DEVELOPMENT, DIAPAUSE AND SEASONAL ECOLOGY
OF THE INSECT PARASITE, APANTELES RUBECULA
(HYMENOPTERA; BRACONIDAE).

by

VINCENT GRAHAM NEALIS

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Department of Plant Science

The University of British Columbia
1956 Main Mall
Vancouver, Canada
V6T 1Y3

Date August 26, 1983
ABSTRACT

Apanteles rubecula is a solitary insect parasite of Pieris rapae (small cabbage white butterfly, imported cabbageworm). The parasite has been successfully introduced to Australia and Vancouver, Canada but has failed to become established at other North American release sites. This practical problem illustrates a fundamental aspect of insect ecology. The seasonal biology of insects is interpreted here as an interaction of responses to ambient conditions. Emphasis centers on the rates at which life history phenomena occur and the importance of the insect's biological chronometers on the outcome of its ecological relationships with its host and its local climate. Comparisons are made between Canberra, Australia and Vancouver, Canada.

The parasite's developmental response to temperature is similar in Canberra and Vancouver but the host response differs. Canberra A. rubecula have a longer generation time relative to the host at low temperatures, but shorter generation times at higher, midseason temperatures. Vancouver parasites always have faster generation times than their hosts but the season is truncated in August by a diapause response to daylengths shorter than 15h. The beginning of the season is delayed until late May by the high thermal requirement to terminate diapause. These local responses to temperature and photoperiod result in different phenologies which, while appropriate locally, are disastrous elsewhere. The failure of
North American attempts to establish Vancouver A. rubecula is attributed to the diapause characteristics of the released insects. They entered diapause while ambient temperatures remained warm enough for morphogenesis and were unable to survive the obligatory period to diapause termination.

Manipulation of the diapause response is one technique in ecological pest management. A methodology for a breeding program and its analysis is presented. Practical suggestion for biological control efforts are made and the role of individual physiological responses in insect seasonal ecology are discussed.
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Thanks to the insect participants seems irreverent. Rather, an apology from Fred Cogswell's "Butterfly":

Bedraggled now and crushed,
frail soul of fluttering things,
forgive my hands that brushed
the sun dust from your wings;

VINCENT NEALIS

Vancouver, B.C.
July, 1983
CHAPTER 1

INTRODUCTION

Time is the most elusive of physical quantities. Changing concepts of time mark revolutions in modern scientific thought. Newton limited time to an instant and so described a universe in which relationships change with a continuous and constant flow of time. His methods still dominate applied sciences but Newton's cosmology has been replaced by Einstein's relativity and time intervals have come to depend upon your point of view. The universe behaves in a surprising fashion at the level of the quanta.

Natural philosophers knew the earth and its organisms changed. Life grew, reproduced and died in apparent harmony with its environment. Darwin understood change and pondered the variants and the exceptions. Darwin's revolution showed where these variations could lead, if only given enough time.

Ecologists seek to explain the distribution and abundance of organisms. An evolutionary approach must explain how organisms "cope" with the deluge of changes encountered in a single, precarious lifetime. We are reminded that the size and importance of changes depends on your point of view. In insect ecology, it is first of all necessary to gain the insect's point of view.
This thesis examines one level of time and seasonal rhythm in a host-parasite relationship. It proposes that the dynamic nature of ecological relationships between insects can only be understood against a background of daily and seasonal responses to ambient weather and photoperiod.

Parasites have a clear objective. They must have a life history which ensures a period of reproductive activity concurrent with suitable hosts -- they must be in the same place at the same time. Their intimate relationship with the host make parasites a good starting point for the comparative dynamics of interacting populations.

The remainder of this chapter introduces the host and parasite and my experimental approach. Chapter 2 describes continuous growth and development as temperature-dependent rates. Chapters 3 to 5 examine the biology of diapause in the parasite. The last chapter discusses the parasite's phenology and diapause and compares the success of its life history strategy under different ecological situations and relevance to biological control.
THE INSECTS

PIERIS RAPAE (Lep., Pieridae)

Pieris rapae L., the small cabbage white butterfly, is a native of Europe where its larvae are minor pests of cultivated crucifers. Richards (1940) is the best source of information for the biology of P. rapae in Britain. Recent studies by Dempster (1967, 1968) provide a life table approach and analysis of mortality factors in England.

The small cabbage white's rapid dispersal through the countries of introduction is documented by Beirne (1971) CANADA, Muggeridge (1942) NEW ZEALAND and Peters (1970) AUSTRALIA. In North America, P. rapae is also known as the imported cabbageworm. What has been unfortunate for cabbage growers has been a boon to entomologists interested in the comparative population dynamics of insects. The imported cabbageworm is readily sampled and easily reared so that extensive life table statistics have been compiled from a diversity of locations (Harcourt 1962, 1966; Ito et al. 1960, 1975; Parker 1970; Parker et al. 1971, 1972; Pimental 1961). P. rapae has been the subject in studies on behaviour (Jones 1977a,b; Jones and Ives 1979), dispersal (Jones et al. 1980) and growth and development (Jones et al. 1982).

Female butterflies lay their eggs singly on the underside of the outside leaves of wild and cultivated crucifers. The five larval instars and the pupae develop within a temperature range of 10° to 30°C (Richards 1940; Jones and Ives 1979). At
at an average temperature of 17°C, a complete generation requires five to six weeks. Development is continuous until a combination of photoperiod and low temperatures, acting on late larval stadia, induces diapause in the pupa. Richards (1940) cited three and a partial fourth generation per year in England but Dempster (1967) claims that only in exceptionally warm years would three generations be completed. There are three generations in Ontario (Harcourt 1963) but only two in Vancouver (Jones and Ives 1979). There may be as many as six generations in the southern United States (Parker et al. 1971) and in Canberra, Australia (Jones and Ives 1979).

APANTELES RUBECULA (Hym., Braconidae)

Apanteles rubecula Marshall is a braconid parasite of the larvae of *P. rapae*. It is native to Europe and Britain but has been introduced to Australia (Wilson 1960) as a biological control agent of the cabbageworm. *A. rubecula* has not become established throughout its host's range in Australia; it has not been recovered in Tasmania or Queensland. The Vancouver population was introduced accidentally (Wilkinson 1966) and I have collected the parasite in the Okanagan Valley at Summerland. Several attempts to establish *A. rubecula* in North America outside British Columbia have failed (Oatman and Platner 1969, 1972; Puttler et al. 1970; D.G. Harcourt and J. Heraty, personal communication). Its potential for control of the imported cabbageworm has been demonstrated (Parker and
Pinnell 1972), but releases must be renewed for reasons which will be discussed later in this thesis. *A. rubecula* had apparently become established in China before biocontrol workers were able to make releases of Canadian material (Hu et al. 1981).

The original *A. rubecula* was described ex *P. rapae* (Marshall 1885) but Schenefelt (1972) catalogues six other hosts from various sources. In his review of the British *Apanteles*, Wilkinson (1945) was convinced that most of the alternate host records were due to either a misclassification of the host or of the parasite. Moss (1933) was unable to rear *A. rubecula* from the closely related *Pieris brassicae* (L.) and Hamilton (in Richards 1940) failed to get oviposition in either *P. brassicae* or *Pieris napi* (L.). Krombien et al. (1980) list *Pieris protodice* Boisduval and LeConte as an alternate North American host but a search of their references cited does not support this claim. Modern workers, with the exception of cataloguers, consider *A. rubecula* to be an obligate parasite of *P. rapae*. 
Biology

The genus Apanteles is a large group of temperate-zone braconids utilizing lepidopterous larvae as hosts. Our knowledge of their biology is fragmentary (Matthews 1974). Gautier and Riel (1921) published the first notes of the biology of A. rubecula.

Free-living adults probably feed on nectar and pollen. In captivity, they feed readily on honey droplets and do not seem to require protein supplements to sustain egg production for several days. Adult behaviour shows that odour plays the principle role in host location, as has been found in other braconids (Read et al. 1970; Sato 1979; Vinson 1976). Visual cues, and chemoreceptors in or near the ovipositor, may be necessary for final acceptance of the host by the parasite (Fisher 1971). Apanteles wasps attack by thrusting the abdomen between the legs and jabbing with the ovipositor. In A. rubecula, which lays a single egg, oviposition requires less than a second and is followed by a change in wasp behaviour; the female moves out of the immediate vicinity and grooms extensively.

Delucchi (1950) provides morphological descriptions and figures of the larval instars of A. rubecula. The single elliptical egg is injected into the host haemolymph and is initially nourished by the trophamnion. The caudate I-instar parasite can often be seen within the trophamnionic membrane. The II-instar is vesiculate (proctodaeum evaginated) and the
last instar typically hymenopteriform (mandibulate, apodous, white cylindrical body). Schisler (1981) reports that A. rubecula remains a haemolymph feeder during the first two instars but feeds on host tissues during the last instar. The mandibles of the last instar are certainly functional as it emerges from the host by biting through the caterpillar's body wall between the third and fourth abdominal segments. It then spins a cream-coloured cocoon. The insect either diapausess at this prepupal or eonymph stage, or develops to an exarate pupal form and finally to an adult, which bites a hatch and pushes its way out of the cocoon.

Mating is similar to that described for Apanteles glomeratus (L.) (Tagawa and Hidaka 1982; Tagawa and Kitano 1981). Males approach females from downwind. A specific sequence of behaviour appears to be necessary before females permit copulation. The male approaches the female from the rear, wings arched and vibrating and antennae held above the female's thorax. Copulation can last thirty seconds to five minutes. The female remains motionless after the male leaves and if she is immediately approached by another male, he too will copulate, uncontested. Once female activity resumes, she appears to be no longer attractive to males. Rahman (1966) estimated female fecundity at about thirty eggs, but I have obtained that many successful ovipositions from a female in one day. Parker and Pinnell (1970) record longevity under mass-rearing conditions as 25.1 days for females and 21.8 days for males. Parker and Pinnell (1972) estimated that adults
survived six weeks during a Missouri autumn.

A. rubecula is attacked by hyperparasites in both Australia and Canada. In Canberra, the pteromalid Eupteromalus braconophagus (Cameron) is an infrequent hyperparasite but in Vancouver, the eulophid Tetrastichus galactopus (Ratz.) accounts for a high mortality toward the end of the season (Nealis 1983) and there are additional hyperparasitisms by various Gelis spp.

DESCRIPTION OF THE STUDY AREAS AND GENERAL METHODS

Parasitic insects present special problems for field sampling. The adult is a small, active predator whose prey are more or less aggregated in particular areas. There may be opportunities to observe wild females but there are no reliable methods for quantitative sampling of populations. Most parasite studies use, as the base observation, the proportion of hosts parasitised. When there is a reliable sampling method for the host population and the proportion parasitised consistent, the immature parasite population may be reasonably sampled. But the unique nature of the host-parasite relationship can cause difficulties in the extrapolation from the sampled host population to the parasite's ecology. For example, there are efficient sampling designs for the imported cabbageworm in
commercial plots (Harcourt 1962) but caterpillars in commercial plots are only a small proportion of the broader population which serve as hosts to A. rubecula. An explanation by way of describing host-parasite ecology may help to clarify the sampling difficulties.

The cabbage white is a vagrant species; the butterfly finds and oviposits on host plants wherever they occur within its range. The distribution of host plants is an important factor in the species' population dynamics. Large patches of host plants, such as commercial cole plots, have a relatively low egg density due to butterfly flight and oviposition behaviour (Jones 1977a) and poor larval survival due to insecticides. But larval survival may be very good on many small, undisturbed patches of host plant. In both North America and Australia, P. rapae is the scourge of backyard gardens. In Canberra, R.Jones and I have made life tables for several cohorts of caterpillars in nine home gardens. They all received large numbers of eggs. Survival of caterpillars varied widely but there was substantial damage in all gardens even though we removed caterpillars after they entered the final instar. Raising cabbages in Canberra requires constant vigilance or insecticides. Yet, A. rubecula was absent from most sites and a minor mortality factor in the remainder. A larger and less disturbed habitat for the cabbage white is represented by a picnic site at Hut Crossing on the Murrumbidgee River near Canberra. This shaded, well-watered area has an annual population of wild mustard (Hirshfeldia) which serves as host
for a small but persistent population of *P. rapae*. The proportion of caterpillars parasitised by *A. rubecula* at this site is consistently high (>50%) from late January until the end of the season in April.

But *A. rubecula* can also exploit large and newly available habitats in particular circumstances. The Hill & Sons Market Garden in Pialligo, near Canberra has been a consistent source of butterflies for several years. Chemical control of cabbage aphid and diamond-back moth make it an area of poor cabbageworm survival. On February 5, 6 and 13, 1981, heavy rains flooded one plot, making the large cabbages unsaleable. No further insecticides were applied. Caterpillar collections on February 17, 20 and March 4, 11 and 20 estimated parasitism rates exceeding 80%. By March 20, parasite cocoons were more numerous than host larvae. *A. rubecula* had thoroughly parasitised the host population. Similar rates in experimental plots are reported by Parker and Pinnell (1972).

In Vancouver, *A. rubecula* can be commonly found parasitising cabbageworms in home gardens but is most consistently collected in areas such as the Burnaby Rental Plots where there is a moderately large population of cultivated crucifers in small, individual plots.

In view of the above habitat associations of the host and parasite, my field samples were opportunistic. Rather than sampling intensively under some schedule, I chose to collect host larvae and parasite cocoons at several sites throughout
the main growing season, concentrating my efforts at key times of the year (e.g., onset of diapause). At each site I would search entire host plants for caterpillars and parasite cocoons until I had enough (50-200) caterpillars to provide an adequate estimate of the rate of parasitism or until it was evident that I must either settle for less or collect every larva in the host population. I kept a record of the search time (1-2 hours) but I do not consider my counts accurate measures of host density. This scheme satisfied the necessities of obtaining field data and experimental material when they were most needed with minimum disturbance to a sometimes sparse population.

My treatment of field-collected insects was as follows. Caterpillars were brought back to the lab and sorted by instar. Depending on the objectives of the collection, each instar was reared separately on potted crucifers under controlled or natural conditions, or dissected under saline so that parasite eggs could be counted. The proportion, per stadium, of parasitised hosts was always obtained. The time to emergence in specific conditions could be used to estimate the approximate age of the parasite on the collection date. The parasite's age and possible superparasitism were observed directly by dissection of the host. The sex-ratio and hyperparasitism were also recorded. These data are the background for subsequent experiments. Interpretation of these field data requires a good deal of qualification and a large part of this thesis is devoted to experimental investigation of hypotheses suggested by the field notes.
Other field data are experimental. A known number of hosts of various instars and/or female wasps were seeded into an area according to a particular experimental design. In some cases, hosts were parasitised in the laboratory and then taken to the field. These methods and those of the laboratory will be discussed with the experiments.

Insect culture

Standardized laboratory conditions cause unavoidable selection in insect stock. It is impossible to anticipate the consequences for laboratory material even when we know the intensity and direction of the selection. In all experiments, I used insects which, if not freshly collected from the field, were no more than three generations removed from it. *P. rapae* pupae and *A. rubecula* cocoons can be stored three weeks at 10°C without increased mortality and the adult wasps live up to six weeks under these same conditions if supplied with honey and water. Butterflies were fed a 10% honey solution absorbed on cotton.

Mating in both the butterflies and wasps is inhibited by artificial light, so newly emerged adults were kept outside or near a window. Recently developed broad-spectrum fluorescent lamps (Vita-Lite) seem to be an improvement but thorough comparisons have not been made.
The imported cabbageworm can be reared on a variety of crucifers but the experiments involving *A. rubecula* utilized Brussels sprouts (Jade Cross) occasionally supplemented by kale (Maris Kestrel) or cabbage (Early Ball). All experiments started with plants six to ten weeks old.

The temperature of each controlled environment facility was recorded continuously and these records were calibrated with mercury thermometers, which were in turn calibrated monthly in ice and boiling water. Temperatures were almost always within ± 1°C of the stated mean. A truly constant humidity is difficult to maintain when there are potted plants in the growth chambers. A relatively constant humidity (approximately 75%) was achieved by keeping the soil in the pots moist and preventing standing water from accumulating in the chambers. Photoperiod was provided by two to six cool, white fluorescent lamps supplemented by two broad-spectrum lamps.
CHAPTER 2

GROWTH AND DEVELOPMENT - RESPONSE TO TEMPERATURE

INTRODUCTION

The time arthropods require to grow and develop during their most active season is largely determined by temperature. As poikilotherms, insects are dependent on ambient temperature to fulfill the thermal requirements for growth, maturation and reproduction. Each process may have different responses to temperature so the biology of the individual, and of the population, is an interaction of all processes in a thermally fluctuating environment. Typically, insects have adapted splendidly and occupy the entire range of climates offered by terrestrial habitats, at all hours of the day.

This relationship between temperature and rate of development means we must calibrate an insect's chronometer with our thermometer. This chapter discusses physiological time in the host-parasite relationship. It describes temperature-dependent rates of growth and development during the major portion of the active season in Vancouver, Canada and Canberra, Australia. These rates may be modified by other factors which are also considered here.
Temperature-dependent time

There are several functions which describe the rate of development of arthropods over a wide range of experimental temperatures (Logan et al. 1976; Stinner et al. 1974). Campbell et al. (1974) argue that field temperatures during the period of greatest insect activity are mostly in the range over which the rate of development is directly proportional to ambient temperature. I fit rate-temperature linear regressions to estimate a threshold $t$, the temperature at which the rate of development will be zero, and a "physiological time" $K$, which estimates the number of degree-days above the threshold required for development to be completed. When average daily temperatures remain close to the threshold, degree-days underestimate the rates and an expression such as Logan et al.'s (1976) may provide a better prediction (J. Regniere, personal communication). Any nonlinear response at low temperatures is not intrinsic to the insect but results from variation in the threshold within the population. Observation of rates at chronically low temperatures are biased by differential temperature selection for individuals with lower thresholds, making the estimate inaccurate (Gilbert et al. 1976). The choice of any particular function should be pragmatic. In this case, the linear model provided an adequate fit over most of the season (Table 2) and allowed simple comparisons with the host. Campbell et al. (1974) describe the empirical estimation of $t$ and $K$ and their standard errors, and I use their methods here.
METHODS

All parasites and hosts were first or second generation laboratory insect, the parental generation was raised on potted cabbage, kale or Brussels sprouts at 22°C 16L:8D. In initial trials with Australian parasites, larval hosts of different stadia were caged with adult wasps for one to two hours at 23°C and then randomly assigned to temperature treatments. In all other trials, host larvae were removed from the parasite cage as soon as an attack was observed, to minimize superparasitism and to avoid using unparasitised individuals. Host larvae were checked daily at the lowest temperatures and twice or three times daily at intermediate and higher temperatures, to determine the survival and duration of host instars and the times when parasite larvae emerged from the host. Once dry (1/2 to 1 day), pupal cocoons were weighed and then returned to the same temperatures until adults emerged. Other _A. rubecula_ were raised at one temperature (25°C) and the cocoons distributed among different temperatures to check whether the conditions experienced by the larvae affected the thermal requirements of the pupae. As there was no effect, pupae with different larval rearing conditions have not been distinguished further. Time to imago and the sex of each individual were recorded. Temperature treatments ranged between 13.9° and 30°C.

In Vancouver, the ability of my estimated t and K values to predict generation times of _A. rubecula_ in the field was checked by rearing cohorts of parasitised hosts in large screen
cages (3m X 3m X 1m high) at the Plant Science Field Station at the University of British Columbia (UBC). Daily maximum and minimum temperatures, recorded at an adjacent meteorological station, were used to compute degree-day accumulation in the field, using the algorithm provided by Frazer and Gilbert (1976).

Fecundity of *A. rubecula*

Preliminary dissections of adult female *A. rubecula* showed that the number of eggs in the swollen, proximal portion of the common oviduct roughly doubled over the first two days after eclosion, and then remained constant for at least three weeks. To avoid confounding weight with differential egg maturation rates, I used females which were two weeks old and of similar, limited foraging history. The adults were anaesthetized, weighed and immediately dissected under saline. All eggs and oocytes were counted. Although this count may underestimate absolute fecundity, it is the comparison for individuals of different weights which is of interest.
RESULTS

Table 1 lists the thermal requirements for the immature stages of *P. rapae* and *A. rubecula* in Canberra and Vancouver. The thermal constants for *P. rapae* are from Jones and Ives (1979). Neil Gilbert provided estimates for Canadian pupae and the development rates of unparasitised larvae shown in Fig. 1.

The egg and larval development rate in *P. rapae* is identical in both countries, but Canadian pupae have a substantially higher threshold than Australian pupae. This difference was confirmed by N. Gilbert for pupae held at 10°C in both places; the Australian pupae eventually produced adults whereas none of the Canadian pupae showed any development. At the same field temperatures, Canadian individuals will develop more slowly than Australian. Parasitism by *A. rubecula* retards development of the host larva (Fig. 1). Note that the early stages of parasitism do not affect host development at high temperatures but later stages slow host development at all temperatures.

In contrast, the host size had little effect on the parasite's threshold or its rate of development. Male and female *A. rubecula* developed synchronously through the parasitic stage so the thermal requirements for egg and larval *A. rubecula* in Table 1 include both sexes from all host sizes. The threshold for these parasitic stages of *A. rubecula* is higher than, but not significantly different from that of its host in either locality.
<table>
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<th>STAGE</th>
<th>LOCATION</th>
<th>t(SE)</th>
<th>K(SE)</th>
</tr>
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<tbody>
<tr>
<td>P. RAPA E</td>
<td>egg, larva</td>
<td>VANC</td>
<td>10.0 (0.8)a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CANB</td>
<td>9.8 (0.7)a</td>
</tr>
<tr>
<td></td>
<td>pupa</td>
<td>VANC</td>
<td>10.4 (0.9)b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CANB</td>
<td>6.7 a</td>
</tr>
<tr>
<td>A. RUBECULA</td>
<td>egg, larva (parasitic)</td>
<td>VANC</td>
<td>10.7 (0.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CANB</td>
<td>11.6 (0.9)</td>
</tr>
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<td></td>
<td>pupa</td>
<td>VANC</td>
<td>11.4 (0.2)</td>
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<tr>
<td></td>
<td></td>
<td>CANB</td>
<td>11.7 (1.0)</td>
</tr>
</tbody>
</table>

**TABLE 1.** Thresholds (t±SE) and degree-day requirement (K±SE) for development of the immature stages of *P. rapae* and *A. rubecula* in VANCouver and CANBerra.  
a) from Jones and Ives (1979); b) from N. Gilbert unpublished.
FIGURE 1. Temperature-dependent rate of development for P. rapae larvae. Open circles are unparasitised larvae, closed circles are larvae parasitised by A. rubecula during the second instar. Bars are 95% confidence intervals. a) third instar rate b) fourth instar rate.
a. III-instar *Pieris rapae*

```
RATE OF DEVELOPMENT
(1/days to develop x 100)
```

```
TEMPERATURE (°C)
```

b. IV-instar *Pieris rapae*
There was no correlation between the degree-day requirement of the parasitic larval stages and that of the free-living pupal stage. Male *A. rubecula* pupae develop faster than female (*F*=25.65 df=1,205 *p*<0.01). The thresholds were identical but males required five degree-days less than females to complete pupal development, about one day less in the field. I do not consider this difference here because it does not result in major differences in total generation time. There was a slight additional effect of weight so that smaller male adults emerged earliest in a cohort. Canadian *A. rubecula* pupae required fewer degree-days to complete development than did Australian (*t*=3.33 df=106 *p*<0.01).

Both Vancouver and Canberra parasite populations had a much lower heat requirement than their hosts. The net effect is that host generation times are shorter in Australia and parasite generation times are shorter in Canada.

How useful are the thermal constants in Table 1 for field prediction? Table 2 lists the chronological and physiological developmental period for Vancouver cohorts of *A. rubecula* larvae reared from caterpillars on cabbage. Four of the five observed values are very close to that estimated in the laboratory. The exceptions are parasites reared during April and May when mean temperatures are close to the threshold. The linear model underestimates the real heat accumulated by the insect in the field. In Chapter 5 I will show that spring
<table>
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<tr>
<th>CALENDAR TIME</th>
<th>PHYSIOLOGICAL TIME MEAN (SE)</th>
<th>N</th>
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<tr>
<td>August 10-30, 1981</td>
<td>119.5 (0.82)</td>
<td>30</td>
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<td>April 28 - June 6, 1982</td>
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<td>10</td>
</tr>
<tr>
<td>July 16 - August 3, 1982</td>
<td>114.4 (0.60)</td>
<td>18</td>
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<tr>
<td>July 31 - August 23, 1982</td>
<td>118.3 (0.54)</td>
<td>47</td>
</tr>
<tr>
<td>August 6-31, 1982</td>
<td>120.8 (1.08)</td>
<td>37</td>
</tr>
<tr>
<td>LAB ESTIMATE (TABLE 1)</td>
<td>119.0 (1.40)</td>
<td>300</td>
</tr>
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</table>

TABLE 2. Chronological and physiological development periods for the parasitic stages (egg to emergence) of *A. rubecula* reared on plants at the Plant Science Field Station, UBC, Vancouver.
emergence of wasps in Vancouver does not occur much sooner than June 1 so that, in practice, I will not have to consider early-season predictions.

Table 3 compares host and parasite generation times at various average temperatures for Canadian and Australian populations. In Australia, _A. rubecula_ will have longer generation times than their hosts at lower temperatures but faster times at higher temperatures. In Vancouver, even at temperatures as low as 15°C, the parasite generation is always shorter than the host. This difference is due to the faster rate of development in Canadian parasite pupae and the extended generation time of the host due to its higher pupal threshold.

Although oviposition in hosts of different ages had a negligible effect on parasite development rate, the parasites emerging from older, larger hosts were certainly larger than those from younger, smaller hosts (Fig. 2) so relative growth rates must be affected by host age. As in many insects, large females had more eggs and unmated females had as many eggs as mated females of the same size (Fig. 3).

Females must grow relatively faster than males since both sexes develop synchronously through the parasitic stage but females are consistently 10% larger than their male sibs. Male weights ranged from 3.60 to 7.83 mg and females from 4.36 to 8.76 mg so there is considerable overlap.

Within the range of temperatures favourable to development
<table>
<thead>
<tr>
<th></th>
<th>VANCOUVER</th>
<th></th>
<th>CANBERRA</th>
<th></th>
</tr>
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<tbody>
<tr>
<td></td>
<td>15°</td>
<td>20°</td>
<td>25°</td>
<td>15°</td>
</tr>
<tr>
<td>P. RAPAE</td>
<td>66.7</td>
<td>32.8</td>
<td>21.7</td>
<td>58.6</td>
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<td>A. RUBECULA</td>
<td>49.1</td>
<td>21.9</td>
<td>14.4</td>
<td>64.7</td>
</tr>
</tbody>
</table>

TABLE 3. Estimated generation times for P. rapae and A. rubecula at three average temperatures in Vancouver, Canada and Canberra, Australia.
(15° to 28°C), parasites reared at higher temperatures were smaller than those reared at lower temperatures (Fig. 2). Oviposition in older hosts produced larger parasites at all temperatures. Parker and Pinnell (1973) made this same observation using a laboratory culture of *A. rubecula* from Vancouver stock. There is no apparent interaction between temperature, host size at oviposition and sex of the parasite; the relationship between weight and these three variables can be expressed as:

\[
WT = 7.49 - 0.109 \text{ TEMP} + 0.25 \text{ HOST} - 0.65 \text{ SEX}
\]

\[R^2=0.29, \text{ df}=295, \text{ p}<0.01\]

where WT is in mg, TEMP in °C, HOST size is 1, 2 or 4 for instar, males are 1 and females are 0.

This equation is based on Vancouver data only. Australian data for these same variables are not so complete; the magnitude and direction of the trends is the same but host size appears to contribute less to final parasite weight.
FIGURE 2. Temperature-dependent final cocoon weight of *A. rubecula*. Open symbols are females, closed symbols are males. Parasitisms began in first instar hosts (circles), second instar hosts (triangles) or third instar hosts (squares). Bars are 95% confidence intervals.
FIGURE 3. Correlation between adult female fresh weight and the number of eggs and oocytes in their ovaries. Standard variables are plotted. Open circles are unmated females, closed circles are mated females. Actual number of eggs and oocytes in *A. rubecula* ranged from 35 to 128.
$r = 0.49$

$df = 55$
DISCUSSION

The parasite and host thermal requirements shown in Table 1 can be compared with those of aphids and their parasites (Campbell et al. 1974, Table 1). The threshold of *A. rubecula* is only slightly higher than that of its host in comparison with the large differences between the thresholds of aphids and their parasites; but the aphid hosts have much lower thresholds than does *P. rapae*. A more important difference here is that, unlike the aphid parasites, *A. rubecula* has a much lower degree-day requirement than its host.

In Australia, generation time in *A. rubecula* is longer, relative to the host, at average temperatures below 17°C but shorter than the host's at higher temperatures. Since 17°C is approximately the mean seasonal temperature for Canberra, parasite generations there are shorter than the host's for half of the season but longer than the host's during the other half. Frazer and Gilbert (1976) have already shown the importance of alternating temperature-driven development advantages in a predator-prey relationship. In Vancouver, *A. rubecula* completes a generation faster than its host at all times of the year. The small number of generations per year in Canada may outweigh any possibility of over-running the host population in Vancouver.

Population growth is a function of development time but it is helpful to view the growth of individuals as a closely associated but distinct process (Gilbert 1983). Size, and therefore growth rate, can vary enormously in parasites being
dependent on sex, temperature and host size among other variables. But even though highly variable in size, most parasites take about the same length of time to complete development because the thermal constants do not vary as widely. A heterogeneous environment does not disrupt the developmental synchrony in parasites; it merely determines their size. This implies high local variability in fecundity compared to timing and is consistent with Cole's (1954) argument that a population's rate of increase is more sensitive to variations in generation time than to equivalent variations in fecundity.
CHAPTER 3

INDUCTION OF DIAPAUSE - RESPONSE TO PHOTOPERIOD AND TEMPERATURE

INTRODUCTION

Diapause is a peculiar physiological state characterized in arthropods by cessation or drastic modification of some metabolic processes leading to a marked reduction in the rate of morphogenesis. Diapause can occur at any stage in the insect life cycle but for a particular species, there is usually only one stage capable of prolonged dormancy. Once initiated, development through the diapause stage requires a particular sequence of events to be completed. Diapause is an adaptive phenomenon enabling insects to live in areas when environmental conditions are unsuitable for activity. It thus serves to synchronize active stages in the life cycle with seasonal periods favourable to growth and development.

Preparation for diapause requires a response under conditions favourable to insect activities and must therefore be initiated by environmental cues which foretell periods unsuitable for continuous development. Several possible cues are recognized; declining food quality and low temperatures were among the first factors investigated, but it is now recognized that, in temperate regions at least, diapause is commonly a response to natural photoperiods (Danilevskii 1965). Photoperiod has the virtue of being a relatively invariant
harbinger of seasonal changes but is not in itself an adverse condition. Moreover the effects of photoperiod on temperature, of far more immediate importance to insects, are delayed, permitting insects to make the necessary preparations for dormancy.

The exact location of the insect photoreceptors involved in the induction of diapause are not known. Eyes and ocelli are not necessary. Control of diapause is definitely neuro-endocrine (Novak 1975) so light may act directly on neurosecretory cells in the cerebral ganglia (Lees 1964). The specific mechanisms of the clocks measuring the light and dark phases and their modification by other variables are fascinatingly complex (Beck 1980; Saunders 1976, 1981).

Diapause in parasites may be influenced by the host (Salt 1941; Vinogradova and Zinovjeva 1972) but in braconids, an independent photoperiodic response has been demonstrated (Dansilevskii 1965; Maslennikova 1959; Rabb and Thurston 1969). Schisler (1981) interpreted failure of A. rubecula to diapause under short days when reared in hosts ligated at the neck as indicative of parasite reliance on the host endocrine system. But the same study showed an effect of parasitism on biosynthesis of juvenile hormone in host larvae: who is controlling whom? I have reared A. rubecula under conditions where approximately half the parasites entered diapause (Chapter 4) and never observed diapause in the unparasitised caterpillars developing side by side with the parasites. In
Vancouver, *A. rubecula* diapause begins two to three weeks before its host, so some degree of independence on the part of the parasite must be recognized.

The adaptive role that diapause plays in synchronizing the insect population with its environment is of primary interest. The important ecological questions pertain to the relationship between seasonal periodicity in photoperiod and temperature, and the induction and duration of diapause.

The photoperiodic response curve expresses the diapause response of a population to a series of stationary photoperiods. Typical of such curves is the critical photoperiod, a period which marks the abrupt change from diapause induction to continuous development (Beck 1980; Danilevskii 1965; Saunders 1976). In the experiments reported below, I added constant, alternating (square wave) and fluctuating (sine wave) temperatures as factors to investigate the interaction between photoperiod and temperature. The interpretation was validated with experimental evidence from the field. I also identified the developmental stages of *A. rubecula* which are sensitive to photoperiod.
METHODS

Laboratory: General

Host and parasite laboratory stocks were taken from Vancouver populations and reared under conditions promoting continuous development (22°C 16L:8D) for one generation before the experiments started. Late-II and early-III instar caterpillars were exposed singly to female wasps. After an attack, the caterpillars were transferred to Brussels sprouts (Jade Cross) in 15 cm pots and then randomly assigned to a particular temperature-photoperiod combination. All laboratory experiments were carried out in controlled environment facilities at the Vancouver Research Station, Agriculture Canada and the University of British Columbia.

Every effort was made to standardize the hosts' food. The inevitable changes in plant condition through the experiment, particularly evident at low temperatures, could have been somewhat ameliorated by replacement of plants at regular intervals but this would have necessitated handling the insects during transfer. Fortunately, caterpillars parasitised by A. rubecula eat very little during the latter stages of parasitism, so food quality then would have a reduced effect. Gilbert (1983) shows that declining food quality affects weight gain but not development time in P. rapae. Moreover, there is little ambiguity regarding the diapause response at short
(<15h) photophases.

The cocoons of the emerged parasites were collected daily, recorded by emergence date and, in some cases, weighed on a Mittler ME-30 electronic balance. They were then held at 22°C 16L:8D. Under such conditions, *A. rubecula* which are not in diapause eclose in about one week (Chapter 2). After 15 days, individuals could be scored as either diapause (D) or nondiapause (N).

Critical Photoperiod

During 1981, experiments were designed to determine the critical photoperiod for the diapause response of *A. rubecula* at different constant temperature-photoperiod combinations. The large number of combinations necessitated splitting the experimental stock into two groups, one for current trials and a second for continuous rearing for the next set of trials. The last trials used third-generation laboratory adults but there were no anomalous responses which could be attributed to artificial selection for or against the diapause response. During these trials, I included two runs at alternating temperatures and 16L:8D.

Experiments in 1982 were designed to see if the photoperiodic response was greatly modified by temperatures which fluctuated daily over a range typical of late summer in Vancouver (15°-25°C). These trials were conducted in identical
controlled environment chambers equipped to permit temperatures to fluctuate as a sine wave with the maximum temperature occurring at the mid-point of the photophase. Photoperiods used were 14L:10D, 14.75L:9.25D, 15.5L:8.5D. A fourth cabinet operated as a control at a constant average temperature of 20°C and a 15.5L:8.5D photoperiod.

Field data

Field data pertaining to diapause are from two sources. Hosts from general field collections were reared on plants in outdoor cages when collections were made during the estimated critical period (July 21 to August 30 in Vancouver, February 15 to March 31 in Canberra). Host caterpillars collected in Burnaby (BBY) on September 16, 17 1981 were caged on potted plants in the laboratory at 22.5°C 16L:8D. Time to parasite emergence was recorded and converted to physiological time. Assuming an average thermal requirement of 120 degree-days above a threshold of 11°C to complete larval development (Chapter 2), I estimated the age at which the parasites were transferred from diapause (field) to nondiapause (laboratory) conditions. These data were used to estimate the photosensitive stage of *A. rubecula* and examine the possibility of disrupting the diapause response.

The second source of field data was the cohorts of parasitised hosts reared on plants in large screen cages (3m X 3m X 1m high) at the Plant Science Field Station (UBC) and, to
a lesser extent, on the adjacent grounds of the Vancouver Research Station. Late-II and early-III instar caterpillars were exposed to adult parasites and, after an attack, placed on potted plants and permitted to settle overnight at 22°C. Plants with parasitised caterpillars were then placed in the field. When parasites emerged, the cocoons were collected daily but kept in a Stevenson screen for two additional days to insure ample opportunity to pupate under ambient conditions. Once they were returned to the lab, diapause was determined by the same criteria as for lab experiments described previously. Insects in diapause were stored in gelatin caps overwinter in the Stevenson screen to determine survival and the timing of spring emergence (Chapter 5).

RESULTS

Critical photoperiod

Table 4 includes the results of all trials to determine the critical photoperiod under controlled conditions. Figs. 4 and 5 illustrate two aspects of the analysis. Figure 4 shows data from constant and fluctuating temperatures and demonstrates the clear photoperiodic response. The critical photoperiod lies between 15h and 16h and appears to be slightly modified by temperature. At constant temperatures less than 19°C, a proportion of parasites entered diapause with a 16h photophase (Fig. 5). The closed circles in Fig. 5 are alternating temperatures plotted at their average daily value.
<table>
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<th>TEMPERATURE</th>
<th>PHOTOPERIOD</th>
<th>N</th>
<th>DIAPAUSE</th>
<th>%</th>
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<tr>
<td>a) 15°</td>
<td>16L:8D</td>
<td>60</td>
<td>45</td>
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</tr>
<tr>
<td>16°</td>
<td>16L:8D</td>
<td>23</td>
<td>15</td>
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</tr>
<tr>
<td>17°</td>
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</tr>
<tr>
<td></td>
<td>12L:12D</td>
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<td>48</td>
<td>100%</td>
</tr>
<tr>
<td></td>
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<td>33</td>
<td>33</td>
<td>100%</td>
</tr>
<tr>
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<td>25</td>
<td>25</td>
<td>100%</td>
</tr>
<tr>
<td></td>
<td>15L:9D</td>
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<td>64</td>
<td>100%</td>
</tr>
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</tr>
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<tr>
<td>22°</td>
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<td>30</td>
<td>30</td>
<td>100%</td>
</tr>
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<td>15L:9D</td>
<td>72</td>
<td>65</td>
<td>90%</td>
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<td></td>
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<td>b) 12°-20°</td>
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<td>60</td>
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<td>c) 20±5°</td>
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<td>14.75L:9.25D</td>
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<td></td>
<td>15.5L:8.5D</td>
<td>68</td>
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<td>-</td>
</tr>
<tr>
<td>constant 20°</td>
<td>15.5L:8.5D</td>
<td>68</td>
<td>36</td>
<td>53%</td>
</tr>
</tbody>
</table>

**TABLE 4.** Diapause response in *A. rubecula* reared under variable temperature/photoperiod combinations.  
a) constant temperatures  
b) alternating temperatures (square wave)  
c) fluctuating temperatures (sine wave)
FIGURE 4. Photoperiodic response curve under different controlled temperatures for Vancouver A. rubecula.
FIGURE 5. Per cent diapause in Vancouver A. rubecula at 16L:8D photoperiod. Open circles are constant temperature conditions, closed circles are fluctuating temperature conditions plotted at their mean daily value. Bars are 95% confidence intervals.
With alternating temperatures, low average temperatures did not induce diapause, provided the maximum was at least 19°C, although the development time was close to what would be expected at the average temperatures. This maximum temperature is regularly reached during the Vancouver season, even after diapause has already been induced in field populations of A. rubecula (Tables 5 and 6). Hence, temperature, although demonstrably operative under experimental conditions, may play a minor role in diapause induction in nature.

The experiments utilizing fluctuating temperatures and a variable photoperiod demonstrate the predominance of the photoperiodic response and limited interaction between photoperiod and temperature in determining the diapause response in A. rubecula (Table 4c). The transition between diapause and nondiapause induction at typical Vancouver summer temperatures is sharp. At less than 15h photophase, diapause is induced in all individuals in a cohort. Within the neighborhood of the critical photoperiod (15h-16h) temperature has some moderating effect; in particular a high daily maximum temperature leads to continuous development even though the same constant average temperature can lead to a substantial proportion of the insects entering diapause.

An additional observation was made from these data. The portion of a cohort which entered diapause consisted of the last individuals to emerge from their hosts i.e., those with the slowest development rates. This association between
development time and the diapause response is not shown here because it would be comparing individuals reared under different conditions. The relationship is examined in Chapter 4.

Field data

Tables 5 and 6 are weekly summaries of diapause incidence in field collections of *A. rubecula* from BBY and cohorts reared at UBC during 1981 and 1982. Temperatures and civil daylengths at Vancouver are given. In the absence of information regarding the spectral sensitivity of *A. rubecula*, I assume the natural photoperiod includes a large portion of the civil twilight periods (see Beck 1980 and Saunders 1975 for a discussion). Civil daylength is, in any case, the period which environmental chambers most closely mimic and it is these data which are compared. The field data confirm laboratory experiments and show that diapause is first induced in the field at photoperiods between 15.5h and 16h photophase. At 15h, almost every individual enters diapause.

In 1981, the first individuals observed to enter diapause emerged from their hosts on August 17; in 1982 on August 7. Most individuals emerging to spin cocoons during the last week of August in both 1981 and 1982 entered diapause despite this being a warmer period during 1982. Diapause incidence was intermediate during the second and third weeks of August. There
<table>
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<tr>
<th>EMERGENCE PERIOD</th>
<th>TEMPERATURE range mean (°C)</th>
<th>DAYLENGTH civil h min</th>
<th>N</th>
<th>DIAPAUSE %</th>
</tr>
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<tbody>
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<td>July 27 - Aug 8</td>
<td>12-25 17.3</td>
<td>15 30</td>
<td>52</td>
<td>0</td>
</tr>
<tr>
<td>August 27-30</td>
<td>10-20 16.1</td>
<td>14 40</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>September 5-8</td>
<td>12-28 18.1</td>
<td>14 12</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>September 10-19</td>
<td>10-26 16.6</td>
<td>13 44</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>after Sept 20</td>
<td>-</td>
<td>&lt;13h</td>
<td>16</td>
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<table>
<thead>
<tr>
<th>EMERGENCE PERIOD</th>
<th>TEMPERATURE range mean (°C)</th>
<th>DAYLENGTH civil h min</th>
<th>N</th>
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</tr>
</thead>
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<tr>
<td>July 11-22 (UBC)</td>
<td>10-24 15.4</td>
<td>17 12</td>
<td>85</td>
<td>0</td>
</tr>
<tr>
<td>July 23-31 (UBC)</td>
<td>10-28 18.3</td>
<td>16 36</td>
<td>39</td>
<td>0</td>
</tr>
<tr>
<td>August 1-7 (UBC)</td>
<td>12-25 16.1</td>
<td>16 14</td>
<td>53</td>
<td>2</td>
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<tr>
<td>(BBY)</td>
<td></td>
<td></td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td>Aug 8-15 (UBC)</td>
<td>9-22 15.2</td>
<td>15 45</td>
<td>29</td>
<td>3</td>
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<td>(BBY)</td>
<td></td>
<td></td>
<td>37</td>
<td>14</td>
</tr>
<tr>
<td>Aug 16-23 (UBC)</td>
<td>12-22 16.6</td>
<td>15 25</td>
<td>87</td>
<td>87</td>
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<tr>
<td>(BBY)</td>
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<td></td>
<td>18</td>
<td>9</td>
</tr>
<tr>
<td>Aug 24-31 (UBC)</td>
<td>12-25 17.4</td>
<td>14 54</td>
<td>45</td>
<td>45</td>
</tr>
<tr>
<td>(BBY)</td>
<td></td>
<td></td>
<td>63</td>
<td>45</td>
</tr>
<tr>
<td>Sept 1-8 (UBC)</td>
<td>13-24 17.4</td>
<td>14 12</td>
<td>58</td>
<td>58</td>
</tr>
<tr>
<td>(BBY)</td>
<td></td>
<td></td>
<td>17</td>
<td>16</td>
</tr>
<tr>
<td>Sept 9-18 (UBC)</td>
<td>8-23 14.5</td>
<td>13 45</td>
<td>73</td>
<td>73</td>
</tr>
<tr>
<td>Sept 19-25 (UBC)</td>
<td>12-22 15.3</td>
<td>13 10</td>
<td>25</td>
<td>25</td>
</tr>
</tbody>
</table>

were a few individuals collected at BBY which did not enter diapause after emerging the last week of August, 1982. This may have been due to temperature; either because daily temperatures at BBY are, on average, warmer than those measured at UBC or because parasitised larvae collected at BBY were reared in small wooden cages which absorbed far more heat than did the large screen cages used for UBC cohorts.

But the final demonstration of the predominance of the photoperiodic response over that of temperature was fortuitous. A cohort initiated on August 15, 1982 began emerging and spinning cocoons on August 30. Seventeen A. rubecula were collected between August 30 and September 9 and were, as expected, all in diapause. On September 8 the cage was relocated behind a greenhouse only 30m away. Greenhouse lights extended the daylength in the vicinity to close to 18h. Only one of the ten parasites emerging one week after this move entered diapause, despite average temperatures during that period which were the coolest since the preceding spring.

When parasitised hosts were transferred from short-day conditions in the field to long-day conditions in the laboratory, the diapause response of the population decreased with the time spent under nondiapause conditions (Table 7). Unlike Schisler (1981) I found that an appreciable disruption of the diapause response required over 40 degree-days, or about one-third of the larval parasite's lifespan be spent under long-day conditions. These data agree with Schisler that
<table>
<thead>
<tr>
<th>DEGREE-DAYS ABOVE 11°</th>
<th>ESTIMATED PROPORTION OF PARASITE DEVELOPMENT COMPLETED AT TIME OF FIELD COLLECTION</th>
<th>N</th>
<th>DIAPAUSE %</th>
</tr>
</thead>
<tbody>
<tr>
<td>23</td>
<td>0.81</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>34</td>
<td>0.71</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>46</td>
<td>0.62</td>
<td>15</td>
<td>8</td>
</tr>
<tr>
<td>58</td>
<td>0.52</td>
<td>23</td>
<td>5</td>
</tr>
<tr>
<td>69</td>
<td>0.42</td>
<td>16</td>
<td>1</td>
</tr>
<tr>
<td>80</td>
<td>0.33</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>92</td>
<td>0.23</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>115</td>
<td>0.04</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

TABLE 7. Diapause in *A. rubecula* larvae collected at BBY on September 16-17, 1981 and transferred to laboratory conditions which promote continuous development (22°C 16L:8D).
A. rubecula larvae mid-way through the developmental period are sensitive to diapause-inducing photoperiods but neither set of data permits distinction between photosensitivity to diapause induction and disruption. It is possible that all immature stages are photosensitive but require a minimum number of short photoperiods before diapause is induced. Diapause would be averted when transfer to long-day conditions occurred early in the developmental period, as Schisler and I have observed. How early such a disruption would occur might depend on temperature, since low temperatures increase developmental time and lead to more photoperiodic cycles per life stage.

DISCUSSION

Vancouver A. rubecula show a photoperiodic response typical of "long-day" insects. Long daylengths (16h) and high temperatures (>19°C) promote continuous development while shorter daylengths and lower temperatures lead to diapause. It is the parasitic larval stage which responds to the photoperiod, although sensitivity may be extended to the prepupal (eonymph) stage (Schisler 1981).

The critical photoperiod for diapause induction of Vancouver parasites lies between 15h and 16h of light per day. The consistency of the response depends to some extent on temperature. Unusually cold conditions could lead to premature diapause in some individuals but the predominant and abrupt photoperiodic response ensures that the transition from
continuous development to diapause is likely to occur over a very short period of time in the field. There is good evidence that absolute daylength is measured because no diapause has been observed when daylengths in the field are decreasing but still above the critical daylength (July in Vancouver; January, February and March in Canberra).

In Vancouver, diapause is noted as early as the second week of August and includes the entire population by the end of the month but in Canberra, diapause is not observed until after the autumnal equinox. This cannot be explained by the relatively warmer temperatures in Canberra. The small moderating effect of temperature on the photoperiodic response established in my experiments was confirmed by Parker and Pinnell (1972) who noted that Vancouver A. rubecula released in Missouri entered diapause in early September, despite the warmer temperatures in their new environment. This early diapause in the Vancouver population may be part of the problem with establishing A. rubecula in warmer locales. I return to this question in the final chapter.
CHAPTER 4

MANIPULATION OF THE DIAPAUSE RESPONSE

INTRODUCTION

Manipulation of the diapause response in insects by selective breeding of both pests and predators is an intriguing possibility for pest management (Chippendale 1982; Hoy 1976, 1978). The general heritability of the diapause response is amply demonstrated by the rapid selection for nondiapause in laboratory strains (Harvey 1957; House 1967; Hoy 1975, 1978). Hybridization of laboratory strains or natural populations differing in their diapause response often yields offspring with a diapause response which is intermediate to that of the parents; an indication of polygenic control (Danilevskii 1965; Hoy 1975, 1978; Tauber and Tauber 1978).

There may be additional nongenetic maternal effects on diapause. Diapause increases with maternal age in some insect parasites (Saunders 1965; Simmonds 1948) and it is the photoperiodic response of the mother which determines the diapause response in the offspring (Ryan 1965; Saunders 1965, 1966). Henrich and Denlinger (1982) showed that the diapause history of the female fleshfly, Sarcophaga bullata Parker, affects diapause in her progeny. Interestingly, the effect was determined, not by diapause itself, but by the diapause-inducing photoperiod experienced by the larva of the maternal
The last chapter showed that the photoperiodic responses of Vancouver and Canberra populations differed markedly. This difference could be due to differences in the original native stock or to divergence following its introduction to Canada and Australia. Either situation implies within-species variability of the diapause response. I suggested that the high critical photoperiod of the Vancouver population has contributed to the difficulties encountered in attempting to establish this population in other parts of North America.

This chapter develops a methodology for a breeding program to modify the diapause response of Vancouver *A. rubecula*. Considering the possibility of maternal effects, experiments to check for effects of maternal age and diapause history were considered prerequisites of any breeding program and are included. The preliminary data illustrate new features of the biology of diapause in *A. rubecula* and suggest a practical approach for future releases of the parasite in North America.
METHODS

Experiments in Chapter 3 indicated that if A. rubecula larvae were reared at 20°C 15.5L:8.5D, only a portion of the cohort would enter diapause. These conditions were chosen as the standard for all experiments described in this chapter.

A kale-based diet modified from Wilkinson et al. (1972) was used as a plug at one end of a 7-dram vial and held in place by a rubber "O" ring. Three parasitised host larvae (late-II or early-III instar) were placed on the diet and the vial placed upside down on a tray in the incubator. Survival rates of host larvae were near 67%, less than that of unparasitised larvae. The time required from oviposition to emergence of the parasite from the host was generally one day longer at 20°C on the diet than it was on potted plants. A similar lag in development time has been noticed in unparasitised P. rapae and is thought by N. Gilbert to be due to an initial reluctance of the caterpillars to feed on the diet.

The first experiment compared the diapause response of progeny from old and young female parents. Old females were six weeks old and had oviposited many times. They had been stored at 10°C, then moved to 16°C for three days before being used in the experiment. Young females had eclosed only two to four days earlier and were held, with males, at 22°C.

The second experiments compared the diapause response of
progeny of females which had entered diapause under the short-day conditions of previous experiments (Chapter 3), with the progeny of females which had never experienced a diapause stage.

Individuals which entered diapause in the experiments on diapause history became the diapause group (D) and were stored at 0°C. Those which continued to develop to adult were the nondiapause group (N) and were mass-mated and their offspring reared at 20°C 12L:12D. All of these progeny entered diapause and were stored with the D-group. So both D and N parents experienced a diapause stage. Total storage time for the diapause group was four months and for the nondiapause group, about three weeks less. These formed the following parental groups:

- D male X D female
- N male X D female
- D male X N female
- N male X N female

plus unmated D and N females.

Differences in maternal age were avoided. All females used in these experiments had been caged with males for two weeks and had limited foraging history.
Analysis

Experiments to detect maternal and genetic effects on the diapause response of the offspring were analyzed in the same way. I was interested in the effects of maternal condition (old vs young or post-diapause vs no diapause) or parental group on the diapause response. I recorded development time because I suspected it would also affect the diapause response (Chapter 3).

This mix of categorical and continuous explanatory variables with a binary response variable (diapause or nondiapause) was analyzed with logit models (Feinberg 1980). These log-linear models employ a weighted regression of transformed variates. Logit analysis extends the log-linear model to allow estimation of parameters and prediction of the binary outcome. Structure of the model, and to some extent its interpretation, is analogous to standard regression analysis (Neter and Wasserman 1974).

The transformed probability, \( p \), of an individual entering diapause under specified conditions is given by;

\[
\text{logit } \hat{p} = \log\left(\frac{p}{1-p}\right)
\]

The logit regression model assumes that the dependence of this
transformed probability of entering diapause on the various explanatory variables can be expressed as a linear relationship such as:

\[ \text{logit } \hat{p} = B_0 + B_1 x_1 + B_2 x_2 + \ldots + B_j x_j + \ldots + B_\eta x_\eta \]

where \( x_j \) is an explanatory variable such as parental group. As in multiple regression, powers of variables and interactions between variables can be included. The models are fitted by the method of maximum likelihood. Alternative models are compared and tested for goodness-of-fit by the method of likelihood ratio. Sokal and Rohlf (1981) discuss the merits of the log-likelihood test statistic.

The analysis of nongenetic maternal effects used a statistical package (BMD:PLR Engelman 1981) but the analysis of the parental groups was extended by Dr. A. John Petkau, Statistical Consulting Service, UBC, to consider contrasts among logits corresponding to the different parental groups. I am indebted to Dr. Petkau for introducing me to logit analysis and for the several hours he spent in analysis and consultation on this problem.

Analysis of parental effects on offspring development rates under constant conditions employed analysis of variance with orthogonal contrasts (Steel and Torrie 1982).

The experiments on maternal age and diapause history consisted of three and six trials respectively. These trials
represent different days of set-up and therefore slightly
different diet qualities. Different trials proved to have a
significant effect of the outcome in both experiments (Tables 8
and 9). In the experiments with parental crosses, a large
number of individuals were set up each day so that the number
of trials was limited to two. Developmental times between
trials were similar and the effect of different diets on the
diapause response was virtually nil in this experiment. Data
from different trials in these genetic experiments were pooled
for the final analysis.

RESULTS

Effect of maternal age and diapause history

The results of the stepwise logit regression analysis are
in Tables 8 and 9. Development time always had the largest
effect on the diapause response. Diapausing individuals were
among the slowest to develop in a cohort (Figs. 6 and 7). In
one case, there was an additional quadratic effect of
development time (Table 9). Including trial (day of set up) as
a variate improved the fit in both cases, indicating the
diapause response was sensitive to differences in the diet,
perhaps via its effect on development rates.

The extreme differences in maternal age had a significant
effect on the diapause response in the progeny but this may
have been due to a high correlation between maternal age and
### TABLE 8. Summary of logit analysis of experiments to test the effect of maternal age on the diapause response of the progeny. Development time in days at 20°C 15.5L:8.5D.

<table>
<thead>
<tr>
<th>STEP</th>
<th>TERM</th>
<th>df</th>
<th>IMPROVEMENT CHI-SQUARE</th>
<th>p-value</th>
<th>GOODNESS-OF-FIT CHI-SQUARE</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Constant</td>
<td>39</td>
<td>163.199</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Development time</td>
<td>38</td>
<td>114.562</td>
<td>&lt;0.001</td>
<td>48.637</td>
<td>0.116</td>
</tr>
<tr>
<td>3</td>
<td>Trial</td>
<td>36</td>
<td>13.146</td>
<td>0.001</td>
<td>35.490</td>
<td>0.493</td>
</tr>
<tr>
<td>4</td>
<td>Maternal age</td>
<td>35</td>
<td>3.310</td>
<td>0.069</td>
<td>32.180</td>
<td>0.605</td>
</tr>
<tr>
<td>5</td>
<td>Dev X Age</td>
<td>34</td>
<td>6.855</td>
<td>0.009</td>
<td>25.325</td>
<td>0.859</td>
</tr>
</tbody>
</table>

### TABLE 9. Summary of logit analysis of experiments to test the effect of maternal diapause history on the diapause response of the progeny. Development time in days at 20°C 15.5L:8.5D.

<table>
<thead>
<tr>
<th>STEP</th>
<th>TERM</th>
<th>df</th>
<th>IMPROVEMENT CHI-SQUARE</th>
<th>p-value</th>
<th>GOODNESS-OF-FIT CHI-SQUARE</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Constant</td>
<td>69</td>
<td>274.329</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Development time</td>
<td>68</td>
<td>170.516</td>
<td>&lt;0.001</td>
<td>103.812</td>
<td>0.003</td>
</tr>
<tr>
<td>3</td>
<td>Dev X Dev</td>
<td>67</td>
<td>12.465</td>
<td>&lt;0.001</td>
<td>91.347</td>
<td>0.026</td>
</tr>
<tr>
<td>4</td>
<td>Trial</td>
<td>62</td>
<td>22.698</td>
<td>&lt;0.001</td>
<td>68.649</td>
<td>0.262</td>
</tr>
</tbody>
</table>

TABLE 8. Summary of logit analysis of experiments to test the effect of maternal age on the diapause response of the progeny. Development time in days at 20°C 15.5L:8.5D.
FIGURE 6. Development period in days at 20°C, 15.5L:8.5D, for the parasitic stages of the offspring of old and young female A. rubecula. Black portions are diapause individuals.
FIGURE 7. Development period in days at 20°C, 15.5L:8.5D, for the parasitic stages of the offspring of female A. rubecula with different diapause histories. Black portions are diapause individuals.
### TABLE 10. Mean development time at 20°C of progeny of young and old females. Analysis of variance used Log (dev time + 1).

<table>
<thead>
<tr>
<th>MATERNAL AGE</th>
<th>N</th>
<th>PROGENY DEVELOPMENT TIME (SE) (days at 20°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>YOUNG</td>
<td>131</td>
<td>14.08 (0.17)</td>
</tr>
<tr>
<td>OLD</td>
<td>114</td>
<td>15.40 (0.18)</td>
</tr>
<tr>
<td>F=28.52</td>
<td>df=1,243</td>
<td>p&lt;0.001</td>
</tr>
</tbody>
</table>

### TABLE 11. Mean development time at 20°C of progeny of females which had, or had not experienced a previous diapause. Analysis of variance used Log (dev time + 1).

<table>
<thead>
<tr>
<th>MATERNAL DIAPAUSE HISTORY</th>
<th>PROGENY DEVELOPMENT TIME (SE) (days at 20°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NO DIAPAUSE</td>
<td>242</td>
</tr>
<tr>
<td>POST DIAPAUSE</td>
<td>145</td>
</tr>
<tr>
<td>F=0.467</td>
<td>df=1,385</td>
</tr>
</tbody>
</table>
developmental period \((r=0.56, \text{df}=34, p<0.05)\). The offspring of old females showed an increased diapause response and also took longer to develop than those of young females (Table 10).

There was no effect of maternal diapause history either before or after the effects of development time and trial were included. Nor were development times of the progeny different (Table 11).

In the genetical experiments, the probability of diapause again increased with development time; in the alternate models in Table 12, all slopes are greater than 0 \((p<0.05)\). There was an additional parental effect (Fig. 8). Of the alternate models in Table 12 and Fig. 8, model A is the simplest and provides an adequate fit but the addition of a term for the interaction of parental group and development time under model B significantly improves the fit. The nature of the interaction is not clear; there were no direct parental effects on mean development time of the offspring (Table 13). By including the interaction, differences between parental groups depend on the developmental period at which the comparisons are made.

At mean development time \((16 \text{ days})\), either model indicates an unusual genetical situation; the offspring of crosses have a lower probability of entering diapause than either inbred line, mated or not (Fig. 8). Normally, one expects crosses to be intermediate to, or least indistinguishable from, the inbred lines.
<table>
<thead>
<tr>
<th>PARENTAL GROUP</th>
<th>MODEL A</th>
<th>MODEL B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dm X Df</td>
<td>0.377 + 1.141 (dev-16)</td>
<td>0.503 + 1.321 (dev-16)</td>
</tr>
<tr>
<td>Nm X Nf</td>
<td>0.805 + 1.141 (dev-16)</td>
<td>0.564 + 0.856 (dev-16)</td>
</tr>
<tr>
<td>Nm X Df</td>
<td>-0.146 + 1.141 (dev-16)</td>
<td>-0.171 + 0.956 (dev-16)</td>
</tr>
<tr>
<td>Dm X Nf</td>
<td>-0.427 + 1.141 (dev-16)</td>
<td>-0.446 + 0.989 (dev-16)</td>
</tr>
<tr>
<td>Nf</td>
<td>0.799 + 1.141 (dev-16)</td>
<td>2.033 + 2.206 (dev-16)</td>
</tr>
<tr>
<td>Df</td>
<td>1.937 + 1.141 (dev-16)</td>
<td>2.256 + 1.406 (dev-16)</td>
</tr>
</tbody>
</table>

GOODNESS-OF-FIT

<table>
<thead>
<tr>
<th>G²</th>
<th>df=62</th>
<th>G²</th>
<th>df=57</th>
</tr>
</thead>
<tbody>
<tr>
<td>57.46</td>
<td></td>
<td>43.37</td>
<td></td>
</tr>
</tbody>
</table>

TABLE 12. Fitted models for logit analysis of diapause response of different parental groups (dev=development time in days at 20°C). D-diapause, N-nondiapause; m-male, f-female.
FIGURE 8. Diapause probability of the offspring of different parental groups. Bars are 95% confidence intervals. Estimates are from models A and B in Table 12. The proportion of males in the associated groups is shown below the abscissa.
<table>
<thead>
<tr>
<th>PARENTAL GROUP</th>
<th>N</th>
<th>PROGENY DEVELOPMENT TIME (SE)</th>
<th>(days at 20°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dm X Df</td>
<td>181</td>
<td>15.8 (0.19)</td>
<td></td>
</tr>
<tr>
<td>Nm X Nf</td>
<td>154</td>
<td>16.3 (0.21)</td>
<td></td>
</tr>
<tr>
<td>Nm X Df</td>
<td>121</td>
<td>16.1 (0.18)</td>
<td></td>
</tr>
<tr>
<td>Dm X Nf</td>
<td>116</td>
<td>15.5 (0.21)</td>
<td></td>
</tr>
<tr>
<td>Nf</td>
<td>97</td>
<td>15.6 (0.27)</td>
<td></td>
</tr>
<tr>
<td>Df</td>
<td>87</td>
<td>16.0 (0.25)</td>
<td></td>
</tr>
</tbody>
</table>

F=2.08 df=5,750 p>0.20

TABLE 13. Mean development time of progeny of each parental group. Analysis of variance used Log (dev time + 1).
<table>
<thead>
<tr>
<th>CONTRAST</th>
<th>MODEL A ESTIMATE</th>
<th>SE</th>
<th>p-value</th>
<th>MODEL B ESTIMATE</th>
<th>SE</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>DmDf - NmNf</td>
<td>-0.43</td>
<td>0.30</td>
<td>0.16</td>
<td>-0.06</td>
<td>0.35</td>
<td>&gt;0.20</td>
</tr>
<tr>
<td>DmDf - NmDf</td>
<td>-0.28</td>
<td>0.37</td>
<td>&gt;0.20</td>
<td>-0.28</td>
<td>0.35</td>
<td>&gt;0.20</td>
</tr>
<tr>
<td>Nf - Df</td>
<td>-1.14</td>
<td>0.39</td>
<td>0.004</td>
<td>-0.22</td>
<td>0.83</td>
<td>&gt;0.20</td>
</tr>
<tr>
<td>DmDf - Df</td>
<td>-1.56</td>
<td>0.36</td>
<td>&lt;0.001</td>
<td>-1.75</td>
<td>0.58</td>
<td>0.003</td>
</tr>
<tr>
<td>NmDf - Df</td>
<td>-2.08</td>
<td>0.38</td>
<td>&lt;0.001</td>
<td>-2.43</td>
<td>0.57</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>DmNf - Nf</td>
<td>-1.23</td>
<td>0.40</td>
<td>0.002</td>
<td>-2.48</td>
<td>0.70</td>
<td>0.001</td>
</tr>
<tr>
<td>NmNf - Nf</td>
<td>0.01</td>
<td>0.34</td>
<td>&gt;0.200</td>
<td>-1.47</td>
<td>0.69</td>
<td>0.030</td>
</tr>
</tbody>
</table>

TABLE 14. Contrasts among logits at mean development time of 16 days at 20°C. D-diapause, N-nondiapause; m-male parent, f-female parent.
The progeny of unmated females show a significantly higher diapause response than any of the other lines (Table 14, Fig. 8 - model B). Their offspring are all males and this provides a clue to a possible explanation of the results. Fig. 8 includes, with each parental line, the proportion of male progeny. The probability of diapause increases with the proportion of males in the experimental cohort. The relative magnitude of this proportion can also explain the apparent parental effects but the data do not permit separation of the two possible covariates. The data could be explained as purely due to sex or genetics or some combination of the two. But if the effect of sex were genuine, and there remains a significant interaction, then there should be an interaction between sex and development time within parental groups. There is not; at least not for nondiapause individuals from all groups. Chapter 2 showed we should not expect any relationship between sex and development time in *A. rubecula* larvae, and these data confirm this. Moreover, in the experiments using old and young wasps, the offspring of older females had an increased diapause response even though the proportion of males was much lower in that group (0.24) than in the young mother group (0.50). So the effect of sex was then in the opposite direction.

In the absence of independent data to distinguish between the effects of sex and parental group, inclusion of either term is, at best, provisional. Given the importance of the interaction between parental group and development time under model B, it is best to consider the model which also includes
the parental group as a main effect. In this model (B), the effects of inbreeding are slight and dependent on where in the developmental period the comparisons are made.

DISCUSSION

Under temperature and photoperiods where only a portion of the parasites of any parental origin entered diapause, the larvae which emerged from the host first were less likely to enter diapause than those which emerged later. This relationship has also been noted in the oriental fruit moth (Dickson 1949). Its similarity to the ageing effect on the photoperiodic response of maternal Nasonia vitripennis (Walk.) (Saunders 1965) suggests a common mechanism. Saunders (1976) subsequently showed that photoperiodism required not only measurement of the duration of the photoperiod but also summation of successive days' information; i.e. a clock and a counter (Saunders 1981). A. rubecula which require longer development times experience more photoperiods and are more likely to enter diapause.

In A. rubecula males and females develop at the same rate so there will be no sexual selection via development time, but the possibility of a direct maternal influence on sex ratio which in turn affects the proportion of progeny entering diapause cannot be ignored. After all, the mother determines the sex of her offspring. The lack of influence of maternal physiology is not surprising since the larva is the stage which
is sensitive to diapause-inducing conditions (Chapter 3).

Analysis of results of the single selection for diapause is inconclusive. The disadvantages of selecting for a binary character such as diapause (we have no idea how 'far away' are parental means) which requires a three-month obligatory incubation period between generations makes selection on the diapause response impractical. But the results suggest an alternative. It should be possible to select, under nondiapause conditions, fast and slow developers. Development rate is a good quantitative character in *A. rubecula* ranging from 11.5 to 22.0 days at 20°C. Since heritability of development time has been demonstrated in insects (Goldschmidt 1980), it would be of more than merely practical interest if selection for development rate also modified the diapause response as both are ecologically related in the control of seasonal development.

There is little reason to doubt that modification of the diapause response in *A. rubecula* should be any more difficult than in other braconid species. But given the existence of the Australian population which does not enter diapause until daylength is less than 12h, the most sensible advice for biological control programs in areas where cabbages are a late-summer or autumn crop is to introduce stock from the Australian, rather than the Vancouver source.
CHAPTER 5

DIAPAUSE TERMINATION AND POST-DIAPAUSE DEVELOPMENT

INTRODUCTION

The conditions and time required to terminate diapause set the clock for the resumption of activity in overwintering populations. Termination of diapause marks the starting point for the phenological model. This chapter takes us back to the first of the season. It considers the effects of storage conditions on diapause termination rates and the developmental response to temperature following diapause. By corroboration with field data, I discuss winter and spring ecology of the parasite A. rubecula.

Andrewartha (1952) was one of the first to recognize that diapause was an active state; physio- and morphogenesis were suppressed but not arrested. He proposed the term "diapause development" to emphasize that diapause was an alternative developmental strategy with specific requirements for its completion. The confusion and controversy regarding diapause terminology (Danilevskii 1965; Mansingh 1971; Sheldon and Macleod 1974; Thiele 1973) reflects the necessity for better understanding of the physiology of diapause and the resumption of normal development.

Yin and Chippendale (1973) have shown that diapause maintenance can be under neuro-endocrine control and, as in
diapause induction, some measurement of time is involved. The termination of diapause may be a response to specific stimuli such as chilling (Schneiderman and Horwitz 1958) or the insect may show a decreasing response to diapause-inducing stimuli (Tauber and Tauber 1976) or simply no response to any stimuli until a certain refractory period has passed (Mansingh 1971).

If diapause is an alternative developmental strategy, it should be possible to characterize its progress and completion as a response to ambient conditions. Photoperiod is the most important factor for induction of diapause but termination and post-diapause development are often temperature responses; photoperiodic sensitivity decreasing after the onset of diapause (Danilevsky et al. 1970). The same lag in the daylength-temperature relationship that produced relatively warm but short days in late summer results in long spring days when temperatures are distinctively cool. Even when diapause termination is a specific response to a critical photoperiod, that photoperiod is usually surpassed in nature while temperatures are too low for appreciable morphogenesis. The insect remains in torpor until temperatures exceed a developmental threshold (Tauber and Tauber 1978).

There is no evidence that diapause termination in A. rubecula is a photoperiodic response. All diapause eonymphs from the experiments reported in Chapters 3 and 4 were transferred from short to long-day conditions immediately after spinning a cocoon and development did not resume before three
months cold storage. There was no diapause when eonymphs were transferred from a 16h to 12h photophase at several temperatures so free-living stadia may not show a photoperiodic response at any time. If that is the case, parasite larvae literally moult their photoperiodic sensitivity.

The experiments reported here investigate diapause termination and post-diapause developmental rates in *A. rubecula*. There is a series of laboratory experiments in which cocoons were incubated under variable storage conditions and then brought to temperatures which promote continuous development. Other cocoons were stored in the field and then brought to controlled conditions in the laboratory and still others were left in the field to determine the dates of diapause termination and adult emergence under natural conditions.

**METHODS**

Experiments in 1982 used *A. rubecula* cocoons from the critical photoperiod experiments of Chapter 3. Earlier trials had shown sporadic adult emergence and high mortality when diapause eonymphs were stored at a moderate temperature (23°C) or for less than three months at low temperatures (0°C or 10°C). It was also noted that although photoperiod experienced by the larva did not affect post-incubation development time, there was a slight effect of larval rearing temperatures, probably via the effects of temperature on final weight (Chapter 2). All
experiments which analyze developmental time used cocoons of larvae reared at 20°C.

To determine weight loss during incubation, weighed cocoons were stored for three or four months at 0°C, then re-weighed and brought to 23°C. Weight after incubation, time to adult emergence and the sex of each individual were recorded. A second series was similarly divided into two storage times, three or four months, and further subdivided into two storage temperatures, 0° and 10°C. These cocoons were not weighed until after they were removed from storage. They were held under the same conditions as the previous trials (23°C). Time to adult emergence and the sex of each individual was recorded. The factors were coded with dummy variates and analyzed by multiple regression (Gilbert 1973).

A parallel series was incubated under natural conditions in a Stevenson screen at UBC on January 20, 1982. Fifteen cocoons were brought to 23°C on March 29, April 23 and May 15. Ten more cocoons were left in the Stevenson screen to determine field emergence dates.

One attempt was made in 1982 to determine post-incubation development time at temperatures between 15° and 28°C and a long day; optimal conditions for development. None of the insects at 15°C terminated diapause and over 25% of the insects at 17°C were still in diapause after sixty days.

The experiments in 1983 were more extensive. I
distinguished diapause termination and post-diapause development times at 17°, 19°, 23° and 28°C.

When diapausing eonymphs were transferred to these warmer temperatures after cold storage for at least three months, morphogenesis did not begin immediately. The eonymph is the mature parasite larva; therefore the midgut is blind and does not open into the proctodaeum. At the final moult, the guts join and the feces and larval cuticle are cast together (the meconium). When illuminated, these post-diapause individuals can be identified by this dark meconium at the posterior of the cocoon. At this point, I consider diapause is terminated and subsequent development is that of the pupa. It should be noted that this definition of diapause termination is strictly operational as active development must occur before the appearance of the meconium.
RESULTS

Although diapause cocoons stored for four months at 0°C lost slightly more weight than those stored for three months, the proportion of weight lost in either group did not differ significantly (F=3.52 df=1,71 0.05<p<0.10). Males and females lost an equal proportion (about 16%) of their weight under these storage conditions. Thus the relationship between sex and weight remained the same after diapause, with females heavier than males. As in continuous development, males develop to adult more rapidly than females (F=27.78 df=1,71 p<0.001). Weight may be an additional determinant of development time since smaller individuals tend to develop more rapidly, but this trend was not as convincing here as it was in the experiments measuring continuous development (Chapter 2). There was a marginal effect of storage time on the developmental period with those insects stored for four months taking less time than those stored for three months at 0°C (F=5.45 df=1,71 0.01<p<0.025).

The second experiments confirmed that after three or four months storage at temperatures below the developmental threshold, females were, on average, heavier than males and required more time to develop to adult (Table 15). Once the sex of the parasite was considered, there were no additional effects of weight, rearing conditions, or storage time on the time to adult emergence.
<table>
<thead>
<tr>
<th>SEX</th>
<th>N</th>
<th>WEIGHT (SE) mg</th>
<th>TIME TO ADULT (SE) (days at 23°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FEMALE</td>
<td>78</td>
<td>5.54 (0.0635)</td>
<td>17.90 (0.202)</td>
</tr>
<tr>
<td>MALE</td>
<td>103</td>
<td>4.93 (0.0552)</td>
<td>15.66 (0.143)</td>
</tr>
</tbody>
</table>

**TABLE 15.** Mean cocoon weights and time to develop to adult for male and female *A. rubecula* after three or four months storage at 0°C or 10°C.
Adding storage temperature did significantly improve the fit of the regression leading to the descriptive model;

\[
\text{DEVELOPMENT TIME} = 17.484 + 0.799 \text{ST.TEMP} - 2.258 \text{SEX}
\]
(days at 23°C)

\[R^2=0.37, \text{df}=178, p<0.01\]

where \text{ST.TEMP}=0 for 0°C, 1 for 10°C; \text{SEX}=0 for females, 1 for males.

Thus females take longer to develop to adult than males and a lower storage temperature decreases post-incubation development time.

Field data from 1982 showed a definite effect of storage time on post-diapause development, with those stored for longer periods taking less time to develop to adult (Table 16). Note that the largest difference occurs between those removed from the field on March 29 and April 23 despite the fact that the period of greatest temperature accumulation was between April 23 and May 15.

The main conclusions of the 1981 experiments were that, given a sufficient storage period, i.e., at least three months below the developmental threshold of 11°C and temperatures greater than 15° to 17°C, the most important determinant of subsequent time to adult emergence was the sex of the insect; males emerged before females. This same emergence pattern was evident in the experiments using conditions promoting continuous development (Chapter 2) indicating winter diapause
<table>
<thead>
<tr>
<th>FIELD STORAGE DURATION</th>
<th>DATE RETURNED TO LABORATORY</th>
<th>N</th>
<th>MEAN DEVELOPMENT TIME (days at 22°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10 weeks</td>
<td>March 29</td>
<td>14</td>
<td>25.2 (0.59)</td>
</tr>
<tr>
<td>14 weeks</td>
<td>April 23</td>
<td>12</td>
<td>19.9 (0.57)</td>
</tr>
<tr>
<td>17 weeks</td>
<td>May 15</td>
<td>13</td>
<td>19.1 (0.49)</td>
</tr>
</tbody>
</table>

TABLE 16. Mean time in days to adult emergence of diapause cocoons taken to the field on January 20, 1982, returned to the laboratory on indicated dates and held at 22°C, 16L:8D.
does not disrupt what appears to be a fundamental difference in male and female developmental biology. This difference is not due to differences in weight, although females are consistently heavier than males. The difference is confirmed under natural conditions where individuals stored outside in a Stevenson screen emerged over a relatively short period of time but males still emerged first (Fig. 9).

Larval rearing conditions appeared to have no effect on development after diapause. In addition, storage conditions had little effect although the particular treatments used, especially with respect to duration were artificially short, so comparisons may not be ecologically relevant. There were consistent indications that increased storage time decreased the subsequent developmental period. This is apparent in the small data set from natural storage conditions (Fig. 9). Individuals not taken to the field until winter emerged later the following spring than did those which had been stored for the entire autumn-winter period.
FIGURE 9. Spring emergence of *A. rubecula* overwintered in the field at Vancouver (1982). Diapause date is the date for the beginning of field storage of diapause individuals. Solid bars are males, open bars are females.
EMERGENCE DATE

Number emerging vs. Diapause Date

June 15

July 15

Dec 15

Oct 1

Jan 15

EMERGENCE DATE
Distinguishing diapause termination from post-diapause pupal development was a significant improvement in the design of the 1983 experiments. I was able to follow Morris and Fulton (1970) and divide the total heat requirement for post-storage development to adult into two parts, \( K_p = K_{dt} + K_m \), where \( dt \) represents diapause termination and \( m \) represents pupal morphogenesis. I will discuss each process separately.

Diapause termination

Tables 17 and 18 give descriptive measures of the time required to terminate diapause at different temperatures following variable storage histories for male and female *A. rubecula*. Males completed diapause development sooner than females. Cocoons stored in the laboratory for four months at 10°C took the longest to terminate diapause at any temperature and this group suffered the highest mortality. A series stored for twelve months at 10°C terminated diapause in three to ten days at 23°C but less than a third of these survived beyond diapause termination. Cocoons stored in the field for the winter required less time to terminate diapause than those stored for a comparable period at 10°C but more time than those stored for longer periods at lower temperatures. Field temperatures at UBC during this period (November to March) were mostly between 0° and 12°C at a mean of 6.4°C and so were intermediate to the controlled storage temperatures.
<table>
<thead>
<tr>
<th>STORAGE MONTHS</th>
<th>TEMP</th>
<th>MORTALITY</th>
<th>SEX</th>
<th>17'</th>
<th>19'</th>
<th>23'</th>
<th>28'</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>10</td>
<td>15%</td>
<td>m</td>
<td>30.8 ± 2.12</td>
<td>23.8 ± 5.14</td>
<td>14.6 ± 3.84</td>
<td>11.4 ± 1.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(25-36)</td>
<td>(17-37)</td>
<td>(10-26)</td>
<td>(10-14)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>f</td>
<td>36.0 ± 2.83</td>
<td>26.6 ± 6.63</td>
<td>14.9 ± 4.04</td>
<td>11.1 ± 0.93</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(34-36)</td>
<td>(17-37)</td>
<td>(11-26)</td>
<td>(10-13)</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>11%</td>
<td>m</td>
<td>8.5 ± 1.60</td>
<td>4.8 ± 1.03</td>
<td>3.1 ± 0.33</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(6-13)</td>
<td>(3-6)</td>
<td>(3-4)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>f</td>
<td>9.0 ± 1.56</td>
<td>6.6 ± 1.52</td>
<td>3.6 ± 0.52</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(7-12)</td>
<td>(5-9)</td>
<td>(3-4)</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>--</td>
<td>m</td>
<td>4.9 ± 1.13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(4-7)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>f</td>
<td>4.6 ± 1.01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(4-7)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>10%</td>
<td>m</td>
<td>11.5 ± 4.23</td>
<td>6.6 ± 2.53</td>
<td>4.8 ± 1.31</td>
<td>3.1 ± 0.30</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(5-16)</td>
<td>(4-13)</td>
<td>(3-7)</td>
<td>(3-4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>f</td>
<td>11.2 ± 0.50</td>
<td>7.3 ± 1.21</td>
<td>7.0 ± 1.87</td>
<td>3.8 ± 0.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(11-12)</td>
<td>(5-8)</td>
<td>(5-10)</td>
<td>(3-4)</td>
</tr>
</tbody>
</table>

TABLE 17 Descriptive measures of time required for male and female A. rubecula to terminate diapause at several temperatures following specified storage conditions. N-number of observations, mean termination time ± standard deviation and the range are given.
<table>
<thead>
<tr>
<th>FIELD STORAGE</th>
<th>MORTALITY</th>
<th>SEX</th>
<th>19°C</th>
<th>23°C</th>
<th>28°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 months</td>
<td>6%</td>
<td>m</td>
<td>16.1 ± 3.30 (14-27)</td>
<td>9.8 ± 1.99 (8-15)</td>
<td>7.4 ± 0.76 (7-9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>f</td>
<td>19.1 ± 3.33 (14-24)</td>
<td>11.3 ± 1.86 (8-13)</td>
<td>7.5 ± 0.55 (7-8)</td>
</tr>
<tr>
<td>5 months</td>
<td>8%</td>
<td>m</td>
<td></td>
<td>5.2 ± 0.58 (5-7)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>f</td>
<td></td>
<td>6.3 ± 1.00 (5-7)</td>
<td></td>
</tr>
<tr>
<td>6 months</td>
<td>12%</td>
<td>m</td>
<td></td>
<td>7.4 ± 0.53 (7-8)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>f</td>
<td></td>
<td>9.0 ± 1.12 (8-11)</td>
<td></td>
</tr>
</tbody>
</table>

**TABLE 18.** Descriptive measures of time required for male and female *A. rubecula* to terminate diapause at several temperatures following storage in the field for varying periods. N-number of observations, mean termination time ± standard deviation and the range are given.
The cocoons stored six, seven or eight months at 0°C had comparable termination rates and were pooled to obtain the following regressions on temperature:

\[
\text{TERMINATION RATE (MALE)} = -0.219 + 0.0191 \text{ TEMP} \\
R^2=0.63, \text{ df}=112, \text{ p}<0.01
\]

\[
\text{TERMINATION RATE (FEMALES)} = -0.188 + 0.0164 \text{ TEMP} \\
R^2=0.74, \text{ df}=57, \text{ p}<0.01
\]

Thermal constants estimated by these regressions show that males and females have the same threshold for diapause termination (11.4°C) but females have a higher heat requirement (61 degree-days compared to 52 degree-days for males).

Although development may proceed slowly at temperatures between this threshold and 15° - 16°C, it appears the actual moult to a pupa requires warmer conditions. On two separate occasions *A. rubecula* has shown no sign of diapause termination after sixty days at 15° - 16°C, even after several months storage. Desiccation then becomes a major mortality factor. It should be stressed that this thermal requirement is peculiar to diapause eonymphs because when eonymphs emerging from the host at 22°C were placed in the same 16°C conditions, they were all able to moult within three days. A nonlinear model would, under these circumstances, provide a more realistic estimate of thermal requirements for the population (see Chapter 2) but would require development times from a wide range of fluctuating temperatures.
Nevertheless, the estimates from the linear regressions work very well in a situation where temperatures do fluctuate -- in nature. Fig. 10 illustrates data obtained in the field. It shows the actual Julian date of diapause termination for Vancouver A. rubecula in a Stevenson screen at UBC in 1983. The first to terminate were males from groups stored six or eight months at 0°C and then taken to the field on April 1, 1983. Only 1 degree-day had accumulated by that date. The rest of the groups are homogeneous despite the differences in the date of diapause induction the previous summer. Using daily temperatures at UBC (shown in the figure), the linear temperature summation model agrees quite well with the Julian dates for diapause termination. The date of 50% emergence may be a few days earlier, depending on the actual distribution of termination times.

Another interesting point to note in Fig. 10 is the role ambient temperature plays in the pattern of termination. During colder periods few individuals terminate diapause and the pattern appears sporadic; but warming periods accelerate rates and "compress" the apparent termination times so that the population terminates diapause over a fairly short period of calendar time (May 15 to 27, 1983).
FIGURE 10. Julian dates of diapause termination in Vancouver *A. rubecula* overwintered in the field, 1982-83. Solid bars are males, open bars are females. *Pm* and *Pf* are the mean termination dates predicted from laboratory data for males and females respectively. Minimum and maximum field temperatures and the thermal accumulation above the threshold *t*, are given.
Post-diapause pupal development

There was no correlation between the time required to complete diapause termination and the developmental period of the pupal stage at any temperature. Nor were there any effects of the different storage temperatures or durations on post-diapause pupal development. Combining data from all laboratory experiments, post-diapause pupal development rate can also be expressed as a linear function of temperature:

PUPAL DEVELOPMENT RATE (MALE) = -0.126 + 0.0112 TEMP

\[ R^2 = 0.83, \text{ df}=182, p<0.01 \]

PUPAL DEVELOPMENT RATE (FEMALE) = -0.107 + 0.0100 TEMP

\[ R^2 = 0.84, \text{ df}=66, p<0.01 \]

The calculated thermal constants from these regressions are given in Table 19. The threshold is similar for males and females and is indistinguishable from the independent estimate in Chapter 2 for pupal development without diapause. The thermal requirement for post-diapause pupal development of both sexes is higher than in nondiapause generations. The real heat requirement must be higher as measurements of post-diapause pupal development time do not include the period from spinning the cocoon to casting the meconium which can take up to two days at 20°C (approximately 20 degree-days).

Employing these estimated parameters in temperature summation following diapause termination at UBC in the spring of
<table>
<thead>
<tr>
<th>SEX</th>
<th>N</th>
<th>t (SE)</th>
<th>K (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FEMALE</td>
<td>68</td>
<td>10.7 (0.85)</td>
<td>99.7 (5.42)</td>
</tr>
<tr>
<td>MALE</td>
<td>184</td>
<td>11.2 (0.47)</td>
<td>89.2 (3.011)</td>
</tr>
</tbody>
</table>

TABLE 19. Estimated thermal constants for post-diapause pupal development in female and male *A. rubecula*. 
1983 predicts a Julian period of adult emergence in the field which is later than actually observed (Fig. 11). It may be just coincidental that this observed distribution of emergence is accurately predicted if the thermal requirements from Table 1 are used. Males clearly emerge before females but once again the emergence of most individuals is compressed into a few calendar days.

On the physiological scale, variation in the total time required for adult emergence is closely associated to variation in the diapause termination period rather than that of pupal morphogenesis (Fig. 12). This is consistent with the suggestion of Danilevskii (1965) and Morris and Fulton (1970) that the thermal requirements for active development show little intraspecific variation, whereas processes associated with diapause are subject to rapid selection and consequently, geographic variation.
FIGURE 11. Physiological time (degree-days) required from diapause termination to adult emergence in same individuals as in Fig. 10. \( P_m \) and \( P_f \) are predictions from laboratory estimates of males and females respectively.
Physiological time

May 29  May 31  June 5

Ln (N+1)
FIGURE 12. Relationship between thermal requirements to complete development to adult (Kp) and the thermal requirements for: a) diapause termination (Kdt) b) pupal morphogenesis (Km). Numbers are frequencies. Squares indicate 10 or more points per cell.
DISCUSSION

After the eonymph enters diapause within the cocoon, there is a period of at least three months when individuals are incapable of continuing development to adult. The longer the incubation period, the more rapid is the resumption of morphogenesis. But this is only true when incubation temperatures are below the threshold for morphogenesis. *A. rubecula* appears to be similar to the fall webworm, *Hyphantria cunea* Drury, where the post-diapause pupal heat requirement decreased to a minimum after six to eight months cold storage and then increased with extended storage (Morris and Fulton 1970). The period of chilling in the field is roughly seven to eight months for both *A. rubecula* and *H. cunea*.

There may be an inverse relationship between temperature and diapause development such that diapause terminates most quickly after an extended period at lower temperatures. Evidence for this is the observation that cocoons stored at 0°C required less time to terminate diapause than did those at 10°C. Insects which overwintered in the field at a mean temperature of 6.4°C required an intermediate period of time to terminate diapause. This same effect of low temperatures on the rate of diapause development has been observed in several insect parasites (Nechols et al. 1980; Schneiderman and Horwitz 1958; Wylie 1977).

Chilling may be a specific cue to terminate diapause but
in *A. rubecula* it is more likely that low temperatures simply preserve the insect during its extended dormancy. A few diapause cocoons stored at 20° to 23°C still emerge after ten to twelve weeks but their emergence is sporadic and mortality very high. After a sufficient storage period (four to eight months) at low temperatures, diapause termination is well synchronized within any one group and mortality low. Diapause then terminates most rapidly at higher temperatures.

Variation in the heat requirement for adult emergence is largely due to variation in the heat required to terminate diapause. This is also similar to that found in the fall webworm (Morris and Fulton 1970). However, in *A. rubecula* the high heat requirement for the post-diapause pupal moult means that diapause termination will not occur until temperatures are consistently high. This facilitates the synchronized termination of diapause and ensures post-diapause pupal development will not commence until daily thermal accumulation rates are high. From a chronological point of view, the intrinsic variability in diapause termination times would be minimized in the field. This is exactly what we observe in nature. Storage at low temperatures for variable periods in the laboratory did not really change the date of diapause termination whether these insects went to the field in late summer (August 19, 1982) or early spring (April 1, 1983). The first insects to terminate diapause are usually males but the relationship between termination rate and sex is not overwhelming.
Post-diapause pupal development is unaffected by larval rearing conditions or storage history and not correlated with diapause termination rates. The thermal requirements are similar to those described for temperature-dependent pupal development in Chapter 2 except the total heat requirement for adult emergence appears to be higher following diapause. This helps delay spring emergence. Males emerge first but most of the population becomes active within a short period of calendar time so mating success is as good as it can be under the circumstances.
CHAPTER 6

PHENOLOGY AND HOST-PARASITE ECOLOGY

To everything there is a season,
and a time to every purpose under heaven
a time to keep silence,
and a time to speak

Ecclesiastes III;1,7

This final chapter reviews the experimental data and
describes the phenology of A. rubecula in Vancouver, Canada and
Canberra, Australia. I discuss some general aspects of
seasonality in host-parasite ecology and conclude with a
discussion of the relevance of seasonal models to our
understanding of insect ecology and biological control.

PHENOLOGY

Phenology is the study of the visible response of
organisms to seasonal changes in their environment. The
recurrence of common biological events (flowering, migration,
hibernation) at particular times of the year give rise to
familiar seasonal cycles and the fundamental ecological tenet
that the distribution of organisms is the result of their
biological interaction with their environment. Descriptions of
the seasonal biology of organisms are as old as the first
observations in natural history. The modern concept of
phenology is well-developed in plant sciences. Coupling precise
meteorological data with biological processes has resulted in "phenological networks" which attempt to map the progress of plant communities throughout the year (Lieth 1974).

The importance of climate and weather in entomology has been stressed in several classic works (Andrewartha and Birch 1954; Uvarov 1931). Local weather impinges on all aspects of the population biology of insects and an appreciation of this interaction between insects and their abiotic environment is necessary to gain the insects' point of view (Wellington 1977).

The conversion to a temperature-dependent time scale, that is from calendar time to physiological time, is a first step. There are several analytic models that make this conversion. Nearly all employ the concepts of a threshold below which development is imperceptible and a total heat requirement to complete development. Throughout this thesis I have used linear regression to estimate these thermal constants. The unreliability of the technique to accurately predict development rates when temperatures are low was a minor disadvantage in timing the spring emergence of overwintering A. rubecula. Over the rest of the season, the regressions worked very well. Their greatest attribute is simplicity as the estimation of standard errors is straightforward (Campbell et al. 1974) and comparisons relatively unambiguous. My interest is not in how accurate can a prediction be made under all possible conditions but in what are the differences and similarities between interacting insect populations and how is
their seasonal biology tuned to broad weather patterns.

The season for *A. rubecula* begins in the spring with the end of diapause and pupation of the parasite within its cocoon. The insect is capable of resuming pupal development after a few months dormancy but in Vancouver, diapause does not end until relatively late (May), almost nine months after it was induced. Part of this delay is due to the high heat requirement to terminate diapause. At least a few days with temperatures sustained over 15°C are necessary for the final moult. The date will, of course, depend on the weather. In Vancouver in 1983, diapause termination occurred over the last two weeks of May; in 1982 it was two weeks later. But termination is synchronous at one location in any year, at least with experimental material. The high heat requirement for diapause termination ensures pupal activity will be delayed until average temperatures are better than just marginal for development.

The estimated thresholds for post-diapause and nondiapause pupal development were similar but post-diapause pupae had a higher heat requirement. Males had the lowest heat requirement and so were the first adults to emerge. Males will attempt to copulate with females immediately. Newly emerged females are ready to oviposit but require a few days before residual fats are depleted and oocyte production complete. In 1982, females were attacking hosts by June 1. The spring of 1983 was warmer and parasites were active in Burnaby by the last week of May.

Temperature summation for both 1981 and 1982 shows there
could be three generations in Vancouver. The second-generation parasites mature before the critical photoperiod is reached although a late spring emergence and cool summer temperatures could restrict populations in some areas to two generations per year. The adults of this generation remained active into September. The last generation parasites emerge from the host from the end of August through September while temperatures are still warm enough for normal development but daylength is shorter than the critical photoperiod. The season ends with diapause in the entire third generation.

There were small differences in the thermal constants between populations from Vancouver, Canada and Canberra, Australia. Australian populations had a higher heat requirement but the most important difference for phenology was the critical photoperiod for the induction of winter diapause. In Vancouver, the critical photoperiod was between fifteen and sixteen hours of light daily so the season was truncated in late summer. In Canberra, activity continued well into autumn; only a small portion of cocoons collected from March 20-23, 1981 (autumnal equinox) entered diapause so there must have been at least one autumn generation. I have not had the opportunity to follow A. rubecula for an entire season in Canberra, but I know it was not common at Pt. Hut until January in 1980 or 1981. Using calculated thermal constants and meteorological data for Canberra in 1981, there would have been three to four generations between January 1 and March 23, 1981. If there were, in addition, a spring generation during
December, there would have been a total of five to six generations of *A. rubecula* during the active season in Canberra.

**Host-parasite synchrony**

As in several insect parasites, the developmental threshold of *A. rubecula* is higher than that of its host. The similar range of the threshold of so many insect species suggests the threshold is primarily a physiological constraint although the difference between host and parasite parameters could be a mechanism promoting host-parasite synchrony (Campbell et al. 1974). Of more interest to this study was the relatively low heat requirement to complete one generation for the parasite. During the main portion of the growing season, the parasite will complete more generations in a given period of time than will the host. There is a theoretical certainty that the parasite population will outstrip that of the host. However, reality prevails when we consider the entire seasonal picture.

In Vancouver, where *P. rapae* has only two generations per year, a high critical photoperiod for diapause induction in *A. rubecula* restricts the parasite to three generations per year at the most. In Canberra, the critical photoperiod is lower and the parasite population could potentially achieve more generations than the host. But the lower thermal requirements of the Australian hosts results in comparatively
short generation periods for the host at the lower temperatures encountered at the beginning and end of the season. Consequently, both host and parasite have five or six generations per year in Canberra.

In both localities, the first parasite adults of the season lag behind the appearance of the first butterflies by several weeks. This is due to the extended dormancy of *A. rubecula* resulting from the high thermal requirement to terminate diapause. The asynchrony in spring emergence enables the host population to get a head start so that when parasites finally emerge, there is a good chance there will be susceptible host larvae available for parasitism.

A recurrent observation in this study was the synchrony in development times of individual parasites. There is little variability in the thermal requirements at any stage so that adult emergence for a cohort at any time of the season occurs over a short period of time, although males consistently emerge before females.

This synchrony in developmental pattern may be significant in parasite ecology. Price (1980) has developed a theory of non-equilibria in which parasite populations are characterized by their frequent extinction in local patches but rapid recolonization and growth in other patches. Parasites, by necessity, occupy ephemeral and heterogeneous habitats. Such a precarious life would be well served by developmental synchrony as it would increase the probability of mating in sparse
populations and insure that parasites in all patches experience the same seasonal pattern irrespective of minor local variations in weather.

Diapause

The characteristics of diapause in *A. rubecula* were examined in detail in Chapters 3 to 5 and need not be repeated. The importance of diapause to phenology has also been stressed. But the difference in diapause response between Vancouver and Canberra populations deserves comment.

The first *A. rubecula* released in Australia were from Switzerland (Wilson 1960) and later material came from Italy, near the southern end of the parasite's range (Delucchi 1950). But we do not know where the Vancouver population originated (Wilkinson 1966) so it is not possible to determine whether these differences in the photoperiodic response reflect differences in the colonizing stock or changes after introduction to new habitats. It would be simple enough to see if the critical photoperiods in the introduced populations fall within the range of variability for European populations.

Whatever their origin, the diapause response in Vancouver and Canberra is remarkably appropriate for local circumstances. In Canberra, where the host is active at least seven months of the year, the parasite also has a relatively long season and as many generations as its host. In Vancouver, the high critical photoperiod ensures a short season. Both strategies permit
A. rubecula to make the most of local host populations and survive local climates.

At first, Vancouver parasites appear to overcompensate, entering diapause well before the end of the summer while butterflies are still laying eggs. However, there are at least two additional risks to late season Vancouver parasite populations. The first is weather. Autumn temperatures fall more precipitously at higher latitudes. Although larval A. rubecula can develop at temperatures down to 11°C, if conditions are cool and moist when they emerge, the silk cocoon, the insect's primary protection, is not properly formed. Cocoons spun during October in Vancouver were misshapen and thin even when the insect was reared from hosts on young plants under laboratory conditions before being taken to the field. None of these insects survived to pupate. In Canberra, where autumn days are relatively clear and dry and often warm for at least a few hours of the day, this may be less of a problem.

The second late-season risk to Vancouver A. rubecula is predation. Hyperparasitism by T. galactopus is substantial in Vancouver during September (Nealis 1983). T. galactopus is a true hyperparasite; it oviposits directly into the primary parasite through the body wall of the primary host. It is incapable of hyperparasitism once A. rubecula has formed a cocoon. Hence it is the parasitic stages and not diapause eonymphs which are at risk. In contrast, hyperparasitism in
Canberra is practically nonexistent. My collections of E. braconophagus were the first records for Australia (I. Naumann, personal communication).

Thus, diapause may serve several ends. After years of watching insect activity, I am finally impressed by the importance of doing nothing.

BIOLOGICAL CONTROL

One of the few benefits of the pesticide treadmill was the belated realization that pest management is an ecological problem. At times, it may seem that theoretical zeal distracts the practical perspective (Wellington 1977) but taken together, theory and practice in insect ecology contribute to our understanding of natural systems. And even if, as Holling (1978) and others suggest, understanding natural systems is not necessary for their management, the more complete is our knowledge of basic ecological relationships, the more able will we be to respond to new situations when things go wrong.

As an ecological approach to pest management, biological control demands not only that the basic biology of the participants be understood but that we formulate some hypotheses about the nature of interactions between trophic levels. Studies in biological control can make a virtue of necessity and truly become large-scale field experiments on natural populations (Myers 1978).
This study began with the observation that despite the wide distribution of a pest species, its specific parasite seemed far less adaptable and consequently, more restricted. Several attempts to introduce the parasite using innovative methods demonstrated the effectiveness of *A. rubecula* to control the imported cabbageworm but establishment was unsuccessful (Parker and Pinnell 1972; Puttler et al. 1970). The clue for these failures was actually contained in Parker and Pinnell (1972) who observed that in Missouri, *A. rubecula* obtained from Vancouver entered diapause in early September even though the host was fully active for several more months. It is now clear why this must be so. The long obligatory dormant period for Vancouver parasites meant they would remain in diapause while ambient average temperatures were greater than 15°C, conditions which we can now recognize as lethal. To restate my proposed solution, the Vancouver stock should remain in Vancouver. Parasites from Australia are more promising candidates for the southern United States.

The importance of finding natural enemies with the appropriate climatic adaptations for a biological control program has been demonstrated many times (Messenger and van den Bosch 1971). These workers combined entomological knowledge with simple experiments to initiate the integrated pest management approach (Huffaker 1980). Their methods have been updated, although not always improved, by current attempts to quantify all the processes and model the entire system.
One such class of models, and perhaps the simplest, are phenological models. They require precise biometeorological data and good measurements of environmental physiology and the recognition that there may be several explanations for a phenomenon, depending on your point of view. It is the ecologist's task to identify which point of view offers the more satisfactory explanation (Gilbert et al. 1976).

A descriptive model, such as outlined here, can offer considerable insight and a simulation model can provide an opportunity to investigate theoretical consequences. But no one; entomologist, ecologist, modeller or insect can predict tomorrow's weather with certainty. It is this uncertainty which makes insect ecology complex and nature so fascinating.
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