One Hundred Years of Parasitoids

The phenomenon of insect parasitism was first described around a thousand years ago by Lu Dian (China, 1042–1102) based on observations of the life cycle of tachinid flies[1]. Further descriptions of parasitism by insects are credited to European 16th and 17th century naturalists, including Jan Jacob Swammerdam (assisted by a painter, Otto Marsilius), and the better known work of Antoni van Leeuwenhoek[2]. It was not, however, until one hundred years ago that the term 'parasitoid' was coined: German entomologist Odo Morannal Reuter introduced it in his book[3] on insect habits and life-histories, *Lebensgewohnheiten und Instinkte der Insekten*. He used the term 'parasitoidea' (parasitoid predators) to distinguish insects that live in close association with their host as immatures, killing it during their development and living freely as adults, from 'parasites' (true parasites) in which both adult and immature stages feed on the host. In defining parasitoids, Reuter had particularly in mind members of the Hymenoptera, such as ichneumonoid and chalcidoid wasps, and these also form our focus here. In reviewing Reuter's book, American entomologist William M. Wheeler[4] mostly downplayed the utility of the term although his criticisms were tempered due to the fact that Reuter has been blind for several years beforehand. Despite Wheeler's critique, the term has now become very widely used, especially in the last 30–40 years, and today a *Web of Science* search on 'parasitoid' returns well over 66,000 articles. We have not been able to cite let alone read all of these! Rather, we here provide a narrative overview of selected highlights of parasitoid research from just prior to Reuter's terminological advance to the present time.

Parasitoids were intentionally utilized as agents of biological pest control before they were so named. In 1883, Valentine Riley, a US Department of Agriculture entomologist, directed the first successful introduction of a parasitoid, the braconid wasp *Apanteles glomeratus*, from the UK to the USA for control of the imported cabbageworm[5]. Since then, research on parasitoids has thrived, broadening from the initial focus on agricultural applications to now include a vast array of topics within genetics, physiology, behaviour, ecology and evolutionary biology. The first comprehensive review of parasitoid biology was provided by Curtis Clausen in his classic *Entomophagous Insects* [6]. Later, Paul DeBach's book[5] *Biological Control of Pests and Weeds* and DeBach and Rosen's[7] *Biological Control by Natural Enemies*' gave full descriptions of biocontrol programmes using parasitoids and a wealth of information on their general biology.

The first models of population dynamics of animals with discrete generations were put forward by Thomson[8] in the 1920s and by Nicholson[9] in the 1930s, both were entomologists working on parasitoids. Extensions to basic models proposed by Nicholson, working with V.A. Bailey, a physicist, continued throughout the rest of the century[10,11] indicating new areas of exploration including how parasitoid behaviour could affect influential model parameters, such as searching time. Meanwhile, George Salt's physiological and behavioural studies, from the early 1930s, set the stage for further advances on numerous topics such as superparasitism and within-host competition, host selection and the immunological and biochemical effects of hosts on parasitoid development and *vice versa*[12,13]. Towards the end of the century, the discovery that parasitoids search for hosts using chemical cues emanating directly from the host[14] and host-feeding induced plant volatiles[15] generated a comprehensive research programme on the chemical ecology of host–parasitoid interactions, that is ongoing today[16].

During the decades that parasitoids were increasingly deployed as biocontrol agents, important advances were also occurring in the fields of behavioural and evolutionary ecology. Ideas originating in studies on avian clutch size by David Lack[17], that selection maximizes the number of young produced per nest, were adopted for parasitoids by Klomp and Teerink[18] generating many productive extensions to clutch size theory and, more generally, optimal foraging theory[19–21]. Many further advances in evolutionary ecology can readily be traced back to W.D. Hamilton's 1960s insights into how genetic relatedness influences the evolution of social behaviour and how sex ratios are influenced by population structure[22,23] plus John Maynard Smith's 1970s developments of game-theoretic thinking, especially concerning contest behaviour[24]. Early developments in contest theory had little to do with the study of parasitoids, but numerous species of parasitoids exhibiting aggressive behaviour have since been used to test and develop contest research[25]. In contrast, parasitoid wasps and other hymenopterans were central to the stimulation and testing of some of the key developments in social behaviour and sex ratio theory: it is no accident that a parasitoid wasp, *Nasonia vitripennis*, is depicted on the cover of the volume collecting Hamilton's works from this period[26].

The extreme female bias of many parasitoid species is often explained by Hamilton's theory of Local Mate Competition[23]. Around a decade later the tendency for parasitoids to lay female eggs in larger (high-quality) hosts and male eggs on smaller (lower-quality) hosts, a phenomenon which had been commonly observed by biological control practitioners[27], was explained by Charnov and co-authors[28,29], borrowing concepts from mammal-oriented theory. These theories show how sex ratio bias arises from sexually differential returns from parental investment and, together with R.A. Fisher's frequency-dependent explanation for unbiased sex ratios, form the basis for arguably the most detailed and elegant area of understanding within evolutionary biology: parasitoids have played no small part in this[29–31]. Hamilton's Local Mate Competition paper[23] also laid the foundations for understanding the influence of symbiotic organisms on the sexual reproduction of their hosts. Parasitoids have played an important role in this, notably the discovery that *Wolbachia* bacteria cause parthenogenesis in *Trichogramma* wasps[32]. Today it is established that symbiotic organisms, either in hosts or in parasitoids, have enormous significance for ecological and evolutionary interactions[33–35].

From the early 1980s parasitoids increasingly captured the interest of evolutionary and population ecologists due to the many interspecific variations around the relatively simple core life history (it often seems possible to find a parasitoid to fit almost any set of modelling assumptions) and to the rather direct fitness and population dynamic consequences of parasitoid host handing decisions[11,21]. At the same time, biological control researchers became increasingly familiar with advances in evolutionary ecology; functional explanations for how decisions maximize reproductive success can be applied to enhance the mass rearing of parasitoids for release in biocontrol programmes and how to further conserve them in agroecosystems[36,37]. H.C.J. Godfray's 1994 monograph[21] on *Parasitoids: Behavioral and Evolutionary Ecology* was paramount in capturing and explaining a vast amount of literature accumulated up to that time. Various other landmark books on insect parasitoid biology, ecology and use in biological control appeared during the next decade and a half[10,38–40]. This was definitely the era in which parasitoid research bridged the gap between basic and applied science, as exemplified by a European research consortium explicitly focusing on applying parasitoid behavioural ecology to biological control and the associated book[41] *Behavioural Ecology of Insect Parasitoids: From Theoretical Approaches to Field Applications*.

One hundred years of parasitoid research have left us highly informed and yet somehow there is still so much left to discover and to achieve. In coming years it is anticipated that the use of biological control will increase as a sustainable alternative to chemical pesticides and, as parasitoids are among the most deployed natural enemies, parasitoid research should be the vanguard of this. Further, parasitoids will assuredly continue to serve as model systems for probing various questions in behavioural, evolutionary and population ecology. For instance, they remain ideal for researching the evolution of sex ratios, which connects to a number of general issues in evolutionary biology[31], and are currently being developed as genetic model organisms[42]. In conclusion, in defining the characteristics of parasitoids that mark them as distinct from predators and from parasites, Reuter, though blind, was far-sighted. For our part, we envisage no reason that research on insect parasitoids will lose its impetus in the century to come. This is because parasitoids are important for both pure and applied biology and for the synergistic interplay between the two.

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