Summary of the Book

1. This book reviews dormancy as an aspect of the ecological adaptations of insects to chiefly seasonal events. Environmental conditions differ greatly from one region to another, and over time in one place. Moreover, so many aspects of insect life cycles can be adjusted in response to seasonal conditions that dormancies can differ in all elements of their timing, form and control. Therefore, the overwhelming diversity of dormancies can be understood only if life cycles are viewed from a broad ecological orientation. Such an approach is the basis of this book, which extends the discussion of dormancy beyond the mainly physiological aspects (such as biological clocks and hormonal controls) previously emphasized.

2. Dormancy is either: quiescence, a stoppage of development due to currently adverse conditions; or diapause, in which morphological development is suppressed (whether or not growth ceases completely) through a central control, not simply by the direct action of environmental factors. Most of the complexities of insect dormancy stem from forms of diapause. Various stages of diapause have been named; the terms preferred here are shown in the first column of Table 2. Attempts to classify diapause are unsatisfactory, because the developmental programmes of different species are so diverse: diapauses are a series of cases in a continuum of adaptations to a variety of circumstances.

3. Individuals that become dormant, especially those in diapause, usually differ in the amount of stored food, external and internal structures, colour, size, metabolism, biochemistry and behaviour from those developing continuously. The most conspicuous changes for diapause often include sequestering of fats (Table 4), marked depression of metabolism (Table 5), seeking of sheltered sites and construction of special cocoons (Table 6). With features such as thicker wax layers on the cuticle, these changes appear to provide additional protection, resistance to desiccation, and reserves of food, which favour survival of the inactive stages. Some changes appear to have no adaptive significance of this sort, although many of them are useful indicators of the diapause condition. In some species the subsequent fecundity or other features of individuals that enter diapause are altered. Other simultaneous structural or metabolic adaptations, such as cold-hardiness, usually appear to be independent of the diapause state, even though they may be induced by similar environmental factors (e.g. photoperiod).

4. Development is controlled by factors that act indirectly (cues, environmental tokens), directly, or as short-term stimuli. Some life cycles are controlled by direct effects (especially in sheltered habitats where conditions change regularly and predictably), but most insect life cycles include control by cues. Even so, the resumption of seasonal development often depends on direct control by temperature, moisture, or other factors, because diapause itself usually ends before favourable conditions return.

5. Although diapause is confined to a single stage in most species, it can be found in insects in general at any stage of the life cycle: egg, pharate larva, larva in any

instar, pupa, pharate adult, adult. However, diapause is somewhat more common in resting or less active stages (egg, prepupa, pupa, pre-reproductive adult) than in fully active ones. Related species tend to have the same diapause stage (Table 9). However, the greatest factor determining the dormant stage is the biology (habitat, food, etc.) of a particular species. Almost any stage can be sensitive to inductive cues, but sensitivity is somewhat more prevalent in active than in passive stages. Most commonly, the sensitive stage immediately precedes the responsive (diapause) stage, so that conditions are assessed just before a developmental decision is made (cf. Table 12). Sensitivity over preceding stages may be added so that conditions are monitored over a longer period. Occasionally, sensitivity occurs much earlier, even in the previous generation (Table 14).

6. Environmental cues vary in how reliably and predictably they are correlated with the seasons, how frequently they occur, and how readily changes in the cues can be recognized (Table 16). Photoperiod normally is the most reliable cue. Thermoperiod shares a similar though less marked reliability. Although overall long-term patterns of temperature are reliable, especially in sheltered habitats, typical short-term patterns are not. Moisture, food quality and quantity, and other cues are reliable indicators of seasonal position only under certain circumstances.

7. Photoperiodic and temperature cues that induce diapause in different species elicit qualitative and occasionally quantitative responses to absolute values. A few species respond to change across a threshold or to directional change. The quality and quantity of food (particularly in phytophagous species, in many parasitoids, and in several predators), and rarely chemical substances or the density of individuals, sometimes modify induction. Photoperiod is the major seasonal cue for the induction of diapause in most insects from temperate regions. Normally it acts simply through a critical daylength (nightlength) beyond which diapause is induced. However, the range of effective photoperiods varies widely among species (cf. Figs. 16–19). Responses to different factors, especially photoperiod and temperature, usually interact. The nature of the responses to inductive cues shows that induction is a dynamic process and not a single event.

8. Diapause intensity is the duration of diapause under given conditions. It can be modified in some species by cues (notably photoperiodic ones) perceived during induction. Diapause development leads to the end of diapause. Its rate depends, according to species, chiefly on photoperiod and temperature, although in most species development eventually resumes spontaneously even without the cues that normally end diapause. Photoperiodic responses may require qualitative signals or more rarely quantitative signals or changes from one daylength to another. Many species from temperate regions require prolonged low-temperature exposure, but other species require exposure to higher temperatures. Moreover, the rate of diapause development differs at different temperatures, often in a complex way, and sometimes interacts with photoperiod. Diapause development evidently comprises more than one stage, usually with different requirements of photoperiod or temperature for maintenance or completion. Diapause development (unlike post-diapause development) very rarely depends on moisture. In a few predaceous species the presence of food ends diapause.

Development after diapause has been induced therefore relies on the monitoring, summation and integration of environmental information against a partly programmable requirement for such information. Diapause development, like induction, therefore is a dynamic process, not just an isolated event.

9. The extent, intensity and environmental controls of diapause differ markedly among geographic races of a species. In general, as latitude (or its climatic equivalent) increases, the incidence of winter diapause increases, the critical photoperiod for its induction increases (cf. Table 24), the inductive temperature decreases, and the intensity of diapause increases (cf. Table 25). Univoltinism persists across a wide latitudinal range in some species, but in others the number of generations increases at lower latitudes. Individuals within a single regional population also vary markedly in diapause characteristics. There may be sexual differences in the occurrence of diapause, in its intensity and in the rate of post-diapause development. Some populations are partitioned into temporal sets, within a season (Table 26), or among seasons (prolonged diapause, Table 27). These responses accord with unpredictability of resources. In several species, an interval timer or endogenous pattern appears to inhibit diapause in the progeny of individuals that entered diapause, but the mechanism and even the existence of many of these "timers" has not been confirmed. Diapause can be selected readily for and against in the laboratory in many species (Table 30), but the last traces of diapause are very difficult to eliminate. The genetic control of diapause usually is relatively complex and polygenic (Table 31), although simple Mendelian and "supergenic" systems have been identified. Detailed genetic work has been done in very few species, but sex linkage (Table 32) and other features have been reported.

10. Dormancy is only one element of the life cycle; growth rates and other characteristics are integrated with it. Photoperiod and other cues, especially crowding, can modify growth as well as development by their indirect action (Tables 33, 36). Several other features, including changes in larval size and adult fecundity, coincide with particular seasons through the effects of photoperiod and temperature independent of any diapause response. The life cycle can best be viewed as a series of alternative pathways, the alternatives being chosen during the development of each individual by a variety of internal (genetically programmed) and external (environmentally determined) mechanisms. The more complex control systems (cf. Table 40) increase the possible flexibility or variability and the precision of the developmental response. They include a larger number of dormant stages, multiple pathways for development within a single dormant period, a wider variety of environmental controls used to time the stages, and the control of growth as well as development by environmental cues.

11. Chapters 11–13 briefly treat physiological aspects of diapause. Existing information on response thresholds and spectral sensitivity for photoperiodic cues (Tables 42, 43) is fragmentary and often has not been reported in a standard manner. Nor has the influence of habitat usually been assessed. Photoperiodic cues are received directly by the brain in most species. Reception of temperature and other cues has been little investigated.

12. Many models, including very complex ones, have been proposed for the

"biological clock" that measures daylength for the photoperiodic responses of diapause. New information often has prompted revision of earlier models, but there is no reason why one type of biological clock should be universal in insects. Unfortunately, hypotheses for clock function are based exclusively on the results of the time-keeping systems (such as diapause responses) and not on their actual mechanisms, which remain unknown.

13. Diapause is programmed internally through the action of a few powerful hormones that control normal development and metamorphosis, the manufacture or release of which is modified during diapause. These hormones have many different simultaneous or successive actions in the developing and diapause insect and thus the hormonal control of diapause can be organized in many possible ways, increasing the difficulty of understanding the control.

14. The complexity of diapause responses creates many potential difficulties in designing unambiguous experiments and in reporting the results (cf. Table 44). "Flow charts" of development usefully summarize complex diapause responses.

15. Dormancy and other responses to the environment are integrated throughout the life cycle. Seasonal problems vary so widely that different demands are placed on different species and on the same species in different places. Similar responses can evolve independently, and parallel responses occur also in organisms other than insects. As already noted, the wide range of adaptations includes arrested, retarded or accelerated development, sensitivity and response to a wide range of environmental cues in almost any stage, and variation in the extent and duration of sensitivity (cf. Table 45). However, a relatively small number of successive developmental choices can generate many different routes of development. Pathways of development can be active (the internal programme causes development to continue uninterrupted unless signalled otherwise) or passive (development ceases unless signalled otherwise), and requirements for either alternative may change with time. These different possibilities have not previously been clearly recognized, resulting in some argument and confusion about the nature of dormancy. Diapause may have evolved in tropical regions, but in any case probably can evolve relatively easily. Its prevalence and control are correlated with habitat as well as latitude, which influence both the actual seasonal constraints and the clarity and reliability of seasonal cues. Adaptive syndromes such as diapause are integrated responses to the average, the normal range, and the predictability of environmental circumstances. The temporal or spatial uncertainty of some habitats is reflected by adaptations such as intraspecific variation in prolonged diapause and other traits. Future work should attempt to interpret the ecological meaning of life cycles by understanding the different developmental pathways that are available to a given individual or a given species. Many of these pathways diverge on the basis of dormancy and allied responses.