had maps and photos of their sites so we were able to find every site again very easily. I-Ching Chen was interested in elevational transects, so she repeated the transect for her PhD project and her results showed, for the first time, how insects are responding to climate warming. She has continued working with Jeremy on the material that she collected."

National data sets

"I have been lucky that funding bodies have been interested in butterflies, habitat loss and climate change across my career. I have also enjoyed my interactions with Butterfly Conservation and the Centre for Ecology and Hydrology (UKCEH), because the data sets they hold are just brilliant for tackling ecological problems. There is just so much you can do with these data for understanding insect conservation; nowhere else in the world has such good data, and these data sets go back such a long way. Other places are getting good, but the UK has at least a 40 year head start. The reason for this is that the UK is a crowded country, with low biodiversity and a population with a tendency to be slightly obsessive about their natural history recording – a tendency which has led to the best documented fauna and flora available anywhere in the world."

Gender Equality

"When I started my career, there were far fewer woman in science, but when I moved to York I noticed it was different. It had a good reputation for equality and there were more female academic staff than other places I had worked, with great role models and women in senior positions. Fortunately, ideas for improving gender equality have spread and I can't remember the last time I was the only female in a meeting, which was not uncommon when I started out in my career.

I have inherited from my mother the sense that 'You don't put up with stuff. You stand up and make changes if things don't seem fair'. There is still a long way to go of course; the more you do the more you realise there is to do! There is still a huge problem about the gender pay gap and it is still difficult for women to reach senior positions in academia. Things are changing, but very slowly, and I get depressed how many decades it will take before we have gender equality in science. Nevertheless, the next generation of early career female scientists have great ideas and continue to challenge the status quo. Girls know that science is fun and that it can lead to an exciting job, but academia needs to do more to support women and help them to stay in science and follow their career aspirations."

New projects

"One of the very exciting things I am doing at the moment is working with the NHM's British butterfly collection. We are taking samples of DNA from historical specimens and comparing it with the DNA from modern material from the same locations to see how much evolution has occurred over time. The NHM has recently digitised its UK Lepidoptera collection, so it was easy to find where species had been collected in the past and then revisit the site to resample those populations."

Over the course of these interviews I have noticed a pattern: all of the Hon. Fellows I have spoken to so far have been in the right place at the right time, and Jane is no exception. Her initially parallel careers have been initiated and propelled by chance meetings. These initially separate paths have interlinked and influenced each other before finally coming together. As Jane said, "initially I viewed my UK and SE Asian work as very different, but recently I have come to see them as very similar". This more holistic view has become a hallmark of her work. Jane's ability to seize some less obvious opportunities has enabled her to forge a body of work that has remained at the forefront of our understanding of human impacts on the natural world, and has pioneered some of our responses to them.

Jane's unassuming, matter-of-fact approach belies the fierce determination with which she pursues her work – a trait that has also seen her champion gender equality in academia; that "not putting up with stuff" attitude has won the Biology Department at York a gold award from Athena Swan in recognition of its commitment to advancing the careers of women in higher education and research.

Jane's butterflies have taken her to some extraordinary places and will continue to do so for many years to come. Like her butterflies, she restlessly searches for new questions. Her enduring relationship with butterflies will ensure that they continue to cooperate and provide answers and solutions, but of course only in warm sunny weather. I hope many more biologists will have the pleasure of chatting with Jane about butterflies over a meal of sweet and sour fish in the shadow of the magnificent rainforests that she loves.

Alfred Russel Wallace Award 2019

The RES's Wallace Award was created to recognise "*post-graduates who have been awarded a PhD, and whose work is considered by their supervisory team to be outstanding*". Once again, all applications ably met these criteria in 2019, with three finalists being invited to submit their theses in full ahead of presenting their work to a panel of judges. In a change from previous years, COVID-19 restrictions dictated that all finalists presented remotely, with the pandemic pushing back the panel interview and discussion to the end of June 2020.

On the day, Dr Jonathan Finch was the first to present, covering his work on 'Dynamics of an obligate pollination mutualism in the Australian Phyllanthaceae', followed by Dr Gerardo Arias-Robledo on his thesis '*Lucilia* blowflies: their ecology, taxonomy and evolution of obligate amphibian parasitism'. Both provided the panel with excellent presentations and informative discussion, but in the end a unanimous decision was reached to award the 2019 prize to the final presenter, Dr Jesamine Bartlett, for her hugely impressive work on 'Ecophysiology and ecological impacts of an Antarctic invader: the chironomid, *Eretmoptera murphyi*'.

Our congratulations go to Jesamine, as well as to our two runners-up. Summaries of all three finalists' PhDs are provided below.

Dave George (on behalf of the 2019 judging panel)

Finalist and overall winner:

Dr Jesamine C. Bartlett

Awarding institution: University of Birmingham, UK

Ecophysiology and ecological impacts of an Antarctic invader: the chironomid, Eretmoptera murphyi

Aliens exist! No, I'm not talking about little green men from outer-space, but rather plants and insects of earthly design that are new species to a region or ecosystem. One such alien is a small, flightless midge from the family *Chironomidae*, which we unwittingly transported to the most other-worldly of places – Antarctica. My thesis explores how this species is not just surviving, but thriving on its new Antarctic island, where now, thanks to the lack of nearly all other terrestrial animal life, it reigns supreme as the largest land animal on Signy Island.

Antarctica is enduring rapid change: the pressures of climate change plus an increase in human activity, are opening the least invaded continent on Earth to new species. As the ancient ice retreats, lands ripe for colonisation by both humans and alien species are increasing in size, and so must our knowledge of the biology, ecology and impact of these invaders. Using the midge, *Eretmoptera murphyi*, as a model invasive organism, we explored these issues.

Through experiments and field observations, my work confirms that this remarkable alien is asexual, with no males to be found. The adults emerge continuously throughout the summer season, a trait that may give them an advantage over their sexually reproductive cousins. But could it even survive on the Antarctic Peninsula in competition with its native cousin, *Belgica antarctica*? Evaluations of its ability to withstand heat, and cold, found that life stages respond differently, and at various points in the life cycle these aliens must successfully endure temperatures from +30 °C to -20 °C. In short, the whole Peninsula is its oyster, if it can get there.

This insect is tough, and this work also found that it is expanding its distribution, doubling its range within the last decade. Its ability to reproduce throughout summer means that, in places, you can find over 100,000 individuals in just 1m^2. Furthermore, its voracious appetite for decaying organic matter means that, where it occurs, it changes the soils, bringing nitrogen content up to levels more typically associated with seal colonies! It is essentially doing the job of an earthworm, in a landscape that has never known anything like it. Our tiny alien has the potential to change local vegetation and is arguably a new keystone species.

Given *E. murphyi's* potential, an examination of existing biosecurity measures was required, and, unfortunately, these were found wanting. Current measures are unlikely to limit its spread, which appears to be tracking footpaths across the island. Larval stages are also able to survive several weeks in sea water, and as it lives on the coasts it seems there is little to stop its eventual colonisation of other islands and the Antarctic Peninsula, where it would likely flourish.

In short, my thesis found that just a single, and seemingly innocuous, alien midge has the potential to change an Antarctic terrestrial ecosystem. But, do not blame this insect; it is humans, the greatest invader of all, that are the "space-ships" transporting these earthly aliens.

Finalist:

Dr Gerardo Arias-Robledo

Awarding Institution: University of Bristol, UK

Lucilia *blowflies: their ecology, taxonomy and evolution of obligate amphibian parasitism*

Blowflies are of evolutionary, ecological and economic importance, performing essential ecosystem services as carrion consumers, and delivering 'dis-services' as parasites, for example as facultative agents of livestock myiasis. The ecological differences that facilitate coexistence within the blowfly community are not fully understood. To quantify these differences, three habitats were sampled (open, hedgerow and woodland) at two different sites in South-West England. A total of 17,246 specimens were caught and identified. *Lucilia sericata* was the dominant species in open habitats, whereas *Lucilia caesar* was the most abundant species in shaded habitats.

The results demonstrate that *Calliphora* and *Lucilia* species show strong temporal and spatial segregation, mediated by temperature, and that species of the genus *Lucilia* show differences in habitat use which are likely to be driven by differences in humidity tolerance and light intensity. These factors in combination result in effective niche partitioning. Within the genus *Lucilia* only one species is generally recognised as an obligate agent of myiasis in Europe, *Lucilia bufonivora*, which exhibits high host-specificity for amphibians. Nevertheless, the species responsible for amphibian myiasis has been debated for years due to taxonomic confusion with *Lucilia silvarum*. To solve this, larvae from 20 diseased toads from the UK, Germany, the Netherlands and Switzerland were subjected to DNA analysis.

Sequence data from *COX1* and *EF1* suggest that amphibian myiasis is exclusively caused by *L. bufonivora*. Similarly, the latter species was thought to be absent in North America, where amphibian myiasis is attributed to *L. silvarum*. In this work, a DNA extraction protocol as well as PCR procedures were designed to successfully extract and analyse DNA from single-leg samples of flies to avoid morphological damage of the sample. DNA-based identification methods from pinned museum specimens, and the analysis, confirmed the presence of *L. bufonivora* in North America. Moreover, it was found in amphibian myiasis cases that were originally attributed to *L. silvarum*.

To investigate the evolution of obligate amphibian parasitism and host-specialisation, molecular clock-dating was performed with a concatenated data set of 3 genes: *COX1* (mtDNA), *ITS2* (non-coding) and *per* (nDNA). Unlinked substitution and relaxed clock models were implemented to allow evolution to vary amongst lineages. Obligate amphibian parasitism probably evolved just once around 4mya after the niche displacement of a saprophagous ancestor from the carrion-fly community. Consistent paraphyly of *L. bufonivora* across single-gene phylogenies and high mtDNA sequence divergence between Palearctic and Nearctic lineages suggest on-going cryptic speciation of *L. bufonivora* in these two regions for at least 2mya. Thus, due to its relative rarity, it has remained unrecorded until recent studies.

The patchy and ephemeral nature of carrion is the key to understanding the ecology and evolution of the Calliphoridae, since this facilitates evolution of niche partitioning and specialisation. This work provides updated results on the ecology, taxonomy and evolution of *Lucilia* blowflies. It also offers accurate molecular procedures that could aid in further entomological research that requires molecular data from museum specimens without damaging their morphological features.

Finalist:

Dr Jonathan T. D. Finch

Awarding Institution:
Western Sydney University, Australia

Dynamics of an obligate pollination mutualism in the Australian Phyllanthaceae

Obligate pollination mutualisms or brood mutualisms are highly specialised pollination interactions. In brood mutualisms, insect pollinators lay eggs within the flowers of a single species of host plant. Pollinator larvae then feed on the fertilised seeds. Plants in brood mutualisms thereby sacrifice their offspring for a dedicated pollination service. In return, pollinators gain a reliable food source for their larvae.

Approximately 700 species of leaf-flower plants (Phyllantheae) have evolved brood mutualisms with a similar number of leaf-flower moths (*Epicephala*: Gracillariidae) across Asia, Australasia, Polynesia and the Americas. These recently-discovered interactions are outstanding examples of plant–insect coevolution. Although their evolutionary origins are now relatively well understood, we know little about the natural history of most species involved, or about variation in their ecological interactions. My thesis aimed to address this knowledge gap.

Breynia oblongifolia occurs in eastern Australia and was known to have a brood mutualism with one moth species, but previous sampling was limited to just one site. Almost nothing else was known about the interactions between these mutualists. My thesis investigated the life history of *Breynia*, its pollinators and the associated insect community.

Through a combination of phylogenetic analysis, behavioural observations and morphological study, I discovered that *Breynia* is pollinated by two co-occurring leaf-flower moth species, adding new complexity to the mutualism. Several leaf-flower moth species have been described from Australia, but the descriptions lack information on the genitalia, which is essential for identification. My morphological descriptions and published genetic data will be invaluable to taxonomic revision of these species and future study of leaf-flower moths.

In addition, I identified a third species of moth in the genus *Herpystis* (Tortricidae) that occurs in *Breynia* fruits as a non-pollinating, seed-eating parasite. This species was previously only known from a single undescribed museum specimen, with no life-history information. *Herpystis* consumes more seeds than either species of leaf-flower moth and decreases host-plant seed production considerably. Parasitic species can have important effects on the evolution of brood mutualisms. How widespread this parasite is amongst *Breynia* species and its evolutionary consequences remains to be seen.

Highly specialised interactions may be vulnerable to fluctuations in the occurrence of mutualistic partners. However, these issues have never been explored for leaf-flower moths. Through statistical modelling of my field data, I showed that *Breynia* fruiting follows irregular large rainfall events and the emergence of adult moths is strongly synchronised to fruiting. Prior to rainfall events, pollinated female flowers remain dormant. My observations show that these dormant flowers frequently contain pollinator eggs that develop with the fruits. I argue that moths use diapause to synchronise their emergence with their host plants. This new mechanism thereby allows specialised pollinators to avoid potentially disastrous mismatches.

In summary, my thesis has greatly developed our understanding of the ecology of leaf-flower moths. The knowledge generated sheds new light on the nature of those interactions and provides a solid basis for the study of this fascinating group of insects across the Australasian region.

SCHEDULE OF NEW FELLOWS AND MEMBERS

as at 7th October 2020

New Honorary Fellows (as at 3.6.20)

Dr Richard Lane
Dr Roger Blackman
Dr Stuart Reynolds
Prof. Jeremy Thomas
Prof. Michael Hassell
Prof. Walter Blaney
Prof. Claire Kremen

New Fellows (1st Announcement)

Dr Pierfilippo Cerretti
Dr Laurel Haavik
Dr Gadi V.P. Reddy
Mr Peter H. Tantius
Dr Philip Barton
Dr Polura Venkata Rami Reddy
Prof. Ramaiyer Varatharajan
Dr Amr Ahmed Mohamed
Dr Akkati Venkat Reddy
Mr Stuart Paul Masson Roberts
Dr Srinivasa Murthy Kotilingam
Dr Angeliki-Kelly Martinou

Upgrade To Fellowship (1st Announcement)

Dr Joe Roberts

New Fellows (2nd Announcement and Election)

Dr Peter William Edward Kearns (as at 3.6.20)

Upgrade To Fellowship (2nd Announcement and Election)

Mr Dafydd Vaughan Lewis (as at 3.6.20)

New Members Admitted

Mr Paul Michael Westgate (as at 3.6.20)
Mr Matthew D. Travers (as at 3.6.20)
Miss May Webber
Dr Alice Evans
Mr Charlie Linton
Miss Giulia Dipietrantonio
Dr Frauke Fedderwitz
Mrs Helen Boyce
Dr Chay Paterson
Mr Peter Gerard Martin
Mr Marcus Maisey
Ms Helen Gilks
Mr Niran Adigun
Miss Annabel Louise Moore
Dr Anusha Challa
Miss Elizabeth Cooper
Mrs Elizabeth Anne Pretorius
Mr Graham Hayden Fisher

New Student Members Admitted

Miss Diana Tixi
Miss Sonal Ladwa
Mr Michael O’Shea
Miss Apithanny Bourne
Ms Christine Lorna Culverwell

Re-Instatements to Fellowship

Dr Joanna Staley

Re-Instatements To Membership

Mr Paul Andrew Cawsey (as at 3.6.20)
Mr Christopher Ahuchaogu

Deaths

Mr Trevor John James, UK, 1986
Prof. Willi Sauter, CH, 1966
Mr Michael Charles Day, UK, 1967

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

COVID-19

(at the time of writing)

We are following the latest UK government advice and working from home as much as possible.

You can still apply for Membership and Fellowship, our journals are still open for submissions, the insect identification service is still operating and our events are now online with free registration.

Our Mansion House headquarters are not open every day, but our online shop is still open, though deliveries may be subject to some delays. The Librarian will not have access to our collections from home, but will be happy to try and locate material online.

We hope that everyone stays safe and well.

2021 Verrall Lecture
Wednesday, 3 March, 2021

Aphid Special Interest Group meeting (online)
Thursday, 15–16 April, 2021

EntoSci20
Thursday, 29 April 2021

Pollinators in Agriculture meeting in collaboration with the AAB
Tuesday, 29 June – Thursday 1 July, 2021
Venue: Copthorne Hotel, Slough.

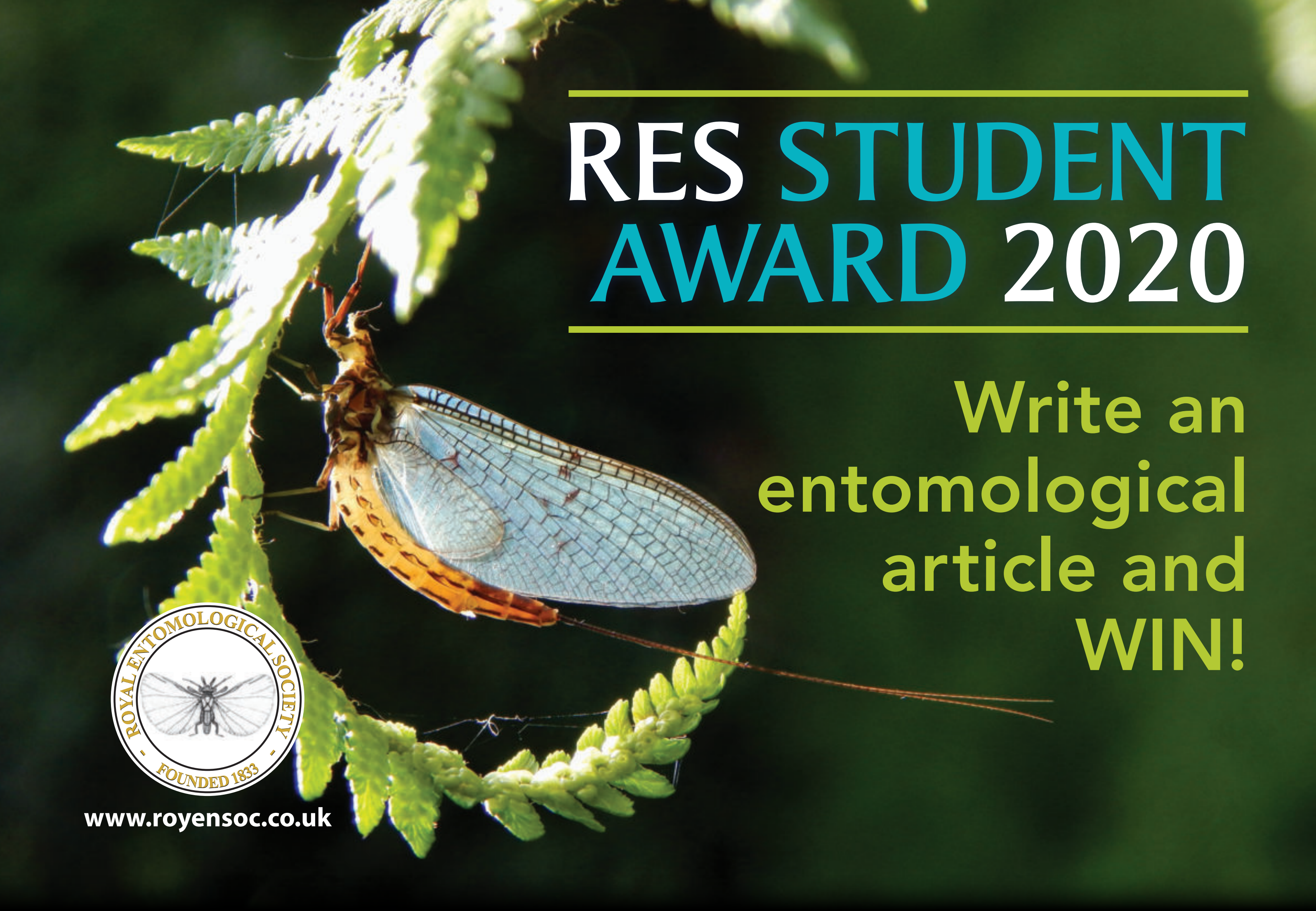
Orthoptera Special Interest Group
Wednesday, 3 November, 2021

NON-SOCIETY MEETINGS

XXVI International Congress of Entomology, Helsinki, Finland, Re-scheduled 19 July – 24 July, 2021
'Entomology for our planet'

International Conference on Urban Pests, ICUP2020, Re-scheduled 13 September – 15 September 2021, Barcelona

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



RES STUDENT AWARD 2020

Write an entomological article and WIN!

www.royensoc.co.uk

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 kirsty@royensoc.co.uk

Alternatively, complete the attached entry form, and submit it with five copies of your entry to:

The Registrar,
Royal Entomological Society,
The Mansion House,
Chiswell Green Lane,
St Albans, Herts
AL2 3NS

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. student I.D. card

THE JUDGES

The judges 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 2020. The winner will be announced in the Spring 2021 edition of *Antenna* and on our website.

PLEASE CUT AND RETURN THIS PORTION WITH YOUR ENTRY

Article title: ____________________

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Student name: ____________________

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Address: ____________________

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Telephone: ____________________

E-mail: ____________________

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Name of academic institution:

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