Valerie K. Brown
Ivo Hodek (editors)

DIAPAUSE AND LIFE CYCLE STRATEGIES IN INSECTS

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Edited by

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and

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This volume is dedicated to
Professor Anthony D. Lees, F.R.S.
upon his retirement from the
Chair of Insect Physiology,
Imperial College, London

PREFACE

The theme of this volume evolved at the XVIth International Congress of Entomology in Kyoto, Japan, in 1980. One of the Symposia, entitled 'Life cycle strategies: seasonal and geographic adaptations', highlighted some of the recent discoveries of variation in diapause responses and their significance in evolutionary ecology. The Symposium attracted so much enthusiasm and lively discussion from participants and audience alike that it was felt a publication on the subject was timely. Many of the contributions to this volume are from invited speakers at the Symposium. However, it is our aim to present as comprehensive a coverage of the field as possible and to achieve this end, other contributions have been sought to cover aspects which did not feature in the Symposium. In addition, many of the Symposium participants have subsequently expanded and somewhat modified the version of their papers given in Kyoto.

To reflect the active growth and diversification of the subject, authors have been invited to present their own original research in preference to purely review articles. The fact that this approach poses more questions than it answers is surely evidence that the subject is in one of its most exciting eras. A major, underlying reason for this is that the elegant work of the laboratory physiologist is now being tested in field studies. It is, therefore, hardly surprising that a large number of the contributions emphasize the ecological and evolutionary significance of the seasonal adaptation strategy employed by insects. Furthermore, many of these contributions involve long-term population studies in addition to considering results in the light of modern ecological theory. The volume is arranged in three parts. The first includes five papers and deals with the mechanisms regulating seasonal adaptation; two focus on adult reproductive diapause and two on larval diapause with the final paper describing the specialised case of insect parasitoids. The second section of four papers is devoted to examples of life-cycle polymorphism in terms of both seasonal and geographic variation. The final section takes a closer look at the evolution of life-cycle strategies, two of the papers consider the evolutionary significance of migration, one the allocation of energy for reproduction and the other two the evolution of different phenologies. There is no clear-cut distinction between the papers in each section; this is an ample reminder of the close collaboration between workers in the field, and the even closer integration between a species' physiological responses and its evolutionary ecology.

The volume is dedicated to Professor A.D. Lees. Tony is undoubtedly one of the leading pioneers in the study of diapause. One only has to look through the references associated with each paper to see that many authors cite his excellent monograph written in 1955, not to mention the wealth of research papers published subsequently. We hope this volume will pay tribute to his expertise as an insect physiologist. However, it must be the aim of any great scientist to stimulate thought peripheral to his own speciality. We trust that in the papers of this volume some of Tony's earlier findings may be seen in the light of population ecology and evolution.

All thanks are due to our Japanese hosts at the Symposium and especially Sinzo Masaki who, together with Hugh Dingle, co-ordinated the event. It is only fitting that Sinzo has contributed the Introduction to the volume and a number of his Japanese colleagues are participants. The international flavour of the volume, with authors from seven countries, highlights the extent of interest in diapause and seasonal life-cycle strategies of insects and the need for further work. Ideas for the latter are made so lucidly by Hugh Dingle in his Concluding Remarks.

We have enjoyed our work as editors and hope that our enthusiasm will be shared by the readers of the volume. We extend our grateful thanks to all those who have kindly reviewed manuscripts and to publishers who have given their permission to reproduce figures or tables. Finally, we wish to thank Junk Publishers and especially W. Peters and his staff for their careful handling of this volume.

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CONTENTS

INTRODUCTION

SINZO MASAKI

Most insects show seasonality in their life cycles. This fact might even have been noticed by early man, for he was seasonally affected in various ways by insects in his surroundings. Certain species of insects have been exploited as a source of food, and information on the seasonal occurrence of edible ones might well have been communicated from generation to generation, like in the tribes of Australian aborigines collecting bogong moths in aestivation caves (Common 1954). From the beginning of agriculture, farmers were prompted to watch carefully the life cycles of insects infesting their crops, and silkworm growers tried to keep hibernating eggs in good condition for the next season. The special physiological nature of those eggs was demonstrated for the first time in the latter half of the last century by means of cold-exposure experiments (Duclaux 1869). The diapausing state itself is, however, only one side of the seasonal regulation system. More than a half century elapsed before the other side, the timing mechanism, was revealed by Marcovitch (1923) who performed the first photoperiod experiments with aphids. This was soon followed by an outstanding analysis of photoperiodicity in the silkworm (Kogure 1933). The modern approach to the subject of seasonal adaptation in insect life cycles was thus founded by these pioneers.

Since then, there has been an exponential growth in research activity up to the present time, as represented by the number of insect species in which some kind of photoperiodic response has been found (Fig. 1). Even a cursory survey of the literature distinguishes two periods after the discovery of insect photoperiodism. In the first period, two or three dozen species became known to be sensitive to daylength, and more work was devoted to temperature relations or other physiological aspects of diapause. The neuroendocrine mechanism, metabolic patterns, and cold-hardiness characteristically associated with diapause or hibernation were elucidated to some extent and provided a sound basis for further advances. The first general account of diapause was given as a lecture at the IXth International Congress of Entomology (1951) in Amsterdam (Bodenheimer 1952), and the first comprehensive review on diapause was published in the next year (Andrewartha 1952). This was not mere coincidence; the time was ripe for the synthesis of accumulated information to initiate the second period of research on the seasonality of insect life cycles.

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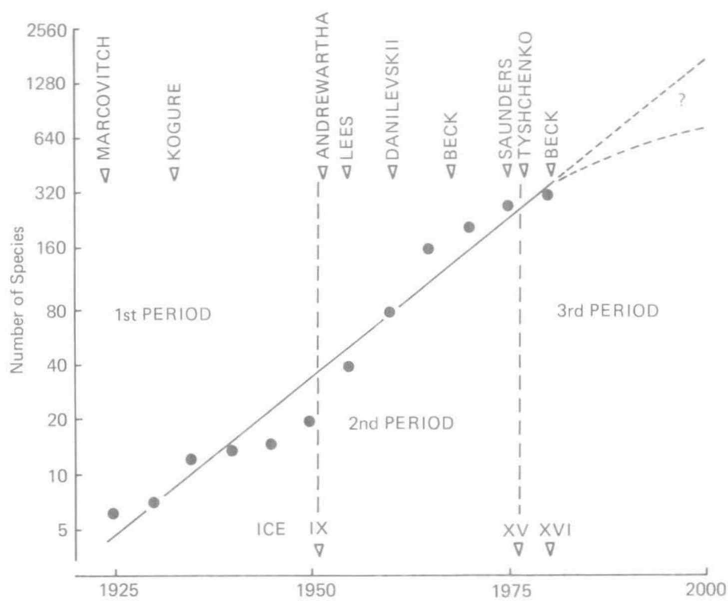

Fig. 1. The cumulative number of insect species in which the response to photoperiod has been elucidated. Species showing different kinds of photoperiodic responses are counted repeatedly. (From tables compiled by Beck 1980.) I.C.E. = International Congresses of Entomology.

Figure 1 shows that the number of species subjected to photoperiodic tests has increased by nearly 20 times during the last 20–30 years. In accordance with this accelerated rate of growth, the second period was characterised by an outburst of review articles dealing with insect seasonality. There are perhaps more than 20 such works, which means that at least one review has been published every one or two years! What is more, several of them are comprehensive books of high quality written by single authors (Lees 1955; Danilevskii 1961; Beck 1968, 1980; Saunders 1976; Tyshchenko 1977). Although the scope differs from one volume to another, the situation is quite remarkable in the world of science.

As an increasing number of species were examined, the unity among insects in the seasonal adaptation of their life cycles became clear. Most, if not all of them, are now known to use daylength as a primary seasonal cue. At the same time, diversified pictures emerged. The seasonal responses of insects are much more complicated than previously thought. In many species, including univoltine ones, photoperiod controls not only the induction but also the maintenance or termination of diapause. In others, the developmental requirements for photoperiodic and temperature conditions are by no means fixed, and the response threshold varies with the season. In still others, not only the absolute level but also the change in daylength is important in determining the response. Moreover, seasonally controlled polyphenism is fairly common and manifested in various ways; body size, colour, wing form, the shape of reproductive organs, the surface structure of cuticle, etc., may be modified by photoperiod. Some of these sorts of polyphenism are component parts of adaptation. It seems highly probable that a number of coadapted responses form an integrated system of seasonal adaptation.

Extrapolation of the trend line in Fig. 1 may predict that Professor Beck will have to undertake the tedious task of compiling a very long species list for photoperiodic responses, should a future edition of his book be published at the end of this century. There will be more than 2000 species! Even though this is still a small sample compared with the number of insect species, a further increase in sample size does not seem very meaningful. We are probably coming close to an asymptote, and what is appropriate at this moment is to explore a new approach for the third period.

Some of the physiological studies have been well orientated in the second period, and a rich harvest will be expected, especially from the field of photoperiodic clocks. Other physiological or biochemical studies will also be elaborated further, and they are of course essential to answer 'how' questions. They can clarify proximate factors involved in the physiological processes underlying seasonal life cycles. However, they do not necessarily answer 'why' questions, asking ultimate factors responsible for the 'decision' of a seasonal strategy. Elucidation of the evolutionary background is most important in any biological phenomenon, and particularly so in the case of seasonal adaptation since this is one of the most significant events in the whole evolutionary history of insects.

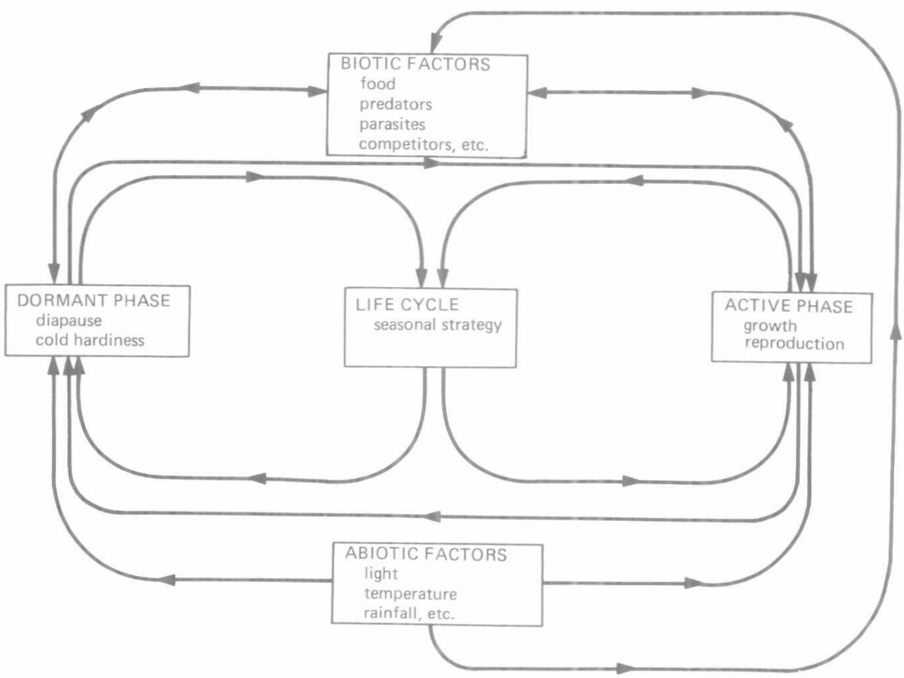

Fig. 2. Schematic representation of factors involved in the evolution of seasonal life-cycle strategies. Arrows indicate the direction of selection pressure.

Here, there is an important role to be played by the ecologist who looks for factors of selection operating in the natural habitat. Why does an insect enter diapause as a pupa but not as an egg? What is the cause of divergence in the diapause stage among closely related species? Why are some species polymorphic in their life cycles? Why do some insects migrate for dormancy while others do not? All these questions are intimately related to evolution and can hardly be solved by physiological methods alone.

In attempting any ecological approach, it must be kept in mind that, in the course of evolution, there may be intricate interactions between different stages within each life cycle and also between life cycles of different species (Fig. 2). The diapause stage necessarily affects the seasonal arrangement of the entire life cycle. Consequently, the environmental pressures exerted on other active stages depend, to a greater or lesser extent, on the stage at which diapause occurs. For example, larvae should find different qualities of food plant or different intensities of predation, if they hatch at different times of the year. The hatching time in turn is primarily determined by the hibernating stage. It is clear that an optimal seasonal strategy is selected for in terms of the fitness of the life cycle as a whole. Various ecological phenomena that can be recognized at the population or community level, such as predation, competition, mimicry or many interspecific relations are ascribed to the temporal relationship between the life cycles of the species involved. In some cases at least, this kind of interaction is important in the evolution of a seasonal life-cycle strategy.

From these arguments, one obvious line of approach to the problem of seasonality is to interweave environmental-physiological analyses with modern methods and theories of ecology, evolution, and population genetics. Undoubtedly, a start in this direction was made at the symposium 'Evolution of Escape in Space and Time' at the XVth International Congress of Entomology (1976) in Washington, D.C., USA (Dingle, 1978). Four years later, the symposim 'Life Cycle Strategies: Seasonal and Geographic Adaptations' at the XVIth Congress (1980) in Kyoto, Japan, gave further impetus to the ecological and evolutionary approach to diapause and the life-cycle strategies of insects. One can only hope that this volume will stimulate yet further interest in this aspect.

ACKNOWLEDGEMENTS

I am deeply grateful to Hugh Dingle who shared the responsibility with me of organizing the symposium, and also to all the speakers who contributed enjoyable papers. I am especially pleased that many of the profits derived from the symposium can be widely disseminated due to the efforts expended by Valerie Brown and Ivo Hodek. I thank them very much.

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PART ONE

MECHANISMS REGULATING SEASONAL ADAPTATION

The evolution of scientific disciplines has to pass through two periods; first, the accumulation of new facts and second, generalisation and synthesis. The formulation of a new theory is succeeded by a short 'happy' period, when new facts can be interpreted with ease. Thereafter, facts are accumulated which do not fit the accepted generalisation. Although this may stimulate the discoverer, the contradictory interpretations may be misleading to new students in the field.

We are currently at a time when relatively recent certitudes are being questioned by discoveries of more complex and more diversified mechanisms. The five papers in this section deal with several such findings and interpretations: (1) the importance of intermediate daylengths and changing daylengths in photoperiodic regulation (Tanaka); (2) the postdiapause recurrent photoperiodic response in females of *Aelia acuminata* and *Coccinella septempunctata* (Hodek), in males of *Oedipoda miniata* (Pener and Orshan), and in nymphs of *Pteronemobius nitidus* (Tanaka); (3) some flexibility in 'choosing' the developmental stage in which diapause occurs (the possibility of completion of diapause development *before* the diapausing stage is attained (Fujiyama)); (4) interrelationship between diapause development and activation in *Tetrastichus julis* (Tauber *et al.*) and *Pyrrhocoris apterus* (Hodek); (5) the complexity of the interactions between the cues from the external environment and the internal milieu of the host's physiology in parasitoids (Tauber *et al.*). The role of cold for diapause development has also been re-evaluated (Hodek, Tanaka). Some of these findings have led to conceptual reconsideration, concerning the definition of diapause (Tauber *et al.*) and the termination of diapause (Hodek).

As the physiological basis of diapause still remains unknown the analytical procedure has to be limited to the evaluation of experimentally manipulated ecological factors. The measurable events may be larval ecdysis (Tanaka, Fujiyama), adult emergence (Tauber *et al.*), pupation, or reproduction (Hodek, Pener and Orshan). Such an experimental approach is fully adequate and should not be criticized for the absence of biochemical criteria. The individual approaches (ecological, morphological, endocrinological,

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