

Parasites and Pathogens of Insects

Volume 1: Parasites

Edited by

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Preface

The focus of this two-volume set is the interface between insects and their associated parasites and pathogens, with particular emphasis placed on the basic biology, biochemistry, and molecular biology of these intimate and intriguing relationships. The initial inspiration for this book was the recognition that although the potential use as biological control agents of many parasites and pathogens of insects has been intensively investigated, few recent works have attempted to address the biochemical and molecular interactions occurring between insect hosts and their invaders. Yet these interactions clearly are critical to the ultimate outcome of the confrontation between any invader and its host. The parasite or pathogen must evade or suppress the host immune response and, while ultimately completing its development in the host, must not stress it prematurely such that the survival of both partners is compromised. In addition, the host environment must satisfy the parasites' nutritional and metabolic needs.

Our intent is to summarize developments and technological approaches currently being exploited to monitor the biochemical, immunological, metabolic, and behavioral alterations in insects infected with parasites and pathogens, with particular emphasis on interactions occurring at the molecular level. Additionally, our authors present several novel ideas for exploitation of this information in the manipulation of insect pests.

Pressure to minimize synthetic chemical insecticides in insect control programs has led to increased interest in the use and study of parasites and pathogens capable of limiting insect populations. This interest, in combination with rapid advances in the techniques now available to study biological systems, has resulted in an enormous increase in knowledge about the biochemistry and physiology of the parasites and pathogens that attack insects, as well as their interactions with the host. This knowledge is so diverse and extensive that most journal reviews deal only with highly specialized aspects of the overall field. While such reviews are of great value, our intent for these two volumes was to assemble a more extensive survey of this rapidly developing field by publishing reviews on selected topics dealing with interactions with parasites (Volume 1) and pathogens (Volume 2) of insects. It would be

impossible, even in two volumes, to review all of the recent findings considered major advances. Therefore, in selecting our topics, we chose to focus on subject areas of long-standing interest (e.g., insect antibacterial proteins and parasite–host developmental interactions) and those dealing with recent breakthroughs that appear significant and likely to be of value in controlling insects (e.g., development of recombinant baculoviruses and formulation of “super” pathogens).

The intended audience for these volumes includes upper-level undergraduates with specialty interests in parasitology and entomology, graduate students, and post-graduate researchers who may use this information to devise new technologies for manipulation of insects of importance to agriculture and human health. We hope these volumes will find a niche on bookshelves in many personal and professional libraries focusing on parasitology, entomology, immunology, epidemiology, physiological ecology, evolutionary biology, and other areas dealing with various aspects of host–parasite relationships.

Insect parasitology and pathology have clearly become multidisciplinary fields. For example, the development of new technologies for gene transfer and arthropod transformation may benefit from the exploitation of naturally occurring transposable elements in insect virus genomes. Useful target genes for manipulation might include those that are critical to the normal functioning of the immune system as well as those parasite-associated factors invoking developmental disruption or sterility of insect pests (i.e., endocrine regulators). Genes associated with refractoriness in vector arthropods are also important and are under scrutiny as possible means for generating engineered vectors with reduced capacity to transmit parasites.

In contrast to the relatively limited information available on molecular host–parasite and host–pathogen interactions in insect hosts, a wealth of recently published material describes the relationships between parasites and pathogens of mammals with their respective hosts. In part, this difference reflects intense research efforts directed toward developing new therapeutic treatments for disease based on these interactions in the hope of identifying critical points of vulnerability that may be manipulated by drugs or other agents. A similar extensive literature describing the molecular interactions of plants with pathogens and parasites also now exists. Our knowledge of the molecular mechanisms of interactions between plants and plant pathogens is thus much more sophisticated than our understanding of the molecular mechanisms operating in insects as they confront invaders. While we have yet to identify virulence genes or avirulent mutants of those genes in species that attack insects, for example, such genes already have been isolated in species that are pathogenic to plants and mammals. Moreover,

though mechanisms of virus resistance have been pinpointed in plants and mammals, our information about insect antiviral defenses remains rudimentary. Induction of resistance has been documented, but its mechanisms remain to be identified.

Nevertheless, we do have significant information about the complexity of some processes, such as the antibacterial defenses of insects, and how they parallel similar processes in mammalian hosts. Hormonal host–parasite relationships have been intensively scrutinized in several invertebrate species, including many insects, which appear to be particularly appropriate models for studying endocrine interactions. Moreover, the association of third-party elements with parasites is perhaps best illustrated by species that attack insects; for instance, both wasp and nematode parasites show intimate relationships with viruses and bacteria, respectively, during parasitism of insect hosts.

In the short term, these volumes are directed at filling a void in the literature by emphasizing basic interactions at the biochemical and molecular levels. In the long term, we expect that many of these interactions will provide avenues for exploitation to either enhance the rates of “beneficial” parasitism (in biological control, for example) or reduce the rate of disease transmission and the rate of infection of vertebrate hosts. Our hope is that the information assembled here will have significant impact on agriculture and human health and that these volumes will stimulate fresh approaches to the investigation of these fascinating and intricate interactions.

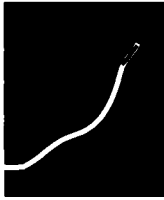
We express thanks to the authors for their timely contributions. In addition, the scope and depth of this work demanded that we enlist the assistance of many scientists to review the chapters. For their time and outstanding efforts in this endeavor, we sincerely thank the following individuals: Drs. Theodore Andreadis, Christopher Bayne, Gary Blissard, Drion Boucias, John Brown, Peter Bryant, John Burand, Thomas Coudron, Samuel Dales, Robin Denell, Douglas Dahlman, Gordon Gordh, Robert Granados, Patrick Greany, Leah Haimo, Alfred Handler, Kiyoshi Hiruma, Hilary Hurd, Davy Jones, Michael Kanost, James Kerwin, Karl Kramer, Leslie Lewis, Michael Locke, Robert Luck, Lois Miller, Louis Miller, Ed Platzner, John Postlethwait, Lynn Riddiford, Justin Schmidt, Don Stoltz, Michael Strand, Just Vlak, Bruce Webb, John Webster, Alan Wood, Timothy Yoshino, Rolf Ziegler, and Marlene Zuk.

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Chapter 1



Patterns of Development in Insect Parasites

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I. Introduction

Successful parasitism by insect parasitoids² requires the solution of three kinds of general problems: (1) which host to select; (2) how to integrate development and growth with those of the host; and (3) what life-history tactics to adopt. The first problem concerns behavioral adaptations relating to host selection and progeny allocation by the adult female (Charnov and Skinner, 1985; Waage and Godfray, 1985; van Alphen and Vet, 1986; Waage, 1986) and will not be considered here for this reason. Instead we will focus mainly on the third and, to a lesser extent, the second problem, both of which concern parasite growth and development.

Most early studies have emphasized mechanisms of parasite growth and development, with less attention paid to the adaptive significance of these mech-

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²Henceforth we use the term *parasite* to mean *parasitoid*. These protelean parasites include a large group of mostly hymenopteran and dipteran species that, as immatures, are obligate parasites of insects and other arthropods and are free-living as adults. Hymenopterous parasites often are called parasitic wasps as opposed to the nonparasitic, aculeate wasps and bees.

anisms. In a causal approach, parasite development and growth may be characterized in terms either of the effects of parasitism on the host (e.g., Douthett, 1963; Salt, 1964; Smilowitz and Iwantsch, 1973; Cloutier and Mackauer, 1979, 1980; Lawrence, 1982; Thompson, 1982, 1983; Beckage and Templeton, 1985, 1986; Strand, 1986; Gunasena *et al.*, 1989; Vinson, 1990; Strand and Dover, 1991) or of the parasite's response to variations in the nutritional state and physiology of the host (e.g., Corbet, 1968; Weseloh, 1984; Hébert and Cloutier, 1990; Lawrence, 1990; Kouamé and Mackauer, 1991; Strand *et al.*, 1991; Sequeira and Mackauer, 1992a,b). In this regard, Lawrence (1986, 1990) considered host regulation (Vinson, 1975; Vinson and Iwantsch, 1980a) and flexibility of parasite development (Corbet, 1968; Weseloh, 1984) as alternate developmental strategies. This viewpoint stresses proximate mechanisms of parasite survival based on qualitative descriptions of the physiological and biochemical interactions between the parasites and their hosts.

However, functional constraints on the parasite's growth and development on or in different hosts can also be considered as variables within a broader evolutionary framework. This approach emphasizes questions about the fitness value of developmental characteristics and patterns of host utilization. Because protelean parasites depend exclusively on host-derived nutrients for their larval development and growth, natural selection would be expected to favor mechanisms that maximize the efficient utilization of these resources. Optimal resource allocation to adult body size, considered the perhaps most important component of Darwinian fitness in parasitic wasps (King, 1987), depends on the insect's growth rate and development time. The allocation of limited (host) resources to competing fitness functions may result in trade-offs that determine an "optimal character set" and, in doing so, may shape the evolution of a species' life-history strategy (Sibly and Calow, 1986).

We use the term *strategy* in accordance with Dominey (1984) to refer to a set of general rules that specify which alternative pattern of responses will be adopted in a particular situation; these rules are typical for each species and determine its adaptedness to the environment, here the host. Tactics, by contrast, refer to several alternative options or mechanisms by which these evolutionary objectives are achieved; these option sets may vary among different individuals or phenotypes. Also, we distinguish between host suitability (Salt, 1938; Vinson and Iwantsch, 1980b) and host quality, two terms often used synonymously. A host species is suitable if it normally supports the successful development of parasite offspring; consequently, suitability is a characteristic of the host species and is genetically determined, or largely so. In comparison, we use the term quality to describe variations in the state or condition of the host that affect process dynamics, such as the rates of parasite growth and development. Such state variables include, or may be correlated with, host age, stage of development, size, sex, and nutritional status.

The chapter is organized as follows. First, we introduce the idiobiont–koinobiont dichotomy, which we use as a (macroevolutionary) organizing scheme. Second, we describe several developmental patterns that characterize broad differences between idiobiont and koinobiont parasites. Next, we discuss seasonal adaptations and the influence of host nutrition on parasite development, including superparasitism and starvation. Finally, we propose three models of parasite development in response to host constraints. We suggest that the essential components of any developmental strategy are the parasite's growth rate, development time, and adult biomass, which are constrained by host quality in an association-specific manner.

II. The Idiobiont–Koinobiont Dichotomy

Haeselbarth (1979) first drew attention to an important macroevolutionary division between parasites developing in hosts that continue to grow and metamorphose during the initial stages of parasitism (called koinophytes) and those that develop in nongrowing and paralyzed hosts (called idiophytes). Askew and Shaw (1986) introduced the terms koinobiont and idiobiont to describe these alternative host-exploitation strategies.

Because the host of an idiobiont does not feed, grow, or metamorphose during the course of the interaction, it contains a fixed amount of resources for the parasite larva, with large hosts being assumed of higher quality than small hosts. However, unless the host is killed by the female at oviposition, age-related variations in quality may result from developmental changes within a particular host stage, such as eggs and pupae (Strand, 1986; King, 1990a). By contrast, hosts parasitized by a koinobiont continue to feed, grow, and develop during much of the interaction. Consequently, host quality as a resource for the parasite larva is influenced by future host growth, which depends on the host's age and stage of development, rather than on its size, at the time of parasitization (Mackauer, 1986; King, 1989; Kouamé and Mackauer, 1991; Sequeira and Mackauer, 1992a).

Blackburn (1991) noted that koinobionts have longer pupal periods and preadult life spans than idiobionts, suggesting that these two groups have probably evolved under different constraints with regard to resource usage. Askew and Shaw (1986) compared idiobiont and koinobiont strategies as a correlate of host range. They proposed that koinobionts are more likely to show a narrow specialization because of their greater dependence on host physiology and development. Gauld and Bolton (1988) noted that idiobionts typically are synovigenic (i.e., females mature eggs continuously throughout life), produce relatively large, lecithal (or anhydropic) eggs containing sufficient resources for early embryonic development, and develop as ecto-

parasites on concealed hosts. Koinobionts, by contrast, are typically endoparasites, produce small nutrient-poor, alecithal (or hydroptic) eggs, and attack free-moving hosts.

Idiobiont and koinobiont strategies show poor correlation with solitary and gregarious development (Askew and Shaw, 1986). Theoretical results (Godfray, 1987), and some experimental evidence (Cruz, 1981), suggest that solitary and gregarious development represent distinct reproductive and/or developmental strategies (Waage, 1986). However, many groups of parasites, including several genera such as *Cotesia*, contain both solitary and gregarious species. In most cases it is not clear whether such developmental variations are due to host-related conditions (le Masurier, 1987, 1991) or reflect phylogenetic constraints (Gauld, 1988; Gauld and Bolton, 1988), or both.

III. Patterns of Parasite Development and Growth

A species' life-history strategy represents a unique combination of responses (tactics) that are shaped by natural selection from an option set associated with each phenotypic character. Option sets may be empirically defined as the quantitative responses of their corresponding life-history characters. With regard to host-parasite interactions, it is convenient to distinguish between two response categories: the influence of the host's phenotype on the parasite's phenotype, and the fitness consequences of variations in the parasite's phenotypic attributes. The first category includes the influence of the species of host, of its stage of development, and of its nutritional status on the parasite's growth rate, development, and size at maturity.

In this and the following section, we use selected host-parasite associations to identify variables that are likely to represent major components of microevolutionary strategies.

A. Idiobionts

1. Egg Parasites (*Trichogramma*)

The generalist egg parasites of the genus *Trichogramma* are among the most thoroughly studied idiobionts. These species are easily reared in the laboratory on their habitual as well as on various factitious hosts (Bigler *et al.*, 1987; Schmidt and Smith, 1987). In his seminal studies, Salt (1940) demonstrated a close correlation between the size of host eggs and the adult size of the parasite. Eggs that were too small to satisfy all the nutritional requirements of the developing parasite larva produced "runts" with structural pecu-

liarities characteristic of starvation. Also, development time varied with the egg's size and the thickness of its chorion.

Although species of *Trichogramma* exhibit distinct patterns of host-size and species usage (Hintz and Andow, 1990), accurate assessment of adaptive life-history variation and developmental strategies is made difficult by facultative gregarious development. Pak (1986) recognized six distinct patterns in the relationship between host age at parasitization and developmental success in *Trichogramma*. Five of these patterns were nonlinear, a fact indicating that host quality for parasite development is a nonlinear function of host age and, more important perhaps, that these quantitative relationships are association-specific. While parasite size and fecundity increased with host size (Reznik and Umarova, 1990), development time varied nonlinearly with host size, possibly reflecting differences in relative host quality rather than in absolute host size or age. Barrett and Schmidt (1991) suggested that, in small host eggs, the parasitoid's size is restricted by the nutrients and space available. However, in hosts above a threshold volume, the size of the resulting wasps depends on the number of eggs allocated by the female at oviposition.

Eggs may be considered as transitory host stages in that rapid embryogenesis can quickly deplete the amount and the availability of stored resources (Anderson, 1972). Thus, egg parasites are under selection to minimize development time and to maximize growth rate (Strand, 1986). Strand (1986) suggested that, in *Trichogramma* species, polyphagy may be a consequence of the physiological uniformity of insect eggs as a food resource, especially because eggs lack significant cellular defenses and are often unprotected. If this hypothesis is in fact correct, we would expect little variation in the growth rates of generalist (egg) parasites. However, more detailed studies of the growth, development, and bionomics of egg parasites may well reveal substantial host-related variation in parasite performance (Marston and Ertle, 1973; Bigler *et al.*, 1987; Reznik and Umarova, 1990; Barrett and Schmidt, 1991).

2. Pupal Parasites (*Pimpla*, *Coccygomimus*)

The growth and development of pupal endoparasites and of those that kill the host at or shortly after oviposition is less well studied. Arthur and Wylie (1959) showed that, in the ichneumonid *Pimpla turionellae*, body size increased with the pupal size of different host species, while development time was generally longer in large than in small pupae. Sandlan (1982) found that the adult size of *Coccygomimus turionellae* decreased with an increase in host age within a host species but was not correlated with size differences between host species; however, parasite development time increased with pupal age.

Host size-, age-, and species-usage patterns in pupal parasites, indexed by the percentage of parasitism, may vary within and between host species