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SIMULATION OF HUNGER, FEEDING AND EGG PRODUCTION IN THE CARABID BEETLE *Pterostichus coerulescens L* (= *Poecilus versicolor* Sturm).

P.J.M.MOLS
Med. 355 Biologisch Station Wijster.

Wageningen Agricultural University

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ABSTRACT

This study is a part of a broad investigation of the behaviour of the carabid beetle *Pterostichus coerulescens L. (= P. versicolor* Sturm) at different densities and distributions of its prey. In this paper the driving force ('the motivation') for searching, feeding and egg production was elucidated. A simulation model was constructed that continuously estimated the internal condition of an individual beetle and that estimated the egg production as a result of feeding under different sets of conditions such as fluctuating temperatures and feeding time intervals.

In this Carabid the driving force for feeding appears to be the relative emptiness of the gut, which depends on the gut content and on the apparent gut capacity. The latter appeared to be a function of the weight of the ovaries together with the quantity of eggs in the oviduct, and of the quantity of reserves stored in the body. These relationships made it necessary to quantify the processes that influence the rates of change of these state variables. Therefore, the rates for ingestion, egestion, assimilation, respiration, storage of reserves, egg formation, egg resorption and egg maturation in the oviduct were quantified experimentally in relation to temperature or estimated from literature. The simulated egg production was in satisfactory agreement with the results of independent egg production experiments carried out at field temperatures.

1 INTRODUCTION

Many ground beetles are well known predators of arthropods of various groups. Their prey include potential pest species on many beneficial plants. Research done by Wishart (1956), Wright and Hughes (1959), Scherney (1959, 1960, 1962), Coaker and Williams (1963), van Dinther and Mensink (1965), Frank (1967), Dubrovskaya (1970), Basedow (1973) Edwards et al., 1979 and Sunderland et al., 1980, 1985 suggests that carabids can considerably reduce the numbers of certain pest species. The reduction depends on the composition of the carabid fauna, on prevailing environmental conditions and on the behaviour of the beetles. Thiele (1977) has presented an extensive survey of this, concentrating on the composition of the carabid fauna. From Varley et al. (1973) it can be concluded that the highly density dependent mortality of the pupae of the winter moth (*Operophtera brumata*), caused by carabids (among other polyphagous predators) might be the result of an area restricted search in prey aggregations. In nature arthropods are often distributed in aggregations (Southwood, 1966). This implies that predators would forage more efficiently if they reacted with a special searching behaviour to those prey aggregations. Such behaviour might result in a better chance of survival and more offspring. It is common for the predators of several species to stay longer in an area where they meet prey than in an area where no prey is available. This phenomenon has been observed in unicellar organisms (Fraenkel and Gunn, 1940; MacNab and Koshland, 1972) as well as in insects (Laing, 1938; Fleschner, 1950; Banks, 1957; Dixon, 1959, 1970; Hafez, 1961; Mitchell, 1963; Murdie and Hassel, 1973: Hassel and May,1974; Evans, 1976, Cook and Hubbard, 1977; Waage, 1977). This tendency may be due to changes in behaviour after an encounter with food items or as a reaction to kairomones (Pak, 1988, Dicke, 1988). Some birds change their searching patterns in prey aggregations (Royama, 1970; Goss-Custard, 1970; Smith and Dawkins, 1971; Krebs et al., 1972; Smith and Sweatmann, 1974) and seem either to develop a searching image of that prey (Tinbergen et al.,1967; Croze, 1970; Dawkins, 1971 a,b) or of the locality where foraging was profitable. Some fishes (Beukema, 1968) and mammals (Taylor, 1977; Trombulak and Kenagy, 1980) also react to differences in prey densities.

1.1 Aim of the study

The ultimate aim of this study was to consider the impact of spatial distribution and density of prey on predatory behaviour and on the resulting egg production of the carabid beetle *Pterostichus coerulescens* L. (= *Poecilus versicolor* Sturm). This predatory beetle rarely flies thus all vital behavioural functions,

such as searching for food, finding a mate, avoiding to be predated itself by birds and toads etc. (LaRochelle 1974a, b, 1975a, b,) occur by walking. This implies that the patterns of movement determine the chance of survival as well as the rate of feeding and reproduction of the individual.

1.2 Approach to the problem

Changes in the distribution of individuals within the preferred habitat can be studied by releasing marked individuals and ascertaining their positions after successive time periods (Rivard, 1965; Baars, 1979). The results obtained by this method of studying displacement in the field gives results which depend on the conditions prevailing during the observations, and therefore do not elucidate the relationship between predator movements and prey density and distribution, because since the processes that govern the predator movements in the field are not known. To gain insight into these relationships and thus to be able to predict the quantitative results of the different types of movement under different sets of environmental conditions, the factors that influence the movements of the individual predatory beetle must be known. The ultimate significance of this behaviour appears from the size of reproduction and from the chance of survival of the predator. Factors which influence the movements of the individual can be devided into internal and external factors. The internal factors originating from the physiological condition or state of the beetle compose the 'motivation' of the animal. This 'motivational' state may be the result of the states of different organs. 'Motivation' is connected with feeding and digestion, which are determined quantitatively by characteristics such as emptiness of the gut, reproductive or non reproductive state, body size, etc. These internal states are influenced by external factors like: temperature, day length and sometimes humidity. As a result of 'motivation' a searching and capturing behaviour occurs which can also be influenced by external factors such as temperature, type and structure of the soil surface (Mossakowski, 1986) and the vegetation. Some of the most relevant components of searching and capturing behaviour are walking speed and direction, locomotory activity and succes ratio. These were also distinguished by Holling (1963, 1964, 1965, 1966) in his study of the predation process of the mantid *Hierodula crassa* and by Fransz (1974), Rabbinge (1976) and Sabelis (1981) in studying predation in acarine systems.

Therefore to get insight into the searching and predatory behaviour research was carried out:

a) To elucidate the driving force ('the motivation') for feeding, searching and predatory behaviour of the beetle.
b) To determine the most important components in the predatory behaviour of the beetle.
c) To quantify the relationships between these components and the 'motivation'.

The information on the 'motivation', on the relevant components of predatory

behaviour and their interactions was used for the construction of a simulation model. With this model the predatory behaviour of the predator resulting in feeding, egg production and dispersal can be estimated at several densities and distributions of the prey.

In this paper the relationship between feeding, physiological state of the beetle and egg production is described. The internal factors which comprise the physiological state of the beetle were integrated in a simulation model. The output of the model was compared with the results of experiments to show whether it is possible to use this model to estimate continuously the 'motivational state' as an internal governing variable for the components of behaviour.

In a subsequent paper the impact of 'motivation' on various components of searching behaviour, and the effect of prey density and prey distribution on survival, egg production and dispersal will be shown.

1.3 'Motivation' for feeding

Hunger is a very important internal driving force for the behaviour of an animal. When insects are deprived of food changes occur in a variety of behavioural components, resulting in feeding. In the blow-fly *Phormia regina*, locomotory activity increases with length of the deprivation period and drops sharply immediately after feeding (Barton-Browne and Evans, 1960; Green, 1964). Predatory mites (Sandness and McMurtry, 1970), tse-tse flies (Brady, 1972) and springtails (Joosse and Testerink, 1977) show an increase in locomotory activity after being deprived of food. Grum (1966) working with carabids, observed an increase in mobility up to the second or third day after the beginning of food deprivation, followed by a decrease when starvation set in. Ernsting (1977) demonstrated that in another carabid *Notiophilus biguttatus*, food deprivation influences locomotory activity in a comparable way. In Holling's (1966) model of the mantid *Hierodula crassa* the driving force for feeding is hunger, which is defined as the degree of emptiness of the gut. Hunger increases through the combined action of assimilation and defaecation, and decreases during feeding. It approaches a minimum when the gut is filled completely. Feeding behaviour is governed by the hunger level. Holling distinguished thresholds for different components of behaviour such as search, pursuit, capture and consumption of prey. Fransz (1974) considered the driving force for the behaviour of the predatory mite *Typhlodromus occidentalis* to be satiation level, which is the complement of hunger. In other investigations it has also been shown that the satiation level of predatory mites is the major factor that influences predation, preference and consumption of the different stages of prey (Rabbinge,1976; Johnson et al.,1975; Sabelis, 1981). The implication is that insight into the driving force for predation of the ground beetle *Pterostichus coerulescens* can only be obtained if the predation process is studied in relation to the hunger level of the predator.

Regulation of food intake, and therefore the driving force for feeding is, in the studies cited above, thought to be governed solely by the emptiness of the

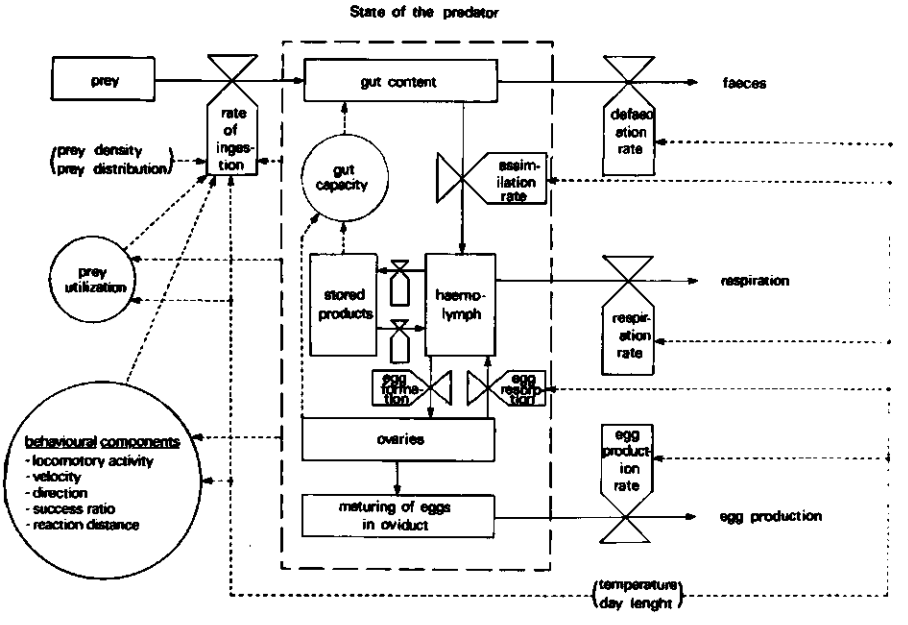


FIG. 1. Relational diagram of the 'motivational' state of the carabid beetle *P. coerulescens*. The rectangles indicate states, valves correspond with rates of change, ccircles with auxiliary variables, solid arrows with the flow of material, broken arrows with flow of information, and forcing variables are given in brackets.

gut. A more holistic approach is described by Gelperin (1971), Dethier(1976) and Holling (1976) for the process of feeding in the blow fly *Phormia regina* (Meigen). Gelperin (1971) states:

'The regulation of food intake is part of a mechanism which aims at metabolic homeostasis. By metabolic homeostasis is meant the metabolic energy flow into and within the animal. Feeding behaviour involves the introduction of energy stores into the animal, gut content determines the rate of delivery of these stores to the blood, and a third set of controls operates to control delivery of energy stores from blood to tissues. If information is available at all these levels of analysis, one should be able to trace the causal sequences of events between cellular energy expenditure and the behaviour of energy ingestion'.

When the delivery of energy to the ovaries is included in this conceptual model a general and simple model of conversion of ingested food to egg production is obtained. The contribution of the feeding behaviour for the survival of the group is best expressed in the fecundity.

As a result of the studies mentioned above a general and simple relational diagram that comprises the dominant state variables connected with feeding and egg production is constructed (fig 1.). In this diagram food is ingested at a certain rate that depends on the prey species and probably on the hunger of the predator. It is digested in the gut, a fraction is egested as faeces and the

remainder is assimilated. The assimilated food is delivered from the haemolymph to the tissues, where it may be metabolized, stored or used for the formation of eggs, depending on the physiological state of the animal. As prey ingestion generally occurs in discrete units (meals) the intake of energy is discontinuous, whereas the utilization is a continuous process. The organism is organized such that energy stored in the body is made available in the intervals between meals so that the animal is free to engage in other activities. All these activities are affected by the principal external governing variable: the temperature. Other factors like daylength and circadian rhythm may play a role.

To be able to construct a simulation model of the 'motivation' of the beetle, the hunger level of the predator was quantified. It was nescesary to estimate the following variables:

1. Gut capacity in relation to the size of the beetle (because this capacity determines maximum meal size).
2. Gut emptying rate and assimilation rate, which determine the rate of change of the gut content and therefore the hunger level.
3. Respiration rate at several temperatures and physiological states.
4. The rate of formation of reserves and the delivery of energy for metabolism and reproduction.
5 The rate of egg formation and egg resorption.
6. The residence time of eggs in the oviduct.
7. The rate of ingestion and prey utilisation.

These variables were established in different reproductive and non-reproductive states of the predator to ascertain the predator's dependence on these states. By quantifying the relationships mentioned above it is possible to estimate the egg production that results from a specific predatory behaviour.

2 BIOLOGY OF *Pterostichus coerulescens* L. (= *Poecilus versicolor* Sturm).

2.1 Description, distribution and habitat

The ground beetle *Pterostichus coerulescens*, fig. 2.1. varies in length between 8 and 11.5 mm. Its general colour is black but the elytra and pronotum are iridescent brown to green and sometimes turn blue and even black as the beetle grows older. According to Freude et al. (1976), *P.coerulescens* is distributed over the whole of Europe with the exception of the extreme North. It is also found in the Caukasus, Siberia and Japan. The species is most abundant in the central parts of Europe especially in the mountains. *P.coerulescens* is most frequently found in open, dry localities. Heydemann (1955) considers it to show highest numbers in cultivated areas with sparse vegetation, where light can easily reach the soil, for example in dry grassy fields on sandy soils with a low humus content. In the Netherlands *P. coerulescens* is most abundant in semi-moist to dry grasslands on sandy soils and less numerous but still abundant in heath areas.

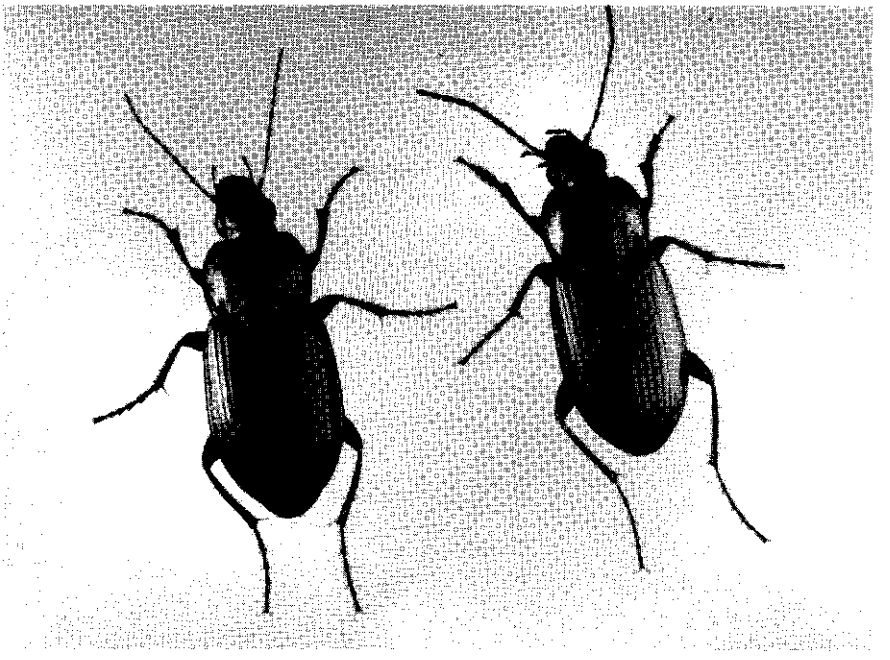


Fig. 2.1. The ground beetle *P.coerulescens* (left female, right male).

2.2 Life cycle

P.coerulescens is diurnal, only a few animals show some nocturnal activity (Greenslade, 1963; Thiele, 1977). Like most carabids *P.coerulescens* is univoltine in the temperate zones. It is a spring breeder with autumn activity. In spring when temperature rises above 8 °C the adults leave their winter shelters and start feeding. Males appear a slightly earlier than females (van Dijk, 1979). After a pre-oviposition period which depends on temperature and food consumption, egg production generally starts in May. The locomotory activity of the beetles peaks just before and at the start of the reproduction period. From the end of June until mid July the activity declines, egg production stops and fat reserves in the body accumulate until the adult beetle hides in the soil, where it stays until the next spring. After hibernation the adult beetle becomes active again the following spring. The eggs are deposited in the soil and hatch after approximately three weeks. The larvae crawl around in the soil and pass through three larval stages before they pupate after approximately eight weeks. The pupal stage lasts approximately two weeks i.e. young beetles appear circa 13 weeks after the eggs were deposited. They can be found in the field from the end of August until the end of October. They remain active until they have built up a considerable amount of reserves which supply energy for hibernation and also enable sufficient glycerol to be synthesized to sufficiently depress the super-cooling point (Baust & Miller, 1970). Activity may stop earlier if the temperature becomes too low i.e. 5 °C. In those cases the chance of a successful overwintering decreases, because the beetles do not succeed in building up sufficient quantities of reserves. The beetles may pass through several reproduction cycles, as even 4 years old beetles have been caught (van Dijk, 1979; Baars, 1979).

2.3 Feeding and food

P.coerulescens digests its food internally like all Pterostichini. They possess thin-walled crops that can expand widely and may fill a considerable part of the abdomen. This is different from species belonging to the genus Carabus where digestion is external and which have relatively small crops. Prey is seized by the mandibles, which penetrate into the cuticle of the prey animal so that the chance to escape is small. Swallowing by cooperative work of the mandibles and maxillae is described in great detail by Evans (1965) for the ground beetle *Nebria brevicollis* F. The crushed food enters the large thin-walled crop and passes through the posterior part which contains a short muscular proventriculus or gizzard. This gizzard operates as a filter, a crusher and a valve, and regulates the flow of food between the crop and the midgut (Evans, 1965). Digestion occurs mainly in the midgut from where the food is assimilated through the gut wall into the haemocoel of the beetle. The undigestible parts pass the hind gut and are excreted.

During the passage through the hind gut part of the water is resorbed. Because

of the internal digestion remains of prey can be found within the crop. Crop-content analyses may help to identify the kinds of prey species captured by the beetles in the field (Davies, 1953; Smit, 1957; Hengeveld, 1980). However, not all prey leaves recognizable remains. For example, Lepidopteran and Dipteran larvae with a soft cuticle (Hengeveld, 1980) do not leave recognizable residues.

Hengeveld (1980) has demonstrated that smaller arthropods are a popular food item of *Pterostichus coerulescens*. Sometimes the beetles can also be found on dead bodies of lizards, mice and on other carrion. Thus, the beetle seems to be very polyphagous.

3 QUANTIFICATION OF THE HUNGER LEVEL

3.1 GUT CAPACITY AND BODY SIZE

3.1.1 Introduction

Gut capacity is determined either by the morphological limits of the gut itself or by factors that limit the expansion of the gut. Here it is defined as the maximum amount of fresh food the gut can contain in different physiological states. This definition implies that the average meal size to satiate a beetle need not equal the gut capacity but in general will be smaller then the gut capacity. Since gut capacity is a morphological characteristic, it will depend on body size, and therefore it will be a characteristic for each individual animal. This has been shown for larval stages of insects (Mathavan and Muthukrishnan, 1980) and for spiders which grow continuously (Nakamura, 1968).

To account for individual differences in body size the satiation level, or the relative gut content (RELGUT), is usually defined as the gut content divided by the gut capacity.

In the experiments done by Davey and Treherne (1963), Green (1964), Holling (1966), Nakamura (1972) and Fransz (1974) it is implicitly assumed that the gut capacity is a constant for a given body size. This is probably true for larval stages and for spider mites, but in adult beetles it also depends on their physiological state. In the present study this became evident when female beetles of *P.coeruleascens* in different states were dissected. Starved beetles showed an abdomen in which the crop could expand to its full extent, because the fat body was almost absent and in female beetles the ovaries had been resorbed. On the other hand, in well fed reproductive females the abdomen was filled with eggs and some fat making it impossible for the crop to expand fully. Therefore it was assumed that the gut capacity depends on the size of the ovaries, the number of maturing eggs, and the quantity of products stored in the fat body. In particular the room left in the abdomen by these organs may indicate the possible expansion of the crop. The variation in the room left will thus depend on the development of these organs. Therefore, the states of these organs expressed in their fresh weight will determine the gut capacity.

The total weight of a beetle is the sum of the weights of:

a) The integument.
b) The vegetative tissues and organs (a + b is minimum fresh weight (MINFW)).
c) The haemolymph (HEMO).
d) The reserves stored (FAT).
e) The active reproductive organs (OVAR).

f) The mature eggs in the oviduct (EGGOV).
g) The gut content (GUTCON).

In non-reproductive beetles the ovaries are so attenuated that any increase in net body weight is caused only by storage of reserves. Then the relation between net body weight and the ingested meal, when abundant food is available, gives information on the influence of weight of the reserves on the possible expansion of the gut. In reproducing female beetles, any increase in net body weight is mainly attributed to the increase in weight of the ovarioles and the number of maturing eggs. Thus, knowledge of the relationship between the changing net body weight and the gut capacity of beetles in different states allows the effect of either the reserves, or the ovarioles and the maturing eggs to be estimated. Therefore, experiments were carried out with non-reproductive beetles in autumn, and with reproductive beetles in spring.

3.1.2. General methods

The general methods needed to quantify the state of the predator are described in this section. The quantitative relationships between reserves, ovarioles, eggs and gut capacity were established gravimetrically. Most relations are based on the weights of fresh food and of living animals. The quantity of ingested food was determined by weighing a beetle before and after consumption of a meal. In general, reproductive beetles were starved for 3 days, and non reproductive beetles for 6 days at 20 °C before the start of the experiments, because the latter have a lower rate of gut emptying. The beetles were kept in petri dishes (9 cm diam.) with ground moist peat mull. After starvation they were offered an excess of blowfly larvae for approximately one hour. This period was long enough to satiate the beetle. Beetles that start feeding with an empty gut usually fill their gut completely. When the beetles refused any further maggots, they were considered to be satiated. When the beetles laid eggs during the experiments or observations, these were removed from the peat mull by the sieve wash method (Mols et al.,1981). If experiments deviated in their experimental set up from this general method, this is noted in the appropriate sections.

When studying the feeding behaviour of reproductive beetles, mainly females were focussed on. It is assumed that formation and storage of spermatophores (2-3 mg per spermatophore) in the male abdomen play a similar role in the occupation of room in the abdomen as the growth and storage of eggs does in the female abdomen.

3.1.3. Body weight in relation to beetle size

Both maximum and minimum weight depend on the size of the beetle. Therefore, abdomen capacity will also depend on beetle size. As the surface of the elytra is supposed to vary proportionally with the size of the beetle, this relationship was estimated as length times width of the elytra (LEWI). (Width is the distance between the shoulder angles, and the length is measured along the suture). Maximum weight was determined in feeding experiments with reproduc-

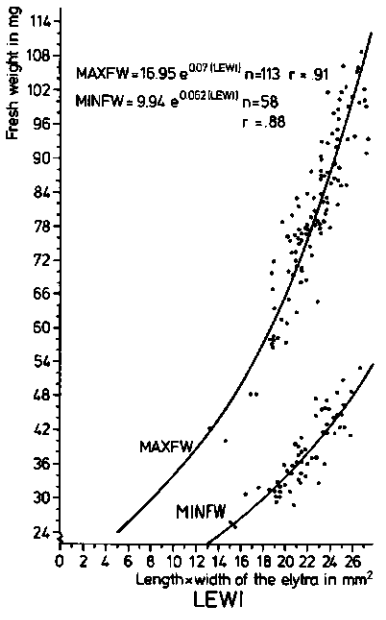


FIG. 3.1. The relationship between length times width of the elytra (LEWI) in mm^2 and maximum (MAXFW) and minimum (MINFW) fresh weight of *P.coerulescens* expressed in mg.

tive and non reproductive beetles (section 3.1.4.). Minimum weights were derived from starvation experiments done to estimate respiration (section 3.7).

Results

The relationships between size of the elytra (LEWI), and maximum (MAXFW) and minimum (MINFW) fresh weight are given in fig.3.1. These are described best by exponential formulae, because they represent relationships between surface (LEWI) and content expressed as weight.

$$MAXFW = 16.95 * e^{0.07 * LEWI} \qquad n = 113\ r = .91$$
$$MINFW = 9.94 * e^{0.062 * LEWI} \qquad n = 58\ r = .88$$

Thus when the size of a specific beetle is known, the corresponding abdomen capacity (ABDOM = MAXFW-MINFW), which is the room available for ovaries, reserves, haemolymph, eggs and gut content, can be estimated.

3.1.4. Gut capacity experiments

3.1.4.1. Non-reproductive beetles

Gut capacity of non-reproductive beetles was estimated both for beetles collected in the field and for beetles reared in the laboratory. Beetles were collected in the field at weekly intervals with pitfall traps during september and october 1977 . They were starved for three days at 20 °C. weighed and then offered abun-

dant food so that they became satiated and were then reweighed. In this way the effect on the meal size of the increasing reserves, stored in the field, could be determined (table 3.1.). However, neither the feeding history nor the age of the beetles captured were known, and since factors such as initial body weight, time of hatching and day length may affect the size of the meal, these have to be known beforehand. Therefore, another group of beetles (10 males and 10 females), reared in the laboratory, were monitored for a period of 10 weeks after hatching. These beetles were not given a meal after hatching, so that at the start of the experiment their guts were completely empty. Meal sizes were then measured in experiments, according to the general method, which were executed at intervals according to table 3.2 at a constant temperature of 20 °C and a day length equal to outdoor conditions. This feeding experiment was repeated in November 1977 with another group of beetles reared under the same conditions and which had hatched early in September. Immediately after hatching these animals were starved at a constant temperature of 8.5 °C. As respiration is very low at this low temperature, approximately the same net body weight as in the previous group of beetles was maintained. The day length was now kept at 8 hours to see whether short day length might influence feeding 'motivation' and thus the estimation of the gut capacity.

Results

Non-reproductive beetles collected in the field.

The average weight of groups of non-reproductive beetles collected in the field did not exceed 50 mg (table 3.1). In autumn it is difficult to catch heavy beetles in the field. To include heavy beetles in the experiment, 3 groups of 15 beetles of each sex were taken from those captured in the field at the beginning of the experiment. These were kept and fed in the laboratory, and are the last three groups in table 3.1.

Beetles with low initial body weight very quickly consumed the maggots offered, so that their body weights also increased rapidly. This consumption continued, mostly without interruption, until satiation and took approximately half an hour.

When satiated, beetles with an initial body weight between 45 and 50 mg, had an expanded abdomen protruding outside the elytra, with the membranes between the abdominal segments clearly visible. The relation between the initial net body weight (NBODYW) and the meal size of these beetles with sizes of LEWI between 19 and 21 mm^2 is given in table 3.1 and fig.3.2a. The meals of the beetles with low initial body weight were all approximately of the same size: 21 mg for the males, and 24 mg for the females. As soon as the net body weight exceeded 46 mg, by storage of reserves, meal size decreased sharply. The quantity of the reserves was estimated by the difference between body weight just before the start of feeding and minimum body weight according to size (FAT = NBODYW-MINFW, from fig. 3.1). At the initial weight of 46 mg, FAT is 12 mg and a meal size of 22 mg can still be ingested. This gives a total maximum satiated weight of 68 mg. This maximum satiated weight is the same as the maxi-

TABLE 3.1. Average meal size (in mg ± SD) of groups of non-reproductive beetles collected in the field in relation to the net body weight (in mg) with empty gut (starvation period at least 2 days). LEWI of the elytrum between 19 and 21 mm^2.

Males			Females		
n	Initial weight	Meal size	n	Initial weight	Meal size
13	37.7 ± 6.4	19.8 ± 5.6	14	37.2 ± 4.5	21.5 ± 6.5
13	41.0 ± 6.4	19.0 ± 6.0	30	40.0 ± 4.2	23 9 ± 4.2
26	41.2 ± 4.4	19.8 ± 4.0	14	41.7 ± 5.3	24.5 ± 4.8
13	41.9 ± 7.6	23.4 ± 3.5	20	42.2 ± 4.9	26.8 ± 3.6
17	43.3 ± 4.9	23.1 ± 3.2	15	42.9 ± 6.3	23.3 ± 5.9
26	44 2 ± 6.4	22.2 ± 4.7	28	44.9 ± 6.0	23.7 ± 6.3
23	48.4 ± 4.1	15.4 ± 5.3	14	45.7 ± 7.9	17.9 ± 4.7
11	49.7 ± 7.0	17.8 ± 4.5	16	48.2 ± 6.9	15.7 ± 4.8
15	53.7 ± 5.9	6.5 ± 4.1	15	57.6 ± 10.1	5.5 ± 2.5
15	58.1 ± 5.9	3.6 ± 2.0	15	58.9 ± 9.3	3.1 ± 2.8
15	54.1 ± 5.4	6.0 ± 4.4	15	60.6 ± 10.1	3.5 ± 2.3

TABLE 3.2. Average meal size (in mg) of groups of non-reproductive beetles (10 males and 10 females) in relation to their net body weight (in mg) just before feeding, after a starvation period to empty their gut. Beetles were reared in the laboratory and fed on the dates in the table. Size of LEWI varied between 22-24 mm^2.

Males (n = 10)				Females (n = 10)	
Date	Days from start	Initial weight	Meal size	Initial weight	Meal size
30/9	0	42.6 ± 4.5	15.8 ± 5.0	39.6 ± 4.5	20.7 ± 4.1
7/10	7	47.5 ± 5.3	21.5 ± 5.4	45.6 ± 4.1	24.0 ± 5.2
18/10	18	52.2 ± 6.0	21.4 ± 3.3	52.1 ± 6.6	23.0 ± 6.7
26/10	26	57.9 ± 10.3	15.7 ± 5.9	57.4 ± 7.0	15.8 ± 7.4
2/11	33	59.2 ± 6.3	9.3 ± 4.8	59.6 ± 6.8	11.1 ± 6.1
8/11	39	61.2 ± 4.6	4.9 ± 3.0	61.4 ± 7.1	8.1 ± 4.0
25/11	56	59.1 ± 4.7	5.0 ± 2.3	59.5 ± 5.8	4.9 ± 5.3
2/12	63	59.9 ± 4.1	2.2 ± 3.3	60.3 ± 6.0	1.4 ± 2.4
8/12	69	60.0 ± 4.5	3.2 ± 3.2	59.7 ± 6.0	2.1 ± 3.4
16/12	77	60.1 ± 5.0	3.5 ± 5.1	59.5 ± 5.1	3.8 ± 3.8

mum fresh weight corresponding with the size of the beetle (see fig.3.1). This implies that when the weight of the stored reserves exceeds 12 mg, the ingested meals will always be smaller then 22 mg, because of lack of room. However, when the initial body weight exceeded 46 mg, meal size did not decrease with a slope of 45 degrees, as was expected if only lack of room was responsible, but decreased more rapidly. This indicates that beetles with a higher reserves weight than 12 mg did not fill their gut so that not all the room available in the abdomen was used up. Fig 3.2a shows that the weight of completely satiated

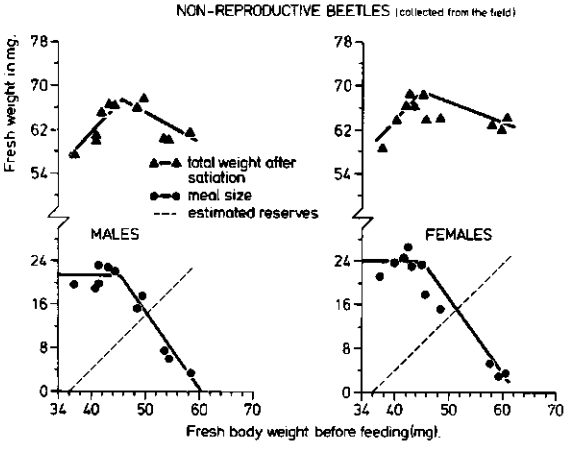


FIG. 3.2a. The relationship between initial net body weight (NBODYW) and the meal size of beetles captured in the field. LEWI is between 19 and 21 mm^2.

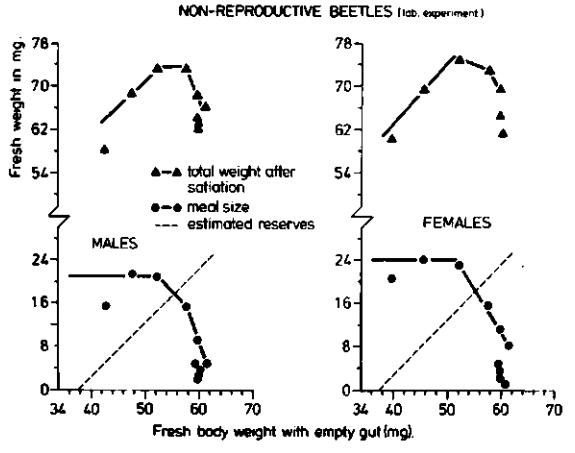


FIG. 3.2b. The same relationship, but now from beetles reared in the laboratory. LEWI is between 22 and 24 mm^2.

beetles did not remain at the maximum level. It dropped when the reserves had reached a weight of about 12 mg. The summation of the weight of the reserves and mealsize is then $12+21=33$ mg for males, and $10+24=34$ mg for females. In the three groups of well-fed beetles added in the experiment, the reserves reached a weight of approximately 23-25 mg, which is approximately 30% of the net body weight. Thus approximately 9 mg could potentially be ingested. In reality only 4-5 mg was ingested. Beetles apparently avoid filling their abdomen completely if they have enough reserves stored.

Non-reproductive beetles reared in the laboratory.

From the start of this experiment the laboratory beetles showed a series of

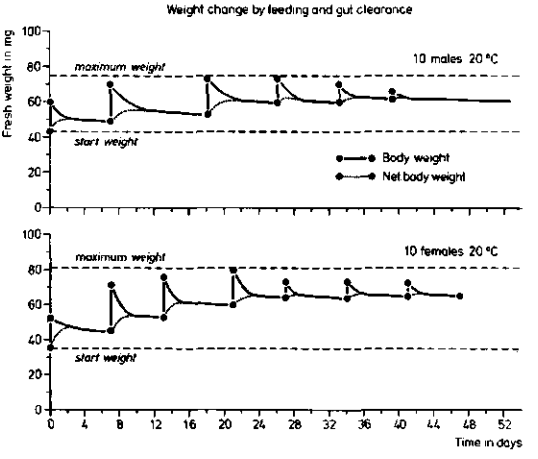


FIG. 3.3. Change in weight by feeding and gut emptying. The solid line corresponds with total fresh body weight, the dotted line with body weight without gut content. In the latter, increase of reserves by assimilation of the ingested food can be observed.

bouts of rapid weight increase (feeding) followed by a gradual but exponential weight decrease caused by egestion and respiration (fig. 3.3.). During the intervals between feeding the beetles showed a gain in net body weight by storage of reserves (table 3.2 and fig.3.2b). When net body weight before feeding was higher then 52 mg the meal size decreased (table 3.2 and fig.3.2b.). The first meal consumed in the experiment (which was also the first meal after hatching) was smaller than the second and third meals. The males consumed less then the females, perhaps because they were smaller. When this experiment was repeated later in autumn with another group of beetles, but with a day length of 8 hours, the same pattern of changes in weight caused by feeding, assimilation and egestion could be observed. This suggests that in non-reproductive beetles only the quantity of reserves present in the beetle influences the meal size. Differences in day length did not give a difference in meal size in these experiments. Since the results are the same as those of the previous experiment they are not given here. In the following paragraph only the result of the first group will be discussed in detail.

The level of the maximum meal weight (MAXGUT) in the laboratory beetles was equal to that found in the field beetles, but in the laboratory beetles, meal weight decreased after the reserves had attained a higher level (compare fig.3.2a and fig.3.2b).

Satiated laboratory beetles were also heavier than beetles taken from the field, because they were bigger. When during this experiment net body weight exceeded approximately 60 mg, locomotory activity dropped almost to zero. The beetles then hided in small holes in the peat mull, and hardly responded to prey. This suggests that beetles do not walk about when they have stored enough food to survive winter. The results of the second group of beetles with day length of 8 hours confirm this pattern. These beetles were very active at the start of

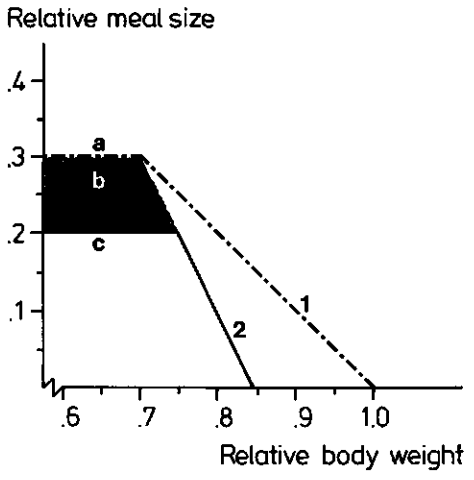


FIG. 3.4. Relationship between net body weight (NBODYW) and meal size (MEALW) both relative to the maximum fresh weight (MAXFW): (a) Relative maximum gut capacity. (b) Relative average meal size to satiate non-reproductive beetles. (c) Relative average meal size to satiate reproductive beetles. (1) Relative gut capacity depending on the room in the abdomen. (2) Relative average meal size to satiate the beetle when the gut expansion is limited by the room in the abdomen.

the experiment when placed in the petri-dishes and their locomotory activity also decreased when enough reserves were stored. Thus, day-length hardly influences the feeding behaviour of non-reproductive beetles. A comparable phenomenon is found in the carabid *Nebria brevicollis* (Penney, 1966).

Differences in body size between laboratory reared and field-collected beetles explain the differences in meal size between the experiments. To eliminate this effect on meal size, both initial net body weights and the weights of the meals of the beetles in both experiments were expressed as fractions of the maximum weight of satiated beetles (MAXFW= maximum SATW), i.e. MEALW/MAXFW and initial NBODYW/MAXFW respectively. This relationship is shown in fig.3.4 . The figure shows that if the relative net body weight is below 70% of its maximum: (a) maximum meal weight (MAXGUT) is approximately 30% of maximum body weight, and (b) the average meal weight is 26% of maximum body weight. When net body weight exceeds this level, meal size decreases, finally becoming zero when net body weight exceeds 85% of the beetle's maximum fresh weight (MAXFW). Since non-reproductive beetles gain in net body weight by the storage of reserves, the quantity of reserves present partly determines the driving force for feeding. Thus in non-reproductive beetles hunger is determined by the emptiness of the gut and by the quantity of reserves.

3.1.4.2. The gut capacity of reproductive beetles

To estimate the gut capacity of reproductive beetles 20 females reared at 20 °C in the laboratory, and which had hibernated at a constant temperature of 8.5 °C and a day length of 8 hours, were given abundant food until the experiment

started. They were then transferred to a constant temperature of 22 °C and 16 h day length. During their reproductive period of approximately 35 days the animals were given abundant food every two days for one hour. Further they were treated according to the general method. Every two days the satiated beetles were removed to new dishes and eggs were collected from the peat mull with the sieve-wash method (Mols, et al.,1980). The same procedure was used for beetles caught in the field, which had hibernated at 8.5 °C. With these beetles experiments were carried out in the laboratory at constant temperatures of 15 and 27 °C. To ensure that the females were fertile,they were given the company of males once a week.

Results

Reproductive beetles reared in the laboratory.

The laboratory-reared beetles used in this experiment were in general bigger (LEWI = 23.4 $\pm$ 1.8 mm^2) than the non reproductive beetles in the previous experiments, which were caught in the field. The reproductive beetles had an initial net body weight of 58 $\pm$ 5.4 mg.(n = 20). The first meals consumed after the change to long day and 22 °C. weighed approximately 19 mg. With the increase of body weight by assimilation of food meal size decreased in the same way as in the experiments with non-reproductive beetles. The difference with these experiments was that net body weight, which includes the weight of the eggs, now decreased both by respiration and by egg production. Egg production caused a rapid decrease in body weight during the two days of starvation. Sometimes eggs were produced during the feeding period, their weight was then subtracted from the initial body weight. In the oviposition period the relationship between initial net body weight and meal size followed the slope of figure 3.5.

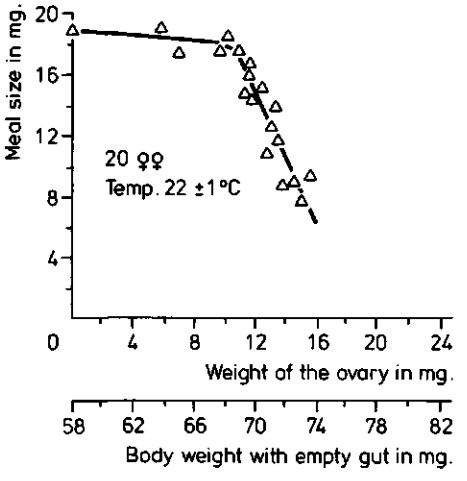


FIG. 3.5. Relationship between initial body weight of reproductive beetles (including eggs) and meal size. LEWI is 23.4 mm^2.

At the same time the weight of satiated beetles remained at the same level, which indicates that they make up for the weight of the eggs produced in the two previous days, by feeding. After eliminating the size effect by expressing the weights as fractions of the maximum weight the same relationship was obtained as in the non reproductive beetles (fig.3.4). The only difference is the relatively small meal size at the start of the experiment needed to satiate reproductive beetles i.e. 20% of MAXFW.

3.1.5. Discussion

As already mentioned in section 3.1.1, these experiments show that in carabids gut capacity depends on how much room is left in the abdomen by the fat mass and by the reproductive organs. The relationship between initial body weight and meal size both in reproductive and in non-reproductive animals clearly shows that availability of room in the abdomen largely determines the amount of food that can be ingested in one meal (fig. 3.4). In non-reproductive female beetles the quantity of stored products mainly determines the expansion of the crop. Thus, at the start of adult life in autumn when the fat mass of the beetle is low, the maximum size of the crop is the main factor which determines the amount of food which can be ingested. By food consumption the reserves increase, and gradually occupy so much roome that they restrict the expansion of the crop, thus limiting meal size. In reproductive females, meal size is mainly determined by the size of the ovaries and by the quantity of maturing eggs in the oviduct. Nevertheless the room in the abdomen is mostly not completely occupied when the beetle refuses more food: the beetle could eat more per meal but does not. This implies, that the meal size only occasionally equals gut capacity, but mostly is smaller. This may be so because of the mechanism that causes the beetle to stop feeding. In most insect species (Barton-Brown, 1975) mechano receptors in the crop can be expected to regulate meal size and duration of ingestion. These receptors will be particularly active when the crop is not inhibited by lack of room and can expand to its full size. When the crop is almost full they will give signals and ingestion stops. When there is a lack of room in the abdomen it is not the stretch receptors in the crop that give off signals to stop feeding, but receptors in the wall of the abdomen (Osborne and Fynlayson, 1962), which warn that a certain expansion of abdomen has been reached. The signal is probably stronger when the initial body weight is higher, thus stopping ingestion earlier than could be expected merely from the availability of room in the abdomen.

Other important information can be derived from the experiments: MAXGUT appeared to be 30% of MAXFW, and is approximately 60% of the difference between MAXFW and MINFW when the crop can expand fully. As MAXGUT will be related to beetle size it is assumed that these percentages will hold for the whole range of beetle sizes (between 16 and 26 mm^2 LEWI). The abdomen capacity for this range of LEWI therefore varies between 30 and 52 mg, and thus MAXGUT will vary between 18 and 31.2 mg . Therefore, beetle size will exert a strong influence on ingestion. The average filling level of the gut that

is required to satiate the beetles was 85% of MAXGUT for non-reproductive beetles and 70% for reproductive beetles. This holds without restrictions by other organs or eggs. During the non-reproductive period almost all assimilated food is used to build up reserves, and therefore the increase in body weight gives an estimate of the amount of reserves stored (section 3.5). This storage is at maximum 30% of MAXFW. In reproductive female beetles almost all the assimilated food is used for egg production (Ganagaraja, 1964). Thus, increase in weight mainly results from growing ovaries and maturing eggs, which means that these greatly determine meal size when the threshold for room in the abdomen is exceeded. For the reproductive beetles all the relations are based on interpretations of changes of weight during the feeding experiments, assuming that in the reproductive period the reserves hardly change in weight. Increasing reserves would have resulted in ovary weight being overestimated in the experiments, whereas decreasing reserves would have given underestimates. The size of the ovaries in the reproductive period of beetles was directly estimated by dissection of beetles (Van Dijk, in prep.).

To show the relationship between meal size and net body weight both are expressed as fractions of maximum fresh weight (MAXFW) to eliminate differences in size (fig 3.4). When the expansion of the gut is not inhibited by the quantity of the organs, meal size varies between .2 and .3 times the maximum fresh weight. When the net body weight exceeds 75% of the maximum fresh weight, the relative mealsize declines steeply and reaches zero when the net body weight exceeds 85% of the maximum fresh weight. Thus 10% increase in net body weight decreases the hunger levels from one to zero.

The relative satiation level (RSATL) is here defined as GUTCON/MEALW. A definition of HUNGER using the part of the gut that actually can be filled by food is then:

HUNGER = 1-GUTCON/MEALW

Since GUTCON may equal MEALW, the satiation level and thus HUNGER varies between 1 (very hungry) to 0 (satiated). Behavioural components can be related to them.

RELGUT (= GUTCON/GUTCAP) may also be used to relate to behavioural components. Unlike HUNGER and RSATL, RELGUT does not vary between 1 and 0, since GUTCAP varies between MAXGUT and 0.5*MAXGUT and GUTCON maximally equals MEALW. Thus RELGUT varies between 0 (very hungry) and 0.88 (satiated) in non-reproductive beetles and between 0 and 0.82 in reproductive beetles. It must be stated also that MEALW is defined as the average weight of a meal to satiate the beetle. Thus in reality MEALW varies around this mean value, and it may sometimes equal GUTCAP (see the definition of GUTCAP). In that case the relative satiation level equals the relative gut content.

3.2. GUT EMPTYING

3.2.1 Introduction

Gut content decreases by the assimilation of food and by defaecation. For some arthropods this process can be described as an exponential decay. This is found in the cockroaches *Periplaneta americana* (Davey and Treherne,1963) and *Leucophaea maderae* (Engelman,1968),the blowfly *Phormia regina* (Gelperin, 1966),the wolf spider *Lycosa pseudoannulata* (Nakamura,1972), the predatory mite *Amblyseius potentillae* (Rabbinge, 1976) and the praying mantis *Hierodula crassa* (Holling, 1966). The general equation for this process is:

$$A = A_0 e^{r*t}$$

where A_0 and A_t are the gut contents respectively before and after the time period t respectively. The relative rate of gut emptying r is independent of the gut content but is very dependent on temperature. The relative rate of gut emptying in *P.coerulescens* can be derived by measuring the decline in weight after satiation, which is the combined result of faeces excretion (FP), respiration (RESPIR), egg deposition (EGG) and sometimes dehydration (fig. 3.6). As all experiments were carried out at a hight relative humidity (RH = ±95%) with water freely available, dehydration could be neglected. When the gut is empty the decline in weight equals the weight loss caused by respiration and egg deposition, because from that moment onwards the beetle stops producing faecal pellets. In fig. 3.6 the process of ingestion and egestion is shown. Data for respiration were obtained from other experiments (see section 3.7).In symbolic form:

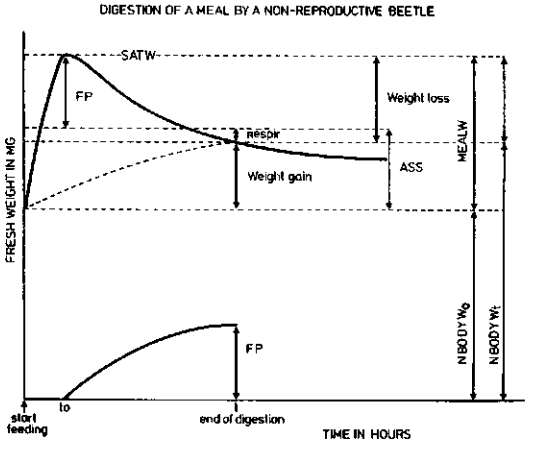


FIG. 3.6. A schematic representation of the changes in weight of the beetle and of faeces produced during and after ingestion of a prey caused by digestion and egestion.

$$WEIGHTLOSS = SATW\text{-}NBODYW_t$$
$$WEIGHTGAIN = NBODYW_t\text{-}NBODYW_o$$

$NBODYW_o$ = Initial net body weight before ingestion (empty gut).
$NBODYW_t$ = Net body weight when the gut is empty again after digestion.
SATW = Satiated weight.

The total quantity of faeces produced during the whole digestion period equals: FP = WEIGHTLOSS-RESPIR-EGG

The total quantity of food assimilated from the gut into the haemolymph is: ASS = WEIGHTGAIN + RESPIR + EGG

The total quantity of food ingested is:

$$MEALW = (WEIGHTGAIN + FP + EGG + RESPIR) = FP + ASS \quad (a).$$

Under the assumption that at constant temperature the gut content of the beetle decreases exponentially by digestion, the general formula becomes:

$$GUTCON = MEALW * e^{-RRGE*dt} = (FP + ASS)e^{-RRGE*dt}$$

or in differential form:

$$d(GUTCON)/dt = -RRGE*(FP + ASS) \quad (b)$$

RRGE = The relative rate of gut emptying.

thus from (b) it follows that:

$$d(FP)/dt = RRGE*FP, \text{ and } d(ASS)/dt = RRGE*ASS$$

These equations assume that the same relative rate of gut emptying (RRGE) can be used as an estimate for the relative rate of faecal excretion as well as for the relative rate of food assimilation into the haemolymph. The RRGE can be estimated from the weightloss caused by faeces production. Therefore the total weight loss measured in the digestion period has to be corrected for respiration and egg production. To take into account the differences in satiation level between different beetles the relative satiation level (RSATL) is used:

$$RSATL = GUTCON/MEALW = 1 * e^{-RRGE*dt}$$

since GUTCON equals MEALW just after satiation the start value of RSATL is 1.

The asssimilation efficiency (EFF) is defined as:

$$EFF = ASS/MEALW \quad (c)$$

Thus from (a) and (c) follows:

$$(1\text{-}EFF) = FP/MEALW$$

3.2.2 Methods for estimating the relative rate of gut emptying

Gut emptying rates were estimated for:

a) beetles that were non-reproductive in autumn, and for
b) beetles in their reproductive stage, especially at the beginning of reproduction in spring.

All beetles were taken from the field in autumn as young recently hatched individuals (which could be recognized by their soft elytra). Some of the animals were immediatly subjected to the gut emptying experiments, the others hibernated in the laboratory at 5 °C and a light period of 8 h. The latter beetles were fed abundantly to build up a reserve supply and were used in the experiments the following spring. During hibernation no food was given. Before starting the experiment the non-reproductive beetles were starved for three days at 20 °C, which was unnecessary for the hibernated beetles because these had already an empty gut. Before feeding the beetles were weighed. They were then fed with an excess of blowfly larvae for two hours; all beetles were highly motivated to eat. After feeding they were reweighed and transferred to clean petri dishes (9 cm diam.) lined with moist white filter paper (to show up feacal pellets and to keep humidity high) and containing a small cup of water to prevent weight loss due to dehydration. Feeding and weighing occurred at 20 °C. After the second weighing the beetles were distributed over temperature incubators, with constant temperatures of 12,17,22,27 °C. respectively and a light period of 8 h. for non-reproductive beetles, and 12,15,19,22 °C. with a light period of 16 h for reproductive beetles.

The non-reproductive beetles were weighed in the morning as well as in the evening with an extra weighing a few hours after the start of the experiment because the decline in weight is fastest then. The reproductive beetles were weighed three times a day because gut emptying appeared to occur more rapidly than in non-reproductive beetles. After each weighing the beetles were transferred to clean petri dishes and the faecal pellets were counted. As the weight of a pellet varies only between 0.8-1.2 mg counting the faecal pellets already gives information on the rate of gut emptying. The following characteristics were estimated:

a) The quantity of food ingested (MEALW).
b) The assimilated fraction of the ingested food (ASS).
c) The mean relative satiation level (RSATL).
d) The weight of faeces (FP) and the cumulative number of faecal pellets produced.
e) The relative rate of gut emptying for each interval period between two weighings (RRGE).
f) The relative rate of gut emptying for the whole period of digestion.
g) The relative rate of gut emptying for the day and night periods separately.

3.2.3. Results and discussion

The decrease in mean relative satiation level (RSATL) estimated from the decrease in weight after satiation for non-reproductive beetles and for reproductive beetles is given in figs. 3.7 and fig. 3.8 respectively. In fig. 3.7 it is clearly shown that the decrease in gut content is complementary with the accumulated production of faecal pellets. In all cases the decline of the relative satiation level was linear when its logarithmic values were plotted against time. The slope of this line is the mean relative gut emptying rate (RRGE) of the whole group,

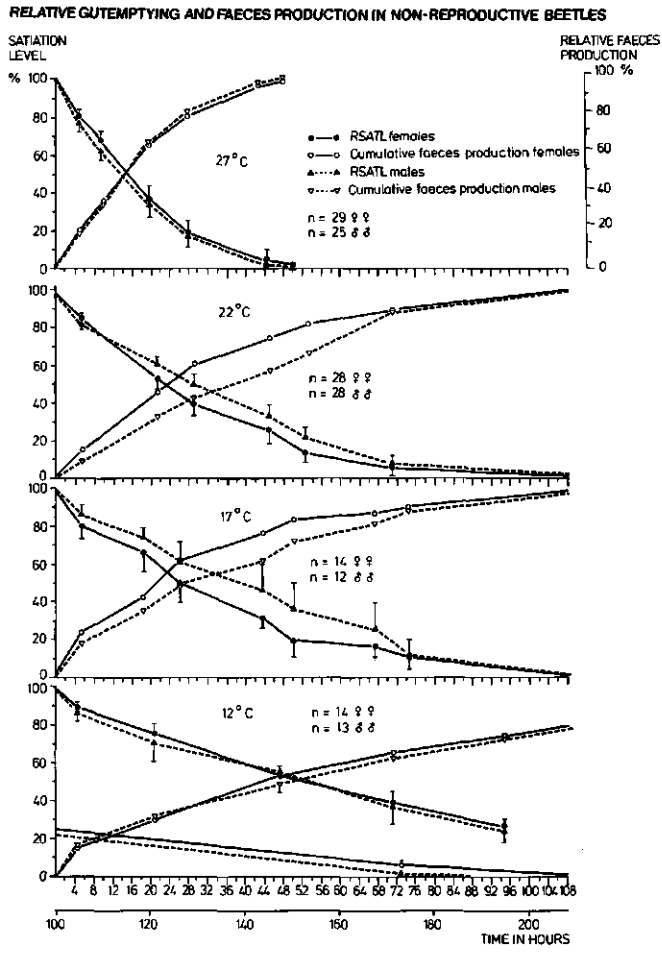


FIG. 3.7. The change of the relative gut content and the relative production curve of faeces after satiation for 12, 17, 22 and 27°C in non reproductive beetles. For 12°C the curve of the relative gut content continues after 96 hrs at the left side of the figure.

which is estimated by linear regression. The same regression method can be used for estimating RRGE of individual beetles. This gives information on the variation between the beetles of the same group. In the lower ranges of RSATL the experimentally obtained values deviate from the theoretical exponential decay. This may be because: (1) The decline of RSATL is a continuous process but faecal pellets are produced at regular intervals in units varying between .8 and 1.2 mg in weight, thus causing a discontinuous weight loss. This discrepancy increases as the gut empties. The calculation of RRGE will thus become less reliable with declining gut content.

(2) A second category of errors arises because gut emptying is a finite process,

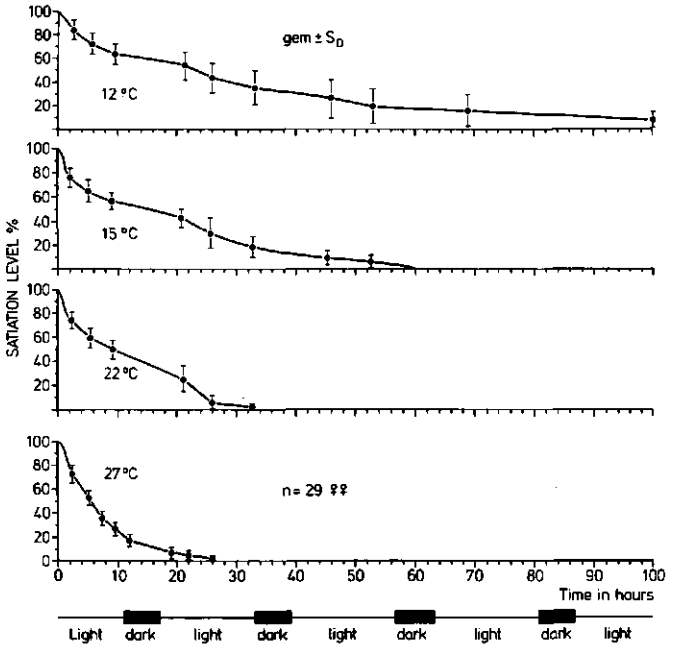


FIG. 3.8. The change of the relative gut content after satiation in reproductive beetles.

and therefore the experimentally determined values will deviate from the theoretically infinite decay, especially in the lower ranges of RSATL. Therefore,

TABLE 3.3. The relative rate of gut emptying (mean ± SD, dimension day^{-1}) of non-reproductive males and females at constant temperatures.
A) RRGE calculated using the average relative gut content of the group.
B) RRGE calculated using the average relative faeces production of the group.
C) RRGE calculated per time period per individual and then averaged.
D) RRGE calculated from the average RRGE per individual.
f = female, m = male

Temperature C	sex	n	A	B	C Day	C Night	D
12	f	14	.38	.34	.63 ± .35	.25 ± .19	.33 ± .07
	m	13	.34	.34	.87 ± .41	.32 ± .40	.43 ± .33
17	f	13	.70	.74	1.06 ± .57	.53 ± .21	.73 ± .27
	m	13	.61	.62	.99 ± .60	.40 ± .26	.60 ± .24
22	f	28	.85	.72	.97 ± .40	.74 ± .38	.87 ± .35
	m	26	.74	.67	.99 ± .45	.60 ± .34	.69 ± .25
27	f	29	1.64	1.69	1.63 ± .71	1.59 ± .94	1.62 ± .69
	m	24	1.50	1.58	1.79 ± .80	1.36 ± .55	1.61 ± .52

TABLE 3.4. The relative rate of gut emptying (dimension day^{-1}) of reproductive beetles at constant temperatures (LD = 17:7)

Temperature °C	n	Average daily maximum RRGE	Average daily minimum RRGE	Average RRGE
5	5	.2	.02	.1 ± .1
12	14	1.25	.15	.7 ± .3
15	58	2.1	.3	1.2 ± .3
19	30	3.2	.6	1.8 ± .5
22	32	3.4	.8	2.2 ± .6
27	29	3.65	2.7	3.3 ± 1.2

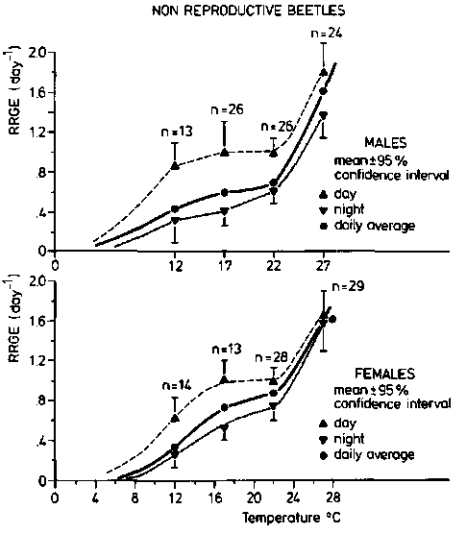


FIG. 3.9. The relative gut emptying rate for both non- reproductive males and females. The average RRGE for the whole day, the night time and the day time is given.

values of RSATL < .2 were left out of the calculation of RRGE. When RRGE is thus calculated for each period between two weighings it appears that the values for the day periods are always higher then those for the night periods (tables 3.3 and 3.4). This might indicate a circadian rhythm in the process of weight loss at constant temperatures, due to a rhythm of alternating high (during day time) and low (during night) relative rates of digestion and egestion.

The average values of RRGE for non-reproductive beetles for all temperatures are presented in fig.(3.9) together with the values for RRGE for day and night. At a temperature of 27 °C no significant difference can be observed between day and night RRGE; at 22 °C a tendency for such a difference can be observed ($0.05 < p < 0.20$), while between 12-17 °C a significant difference occurs. (These temperatures are the same as those to which the beetles are usually subjected to in the field). Because the reproductive beetles were weighed more often during 24 hours, the change of RRGE throughout 24 hours could be plot-

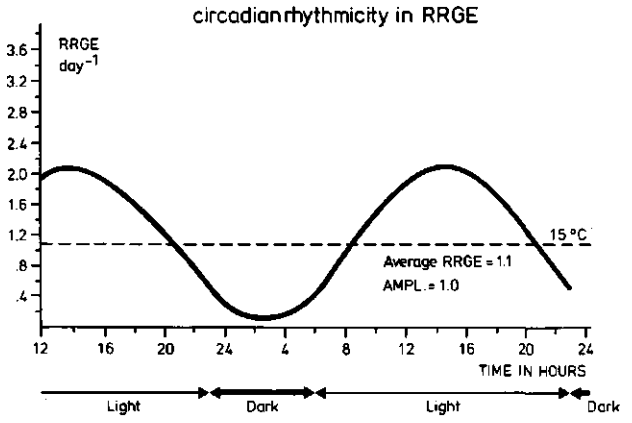


FIG. 3.10. The relative gut emptying rate (RRGE) shows a circadian rhithmicity which can be mimicked by a sinusoid function with an average of:
$(RRGE_{max} + RRGE_{min})/2$ and an amplitudo of $(RRGE_{max} - RRGE_{min})/2$
The time of the minumum is set at 2.00 o'clock, the maximum at 14.00 o'clock.

ted fig.(3.10). This figure shows a rhythmic increase and decrease of RRGE throughout the 24 hours. RRGE reaches a maximum at noon and a minimum at midnight. This process may be described by a sinusoid using the mean (AVDIGS) and the amplitude (AMDIGS) of RRGE.
RRGE = AVDIGS + AMDIGS*SIN(2PI*HOUR/24-PI/2) The mean RRGE

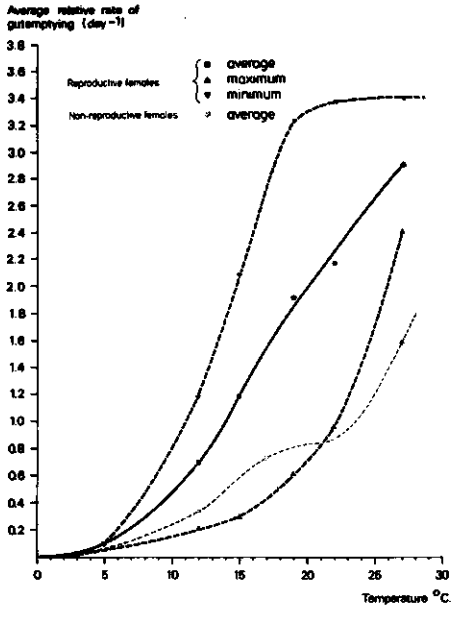


FIG. 3.11. The average relative gut emptying rates (RRGE) both for reproducing and non-reproducing female beetles.

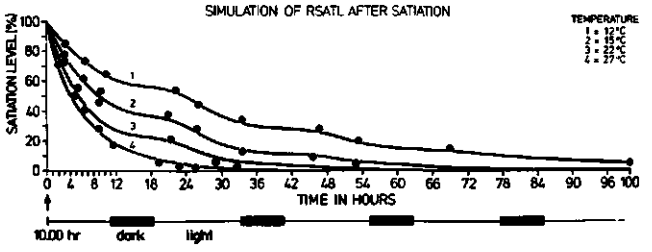


FIG. 3.12. The change of the relative satiation level (RSATL) using the sinusoid function for the circadian rhythmicity of the relative gut emptying rate (RRGE) for 12, 15, 22 and 27 °C in reproducing females. (The black dots are the observed values.)

both of reproductive and non-reproductive beetles for the different temperatures are given in fig (3.11). This figure shows that in reproductive beetles the RRGE is two to three times higher than that of non-reproductive beetles. In fig 3.12 the effect of circadian rhythmicity on the relative satiation level of the gut is shown for different temperatures.

3.3 INGESTION

Ingestion rate

The time needed to ingest a prey depends on size of the prey and on ingestion rate, which will again depend on emptiness of the gut. Together with the time taken to pursue a prey, these determine handling time. *P.coerulescens* prefers slow-moving or almost stationary prey, so that the time of pursuit is usually short. The ingestion rate is greatly affected by the kind of prey. Soft prey like maggots and small caterpillars will be ingested faster than prey with a hard integument. When they are still hungry beetles will nibble inedible parts of a prey for hours. As soft prey most important such were almost always offered in the experiments. To estimate the degree to which the ingestion rate is influenced by the relative gut content, small maggots of known weight were offered to reproductive beetles that had been starved for two days. Maggots weighing between 1.5 and 3 mg, were offered in sequence. After acceptance of a maggot the total consumption time was measured with a chronometer. These observations were carried out in the laboratory at 20 °C. As the gut content could be estimated by the quantity of prey already ingested, the relationship between relative gut content and ingestion rate could be established. The same type of observations were carried out with heather beetle larvae (*Lochmea suturalis*) and with a few aphids (*Myzus persicae*) as prey.

Ingestion threshold

When beetles are satiated it takes time needed for digestion before they are motivated again to attack another prey. To measure the relative satiation level at which beetles start eating again 13 female and 7 male non-reproductive beetles

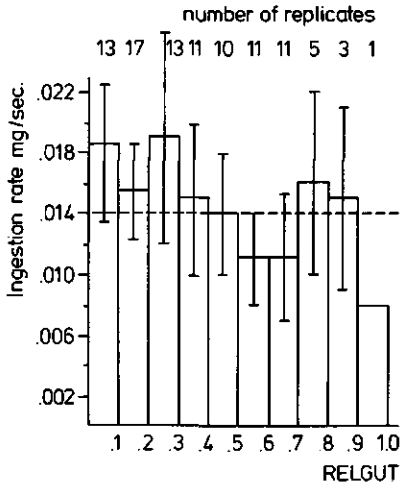


FIG. 3.13. Relationship between relative gut content and ingestion rate in *P.coerulescens*, with maggots as food.

TABLE 3.5. The average ingestion rate of *Pterostichus coerulescens* with 3 kinds of prey.

Prey type	number of replicates	ingestion rate ± SD in mg/sec.
Maggots *Calliphora sp.*	95	0.014 ± 0.008
Larvae *Lochmaea suturalis (Thomson)*	35	0.0125 ± 0.007
Aphids *(Myzus persicae)*	12	0.009 ± 0.006

were observed in petri dishes after having satiated them with maggots. The temperature was 17°C.

Results

Ingestion rate

The relationship between relative gut content and ingestion rate with maggots as food is given in fig. 3.13. It shows that there is a significant tendency of the beetles to eat more slowly when they are almost satiated (Spearman's rank correlation $p = .03$ on esided). However, when the relative gut content is high (>0.8), only a few replicates could be produced, because RSATL is 1.(see section 3.1), and thus acceptation of more prey is very low. The average rates of ingestion with maggots, heather beetle and aphids as prey are given in table 3.5.

Ingestion threshold

In females, after satiation the first beetle started eating again after 6 hours. After 18 hours 50% had resumed eating and the last started after 30 hours. From fig 3.7 it was estimated that the average threshold for ingestion was reached after 18 h when RSATL was 70%.

In males the first beetle started eating after 14 hours, 50% after 19 hours and the last after 28 hours. Thus average threshold for ingestion was estimated from fig 3.7 to be reached after 19 h at a value of RSATL of 75%.

It is assumed that the results of this experiment at 17°C also hold for other temperatures, but that may be beside the truth.

3.4 Prey utilization

Prey utilization depends on the hunger level of the beetle, on its feeding habits and on prey features. The hunger level determines the quantity of prey that can potentially be ingested, whereas the actually ingested amount of prey depends on the ingestible fraction and on the size of the prey. Moreover, during feeding part of the prey will be wasted because it drains to the soil. To establish the fraction of prey ingested, maggots of different weights in the range of 3-40 mg were offered to beetles of known weight, that had been starved for two days.

Results

In fig.3.14 the relationship between weight of the prey and weight of the ingested quantity is given. This experiment shows that the fraction of prey ingested decreases curviform with increase of prey size, even when the beetle is not yet satiated. The simplest explanation for this is that because it takes longer to ingest big prey, than small prey, there is more time for parts of big prey to be lost

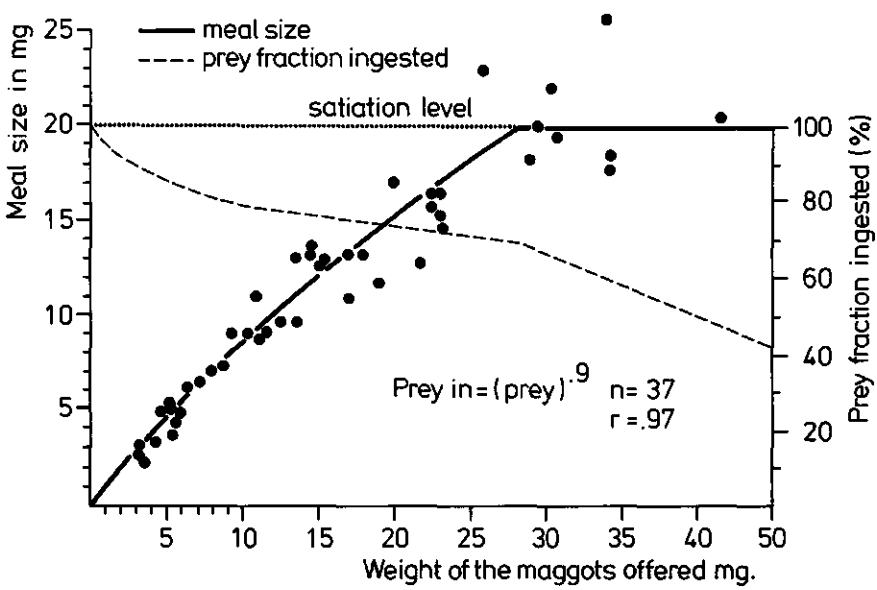


FIG. 3.14. Relationship between weight of maggots offerd and the final quantity of food (PREYIN) ingested. The solid line and black dots represent the weight of the prey ingested. The broken line represents the fraction of the prey ingested.

into the soil. In this experiment the meal size required to satiate these beetles was 20.6 ± 2.8 mg. (n=9). This value did not differ substantially from that obtained when establishing the gut capacity (section 3.1). The relationship between weight of ingested prey (PREYIN) and the weight of the prey offered can be fitted satisfactorily by a power curve of the form:

$$PREYIN = PREY^{0.9} \qquad (n = 37, r = .97)$$

According to this formula prey utilization decreases from 93.3% for a prey of 2 mg to 72.5% for a prey of 25 mg. This relationship only holds when PREYIN is smaller than the quantity of food necessary to satiate the beetle.

3.5 Assimilation

The assimilation efficiency or the approximate digestibility (AD) of the ingested food depends on the quality of the prey, e.g. nutrient composition, fraction of indigestible integument etc. It is normally calculated as: (dry weight of ingested food (DI) minus dry weight of faeces (DF)) devided by DI (Waldbauer, 1968). To estimate the assimilation efficiency of the beetle, dry:fresh ratio's of both beetle and prey had to be established. This ratio may be related to weight, therefore the ratio was estimated both for maggots (n=38 ranging in weight from 2-46 mg) and for beetles (n=101 see section 3.7) of different weight. Their fresh weight was established before they were dried in an oven at 75°C for 48 h. and reweighed.

Assimilation efficiency was estimated from the ingestion and weight gain as these were derived from the gut emptying experiments (section 3.2). It was not possible to establish the dry weight of the faeces, because beetles smear it often throughout the petri-dish. Therefore weight gain was used directly and then it equals (DI) minus (DF). The dry weight of the ingested meal was obtained by multiplying meal weight by the dry:fresh weight ratio of the maggots offered. In general only big maggots were given but in some experiments with reproductive beetles only small maggots were available. In the latter cases meals were multiplied by the ratio appropriate for small maggots.

The asssimilated quantity of fresh food is:
ASS = WEIGHTGAIN + RESPIR + EGG (see section 3.2.1).

The dry weight of ASS is calculated by multiplying WEIGHTGAIN by the appropriate dry:fresh weight ratio belonging to NBODYW of the beetle and by adding this to the dry weight loss from respiration (see section 3.7) and the dry weight of the eggs deposited. The latter of course only in the case of reproductive females. The assimilation efficiency is thus the dry weight of ASS devided by the dry weight of the ingested meal.

Results

Maggots with a fresh weight below 17 mg. show a dry:fresh weight ratio of

TABLE 3.6. Assimilation efficiency of *P.coerulescens* with maggots (*Calliphora* sp.) as food at different temperatures.

Non-reproductive beetles				Reproductive beetles			
Temper-	n	sex ature	ass.eff ± SD	Temper-	n	sex	ass.eff ± SD
12	14	female	0.48 ± 0.06	12	14	female	0.54 ± 0.07
12	13	male	0.55 ± 0.07				
17	14	female	0.42 ± 0.10	15	34	female	0.47 ± 0.11
17	13	male	0.47 ± 0.11	19	29	female	0.50 ± 0.12
22	28	female	0.54 ± 0.09	22	31	female	0.49 ± 0.09
22	26	male	0.55 ± 0.07	27	29	female	0.50 ± 0.09
27	29	female	0.53 ± 0.09				
27	24	male	0.55 ± 0.10				
	average	female	0.49 ± 0.08			average	0.50 ± 0.09
		male	0.53 ± 0.09				

0.23 ± 0.03 (n = 23), while heavier maggots have a higher ratio, viz. 0.32 ± 0.04 (n = 15). The dry:fresh weight ratio of beetles changes with weight and differs from that of maggots (section 3.7).

The estimates of the assimilation efficiency are given in table 3.6. No significant difference in assimilation efficiency could be observed either between the reproductive and non-reproductive beetles, or between the sexes in the non-reproductive beetles. The average efficiency both for reproductive and for the non-reproductive beetles was approximately 50%.

3.6 RESERVES

Changes in net body weight in non-reproductive beetles are only caused by respiration and by storage of reserves (FAT) i.e. they are not affected by the growth of ovaries and eggs. This allows the rate of reserve storage to be estimated, under the assumption that to maintain homeostasis the rate of assimilation of food into the haemolymph has to be balanced by the rate of discharge. This is achieved when the relative rate of food storage (RRFAT) on average equals the relative rate of gut emptying; otherwise accumulation or diminishing of food substances in the haemolymph would occur. In cases of food shortage a delivery of energy from the storage to the haemolymph, which meets the metabolic needs, can be expected to occur. This rate of delivery of energy was estimated from the respiration rates established in experiments for a whole range of temperatures, both for reproductive and for non-reproductive beetles. The maximum quantities of reserves that can be stored were obtained from the feeding experiments for the estimation of the gut capacity (section 3.1). From these experiments it appeared that ingestion stops when approx. 30% of the maximum body weight consists of reserves. The ultimate quantity of reserves will depend on

the size of the beetle, of course. For an average-sized beetle this will amount to 20-30 mg.

3.7 Respiration

3.7.1. Introduction

Respiration rate per unit body weight can be estimated from oxygen uptake or from carbondioxide production. The level of metabolic processes depends on both individual and external factors. Individual factors may be: body size, body weight, age, developmental stage, reproductive state, nutritional state (starving or well fed), and state of activity.

The external factors that affect metabolism are diurnal and seasonal changes in temperature, relative humidity and any other significant environmental factor (Duncan and Klekowsky, 1975). It is tedious and time consuming to quantify respiration rate by estimating oxygen uptake or carbon dioxide production. This method offers no direct estimation of weight loss, because different sources of energy deliverance may be involved, i.e. carbohydrates, proteins or fat. Therefore the gravimetric method was used, which is much simpler and much more correct, although less accurate especially for short time periods. For simple ecological experiments it is the only practical method.

In carabid beetles respiration during starvation causes weight to decline steadily (v.Dinther,1964; Kabacic & Stejgwillo, 1974). Weighing, enables the weight loss resulting from both respiration and transpiration to be ascertained. To eliminate desiccation effects, the experiments were carried out at high humidities and with water freely available. If the water content of the body differs between well-fed and starved beetles, weighings cannot be used directly to estimate repiration but will have to be based on dry weights. A practical disadvantage of the gravimetric method is that it has to be carried out over rather long periods (more then three days), because the weight losses by respiration are relatively small.

Weighing errors caused by condensation or dirt on the beetle will affect the estimations.

3.7.2. Experiments

Respiration rate was measured in four groups of beetles:

1. Post-diapause beetles.
2. Post-reproductive beetles.
3. Diapause beetles.
4. Young, newly hatched beetles.

The experiments were mainly done with females, because in experiments done by Könen (1978) on *Pterostichus nigrita* and *P.oblongopunctatus*, and by Kabacic & Stejgwillo (1974) on *Harpalus pubescens* no significant difference in respiration was observed between the sexes. To check these observations in young bee-

tles of *P. coerulescens*, respiration was established both for males and females.

Post-diapause beetles were caught with pitfall traps from 6-18 April 1978. They were stored at 5 °C in an incubator untill at least 60 beetles had been collected. To ensure that their guts were empty, they were starved for two days at 20 °C before the experiment started. Some beetles were dissected to ascertain the state of the ovaries: No beetles showed developing ovaries. The beetles were divided over four groups and placed individually in plastic petri dishes (9 cm diam.) with moist peat mull and a container of water to keep humidity high. Each group was kept in an incubator at a constant temperature of 12, 17, 22, or 27 °C and a light period as outside (15-16 hours). Every third day the beetles were weighed untill they died, after which they were preserved in ethanol (70%). When all beetles had died from starvation their dry weights were established after drying for 48 h in an oven at 75 °C. The length and width of the elytra were measured,so that size could be related to respiration.

Post-reproductive females that had not laid any eggs for more than one week were placed in incubators at constant temperatures of 5, 8.5, 12. 17, 22 or 27 °C, and with a light period of 15-16 h. They were deprived of food and were weighed once every week for two months. The conditions were the same as in the previous experiment.

Spent but well-fed one-year-old female beetles, considered to be in diapause, were deprived of food in autumn under the same conditions as in the previous experiments and kept in incubators at temperatures of 5, 8.5, 15, or 22 °C. Day-length was 10 h, since the beetles need short-day conditions to stay in reproductive diapause (Krehan, 1970).

Newly hatched, male and female callow beetles were captured in the field in autumn (September 1977). Weight loss experiments were started 5 days after the last consumption of a meal. Conditions were the same as in the other experiments. The beetles were weighed daily over five days. They were kept at temperatures of 17, 22 and 27 °C and at a day length of 10-12 hrs.

To estimate water content, the fresh and dry weights of 101 beetles in reproductive state were compared.

3.7.3. Results

Post-diapause beetles.

In table 3.7 the results of post diapause beetles are shown. At the three lower temperatures the los of fresh weight was about similar but it was 2 mg higher at 27 °C. Fresh weight at the end of the experiment decreased slightly with increasing temperature, as did the dry weight at the end of the experiment. The loss of dry weight increased with temperature. This wasi not caused by higher initial dry weights or by the larger size of the beetles, but probably by a greater depletion of reserves at higher temperatures. Survival periods became shorter as temperature increased.

Because loss of fresh weight was established for each beetle individually, it could be shown that during the whole starvation period the weight decreased

TABLE 3.7. The results of the starvation experiment with post-diapause females. All weights are in mg (mean ± 95% confidence interval).

Temperature °C	12	17	22	27
Number of females	15	13	15	14
Initial fresh weight	52.2 ± 4.5	49.8 ± 4.1	49.1 ± 4.1	50.3 ± 4.3
Initial dry weight	18.8	17.3	16.9	17.6
Final fresh weight	40.2 ± 3.8	37.0 ± 3.4	36.5 ± 3.7	35.5 ± 2.7
Final dry weight	13.1 ± 1.5	11.3 ± 1.0	10.5 ± 1.2	10.3 ± 1.1
Total loss of fresh weight	12.0 ± 1.3	12.8 ± 1.9	12.6 ± 1.7	14.8 ± 1.6
Total loss of dry weight	5.7	6.0	6.4	7.3
Loss of fresh weight in mg/day	0.24 ± 0.05	0.41 ± 0.1	0.64 ± 0.1	0.99 ± 0.14
Loss of dry weight in mg/day	0.19	0.32	0.49	
Initial dry:fresh ratio	0.36	0.36	0.34	0.35
Final dry:fresh ratio	0.33	0.32	0.29	0.29
Dry:fresh ratio of weight loss	0.47	0.47	0.51	0.49
Survival time in days	49.3 ± 9.7	32.3 ± 5.4	19.9 ± 3.6	15.0 ± 1.7
Size (LEWI) in mm^2	21.4 ± 1.3	21.6 ± 1.5	20.7 ± 1.3	20.8 ± 1.5

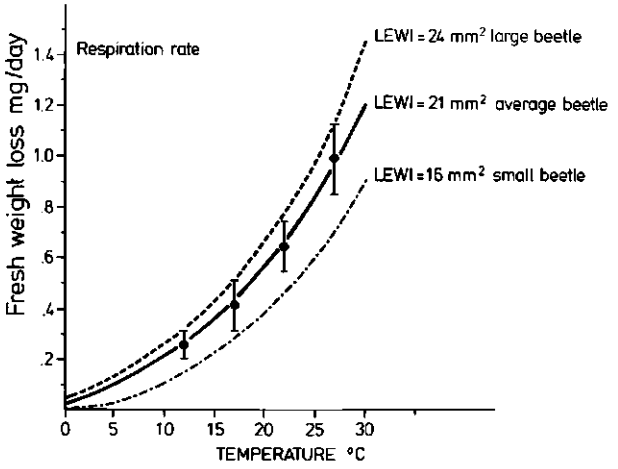


FIG. 3.15. The experimentally established relationship between temperature and the rate of fresh weight loss (RFWL) in mg/day in starved beetles (mean ± SD). The relationship is exponential according to: $RFWL = 0.0935e^{(0.0087 * TEMP)}$
RFWL

with a constant rate. The rate of fresh weight loss (RFWL) could thus be estimated by means of linear regression. For each temperature these individual rates were averaged per group. They are also given in table 3.7.

The rate of fresh weight loss (RFWL) increased exponentially with temperature (TEMP). The best fit for this relationship (fig 3.15) is given by:

$$RFWL = 0.0935e^{0.087(TEMP)}$$

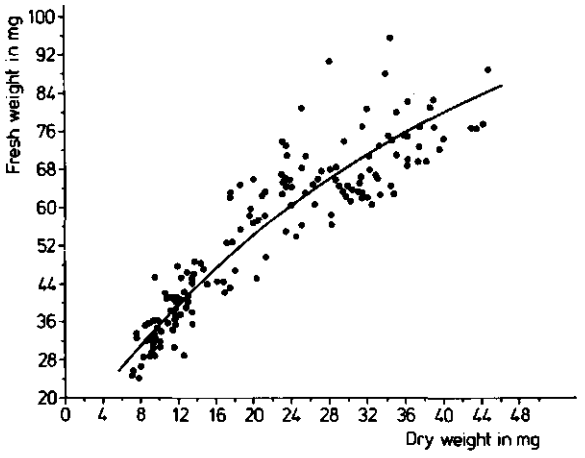


FIG. 3.16. The relationship between dry and fresh weights of beetles varying from starved and exhausted to reproducing and full of eggs.
$DW = (0.1 * FW)^{1.7763}$

To estimate loss of dry weight, the dry weights of the beetles at the beginning of the experiment must be known. Therefore the fresh weights of starved beetles (fresh weight at the start of the experiment in table 3.7) were taken together with the net body weights of 101 reproductive beetles with an empty gut, and all were related to their respective dry weights. The values of post-diapause beetles could be added to those of reproductive beetles because in the field the weights of post-diapause beetles will continuously increase by feeding until they reach the weights of reproductive beetles. This relationship is given in fig.3.16. It can be seen that when weight increases the ratio between dry and fresh weights (DW:NBODYW) does not remain constant but increases also. The relationship between dry and fresh weight follows a power curve, which is best described by the equation:

$$NBODYW = 10(DW)^{0.0563} \qquad (n = 158\ r = .8)$$

or the reverse:

$$DW = (0.1 * NBODYW)^{1.7763}$$

From this equation the dry weight of the beetles at the start of the experiment were estimated (table 3.7). The loss of dry weight during starvation was computed by subtracting the dry weight at the end of the experiment from the expected dry weight at the start of the experiment, as estimated from fig 3.16. Dividing the loss of dry weight per day by the average dry weight of the beetle (= (initial dry weight + final dry weight)/2) gives an estimate for the respiration expressed in mg dry weight per day per mg dry beetle weight (fig.3.17).

This rate of respiration (RRES) shows an exponential relation with the temperature according to the equation:

$$RRES = 0.0021e^{0.01064 * TEMP}$$

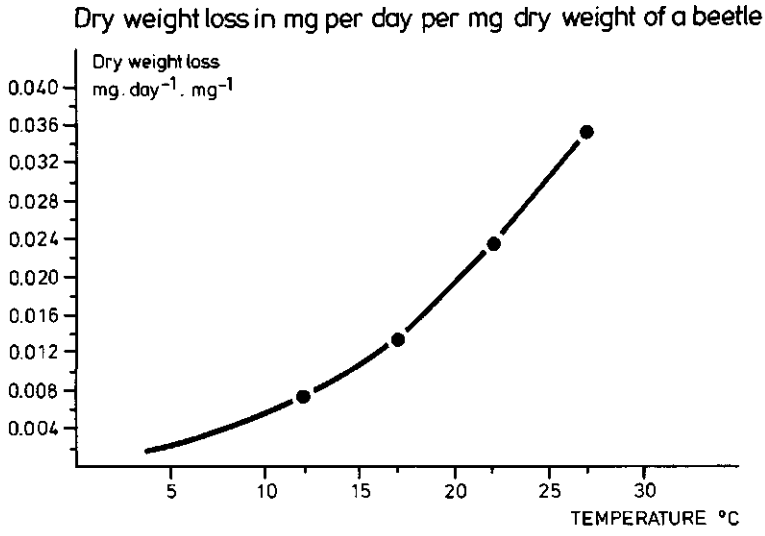


FIG. 3.17. The relationship between dry weight loss expressed in mg per day per mg dry beetle weight and the temperature.

Expressing respiration per mg dry beetle weight results in larger beetles having higher total respiration rates. After recalculation to fresh weight this is supported by fig.3.18 where the size of the beetles (LEWI) is related to the loss of fresh weight. At each temperature a significant positive relation was found

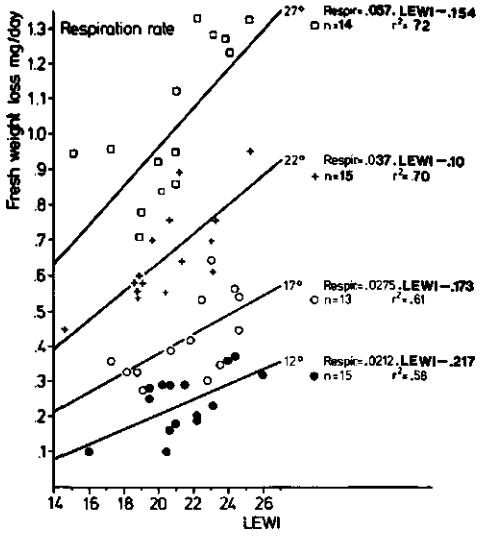


FIG. 3.18. The relationship between the size of the beetle and the fresh weight loss in starved beetles at different temperatures.

between size and weight. Since size and weight are closely related the use of respiration fresh weight loss expressed in mg per mg body weight is justifiable after recalculation from dry weight loss.

The dry:fresh ratio of the weight loss does not show any relation with temperature and is of the same magnitude in all groups. It is important to notice that the dry:fresh ratio of weightloss is higher than the body dry:fresh ratio, 0.48 instead of 0.33 (these values hold for the 38-50 mg body weight range).

Post-reproductive beetles

The weights of the post-reproductive beetles varied from 60-70 mg. Only fresh weight loss was measured (table 3.8.). The weight loss was very low at 5 °C, between 8.5 and 15 °C it stayed at the same level, but at higher temperatures it increased. The beetles retreated to small holes in the peat mull and did not show locomotory activity. At higher temperatures some activity could be observed but at a low level.

Diapause beetles

These beetles showed the same fresh weight loss during starvation as the post-reproductive beetles (table 3.9.). Therefore these data have been combined in fig.3.19, where a linear relationship between temperature and fresh weight loss per day is shown.

TABLE 3.8. Loss of fresh weight of post-reproductive beetles during starvation. The initial weight varied between 60-70 mg.

Temperature	n	Loss of fresh weight mg/day ± SE
5	36	0.018 ± 0.002
8.5	16	0.11 ± 0.01
12	10	0.11 ± 0.01
15	10	0.11 ± 0.01
17	21	0.13 ± 0.015
22	23	0.17 ± 0.04
27	19	0.20 ± 0.02

TABLE 3.9. Loss of fresh weight of diapause beetles during starvation. The initial weight varied between 60-70 mg.

Temperature	n	Loss of fresh weight mg/day ± SE
5	45	0.02 ± 0.002
8.5	11	0.11 ± 0.015
15	10	0.11 ± 0.01
22	19	0.15 ± 0.01

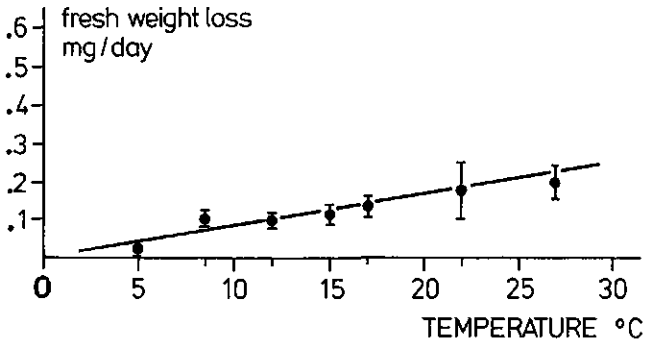


FIG. 3.19. The relationship between fresh weight loss and temperature in starved beetles in the post-reproductive and diapause stage.

Young beetles

The rates of fresh weight loss of young beetles are given in table 3.10. Males and females did not show a different rate of weight loss. For the three temperatures the rates in young beetles are at the same level as those in the post-diapause beetles (table 3.7).

3.7.4. Discussion

From the fact that the dry:fresh ratio of body weight increases with the body weight, while in the experiments it was found that during starvation the rate of fresh weight loss remained constant,it can be concluded that the dry:fresh ratio of weight loss also depends on the body weight of the beetle.

Beetles that have just emerged from diapause are low in weight. They show a higher water fraction than later when they have resumed feeding and are starting to produce eggs. It was found that the dry:fresh ratio of mature eggs is 0.58 (section 3.8). Thus, egg production results in an increase of the dry:fresh ratio of the total body, and this is mainly caused by the growth of the ovaries and

TABLE 3.10. Loss of fresh weight of newly hatched beetles in autumn. The initial weight varied between 40-50 mg.

Temperature	sex	n	Loss of fresh weight mg/day ± SE
17	f	9	0.50 ± 0.03
	m	16	0.46 ± 0.03
22	f	28	0.62 ± 0.025
	m	28	0.61 ± 0.025
27	f	29	0.95 ± 0.05
	m	25	0.90 ± 0.05

the quantity of mature eggs in the oviduct. This is a gradual process, which explains the curvilinear relationship between fresh and dry weight, and it makes clear that fresh weight loss itself is not a reliable estimate for respiration. Therefore, dry weight loss expressed in mg per mg beetle weight per time unit was used as an estimate for respiration.

To make these results comparable with the values for respiration given in the literature for beetles of about the same size, the values were recalculated to express oxygen consumption. Because the composition of the reserves was not known calculations were made with carbohydrates, fats and proteins as sources. The general formula for the metabolization of carbohydrates is:

$$O_2 + (CH_2O)_n = CO_2 + H_2O + \text{energy}$$

When carbohydrates are oxidized completely, 1 mg requires $22.4/30 = 0.7467$ ml oxygen. Oxygen consumption was expressed in ul/hour/mg fresh weight of the beetle using the fresh weight values of table 3.7 The results of these calculations are given in table 3.11 together with the oxygen consumptions when fats or proteins were metabolized, calculated according to the method of McGilvery (1970). They were also estimated for the appropriate temperatures by exponential interpolation (table 3.11) so that these rates could be compared with those found in the literature (table 3.12). The comparison shows that the oxygen consumptions found when fats or proteins are metabolized are of the same magnitude as those of *Pterostichus nigrita, P.oblongopunctatus, P.metallicus* and *Harpalus pubescens* which are all species of about the same size. The oxygen consumptions of the large carabid species are lower. This confirms our finding (above) that large beetles metabolize less energy per mg weight than small beetles. *Pterostichus* spp. are polyphagous predators ingesting much fat and protein, which they also use as the main sources for energy production.

The relationship between respiration and temperature is exponential with a

TABLE 3.11. The oxygen consumption (OC) of post-diapauze beetles, calculated from dry weight loss per hour per mg fresh beetle weight, according to the method of McGilvery (1970) in Gordon (1972). Carbohydrates, fats or proteins as source of energy. The general relationship between oxygen consumption and temperature follows an exponetial curve according to the formula: $OC = a.e^{(b.temp)}$, in which a and b are constants.

Temperature	Loss of dry weight mg/day	Oxygen consumption ul O_2/mg fresh weight/hour		
		Carbohydrates	Fats	Proteins
12	0.115	0.08	0.19	0.10
17	0.19	0.14	0.35	0.17
22	0.32	0.23	0.60	0.29
27	0.49	0.36	0.91	0.45

For Carbohydrates	a = 0.025	b = 0.1
For Fats	a = 0.057	b = 0.105
For Proteins	a = 0.03	b = 0.101

TABLE 3.12. Oxygen consumption of carabid beetles (μl O_2/mg fresh weight/hour.

Temperature C Species	5	10	15	20	23	25	30	Fresh weight mg	Author
Pterostichus nigrita (F.)	0.12	0.19	0.26	0.37	--	0.79	0.80	40-50	Könen, 1978
P.oblongopunctatus (F.)	0.05	0.12	0.13	0.24	—	0.68	0.90	55-60	Könen, 1978
P.oblongopunctatus (F.)			0.167					40-50	Weideman, 1971a.
P.metallicus (F.)			0.163					120	Weideman, 1971a.
P.coerulescens (L.)									
Carbohydrates	0.04	0.067	0.11	0.18		0.30	0.50	40-50	This study
Fats	0.10	0.16	0.27	0.46		0.78	1.31	„	This study
Proteins	0.05	0.083	0.14	0.23		0.38	0.62	„	This study
Harpalus pubescens (Müll)				0.39				150	Kabacic & Stejgwillo, 1974
Carabus cancellatus (Ill.)				0.2				560	Smidt, 1956
C. arcensis (Herbst.)				0.25				?	Smidt, 1956
C. coriacius (L.)				0.15				?	Smidt, 1956
Carabidae					0.31			?	Kittel, 1941

Q10 of 3 in the temperature range between 12-22 °C. At higher temperatures it declines to 2.3 . These kinds of value are often found for poikylothermic animals (Petrusewics and MacFadyen, 1970; Andrewartha and Birch, 1954; Wigglesworth, 1939). Although the gravimetric method is not very accurate, especially in measurements over short time periods, it is an easy way of obtaining a number of estimates on respiration that are in reasonable agreement with values given in the literature. Moreover, with this method it is easy to obtain information on individual variation, which is of increasing importance because it has been recognized that individual variation is a fundamental feature of natural populations.

To compare respiration in the different stages of the life cycle of a beetle, the fresh weight losses measured in the post-reproductive, diapause and young callow beetles respectively had to be transformed to dry weights. This was done with the dry:fresh weight relationship given in fig.3.16. Respiration in post-reproductive and diapause beetles was similar. Post-diapause and young callow beetles also showed similar values but at a higher level. The respiration of the first two resting stages was 60% lower than that of the two active stages of the life cycle. This implies that during aestivation when temperatures vary between 15-25 °C the respiration rate will be such that a well fed beetle can survive for approximately 4 months. If the reserves built up after reproduction are not sufficient, beetles may become active again in late summer or autumn in search for food. This may explain the small numbers of old P.coerulescens beetles captured in pitfall traps in late summer and autumn (see den Boer, 1979, and van Dijk,-pers.comm.).

In late summer and autumn many newly hatched beetles become active in search for food to build up reserves. In the gut capacity experiments (section 3.1) it was shown that after three or four large meals there was a sharp decline in meal weight indicating that the motivation for ingestion became low. Since only about 25 mg of dry weight has to be ingested to build up enough reserves for hibernation when temperature and respiration are low, the activity period for the callow beetles will be short. This explains why fewer beetles are captured in pitfalls in autumn than in spring when the beetle are reproductive.

3.8 Reproduction

From the observations in section 3.1. it appeared that the quantity of maturing eggs in the oviduct and the size of the active ovarioles play a dominant part in the values of net body weight and gut capacity and thus determine meal size. Moreover, during post-diapause in spring the relative rate of gut emptying is two to three times higher than in autumn. This rate stays high during oviposition and decreases again when reproduction stops. This indicates that the processes of egg development and production greatly influence hunger. Therefore the activity of the ovaries, the number of maturing eggs and the rates of egg formation and oviposition are variables that significantly affect the 'motivational' state

of the beetle. These variables were estimated as well as possible in experiments, and supplemented with data from literature.

3.8.1 Introduction

According to Krehan(1970), sexual maturation in *P.coerulescens* is regulated by photoperiod. The females need a change from short-day to long-day conditions to become reproductive. Moreover, to mature the males need a cold period with temperatures between +2 and +7 °C. during the short-day period. In females short-day conditions induce euplasmatic growth of the oocytes (pre-vitellogenesis). Long-day periods following this pre-vitellogenesis enables the oöcytes to incorporate large amounts of yolk material (vitellogenesis). After the change from short to long day conditions the small ovarioles swell by the growing eggs and nursery cells. The rate of this process depends both on temperature and on food consumption. When the eggs have reached their mature size the trophocytes are absorbed and their remains gradually change into a yellow to dark brown body (corpus luteum). The presence of corpora lutea at the start of the reproductive season indicates that the beetle is beginning its second or even its third reproduction cycle (van Dijk, 1972,1979). The fullgrown eggs pass into the oviduct where they mature further for a few days. The duration of the passage through the oviduct depends on temperature. The eggs are deposited in the substrate as soon as conditions are appropriate. Oviposition stops when there is a shortage of food (van Dijk, 1976). Starvation for approximately 5 days at 20 °C causes a premature interruption of oviposition, which can only be started again after a new period with short-days (< 12 h) followed by a long-day period. As the cause of normal termination of oviposition (with sufficient food available) is not known, the duration of oviposition has to be established by experiment.

During aestivation and hibernation the ovaries regress (Krehan, 1970; van Dijk, 1979). In dytiscid beetles (related to the carabids) oöcytes are continually being formed and resorbed during hibernation although the ovaries are regressed (Jolly, 1975). The same process occurs in the Colorado potato beetle *Leptinotarsa decemlineata* (de Wilde, 1954). This continuation of oögenesis is thought to be a characteristic feature of species in which the adult is capable of hibernating more than once (Johansson, 1964), but it has not been confirmed in carabid beetles so far. The qualitative information about reproduction given above was translated into a conceptual model of the processes involved.

1) Temperature and daylength that enable start of vitellogenesis.
2) Rate and duration of incorporation of yolk material into the oöcytes.
3) Resorption rate of eggs if there is shortage of food.
4) Ultimate size of the ovaries when these produce fullgrown eggs.
5) Weight of fullgrown eggs.
6) Residence time of eggs in the oviduct.
7) The period needed to react to changing daylength.

The next sections deal with the quantification of these parameters and variables. The values needed were obtained by experiment or from literature.

3.8.2 Quantification of the processes

3.8.2.1 Day-length thresholds for vitellogenesis

In the field sexual maturity of *P.coerulescens* is achieved shortly after the vernal equinox (Thiele, 1977). This indicates that vitellogenesis will start when daylength exceeds 12 hours, provided that temperature is favourable. So far, in *P.coerulescens* the daylength at which 50% of the beetles reach the state of vitellogenesis is not known exactly. However, extensive data exist on *P. nigrita, P.oblongopunctatus* and *P.angustatus*, which belong to the same kind of spring breeders (Thiele, 1977). In all these species, including *P.coerulescens*, dormancy is obliged at least in the females.

The males sometimes need a different photoperiod and temperature to start their gonad development. In all females and in the males of some species the photoperiod is largely responsible for the duration and termination of dormancy. Therefore in this study the critical photoperiod for *P.coerulescens* was assumed to be the same as found by Thiele (1977) and Könen (1977) for these other spring breeders i.e. 12 h light.

3.8.2.2 Temperature thresholds for vitellogenesis

To establish the temperature threshold for ovarial activity and for the total pre-oviposition period, beetles caught in the field in autumn and kept in the laboratory under short day condition (LD 8:16) and with abundant food, were placed under long-day conditions (LD 16:8) in spring, and divided into five temperature groups. Males and females were placed pairwise in petri-dishes with ground peat-mull and transferred to incubators and kept at temperatures of 12, 15, 19, 22 or 27 °C. They were offered maggots in excess and every day the peat mull was sieved to establish the deposition of the first egg of every female. In table 3.17 the average period needed to reach egg production for each group of beetles is given. From the inverse of this relationship the threshold temperature for ovarial activity could be estimated. It appeared to be 10 °C., which is one and a half degree higher than found experimentally by van Dijk (1979). In his experiments he observed a very low egg production at 8.5 °C. Probably the above relationship is not linear but S-shaped. The latter relationship fits also better to the data. From a sigmoid curve it is impossible to detect a threshold

TABLE 3.17. The relationship between the duration of the preoviposition period, the transition rate of the pre-oviposition period and the temperature.

Temperature °C	n	preoviposition period ± SD	transition rate ± SD
12	16	41.2 ± 18.5	0.029 ± 0.0135
15	10	21.4 ± 10.1	0.0536 ± 0.018
19	11	12.2 ± 1.9	0.0841 ± 0.013
22	13	7.2 ± 1.6	0.1445 ± 0.031
27	42	5.7 ± 1.3	0.1826 ± 0.040

for development, thus the temperature found by van Dijk (1979) will be used as the threshold for egg development.

Together with the first eggs also remains of spermatophores were found, but since one or two days may elapse between copulation and excretion of the empty spermatophores, males probably reach sexual maturity somewhat earlier than females.

3.8.2.3 The rate of ovary growth and the maximum weight of the ovaries

When daylength conditions are adequate, temperature and food are the driving forces for the rate of development of the ovaries. The conversion of food and reserves into yolk depends on the digestion rate of the food. If it is assumed that this rate determines the growth of the eggs, the time for the ovaries to grow to full development can be estimated. Fullgrown ovaries bear eggs in all different stages of development from small oocytes until fullgrown eggs. The total weight of these ovaries is approximately 10 mg, including the nursery cells (van Dijk, 1986); this is approximately 12% of the maximum fresh weight.

3.8.2.4 Residence time of the eggs in the oviduct

The time eggs need to mature in the oviduct was experimentally established for a single temperature of 19 °C. If it is assumed that the relationship between rate of maturation and temperature is linear the values for other temperatures can be estimated.

In the experiment 36 reproductive females were offered coloured maggots after one day of starvation. After satiation 6 beetles were dissected per day for 6 consecutive days, to search for coloured eggs in the ovaries and in the oviduct. At the same time the eggs deposited in the petri dishes were sieved from the peat mull and counted. All eggs were incubated at 19 °C, so that survival under influence of the dye could be observed.

The results of this experiment (see table 3.13) show that one day after con-

TABLE 3.13 The sequence of colouring of eggs above and under the Corpus luteum (CL) by a red dye ingested by feeding, and the deposition of these eggs.

Day after start.	1	2	3	4	5	6
% coloured eggs above C.L.	75.4	91.7	100	100	100	100
% coloured eggs under C.L.	0	5	34.8	66.2	87.3	87.9
% of coloured eggs laid	0	0	1	38.0	70.5	93.1

TABLE 3.14 The total transition time of coloured food from ingestion until the deposition of the first coloured eggs (Exp. van Dijk unpubl.)

Temperature °C	12	15.5	19	22
Transition period in days (mean + sd)	12 ± 4	7 ± 1.8	5.3 ± 1.2	4.3 ± 1.3

sumption of the dye most of the eggs above the corpora lutea (C.L.) were coloured red. After two days the first coloured eggs were observed under the C.L. in the oviduct. After 3.5 days, 50% of the ripe eggs were coloured. Obviously, the maturation of the eggs varies widely, because after 6 days uncoloured eggs could still be found in the oviduct. On average 4.5 days were needed for the growth, maturation and deposition of an egg. Thus it can be concluded that in this experiment at 19 °C the maturation in the oviduct took approximately a single day.

Van Dijk (pers. comm.) did experiments to estimate the total transition time of coloured food through the body at 12, 15.5, 19 and 22 °C. He observed the time needed from the intake of coloured food until the deposition of the first coloured eggs (table 3.14).

The results of the two experiments show different values for the duration of the transition period for the dye at 19 °C. According to table 3.13 it took 4.5 days for coloured eggs to be laid, whereas in table 3.14 one day more was needed (viz. 5.3 days). This may be due to the small number of females dissected in the first experiment and the wide individual variation which apparently exists. In all probability the average residence time of eggs in the oviduct at 19 °C. will be between 1 and 2 days. The average number of eggs in the oviduct from the dissected beetles at 19 °C. was 12.5 ± 5.5 (mean $\pm$ SD). The quantity of eggs in the oviduct is the result of the input rate of eggs from the ovaries, the residence time in the oviduct, and output by deposition. This number also allows the maturation period to be roughly estimated. Ovaries need approximately 4 days to grow to full development (about 9-10 mg), if excess of food is offered. Thus they grow 2.5 mg per day, and about 6 fullgrown eggs are produced per day (an egg weighs 0.4 mg). Thus it takes approximately 2 days for the number of eggs in the oviduct to reach the value found in the experiment. This agrees rather well with the estimations made before.

The maturation time at different temperatures is derived from a supposed linear relationship between maturation rate and temperature with a threshold at 10. °C and an estimated maturation rate at 19 °C of 0.5 (day^{-1}).

3.8.2.5 The reaction time to change in daylength

The time between emerging from diapause and the deposition of the first egg is called the pre-oviposition period. It may be divided into three phases: 1) The period needed to react to changing daylength. 2) A period for growth of the ovaries until the first mature eggs enter the oviduct. 3) The residence time of the eggs in the oviduct.

If the duration of the entire pre-oviposition is known the length of two of the phases can be established and that of the third phase can be estimated.

The average time needed for eggs to grow in the ovaries plus the average residence time in the oviduct were established and these were subtracted from the average pre-oviposition period, to estimate the reaction time to changing daylength conditions (RTD).

The period of ovary growth was simulated with a model, which used the rela-

TABLE 3.15 Estimation of the average reaction time to change in daylength calculated with average duration of egg growth in the ovaries, average residence time of eggs in the oviduct and the total pre-oviposition period ± SD (all expressed in days).

Temperature °C	12	15	19	22	27
Reaction time to change in daylength.	10	10	6.5	3.7	2.4
Growth period of the eggs in the ovaries	24	7.4	3.7	2	2.3
Residence time of eggs in the oviduct.	12	4	2	1.5	1.
Pre-oviposition period.	46±18	21.4±10	12.2±1.9	7.2±1.6	5.7±1.3

tive gut emptying rate as a measure for the relative rate of assimilation of food from the haemolymph to the ovaries. The model is constructed such, that when the ovaries reach a weight of 12% of MAXFW the eggs are dumped into the oviduct.

The experimental established pre-oviposition period and calculations concerning the other periods are given in table 3.15 .

The pre-oviposition period shows an almost hyperbolic relationship with the temperature. The inverse of this period offers the relative rate of pre-oviposition (RRPRO) (fig. 3.20). Linear regression through these points gives equation: $Y = -0.111 + 0.0107 * T$ (where Y = RRPRO and T = temperature). The development threshold according to this equation is 10.4 °C. Observations of Van

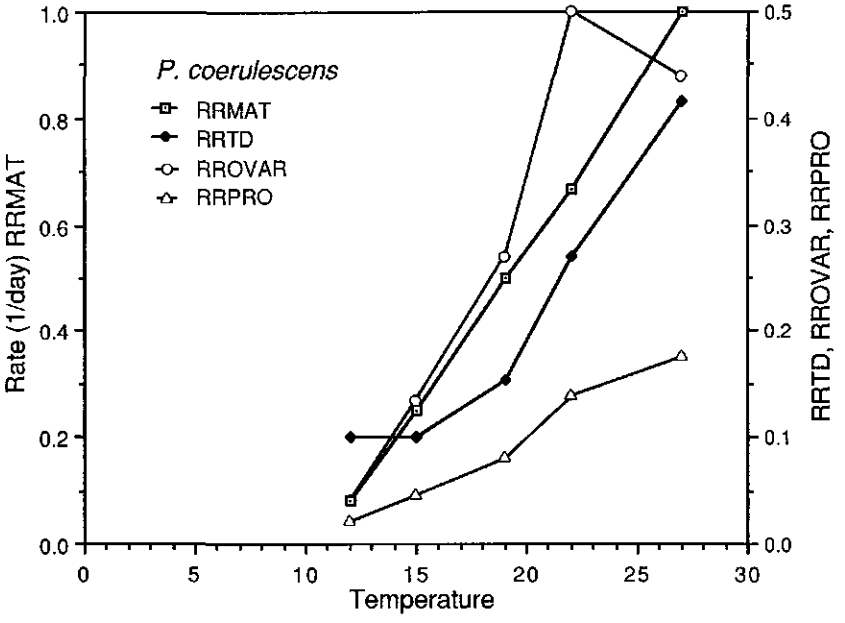


FIG. 3.20. The relationship between the temperature and: RRTD (the relative reaction rate to change in daylength), RROVAR (the relative growth rate of the eggs in the ovaries), RRMAT (the relative maturation rate of eggs in the oviduct), RRPRO (the relative pre-oviposition rate).

Dijk (1979) show that the beetle is able to lay some eggs at 8.5 °C thus, it is more likely that the relationship between RRPRO and the observed range of temperatures is not linear but slightly sigmoid. The levelling of the curve at 27 °C supports this. This is caused by the decrease of the egg formation rate in the ovaries at temperatures above 22 °C (fig. 3.19). In its turn the decrease in egg formation rate is caused by the high respiration rate at those temperatures (see chapter 3.7). The ultimate calculation of the reaction period to change in day length using the duration of the other periods gives a reaction period which decreases in length with increase of the temperature. The inverse of these durations gives the relationship between the relative rate of reaction time to change in daylength (RRTD) and temperature, which is probably a sinusoid with a maximum of 1. (the minimum number of days needed to react to a change in daylength) at high temperatures.

3.8.2.6 The oviposition period

The oviposition period is defined as the period between the deposition of the first and the last eggs. This period differs from the egg formation period, because the latter starts at the moment yolk is incorporated into the oocytes and ends when the last egg is dumped into the oviduct. The formation of the first eggs thus overlaps with the pre-oviposition period. For the simulation of egg production the duration of the egg formation period as calculated by:

Egg formation period = (mean oviposition period) + (mean growth period of eggs in ovaries) − (mean residence time of eggs in the oviduct).

The oviposition period was established from the experiments at constant temperatures and abundant food. The results are shown in table 3.16.

Above 12 °C, temperature appears to be positively correlated with the length of the oviposition period. The same holds for the egg formation period, although weaker. The variation is very wide at 12 °C.

TABLE 3.16 The egg formation time, expressed in days, estimated as: mean oviposition period + mean growth period of eggs in the ovaries − mean residence time of eggs in the oviduct.

Temperature °C	12	15	19	22	27
Oviposition time ± SD	55±40	29±4.2	34±4.5	35±2.8	39.5±3.5
Egg formation time	60	32.4	35.7	35.5	41.0

3.8.2.7 Oösorption

Oösorption is characterized by cessation of yolk deposition (vitellogenesis) thus curtailing further ovulatory cycles, and degeneration of the yolk-containing oocyte and the enveloping cells. In *P.coerulescens* this process is irreversible (van Dijk, 1979). Oösorption may be a response to ecological, behavioural or physiological factors (Bell and Bohm, 1975). Food shortage,either quantitative (Osborne and Finlayson, 1962) or a qualitative nature (Johansson, 1964) is the major cause of it. Lack of protein in the diet may lead to cessation of vitellogenesis

and start of oocyte resorption. Another factor that may have an effect is the absence of males. Virgin females of many insect species start to deposit yolk, but in the absence of mating their oöcytes are quickly resorbed (Bell and Bohm, 1975). The frequency of mating may also influence egg production, probably by triggering the production of juvenile hormones that stimulate yolk deposition. At the population level it will thus have a negative effect when density is so low that males and females do not encounter each other regularly: 'under population' (Andrewartha & Birch, 1954 Chapter 9). It is important to find out which encounter rate and thus which density is critical.

Oösorption caused by starvation has been observed in *P.coerulescens* (van Dijk, 1979). However, the rate of resorption has not been measured. Therefore, it was assumed that in case of starvation the oocytes and the nursery cells have to deliver enough energy to the haemolymph to meet the metabolic need. Since the metabolic need is known (see section 3.7) the rate of resorption can be estimated.

3.8.2.8 Weight of eggs

The total weight of eggs divided by the individual egg weight results in the number of eggs present in the oviduct.

Two possible relationships have to be considered: 1) That between the size of the beetle and weight of an egg, and 2) the dry:fresh weight ratio of an egg.

By measuring beetles of different size and by weighing their eggs no relationship could be found between beetle size and egg weight. This is in agreement with observations of Suzuki and Hara (1976), who demonstrated that eggs seem to be fairly constant intraspecifically, individual beetle size seems to be reflected more in egg numbers. The fresh weight of a single egg is 0.40 ± 0.04 mg. ($X \pm SD$, $n = 137$). The dry weight of an egg is 0.217 ± 0.14 mg ($n = 65$). Thus the dry:fresh ratio of an egg is 0.54.

4 RESULTS OF SIMULATION AND VERIFICATION OF EGG PRODUCTION

A simulation model was constructed using information from literature and the results from the experiments discussed in the previous chapter. The set-up of the model, together with all the quantitative relationships, is extensively described in appendix I . The simulation model was used to compute food consumption and egg production under various conditions, such as fluctuating temperatures, different quantities of food, feeding time or food quality in relation to characteristics of the beetle, such as beetle size, gut capacity, gut emptying rate, respiration rate or maturation rate of the eggs. It is impossible to evaluate the consequences of all these changes experimentally as this would require a tremendous amount of time, whereas in some cases it is even impossible to create the experimental conditions.

In the next sections the general results of model calculations are given. They are compared with results of experiments carried out independently from the previous experiments, with beetles under well defined conditions.

4.1 SIMULATION OF EGG PRODUCTION

The processes involved in the conversion of food to eggs.

In the model the beetle starts feeding. The food ingested during the first period is digested at a low rate. During that period no yolk is incorporated into the oocytes, thus all the ingested food is converted to stored products (FAT). This quantity grows. Some time is needed to react to changing daylength. After this period egg formation starts, the relative gut emptying rate increases and the oocytes in the ovarioles start growing. The quantity of stored products also decreases until a balance is reached between storage and use. When the total quantity of the eggs above the corpora lutea has reached a weight of 12% of MAXFW, eggs are dumped in the oviduct. This happens every time the maximum weight of the ovaries (MAXOV) is exceeded by the weight of an egg. The number of eggs in the oviduct grows until a level depending on input rate from the ovaries and the transition rate in the oviduct is reached. The latter determines residence time and therefore oviposition rate. When egg formation time is over, the last eggs in the oviduct will be deposited. The gut is not longer inhibited in its expansion, a few large meals will be ingested, and all the assimilated food is stored again, which is shown as an increase of FAT.

Fig 4.1a shows the continuous change of a number of state variables such as total weight of the beetle (TOTW), gut content (GUTCON), haemolymph (HEMO), stored products (FAT), ovaries above corpus luteum (OVAR) and the number of eggs in the oviduct (EGGNUM). Food is ingested each time

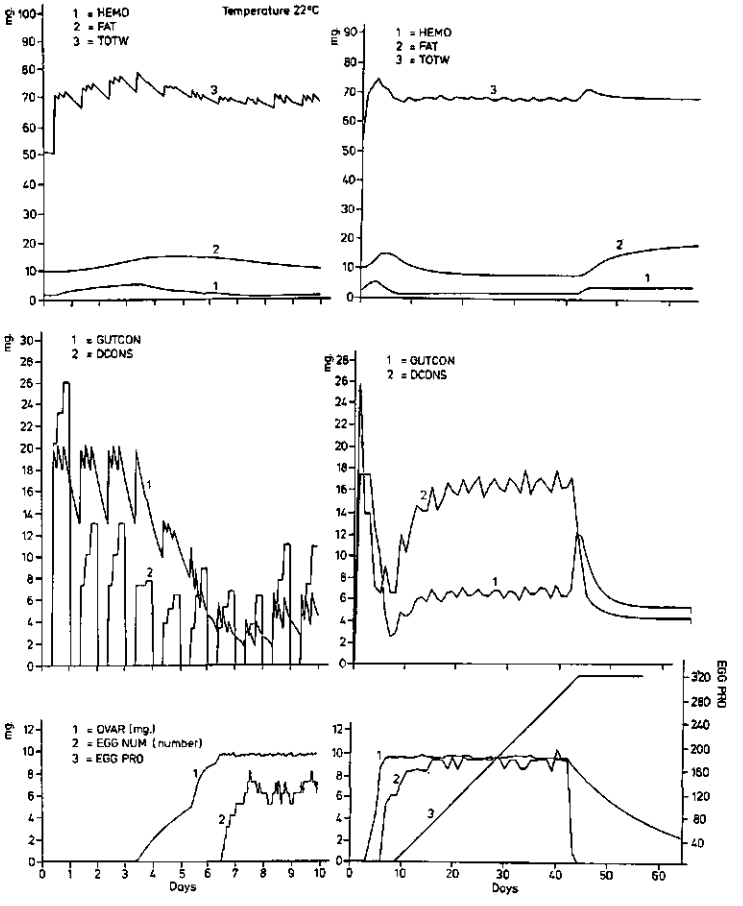


FIG. 4.1a,b. The change of weights at a constant temperature of 22 °C of: the total beetle (TOTW), haemo-lymph (HEMO), stored products (FAT), gut content (GUTCON), daily consumption (DCONS), ovaries (OVAR) and the change of the number of eggs in the oviduct (EGGNUM) and the number of eggs produced. Fig (a) shows the daily change in detail for a period of 10 days. Fig (b) shows the value of weights and numbers at midnight for the whole period of reproduction.

the relative satiation level drops below the ingestion threshold to simulate ample food supply. During the night beetles are not active. Therefore, the gut content decreases during the night, in the morning food is ingested again. In fig 4.1b the change of the same state variables and those of the output variable egg production are plotted on a daily time scale for the whole oviposition period. The values of the variables are those reached at midnight. The decrease in daily food consumption after the fourth day, caused by the growth of OVAR and EGGNUM is particularly striking, illustrating the effect of the limited room in the abdomen on ingestion. When egg deposition starts, more room becomes available and consumption increases again.

4.2 VERIFICATION OF EGG PRODUCTION

In this part of the chapter the verification experiments are described, which were done with beetles under known conditions. The results of the experiments were compared with the results of simulations in which the same conditions were used as input parameters or variables.

4.2.1 Methods

General experimental method.

All the experiments were carried out with beetles in petri-dishes (9 cm diam.). Moist ground peat mull was added to offer a substrate for the beetles to deposit their eggs. The peat mull was inspected for eggs according to the sieve-wash method (Mols et al. 1981). In the experiments maggots (*Calliophora sp.*) were offered as food.

The beetles originated from the grassland Nuil (a place in the neighbourhood of the Biological Station at Wijster). The size of the beetles ranged between a LEWI of 20 and 24 mm^2.

a) Egg production with excess of food.

Experiments were carried out in incubators at 12, 15, 19, 22 or 27 °C. The beetles were given excess of food.

b) Egg production when food is limited.

Experiments were carried out at constant temperatures of 15, 22 or 27 °C. At 15 °C a group of 16 beetles was offered food once every two days, except at the weekends (experiment done in 1979). At 22 °C a group of 20 beetles was offered food every two days, including the weekends (experiment done in 1978). At 27 °C one group of 12 beetles was offered food once a day, another group of 15 beetles was offered food once a day except at the weekends (experiment executed in 1979). In all these groups the quantity of food ingested was measured by weighing beetles before and after the meal. Further, the treatment of the beetles was according to the general method.

c) Verification of egg production at field temperatures.

Egg production experiments were also carried out under changing outdoor temperature conditions. The beetles in the petri dishes were placed outside in an insectarium protected from direct sunlight by a roof. These experiments were carried out in 1978, 1979, 1982 and 1985 by Van Dijk (unpubl.). His results were compared with the simulations for these years. Beetles originated from the poor heath land Schuttingveld and from the grass land Nuil. Beetles captured at Schuttingveld were much smaller in size (females LEWI $= 17.8 \pm 2.3$ $n = 16$, males LEWI $= 17.3 \pm 2.5$ $n = 10$) than those from Nuil. In 1979 LEWI was 21 ± 1.3 ($n = 57$, $X \pm SD$). In 1982 LEWI was not measured but assumed to be the same as in 1985 i.e. 22.7 ± 4.3 ($n = 9$, $X \pm SD$ estimated from the weights at the end of the reproduction period of 1985).

In 1979 experiments were carried out both with beetles originating from Schuttingveld and from Nuil.

4.3 Results and discussion

Egg production with excess of food.

In table 4.1 the daily and total egg production,together with the length of the oviposition period are given. In fig 4.3 the total egg production per female per season, calculated by the model, is given, and compared with the estimates from experiments at constant temperatures of 12, 15, 19, 22, and 27°C from table 4.1. The experiments show a high individual variation in egg production even at constant temperature, due to individual differences in duration of oviposition period, and in rate of egg production per day.

The first experiments at 12°C gave a very low mean egg production. This is probably because of the low fraction of beetles that mated at this low temperature; this greatly influences total egg production. The few females that did mate showed a much higher egg production than those that did not. Later experiments at 12°C, in which most of the females mated, showed a distinctly higher egg production (van Dijk pers.comm.). The estimates of total egg production calculated by the model are generally in good agreement with the experimental results (fig 4.2). A more detailed analysis of the pattern of daily egg production in the model shows an increase of egg production until a specific temperature-dependent level, at which it stays nearly constant for a long period. When egg formation ends there is a rapid decline in egg production at a rate depending on the residence time of the eggs in the oviduct. To test whether this also occurs in reality the egg laying pattern of the individual beetles in the experiments was analyzed. In the experiments much variation occurred in the individual egg production per day, possibly because of an irregular feeding pattern. The average pattern of mean egg production per reproductive female per two days is given in fig. 4.3. In this figure day 1 is the day at which the females start egg production. It can be seen that at 15 and 19°C egg production stays at about the same level

Table 4.1. The results of egg production experiments at constant temperatures and ample food supply.
** experiments done by van Dijk.

Temperature	Number	Egg production per day per female ± SE	Total egg production ± SE	Oviposition period (days) ± SD
12	11	.2 ± .1	9.7 ± 2.3	56 ± 40
12**	17	.6 ± .1	22.6 ± 4.1	44 ± 9
15	15	2.7 ± .6	79 ± 15	29 ± 16
19	44	5.8 ± .6	214 ± 34	34 ± 30
22	28	8.4 ± 1.1	295 ± 31	35 ± 15
27	30	9.6 ± .9	379 ± 58	39.5 ± 19

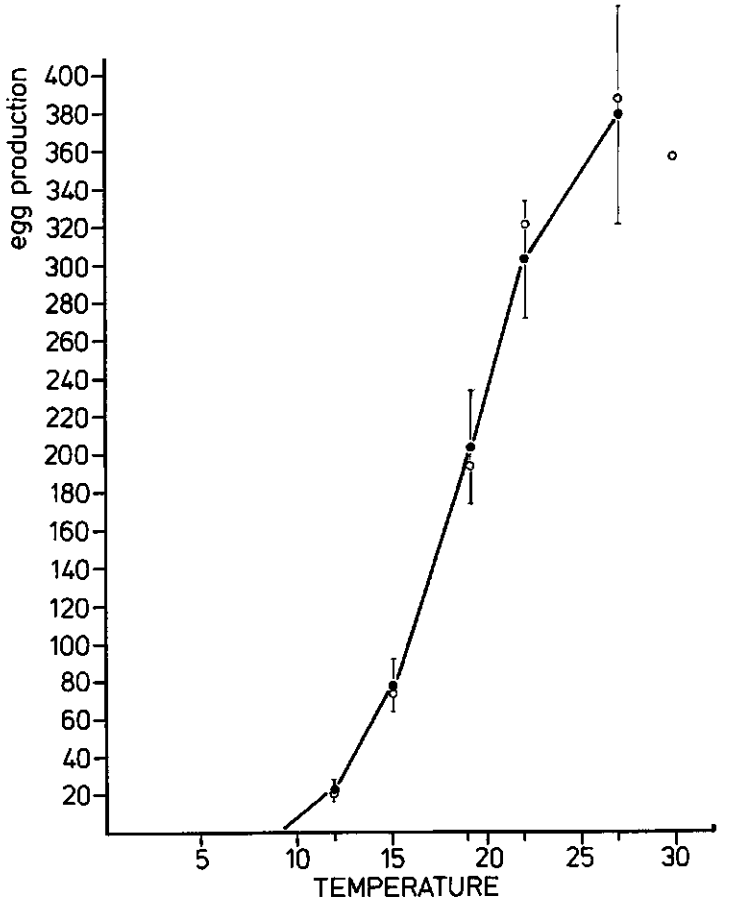


FIG. 4.2. Experimental (black dots) (mean ± SE) and simulated (open dots) results of egg production at different constant temperatures, when food is available in excess.

until the fraction of reproductive females falls below 50%. Then, because of the small number of beetles, the variation in the mean egg production increases. In the results of experiments at 22 and 27 °C an overall increase in mean egg production per female can be observed, because low producers tend to finish egg production earlier. After 40 days the number of reproductive females became so low that variation increased because of individual differences. In all these experiments there was a tendency for animals with a high reproduction rate also to have a longer oviposition period. This tendency is significant in the 27, 19 and 15 °C groups ($p < 0.05$) but not in the 22 °C group. When the egg production of an individual beetle is analyzed it appears that every beetle has its own level of reproduction around which the daily egg production fluctuates. During one season egg production in P.coerulescens seems to be age-independent.

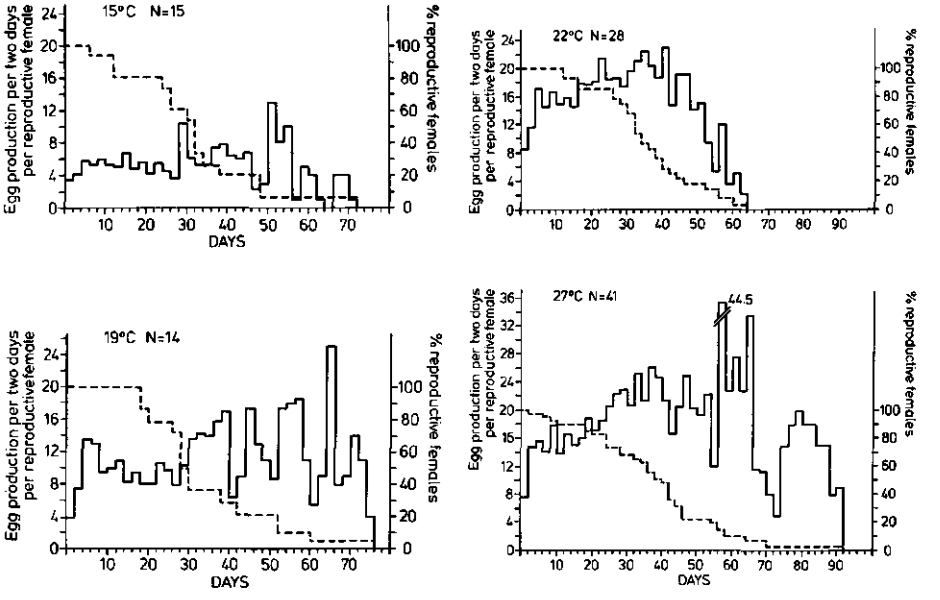


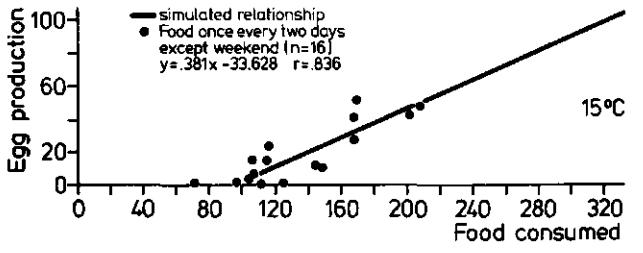
FIG. 4.3. The average egg production per reproducing female per two days (solid line) in relation to reproductive age, and the % females reproducing (broken line) at different temperatures. The start of oviposition of each individual female is taken as day one.

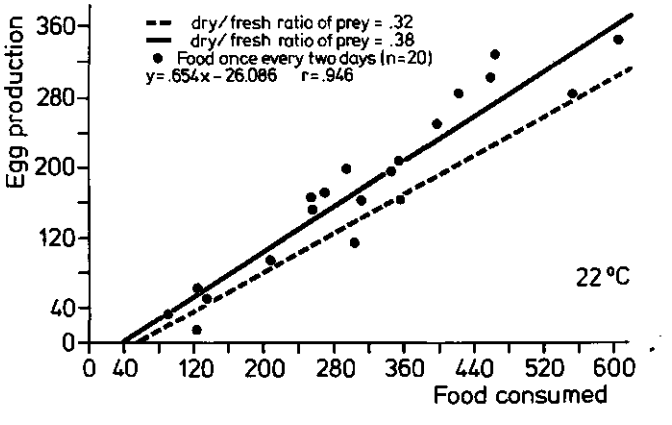
b) Egg production at limited food conditions.

The total consumption during the pre-oviposition and oviposition periods for an individual beetle is related to its total egg production. In fig.4.4 the experimentally estimated relationship between the total consumption of a beetle during adulthood and its total egg production is given at various temperatures.- There is a linear relationship, which implies that, although there are large individual differences in total egg production, the conversion of food into eggs at a specific temperature is more or less the same for all the individuals. The differences in conversion at various temperatures are caused by differences in respiration. The model output at 15 and 27 °C shows the same relationship as found in the experiments. Only at 22 °C the conversion is more efficient in the experiment than in the model. This is probably because of the superior quality of the maggots offered as food in that experiment. A change in the dry:fresh ratio of the prey from .32 to .38 gave the same relation simulated by the model as found in the experiment.

c) Egg production at field temperatures.

The result of experiment and simulation are given in table 4.2 In the model the simulation starts at March 21 (LD 12:12). Simulated egg production corresponded well with the actual situation although there were very strange deviations from the starting date, especially for the year 1979. In the experiment the beetles from Nuil started egg production already at 12 May when the number





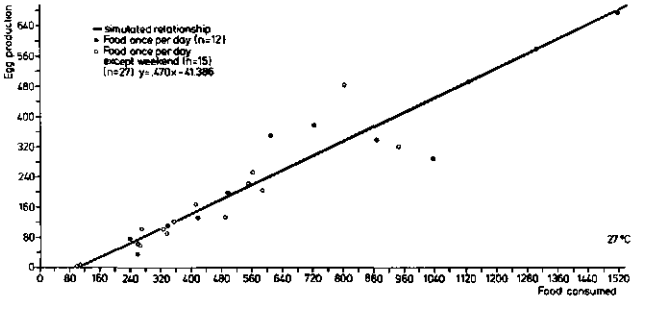


FIG. 4.4. The relationship between total food consumption (from the start of the experiment until the end of the reproduction period) and the total amount of eggs produced per individual beetle at constant temperature. The lines represent the results of simulation with the same conditions.

of day degrees above 10 °C was just 28. This was very low as compared to the expected amount of day degrees in the other years which varied between 65 and 90. Beetles caught in the field may have experienced other temperatures before the start of the experiment than in the simulation, because of their preference for exposed spots in the sunlight during spring. The amounts of eggs simulated for that year were also much higher than found in the experiment. This may be due to the later start of the simulated egg production in the season, because later in the season temperatures were higher.

The changes of the internal states and the variation of the output variables daily egg production (DEGGP) and daily food consumption (DCONS)) resulting from fluctuating field temperatures are given in fig. 4.5, fig 4.6 and fig 4.7 for the year 1985. Food consumption, egg numbers in the oviduct, and daily egg production are strongly affected by fluctuating temperatures. This is also illustrated in the relation between the daily temperature sum above 10 °C (n = 52 days) the daily food consumption (DCONS) in fig 4.8a and in the relation of the temperature sum and the simulated daily egg production (DEGGP) in fig 4.8b. The variation in the first relationship was due to the effect of the restricted room in the abdomen during the pre-oviposition period. Although the temperatures may be high during that period the beetle is not capable to ingest more food then. The variation in the latter figure is due to a delay in digestion, the time needed for egg formation and the passage of the eggs through the oviduct.

TABLE 4.2. Egg production under outdoor conditions for the years 1978, 1979, 1982 and 1985. Experimental and simulated results. a) beetles from the grassland Nuil, b) beetles from the heathland Schuttingveld. Eperiments done by van Dijk (pers. comm.).
* LEWI estimated

Experimental results						Simulated results		
year	LEWI	n	average egg production ± SE	av. starting date	duration of reproduction ± SD	egg production	starting date	duration of reproduction
1978b	17.8*	27	60.5 ± 8.9	20 may	45.0 ± 19.5	65	16 may	44
1979a	21	30	76.6 ± 16.4	12 may	42.2 ± 22.3	97	18 may	40
1979b	17.8	30	53.5 ± 8.9	18 may	36.7 ± 13.6	62	22 may	36
1982a	22.7*	20	148.7 ± 14.8	18 may	39.2 ± 12.2	141	17 may	39
1985a	22.7	9	129.3 ± 78	11 may	54.6 ± 12.6	127	8 may	52

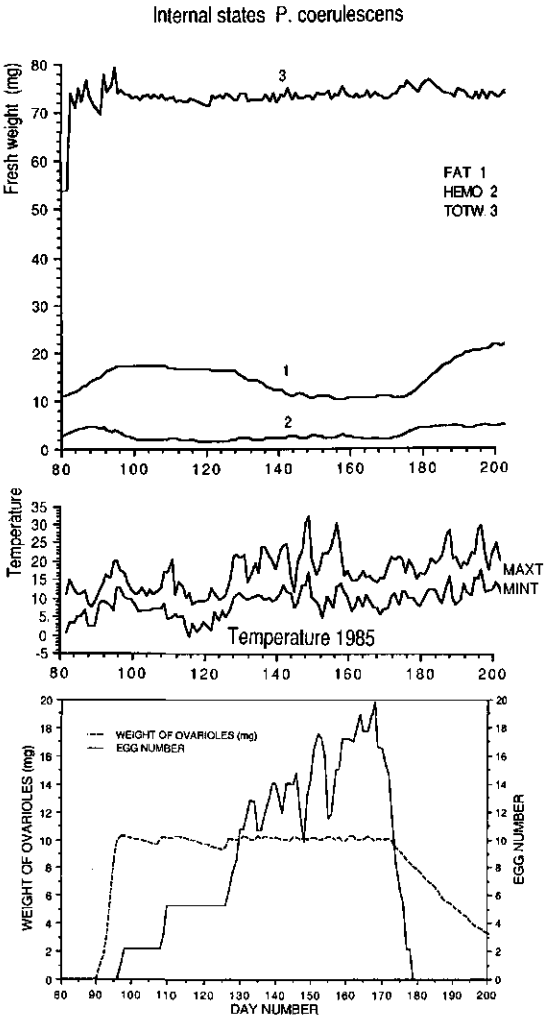


FIG. 4.5a. The simulated change of weights at field temperatures (1985) of the total beetle (TOTW), materials in the haemolymph (HEMO), stored products (FAT),b) the ovaries (OVAR) and the number of eggs in the oviduct (EGGNUM). Food is available in excess.

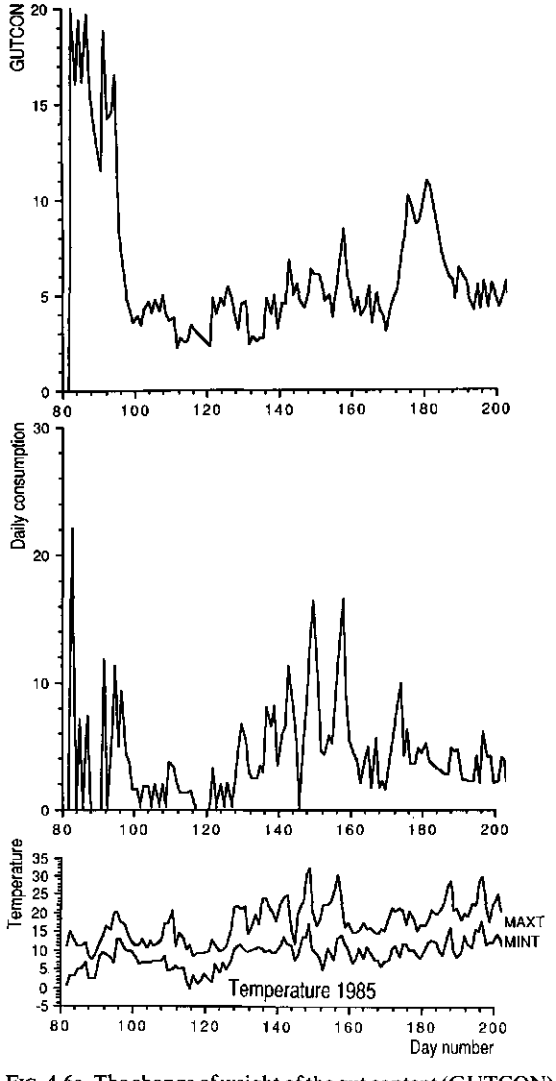


FIG. 4.6a. The change of weight of the gut content (GUTCON). b) The daily consumption (DCONS). during the reproduction period in 1985.

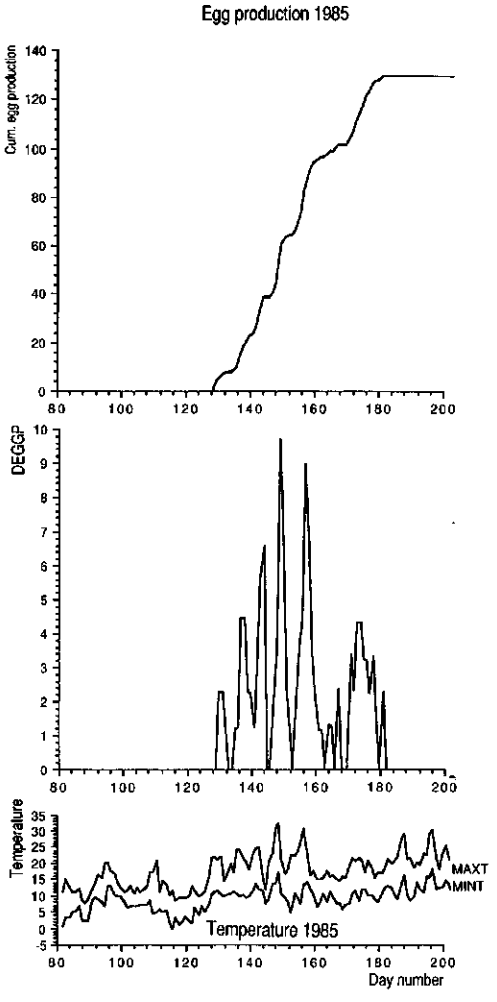


FIG. 4.7. The daily and total egg production at field temperatures for the year 1985. Food is available in excess.

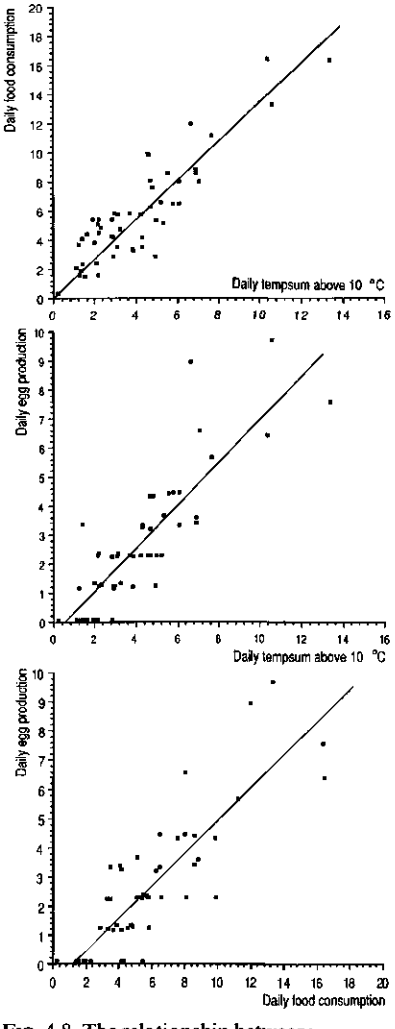


FIG. 4.8. The relationship between:

a) the simulated food consumption of 1985 and the daily temperature sum above 10 °C. ($y = 1.35.T_s$ $r^2 = 0.77$)

b) the simulated egg production and the daily temperature sum above 10 °C. ($y = -0.424 + 0.743.T_s$ $r^2 = 0.74$)

c) the relationship between simulated daily food consumption and simulated daily egg production. ($y = -0.558 + 0.547 * DCONS$ $r^2 = 0.72$)

5.0 SENSITIVITY ANALYSIS

5.1 INTRODUCTION

The sensitivity of the model was analysed in two ways: by making structural changes in the model (coarse sensitivity analysis) and by changing variables and parameters to determine their relative importance for the behaviour of the model (fine sensitivity analysis). The different structural subunits of the model were tested to see whether they correctly describe the phenomenon they represent (see the foregoing sections). To evaluate the effect of a certain structural subunit on the behaviour of the model, the subunit in question was replaced by a constant value.

To ascertain the quantitative importance of the different input relationships and parameters for the model results, the average values of these relationships or parameters were replaced by the average values plus or minus the standard deviation. There are two kinds of output variables: actual state variables, and accumulated values of inflow rates of some state variables. The first group comprises the momentary states of the predator, such as gut content, fat storage, number of eggs in the oviduct, etc. The second group concerns quantities such as total egg production, food consumption or respiration per day or per season.

The relative effect on the model's output of a change in a variable or parameter can be estimated from the amount the output changes relative to the change of the input variable or parameter:

SA = d(output)/(old output)/d(input)/(old input variable)
d(output) = new output – old output.
d(input) = new value – old value of parameter or variable.

When SA = 1, the change of the input variable or parameter has the same relative result on the output. When SA < 1, the change of the value of the input variable is buffered by the model, and when SA > 1 the effect on the output is stronger than the change of the input variable, and thus the variable or parameter may be of great importance for the output of the model. Positive or negative signs may also occur, because if certain input values are lowered (a negative change), the result may be a positive effect on the output, and vice versa.

Because the relationships with respect to temperature are curvilinear the sensitivity analysis has to be repeated to test the specific variables and parameters for different temperatures. This was done for temperatures of 12, 15, 19, 22, 27,and 30 °C or with field temperatures if this was needed (e.g. to ascertain the effect of circadian rhythmicity of the relative gut emptying rate on other processes).

Egg production over a season and total food consumption for the same period were used as output.

5.2 Results

The results of the sensivity analysis on the values of parameters and variables are given in table 5.1. It can be seen that certain changes in input variables or parameters generally lead to relative smaller changes in the model output. Exceptions are found for the relation between prey dry:fresh weight ratio and food consumption and between the size of the ovaries (MAXOV) and egg production. The effect of temperature on the relative changes of the output variables is greatest at both low ($\leq$ 15°C) and high temperatures ($\geq$ 27°C). At these temperatures most relationships deviate from linearity (especially the sigmoidal relationship between the relative rate of gut emptying and temperature: fig. 3.11). It can also be seen that a change in the value of a variable or parameter which leads to higher egg production is buffered more strongly by the model than a change that leads to a decrease in egg production. This is caused by the restricted size of the animal, which forms the physical limits to the system.

The consumption rate is negatively influenced by variables that cause an increase of the storage of fat or eggs, because the physical limits of the system are reached more readily.

5.2.1 Relative rate of gut emptying (RRGE)

In the model the same relative values are used for the processes of gut emptying and for assimilation of food by the ovaries (section 3.8). Therefore, if these values increase, egg production rises, and the pre-oviposition period is curtailed. More eggs are dumped in the oviduct, and the latter limits room in the abdomen thus resulting in a relatively low increase of ingestion. The ultimate result of a 30% change in the relative rate of gut emptying is a 16-29% change in egg production and 6-20% effect on consumption. The effects are strongest at high temperatures, because the residence time of eggs in the oviduct is then too short for high numbers of eggs to be cumulated in the oviduct. Thus, ingestion will not be limited by restricted expansion of the gut.

Circadian rhythmicity of RRGE.

When temperature is constant, replacing the circadian rhythmicity of RRGE by the average daily values, has hardly any effect on the production. However, when the model is run with field temperatures from the years 1978, 1979, 1982 and 1985, a constant RRGE decreases egg production by an average of approximately 10%. The effect of fluctuating temperature on gut emptying is enhanced by the effect of the circadian rhythmicity. During the night, when temperatures are relatively low, RRGE is further decreased by the circadian rhythmic effects. During day time the opposite occurs. Governed by temperature and the circadian rhythmicity of RRGE, and of course depending on the availability of food,

TABLE 5.1. Results of a sensitivity analysis. The effect (SA) of the change of the variable or parameter on the output of the model is expressed relatively.
SA = (d(output)/output)/(d(var)/var)
C = total consumption during an oviposition period in mg.
EP = total egg production.
MF = multiplication factor.
SC = sensitivity on consumption, SEP = sensitivity on egg production.
For information on the normal values of the standard input see appendix 1.

Temperatures °C		12		15		19		22		27		30	
Standard		C 210	EP 20	C 257	EP 71	C 466	EP 193	C 692	EP 326	C 912	EP 387	C 978	EP 345
Variables and parameters	MF	SC	SEP	SC	SEP	SC	SEP	SC	SEP	SC	SEP	SC	SEP
RRGE	0.7	0.27	0.70	0.46	0.81	0.54	0.67	0.64	0.69	0.67	0.82	0.67	0.97
	1.3	0.20	0.59	0.30	0.71	0.49	0.54	0.52	0.56	0.61	0.74	0.55	0.77
FROFAT	0.7	–0.37	–1.04	–0.56	–1.0	–0.48	–0.61	–0.44	–0.49	–0.52	0.65	–0.50	–0.72
	1.3	–0.28	–0.83	–0.10	–0.88	–0.36	–0.41	–0.30	–0.34	–0.41	0.51	–0.38	–0.55
TOFAT	0.6	–0.19	–1.03	–0.41	–1.1	–0.35	–0.63	–0.32	–0.51	–0.53	0.90	–0.51	–1.0
	1.4	–0.14	–1.0	–0.25	–0.64	–0.24	–0.55	–0.26	–0.40	–0.31	0.54	–0.32	–0.62
FROVAR	0.7	–0.20	–1.0	–0.3	–1.0	–0.35	–0.6	–0.3	–0.5	–0.4	0.6	–0.4	–0.7
	1.3	–0.15	–0.8	–0.4	–0.9	–0.3	–0.4	–0.4	–0.4	–0.5	0.5	–0.5	–0.55
TOOVAR	0.7	0.25	0.95	0.38	1.1	0.33	0.74	0.45	0.72	0.54	0.91	0.51	1.0
	1.3	0.22	0.76	0.31	0.83	0.35	0.53	0.34	0.52	0.46	0.77	0.41	1.11
MATT	0.5	–0.08	–0.71	–0.16	–0.4	–0.24	–0.4	–0.25	–0.32	–0.06	0.09	–0.05	–0.1
	1.5	–0.01	–0.33	–0.09	–0.2	–0.19	–0.26	–0.12	–0.20	–0.10	0.16	–0.06	–0.11
RESPIR	0.5	0.47	–0.13	0.34	–0.09	0.22	–0.07	0.19	–0.08	0.25	0.13	0.31	–0.17
	1.5	0.48	–0.08	0.33	–0.08	0.27	–0.07	0.37	–0.07	0.26	0.11	0.31	–0.17
EFF	0.7	0.27	0.7	0.46	0.81	0.54	0.67	0.64	0.69	0.67	0.82	0.67	0.92
	1.3	0.20	0.59	0.30	0.71	0.49	0.54	0.52	0.56	0.61	0.74	0.55	0.77
DWPREY	0.3	–2.55	0.46	–1.93	0.55	–1.39	0.67	–0.74	0.97	–0.96	0.98	–1.77	1.23
	0.8	–1.75	0.13	–1.13	0.25	–1.03	0.33	–0.92	0.52	–0.94	0.38	–0.70	0.22
	1.2	–0.30	0.17	–0.70	0.18	–1.58	0.21	–0.61	0.29	–0.62	0.42	–0.61	0.37
EGGW	0.8	0	–1.	0	–1.	0	–1.	0	–1.	0	1.	0	–1.
MAXOV	0.8	–0.65	–1.56	–0.62	–1.54	–0.65	–0.96	–0.56	–0.87	–0.63	1.0	–0.57	–1.15
	1.2	–0.43	–1.35	–0.41	–1.31	–0.42	–0.96	–0.76	–0.83	–0.46	0.90	–0.57	–1.12

the quantities which can potentially be ingested will be higher during the day then during the night. If the beetle has some food in its gut at the start of the night, the urge to walk about in search for food as a result of hunger (Mols, 1986), will generally be low during the night, because the gut emptying rate is particularly slow then. Thus, having a RRGE that follows a circadian rhythm, with a maximum during day time, is of advantage for a diurnal beetle.

5.2.2 Dissimilation (FROFAT) and formation (TOFAT) of stored products

The rate of fat storage results from fat formation and fat dissimilation (RFAT = TOFAT-FROFAT) (fig 5.1). The balance situation depends on the quantities of FAT and of HEMO via feedback loops. During diapause the quantity of HEMO depends mainly on the supply from the gut and on the rates to and from FAT until a balance is reached. During the oviposition period food is also delivered to the ovaries. Since the demand from the ovaries is much higher than the demand from FAT most of the food is directed to the ovaries, which results in a low level of HEMO and thus in a decrease of FAT. Changing these rates directly affects the quantity of fat stored, and therefore the room in the abdomen, and this is followed by a change in ingestion rate, and as a consequence, in egg production. The relative effect of these variables is the same.

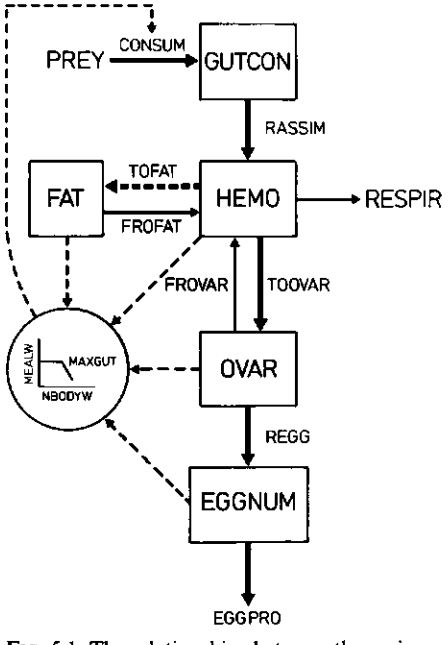


FIG. 5.1. The relationships between the various state variables. The feedback loops between FAT and HEMO and between OVAR and HEMO buffer the fluctuations of HEMO. The ingestion of food is regulated by the combined quantity of FAT, HEMO, OVAR and EGGNUM via the relationship between net body weight and the potential meal weight.

Increase of fat dissimilation provides more room in the abdomen and the same holds for a decrease in fat formation. An effect of temperature can also be observed. To explain this phenomenon the sequence of processes after breaking diapause must be observed in more detail. The model incorporates a reaction time to change in daylength. During this period the assimalated food is mainly stored, thus causing an accumulation of fat. After this period the food is mainly used for the formation of eggs, and the high quantity of fat stored during the reaction period is delivered to the haemolymph at a rate FROFAT= RRFDIS*FAT. In this equation RRFDIS is the relative rate of transport of products from FAT to HEMO. This relative rate is strongly temperature dependent in a curvilinear way. At low temperatures the delivery of FAT to HEMO is so low that the fat quantity hardly decreases and thus limits food ingestion for much longer than at higher temperatures, and the numbers of eggs produced are reduced proportionally. At higher temperatures the effect of a change of the input variable on the output is buffered more. The same explanation holds for the influence of a change of fat formation on consumption and egg production.

5.2.3 Formation (TOOVAR) and resorption (FROVAR) of eggs

The growth of the eggs in the ovaries above the oviduct (ROVAR) is the result of the formation and the resorption rates and the delivery of eggs (REGG) to the oviduct. ROVAR = TOOVAR – FROVAR – REGG.

Both the increase and decrease of the egg growth rate result in the same kind of change in egg production. Decrease of the rate results in an increase of materials in the haemolymph. The reverse occurs when the rate is increased (fig 5.1). When the quantity ofmaterials in the haemolymph increases, the room in the abdomen becomes smaller because more fat will be formed. The pre-oviposition period also depends on the ovary growth rate. An increase shortens this period and the reverse occurs when there is a decrease. Since the total egg formation period is estimated according to the method in section 3.8 a longer pre-oviposition period will result in a shorter reproduction period and therefore in a lower egg production. Changes in relative resorption rates will have comparable but opposite effects to changes in the relative formation rate.

5.2.4 Residence time of eggs in the oviduct (MATT)

If the residence time of the eggs in the oviduct increases eggs cumulate and thus room becomes limiting. The opposite occurs when the residence time is shortened. The effect of a change in residence time on egg production is greatest at 12 °C, though the effect on consumption is negligible. At higher temperatures the residence time is shorter, and then the transition rate through the oviduct is much higher than the egg formation rate. Therefore, accumulation of eggs in the oviduct is not so great that it leads to a proportionally high occupation of room in the abdomen with all the related effects on ingestion.

5.2.5 Respiration rate (RESPIR)

When food is available in excess increasing or decreasing the respiration rate

by 50% has only a minor inverse effect on egg production. It has a somewhat greater – but still small – positive effect on food consumption. The quantities of food used for respiration in comparison with the quantities used for egg production are too small to exert a strong influence on the output. When food is not offered in excess the beetle cannot compensate for an increase in respiration rate by ingesting more. Then an increase in respiration leads to a decrease in egg production equal to the amount of energy needed for respiration. Thus under those circumstances a proportional change in respiration is followed by a proportional change in egg production.

5.2.6 Egg weight (EGGW)

A change in the weight of an individual egg will result in a proportional change in the numbers of eggs produced, because egg number is calculated by dividing the total weight of eggs in the oviduct by the individual egg weight. But this is only of minor practical significance for this model, since egg weight is faily constant.

5.2.7 Dry weight fraction of prey (DWPREY)

Decrease in dry weight fraction of prey, affects consumption rate positively and egg production negatively. At temperatures of 12,15,19 and 30 °C, consumption increases more than proportionally, whereas at 22 and 27 °C a proportional reaction occurs. This results in an egg production that is influenced less than proportionally. If food is limited, and thus prey of low dry weight fraction cannot be compensated by an increase in consumption, the proportional change in egg production is about similar to the proportial change in prey dry weight fraction. Therefore, in field situations, where prey generally is not available in excess (van Dijk, 1986), prey dry weight fraction will be of great importance for the egg production of the beetle.

5.2.8 Efficiency of food assimilation (EFF) and food conversion to eggs

Part of the ingested food is egested as faeces, while the remaining part is converted and used for respiration, egg production or stored as fat. The effect of changing the efficiency of food assimilation is similar to that of changing the relative rate of gut emptying when food is available in excess, because the assimilation rate (RASSIM) is computed according to:

RASSIM = RRGE*EFF*GUTCON

When food is limited there is an effect on egg production which is comparable with changes in prey quality under limiting food conditions. The efficiency of food conversion from ingestion or from assimilation to egg production, can be calculated with the model, just as the proportion used for respiration and the proportion that is stored. For the range of constant temperatures the results are given in fig.5.2 and 5.3. These figures clearly show that the efficiency of the ingested food is very low at 12 °C, increases at temperatures up to 22 °C, where it is most efficient, and decreases again when temperature increases further. At low temperatures the low efficiency is due both to the long duration

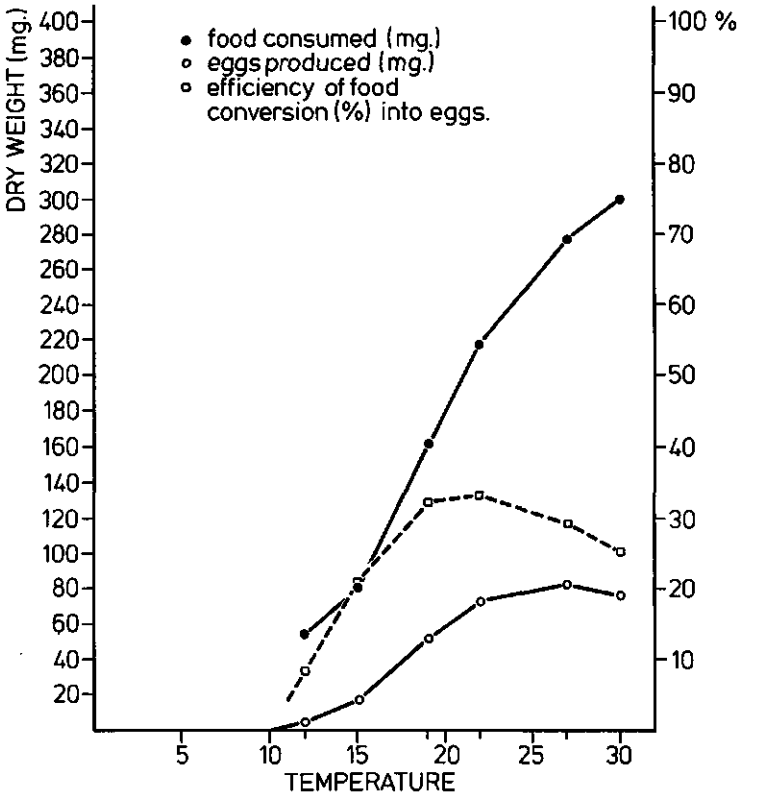


FIG. 5.2. The simulated total quantity of food consumed from break of diapause until the end of the oviposition period, the quantity of eggs produced (both expressed in mg dry weight), and the efficiency of conversion of food into eggs at constant temperatures.

of the pre-oviposition period, which causes a lot of assimilated food to be used for respiration, and to the storage of reserves. The lower efficiency at high temperatures is mainly due to the high respiration rate (Fig. 5.3).

5.2.9 The maximum weight of the ovaries above the oviduct (MAXOV)

The maximum weight of the ovaries together with the ovary growth rate and the reaction time to change in daylength determine the duration of the pre-ovipostion time, and also the room in the abdomen. Increasing the maximum weight of the ovaries has therefore a negative effect, whereas a decrease has a positive effect on egg production and on consumption, which appears to be almost proportional with the change of the input parameter.

5.2.10 Size (LEWI)

In the model the size of the beetle has a very strong influence on the egg production and food consumption because the size of the ovaries (12% of MAXFW), abdomen capacity and respiration rate are closely connected with

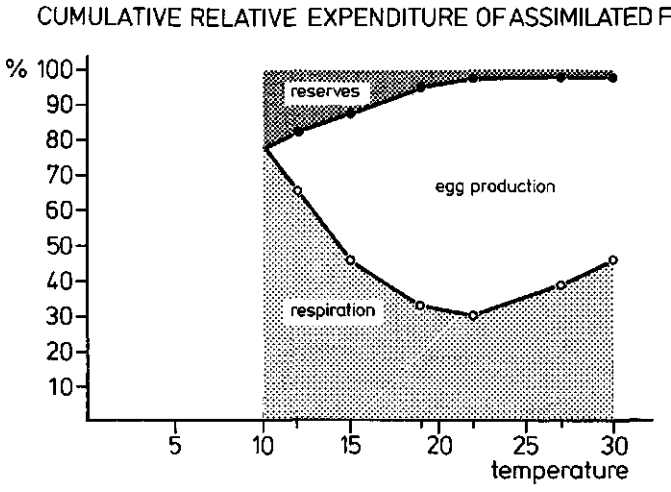


FIG. 5.3. The simulated cumulative expenditure of food assimilated throughout the gut wall used for reserves, respiration and egg production, during the oviposition period at constant temperature.

it. Beetle size influences also the length of the oviposition period. The relationship between beetle size, egg production and food consumption is given in table 5.2. Differences in size may be caused by the food conditions in the larval stages in combination with the temperature.

Beetles captured in different areas often show differences in size. For example beetles captured on the SCHUTTINGVELD heathland were mostly much smaller (LEWI = 17.8) than those captured at the NUIL grassland (LEWI varies from 20-24). This suggests that at SCHUTTINGVELD the food conditions, at least for the larval stages, are worse than at NUIL. The effect is that the average egg production per beetle at SCHUTTINGVELD will probably be more than 30% lower than at NUIL (table 5.2).

Table 5.2 The effect of size (LEWI) on food consumption (mg) and on total egg production, simulated from the break of diapause untill the end of reproduction. Food is available in excess.

Temperature.			12					15					19		
LEWI	16	18	20	22	24	16	18	20	22	24	16	18	20	22	24
Egg production.	5	10	14	20	29	29	39	54	71	93	88	116	149	193	245
Food consumption.	107	138	168	210	268	123	157	200	257	320	232	295	370	466	581
Temperature.			22					27					30		
LEWI	16	18	20	22	24	16	18	20	22	24	16	18	20	22	24
Egg production	151	196	254	326	414	179	233	306	387	490	162	212	276	358	462
Food consumption	345	473	552	692	863	474	590	742	912	1137	522	644	793	987	1208

5.2.11 *The relationship between meal weight (MEALW) and net body weight (NBODYW)*

The effect of the relationship between the weight of a meal a beetle can ingest and its net body weight (section 3.1) on egg production was examined by replacing it by a relationship that allows all the empty space available in the abdomen for the expansion of the gut: MEALW = GUTCAP.

Thus, the ingested meal size equals the abdomen capacity minus the weight of stored products, (haemolymph,ovaries and eggs in the oviduct and the food already present in the gut). The model was run at constant temperatures. At 12 °C egg production is 90% higher, at 15 °C 103%, at 19 °C 61%, at 22 °C 44%, at 27 °C 44% and at 30 °C 49% than normal. These results show that the egg production is much higher when MEALW = GUTCAP, but also that the effect depends on temperature. Below 19 °C the effect is generally twice as high than above this temperature. These results show that the earlier termination of ingestion, probably by the action of stretch receptors in the abdomen, before the ultimate gut capacity is reached, exerts a strong influence on ingestion and on egg production. The significance of this behaviour for the beetle can only be guessed. Some beetles which ingested until their abdomen expanded to their ultimate size, and which were placed in cool very moist petri dishes, showed a high mortality. This may be the result of water diffusing into the beetle, leading to a still greater expansion of the abdomen, which was then ruptured. The prevention of this may be one of the functions of the stretch receptors, and this individual survival value outweighs a higher reproduction.

5.2.12 *Dry:fresh weight ratio of the beetle*

In section 3.7 was shown that the dry weight fraction of the beetle increases with body weight, because of the curvilinear relationship between the dry weight of the beetle and its fresh weight. To evaluate the effect of this relationship it was replaced by a constant ratio. The results of the simulation with dry-fresh ratio's of 0.3, 0.4 and 0.5 respectively are given in table 5.3.

TABLE 5.3 The effect of replacement of the curvilinear relationship between dry and fresh weight by constant ratios on consumption and egg production. The effect is given as the fractional difference with simulation results using the standard ('normal') relationship.

Dry:fresh ratio	0.3		0.4		0.5	
Temperature °C	consum	eggpro	consum	eggpro	consum	eggpro
12	−.32	−.40	−.04	−.05	.24	.30
15	−.35	−.37	−.02	−.04	.22	.21
19	−.35	−.37	−.03	−.05	.22	.18
22	−.33	−.36	−.03	−.05	.17	.14
27	−.35	−.38	−.02	−.03	.23	.28
30	−.36	−.34	−.02	−.02	.34	.27

The simulations show that a constant dry:fresh ratio of 0.4 results in a consumption and in an egg production almost equal to the values obtained with the standard relationship. In the latter a dry:fresh ratio of 0.4 is reached as soon as a few meals are consumed after breaking of diapause. Throughout the whole reproduction period this value will fluctuate closely around 0.4. Therefore, only minor differences can be expected when food is offered in excess. When periods of food excess are followed by shortage of food, the curvi) linear relationship will play a more important role. The table also shows that changing the dry:fresh ratio by 25% to 0.3 or to 0.5, has a strong effect on consumption and on egg production. A decrease of the ratio has a stronger effect than an increase.

5.2.13 Duration of oviposition (OVIP)

The length of the oviposition period is the result of egg formation and residence time of eggs in the oviduct. Knowing the length of the oviposition time and the residence time the length of the egg formation period could be estimated. The relationship between temperature and duration of the egg formation period is not linear (table 3.16), which makes extrapolation outside the range of the experiments difficult, especially below 12 °C. In the simulation of egg production at field temperatures the rate of transition of the egg formation period below 12 °C appeared to determine highly the length of the total oviposition period (Table 5.4). By trial and error it was found that a rate of transition of the egg formation period of 0.004 (day^{-1}) at 10 °C gave oviposition periods which agreed best with the experimentally found values in the different years.

When the transition rate through the egg formation period at 10 °C was decreased, both egg production and duration of the oviposition period increased for those years although there seems to be a limit when the rate becomes smaller than 0.0033 day^{-1}.

The conclusion is that the differences in the length of the the oviposition period between the years apparently depend on the number of days after the start of egg formation (that is when daylength exceeds 12 h plus the reaction time) with a temperature below 12 °C.

TABLE 5.4 Duration of oviposition period (days) and size of egg production when different values for the rate of transition of the egg formation period at 10 °C were introduced.

Transition rate of Egg formation at 10 °C. Year	0.01		0.005		0.004		0.0033	
	ovip	eggpro	ovip	eggpro	ovip	eggpro	ovip	eggpro
1978 b	32	47	38	58	44	65	46	68
1979 a	33	75	38	93	40	97	41	102
1979 b	28	47	34	59	36	62	37	66
1982 a	35	124	38	137	39	141	40	144
1985 a	45	112	49	122	52	127	54	133

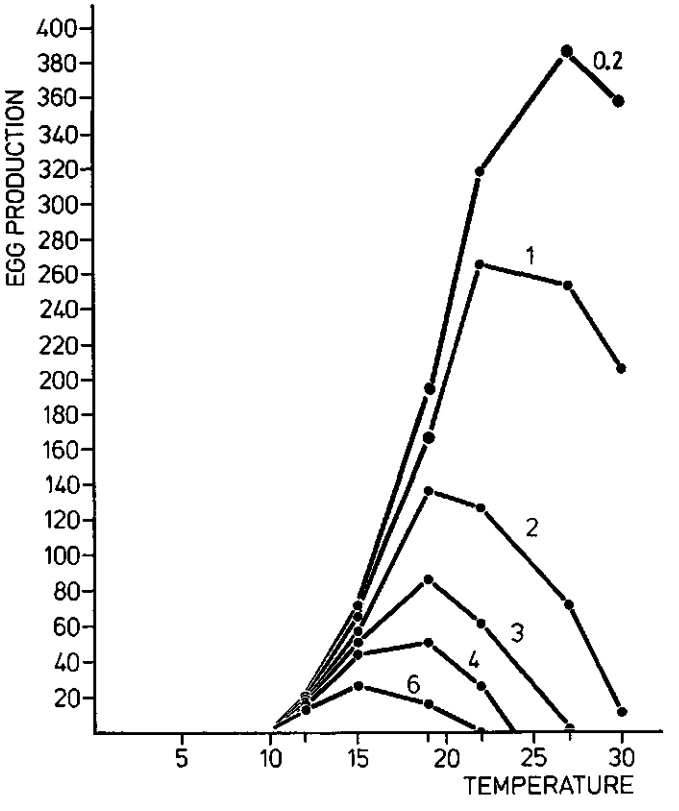


FIG. 5.4. Simulated egg production at constant temperatures but with different intervals of starvation. Feeding varied from 5 times a day (0.2), once per day (1), once per two days (2), once per three days (3), once per four days (4), to once every 6 days (6).

5.2.14 The effect of shortage of food on egg production

Shortage of food was simulated by offering the beetles food in a series of experiments with progressively longer intervals during which they were starved: once every day, or once every two, three, four or six days. The results of the simulation are given in fig. 5.4. This figure clearly shows that the consumption of food strongly influences the number of eggs produced especially at high temperatures, because more food is then needed for respiration. At temperatures under 15 °C periods of starvation longer than a week can be tolerated, with only a slight decrease in egg production.

5.2.15 The threshold for ingestion

The influence of the threshold of the ingestion (CONTD) on food consumption and egg production is estimated by changing the relative satiation level

Table 5.5 The relationship between the threshold for ingestion (CONTD) and the total food consumption (mg), from the start of the simulation until the end of the oviposition period, and egg production at 20 °C.

Threshold	0.1	0.2	0.4	0.6	0.7	0.8	0.9
Egg production	165	182	201	209	211	213	216
Consumption	416	448	479	492	498	504	509

(RSATL) below which ingestion is allowed at the constant temperature of 20 °C. The results of the simulations are given in table 5.5 The results clearly show that when excess of food is offered, changing the threshold for ingestion in the range from 0.9 to 0.4 only had a minor effect on the consumption and egg production. This is because meal size increases when the threshold is lowered, thus compensation occurs. When the threshold becomes lower than 0.4, the compensation by ingestion of a larger meal is less effective and the effect on food consumption and on egg production becomes substantial. If food is limited in size (smaller than the potential meal size), such that compensation by ingestion of a larger meal is only partial, or when food is offered only after specific time intervals, the level of the threshold becomes more important.

6 GENERAL DISCUSSION AND CONCLUSIONS

6.1 THE HUNGER LEVEL

By most authors the hunger level of an arthropod is thought to be only determined by the gut content or by the emptiness of the gut (Holling 1966, Rabbinge 1976, Fransz 1974, Sabelis 1981, Nakamura 1976, Gutierrez et al.,1981). However, this restriction is not appropriate for the carabid beetle *P.coerulescens*. Instead of the single state variable used by these authors, more variables have to be involved in the determination of the hunger level in this beetle.

The state variables gut content, haemolymph, ovarioles, maturing eggs in the oviduct and the quantity of stored products all together determine the hunger level of this beetle. Therefore, the hunger level fluctuates in time to a degree that depends on the combined effect of the changes of these variables.

The rates of change of these variables differ strongly in the course of time depending on the values of the state variables, on the temperature and on the circadian rhythm. Moreover, they are multiple interrelated (see the relation diagram fig 1). Therefore, the ultimate effect on the hunger level can only be estimated with the help of a simulation model.

Changes in these variables do not always have the expected effect (measured in food consumption and egg production) over the whole range of the beetle's weight because of the rigidity of the system (the beetle's body). When almost all the room in the abdomen of the beetle is already occupied, changes in those variables that promote an increase of consumption and/or egg production have less effect than when ample room is available in the abdomen.

The relative hunger level will fluctuate more at high than at low relative body weights (fig 3.4). At net body weights (=fresh body weight with empty gut) below 75% of the maximum weight meals of about 20 mg are needed to satiate the beetle, while with a net body weight above 75% of the maximum weight the meals to satiate the beetle become increasingly smaller. The cause of this phenomenon is that at low body weights the hunger level is predominantly determined by the relative gut content, and at high body weights by the quantity of stored products and the number of maturing eggs. This means that after egg laying the hunger level of the beetle is suddenly increased, which implies that components of behaviour coupled with the hunger level will significantly change after egg laying.

From all this it can be concluded that in beetles which are low in weight the changes of the hunger level are predominantly determined by the degrees of ingestion and egestion. When room in the abdomen becomes limiting, especially the transition rate of eggs through the oviduct and the rate of egg laying become increasingly important, together with changes in the amount of stored products.

The values of the various relative rates differ to such an extent from each other that one may consider food intake to be governed by a combination of long term (storage, usage of fats and respiration) and short term (egestion, egg formation and egg deposition) processes.

For example, respiration depends on both the weight of the beetle and on its physiological stage. To illustrate the latter: at 20 °C in the reproductive period respiration amounts approximately up to 1 mg per day in fresh weight. In the same time 8 eggs per day (=3.2 mg) may be produced, often laid in groups of 2-4 together within half an hour. Egestion may amount up to 7 mg fresh weight for the standard prey (dry:fresh ratio = 0.32). This shows the differences in time constants of the system.

6.2 Food consumption

The food consumption of *P.coerulescens with excess of food and* at a constant temperature, when calculated by the model, can be compared with the results of feeding experiments with other beetles. *P. coerulescens* apparently is a relatively moderate eater, anyhow when compared to the results of the feeding experiments done by Scherney (1959, 1961). In his experiments most carabid beetles took up at least their body weight in food daily. The closely resembling, but slightly larger beetles of the species *P.cupreus* in his experiments consumed up to two times their own initial body weight. However, when the food consumption of P.coerulescens is compared to the data of van Dinther (1966) the daily consumption of the carabids in his experiments was similar to that in our simulations, at least when in the simulation food is offered with a dry:fresh weight ratio equally to that in his experiments. The dry:fresh weight ratio of the prey in the experiments of van Dinther(1966) was 0.16. In our experiments and simulations the food consumption per day of *P. coerulescens* with excess of food is not constant, but changes throughout the reproductive cycle. Just after diapause break, the consumption is highest, approximately 55% of its initial body weight per day. After that period consumption declines rather sharply to 26%, and after the start of egg deposition it increases again to a more or less steady level of 48% of its initial body weight.

In the experiments of van Dinther the daily food consumtion of the carabid beetles *Amara spreta*, *Harpalus rufipes*, and *Harpalus aeneus* was 31%, 28% and 31% of their own initial body weight respectively, when fed with housefly larvae. This consumption is relatively lower than *found in P.coerulescens*. However, other carabid beetles in the same weight range as *P.coerulescens* such as *Pterostichus lepidus* daily consumed 75%, *Calathus erratus* 70% and the smaller *Calathus melanochephalus* 64% of their initial body weight daily. When the model was run with the body size of *P.lepidus* (LEWI = 33 SD = 3 n = 20) also with a dry: fresh ratio of food of 0.16, the simulation with an initial body weight of 90 mg, gave a daily consumption of 60 mg, thus 66.7% of the initial body weight. This is rather close to the experimental results of van Dinther. The model agreed

well because the dry:fresh ratio of the food was known, and because *P.lepidus* is living in the same kind of habitats as *P.coerulescens*, and probably has similar feeding and digestion characteristics. Scherney (1959) gave different kinds of prey such as worms, larvae of the *Colorado potato beetle* and some caterpillars but he did not estimate the dry:fresh ratio's. In the model this ratio influences daily food consumption considerably. If it is halved, daily food consumption almost doubles. Moreover, Scherney did not correct for prey remains in the way Van Dinther did. This may have resulted in a strong overestimation of consumption. Neither did he mention the temperature at which he carried out the experiments, and food consumption is highly temperature dependent.

Another source of error is the loss of fluid from the prey while the predator is eating. This loss should be added up to the prey remains but this is very difficult since it is mostly smeared around. Especially at high prey densities this may give erroneous results because then many preys will be eaten partly only.

All this illustrates how many precautions one has to make to carry out reliable feeding experiments, even in the laboratory, not to mention in the field situation.

6.3 Egg production

In *P.coerulescens* the number of eggs produced per female is a characteristic that varies widely between individuals, but each female has a characteristic level of reproduction which varies only slightly with time (see chapter 4 and Van Dijk ,1979). The differences between internal factors apparently determine the individual level of egg production in the individuals. The importance of the various variables and parameters in this respect was shown by sensitivity analysis. In real beetles changes in parameters and variables will be interconnected, which may lead to an accumulation of effects. This may result in both beetles having high reproductive capacities and beetles which are hardly capable of producing eggs. With the model it is possible to simulate such effects and the whole range of variation in egg production found in real beetles appears to be be simulated by just changing the values of some rate variables. To show this, three rate variables (RRGE, FROFAT and MATT) and two parameters (EFF and MAXOV), which influence egg production most, were simultaneously changed 20% each,an amount of change which is within the standard deviation of their average values. Simulations were also executed with experimentally found but more extreme values of these variables. The results of these simulations are given in table 6.1.

It is shown in table 6.1 that only changing simultaneously the values of the most important factors may increase or decrease the ultimate egg production drastically. The relative ingestion rate and the efficiency determine the quantity of food that can be assimilated per time constant. These rates are strongly affected by the size of the meal and thus by the limits of expansion of the crop. By increasing FROFAT the quantity of stored products is more rapidly used for egg production and more room is available for ingestion. The shorter the residence time of the eggs in the oviduct (MATT) the higher ingestion can be

TABLE 6.1 The effect of a simultaneous change of some variables and parameters on both egg production and on food consumption. Simulation was executed for 20°C.

A: RRGE, EFF and FROFAT times 1.2, MATT and MAXOV times 0.8
B: RRGE, EFF and FROFAT times 0.8, MATT and MAXOV times 1.2
C: Extreme values RRGE times 1.4, FROFAT times 1.5, EFF times 1.3, MATT times 0.5 and MAXOV times 0.7
D: Extreme values RRGE times 0.6, FROFAT times 0.5, EFF times 0.7, MATT times 1.5 and MAXOV times 1.3
Control: All the multiplication factors were 1.
The size of the beetle (LEWI) is kept constant at 22.

	Control	A	B	C	D
Egg production	204	317	118	425	56
Consumption (mg)	482	537	443	545	500

and thus egg production also. The size of the ovaries (MAXOV) determines also the room in the abdomen available for expansion of the crop. If also the food dry:fresh weight ratio is varied and if the length of the oviposition period is changed (the variation in duration of oviposition is approximately 50% of the average) and also beetle size, this will result in still more extreme high or low values for the egg productions per female and per season. In experiments a positive correlation was found between a high daily egg production and the duration of the oviposition period (Chapter 4, Van Dijk, 1979). A 50% longer oviposition period was often found in high egg producers. This implies that in the most favourable combination C total egg production would increase to 630 eggs per female per season at the constant temperature of 20°C. For the worst combination D a shorter oviposition period would decrease total egg production still more until about 30 eggs per female and per season. At higher temperatures individual egg productions varying between 25 and 1000 can be produced in this way.

These examples show that the whole range of egg productions found in *P.coerulescens* by van Dijk, 1979 can be simulated if in the model the appropriate variables and parameters are changed within realistic limits.

6.4 THE GENERALITY OF THE MODEL

In our relatively simple model no neural or endocrinal control mechanisms are explicitly incorporated. But one must be aware that in the relationships found by experiment most of the effects of such mechanisms are involved implicitly. For example, the empirical relationship between body weight and meal size is governed by the action of the stretch receptors in the crop and in the abdomen. Another example is the triggering of egg production by the neuro-endocrinal system as a reaction to day length. Only the ultimate effect, as expressed in time delays, is integrated into the model, not the entire process. It

must therefore be stressed that this model does not provide new insights into the physiological process of egg production. It is just founded on general principles that have been brought together and used to quantify the different rates as well as possible. Hence, this mechanistic model merely describes the main processes involved in the feeding behaviour and production of eggs of an individual beetle. For that purpose it uses the averages of experimentally found values of parameters and variables. The importance of the individual parameters and variables was shown by sensitivity analysis and in the foregoing section.

Since the model is based on general principles it can simply be adapted to other carabid species by just changing certain parameters and thus eventually the relationships between the rate variables and temperature. In most cases the structure of the model will remain the same. However, for the external digesters (*Carabinae* ss), the structure of the model will have to be changed, for they do not have a large crop in which they store their ingested food. They also spend a long time for ingesting their meal (in *Carabus nemoralis* sometimes hours, unpubl obs. by the author). In other *Carabidae* the most important parameters to be changed will be size(LEWI), the maximum weight of the active ovaries (MAXOV), the egg weight (EGGW), the assimilation efficiency of food (EFF) and the dry:fresh ratio of the eggs. The length of the oviposition period in relation to temperature and the temperature threshold for egg development are also important characteristics of a species.

In the *present P.coerulescens* model mostly relative rates (with dimension 1/time) are used. As these describe general physiological processes which can be assumed to be similar in most closely related species, they will not have to be changed.

A simulation with the characteristics of the carabid beetle *Calathus melanocephalus* gave a simulated egg production which was very close to the experimentally found (van Dijk, 1982) numbers. To get that result only size, egg weight, maximum ovarium weight and the duration of the oviposition period were changed.

6.5 The model as an instrument

Since the results of the model correspond reasonably well with both the results from laboratory and those from field experiments it makes sense to assume that the model can be used to predict egg production if the quantity and quality of the ingested prey is known or reversed to estimate the quantity of food of standard quality ingested in the field by the beetle if the egg production and the weight of the beetle are known.

The definition of quality will remain a problem unless besides dry:fresh weight ratios, the fractions of proteins, carbohydrates, lipids, minerals and vitamins in the prey can be quantified and related to the egg production of the beetle. Until that time we will have to work with the dry:fresh ratio of the prey as an index for quality.

The quantity of ingested prey will depend on several variables: prey density, prey availability, prey distribution, the searching behaviour of the beetle and the physiological properties of the beetle as outlined in the motivational state model. If the relationship between the searching behaviour of the beetle and hunger is known it becomes possible to simulate the impact of prey density and spatial distribution of prey on the egg production of the beetle. All kinds of prey distributions should be evaluated, but it is hardly possible to carry this out in the field or even in an arena in the laboratory because the borders of the arena will seriously disturb the behaviour (edge effects).

In natural situations it will be extremely difficult to get insight into the quantity and distribution of prey. If we collect potential prey in the field we do that in a way which differs completely from the beetle's way, because our perception and instrumentation differ. Thus, if we use the beetle as a 'collector' it will give us a less biased view into the availability of food for the beetle. The output of the beetle is not prey quantity, however, but a conversion of prey into body weight and into egg production. By using these variables with the model it is possible to estimate the quantity of food ingested.

The model may also be used to estimate the role carabids may play as predators in agricultural fields. In such systems the numbers of pest insects often can be estimated somewhat easier than in more natural situations; the numbers of carabids can be estimated by pitfall trapping. If the model is adapted for the carabid species concerned the predation over a season can be simulated and the role of these species can be assessed.

For these purposes the relationships between the most important components of searching behaviour and the hunger level will have to be estimated. That will be discussed in the next article.

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REFERENCES

ANDERSON, J.M., 1972. Food and feeding of Notiophilus biguttatus F. (Coleoptera, Carabidae) Rev. Ecol.Biol.Sol.9,177-184.

BAARS, M.A., 1979.Patterns of movement of radio-active carabid beetles. Oecologia, 44,125-140.

BAARS, M.A., 1982. Running for life. Studies on the locomotory activity and population dynamics of Pterostichus versicolor Sturm and Calathus melanocephalus L. (Coleoptera, Carabidae). Phd thesis, VU Amsterdam.

BAARS, M.A., VAN DIJK,TH.,S., 1984a. Population dynamics of two carabid beetles at a Dutch heathland. I. Subpopulation fluctuations in relation to weather and dispersal. J.Animal. Ecol.,53, 375-388.

BAARS, M.A., VAN DIJK,TH.,S., 1984b. Population dynamics of two carabid beetles at a Dutch heathland. II. Egg production and survival in relation to density. J.Animal. Ecol.,53, 389-400.

BANKS, C.J., 1957. The behaviour of individual coccinellid larvae on plants. J.Anim.Behav.5, 12-24.

BARTON BROWNE, L.,1975. Regulatory mechanisms in insect feeding. Adv. Insect Physiol. 11,1-116.

BASEDOW, T., 1973. Der Einfluss epigaischer Raubarthropoden auf die Abundanz phytopfager Insekten in der Agrarlandschaft. Pedobiologia,13,410-422.

BAUST, J.G. and MILLER, L.K., 1970. Variations in glycerol content and its influence on cold hardiness in the Alaskan carabid beetle Pterostichus brevicornis. J.Insect Physiol.10,979-990.

BELL, W.J. and BOHM, M.K., 1975. Oösorption in insects. Biol.Rev.50,373-396.

BERNAYS, E.A., 1985. Regulation of feeding behaviour. In: Insect physiology, biochemistry and pharmacology. G.A.Kerkut and L.T.Gilbert (eds). Vol. 4 ,1-32

BERNAYS, E.A. and SIMPSON, S.J.,1982. Control of food intake. Adv Insect Physiol. 16,59-118.

BEUKEMA, J.J., 1968. Predation by the three-spined stickleback (Gasterosteus aculeatus L.): The influence of hunger and experience. Behaviour, 30,1-126.

BLISS, C.I., 1971. The aggregation of species within spatial units. In: Statistical Ecology. G.P.Patil, E.C. Pielou, W.E.Waters (eds), Penn. State Statistical Series,1; 311-335.

BOOTH, D.A., 1978. Hunger models; computable theory of feeding control. Acad. Press London.

COAKER, T.H. and WILLIAMS, D.A., 1963. The importance of some Carabidae and Staphylinidae as predators of the Cabbage root fly Erioschia brassicae (Bouche).Ent.Exp.Appl. 6,156-164.

COOK, R.M., and HUBBARD, S.F., 1977. Adaptive searching strategies in insect parasites. J.Anim. Ecol.46,115-125.

CROZE, H., 1970. Searching image in carrion crows. Z.Tierpsychol. 5:(suppl.),1-86.

DAVEY, K.G. and TREHERNE, J.E.,1963. Studies on crop function in the cockroach (Periplaneta americana L.) I. The mechanism of crop emptying. J.Exp. Biol.40,763-773.

DAVIES, M., 1953. The contents of crops of some British carabid beetles. Entomol. Mon.Mag.89,18-23.

DAWKINS, M., 1971a. Perceptual changes in chicks, another look at the 'search image' concept. Anim. Behaviour, 19,566-574.

DAWKINS, M., 1971b. Shifts of 'attention' in chicks during feeding. Anim.Behaviour. 19,575-582.

DETHIER, V. G., 1976. The hungry fly. Harvard University press, Cambridge. Mass.

DICKE M., 1988. Infochemicals in tritrophic interactions PH.D thesis, Agricultural University Wageningen, pp. 235.

DINTHER, J.B.M.,1964. Studies on the starvation capacities of some carabid species. Med. Rijksfac. Landbouwwet. Gent,29(3),1088-1096.

DINTHER, J.B.M. van, 1966. Laboratory experiments on the consumption capacities of some carabidae. Meded. Rijksfac. Landbouwwetensch Gent,31,730-739.

DINTHER, J.B.M.VAN, and MENSINK, F.T., 1965. Egg consumption by Bembidion ustulatum and Bembidium lampros (fam. Carabidae) in laboratory prey density experiments with house fly eggs. Mede. Landbouw Hoogesch. Opzoekstns. Gent.30,1542-1554.

DINTHER, J.B.M. VAN, and MENSINK, F.T.,1971. Use of radio active phosphorus in studying egg predation by carabids in cauliflower fields. Med. Fak.Landbouwwetensch. Gent.36,283-293.
DIXON, A.F.G., 1958. A study of the searching behaviour of certain insects feeding on aphids. D.Phil.Thesis, Oxford.
DIJK TH.,S.VAN, 1979a. On the relationship between reproduction,age and survival in two carabid beetles:Calathus melanocephalus L. and Pterostichus coerulescens L. (Coleoptera,Carabidae). Oecologia, 40,63-80.
DIJK, TH.,S. VAN, 1979b. Reproduction of young and old females in two carabid beetles and the relationship between the number of eggs in the ovaries and the number of eggs laid. Misc.Pap. Landbouwhogeschool, Wageningen.18,167-183.
DIJK, TH.,S. VAN, 1982. Individual variability and its significance for the survival of animal populations. In: Environmental Adaptation and Evolution. D.,Mossakowski and G. Roth (eds.). Gustav Fischer, Stuttgard,New York, 233-251.
DIJK, TH.,S. VAN, 1986. On the relationship between availability of food and fecundity in carabid beetles: How far is the number of eggs in the ovaries a measure of the quantities of food in the field. In: Feeding behaviour and accessibility of food for carabid beetles. P.J.den Boer, L.Grum and J.Szyszko (eds.), Rep. fifth meeting of European Carabidologists. Warsaw Agric. Univ.-SGGW-AR,105-121.
DUBROVSKAJA, N.A., 1970. Field carabid beetles (Coleoptera, Carabidae) of Byelorussia. Entomol. Rev.49,476-483.
DUNCAN, A. and R.Z. KLEKOWSKI, 1975. Parameters of an energy budget: (in: Methods for ecological Bioenergetics, eds. Grodzinski et al.) Int. Biol Programme Handbook no 24, Blackwell, Oxford, 97-147.
EDWARDS, C.A., K.D.SUNDERLAND and K.S.GEORGE, 1979. Studies on polyphagus predators of cereal aphids. J. Appl. Ecol. 16,811-823.
ENGELMANN, F., 1968. Feeding and crop emptying in the cockroach Leucophaea maderae. J. Insect Physiol. 14,1525-1532.
ENGELMAN, F.,1970. The physiology of insect reproduction. Pergamonn press., Oxford.
ERNSTING, G.,1978. Predation of springtails.Phd Thesis VU Amsterdam, Drukkerij Ernsting, Wageningen, p.88
ERNSTING,G., and F.A.HUYER. 1984. A laboratory study on temperature relations of egg production and development in two related species of carabid beetle. Oecologia. 62(3), 361-367.
EVANS, D.R. and BARTON BROWNE L., 1960. The physiology of hunger in the blowfly. Am Midl. Nat. 64, 282-300.
EVANS, H.F., 1976. The searching behaviour of Anthocorus confusus (Reuter) in relation to plant density and plant surface topografy. Ecol.Ent.1, 163-169.
EVANS, M.E.G., 1965. A comparative accounty of the feeding methods of the beetle Nebria brevicollis (F.) (Carabidae) and Philonthus decorus (Grav.) (Staphylinidae). Trans Roy.Soc.Edinburgh.LXVI.(1963064), 91-109.
FERENZ, H.J.,1977. Two-step photoperiodic and hormonal control of reproduction in the female beetle Pterostichus nigrita. J.Insecty Physiol. 23,671-676.
FLESCHNER, C.A., 1950. Studies on the searching capacity of the larvae of three predators of the Citrus red mite. Hilgardia,20, 233-264.
FORRESTER, J.W., 1961. Industrial Dynamics. MIT-press, Boston.
FRANK, J.H., 1967a. The insect predators of the pupal stage of the wintermoth, Operophtera brumata (L.) (Lepidoptera:Hydriomenidae). J.Anim.Ecol. 36,375-389.
FRANK, D.H., 1967b. The effect of pupal predators on a population of wintermoth, Operophtera brumata (L.)(Hydriomenidae). J.Anim.Ecol. 36,611-621.
FRAENKEL, G.S and GUNN, D.L., 1940. The Orientation of Animals. Oxford Book, New York.
FRANSZ, H.G., 1974. The functional response to prey density in an acarine system.Simulation Monographs, PUDOC, Wageningen,149 p.
FREUDE, H., HARDE, K.W. and LOHSE, G.A., 1965. Die Kafer Mitteleuropas (Band 2,Adephage I). Goeche and Evers, Krefeld.
GANAGARAJAH, M.,1965. The neuro-endocrine complex of adult Nebria brevicollis F. and its relation to reproduction. J. Insect Physiol.11,1377-1387.

GELPERIN, A.,1966. Control of crop emptying in the blowfly. J. Insect Physiol. 12,331-345.
GELPERIN, A., 1971a. Abdominal sensory neurones providing negative feedback to feeding behaviour of the blowfly. Z.Vergl.Physiol. 72,17-31.
GELPERIN, A.,1971b. Regulation of feeding. Ann.Rev.Ent.16,365-378.
GELPERIN, A., 1972. Neural control systems underlying insect feeding behaviour. Am.Zool.12,489-496.
GORDON, H.T.,1972. Interpretations of insect quantitative nutrition. In: Insect and Mite Nutrition. Rodriguez J.G. (ed.), North-Holland Publishing, Amsterdam,pp 73-105.
GOSS-CUSTARD, J.D., 1970. Feeding dispersion in some overwintering wading birds. In Social Behaviour in Birds and Mammals: Essays on the Social Ethology of Animals and Man. Ed J.H. Crook. pp.3-65. Academic Press, London.
GREEN, G.W., 1964a. The control of spontaneous locomotor activity in Phormia regina Meigen – I. Locomotor patterns in intact flies. J.Insect Physiol.10,727-752.
GREEN, G.W., 1964b. The control of spontaneous locomotor activity in Phormia regina Meigen. – II.Experiments to determine the mechanisms involved. J. Insect Physiol.10,711-726.
GREENSLADE, P.J.M., 1963. Daily rhythms of locomotory activity in some carabidae. (Coleoptera). Ent.Exp.Appl.6,171-180.
GRUM, L., 1966. Diurnal activity rhythm of starved Carabidae. Bull. Acad. Polon. Sci. Sect. Sci Biol., 14; 405-411.
HAFEZ, M.,1961. Seasonal fluctuations of population density of the cabbage aphid Brevicorine brassicae (L.) in the Netherlands and the role of its parasite Aphidius (Diaretiella) rapae (Curtis). Tijdschr. Plantenziekten 67,445-548.
HASSEL, M.P., 1976. The dynamics of competition and predation. London, Arnold, pp.68.
HASSEL, M.P., LAWTON, J.H. and J.R. BEDDINGTON, 1976. The components of arthropod predation. I. The prey death rate. J. Anim. Ecol.45,135-164.
HASSEL, M.P., and MAY, R.M., 1974. Aggregation in predators and insect parasites and its effect on stability. J.Anim. Ecol.,43;693-726.
HEESSEN, H.J.L., 1980. Egg production of Pterostichus oblongopunctatus (Fabricius) (Col. Carabidae) and Philonthus decorus (Gravenhorst) (Col. Staphylinidae). Neth. J. of Zool. 30(1),35-53.
HEESSEN, H.J.L., 1981, On reproduction and survival in two ecolologically related beetle species of the forest floor. Phd Thesis, R.U. Utrecht.
HENGEVELD, R., 1979. The analysis of spatial patterns of some ground beetles (Col. Carabidae). Statistical Ecology Series vol.8, 333-3465
HENGEVELD, R.,1980. Poliphagy, oligophagy, and food specialisation in groundbeetles (Coleoptera, Carabidae). Neth.J. Zool.,30(4), 564-584.
HEYDEMANN, B.,1955. Zur Systematik und Ocologie von Pterostichus cupreus und coerulescens (Col. Carabidae). Bonn. Zool.Beitr. 6,235-239.
HEYDEMANN, B.,1957. Die Biotopstructur als Raumwiderstand und Raumfulle fur die Tierwelt. Verh.Deut.Zool.Ges. Hamburg,1956,332-247.
HILL, L., LUNTZ, A.J. and STEELE, P.A., 1968. The relationship between somatic growth,ovarian growth and feeding activity in the adult desert locust. J.Insect Physiol. 14,1-20.
HOLLING, C.S., 1959. Some characteristics of simple types of predation and parasitism. Can.Entomol. 91, 385-398.
HOLLING, C.S., 1963. An experiment component analysis of population processes. Mem.Entomol. Soc. Can.32,22-32.
HOLLING, C.S., 1966. The functional response of invertebrate predators to prey density. Memoires Entomol.Soc. Canada, no 48,86 p.
JOHANSSON, A.S., 1964. Feeding and nutrition in reproductive processes in insects. In: Insect Reproduction ed. K.C. Highram symp. Royal Entomol. Soc. 2nd. London, 43–55.
JOHNSON, D.M., AKRE, B.G. and P.H. CROWLEY, 1975. Modelling arthropod predation: Waste full killing by damselfly Naids. Ecology 56,1082-1093.
JOLY, P., 1945. La fonction ovarienne et son control humorale chez les Dytiscides. Archives de zoologie experimentale et generale, 84; 49.
JOLY, P., 1950. Fonctionnement ovarien des Carabes. Comptes rendus des seances de la Societe de Biologie, 144;1217-1220.

KABACIK-WASYLIK, D. and B. STEYGWILLO-LAUDANSKA, 1971. Starvation and the average survival time of Carabidae. Ekol. Pol. 19,419-425.

KÖNEN, J., 1978. Physiologisch-okologische Untersuchungen zur steuerung der Gonadenreifung und Fortplanzungsperiodik von Pterostichus oblongopunctatus F. (Coleoptera, Carabidae) in Abhangigkeit von Temperatur, Fotoperiode und Juvenilhormon. Inaugural-Dissertation der Universitat zu Koln.

KITTEL, A., 1941. Korpergrosse, Korperzeiten und energiebalans.II. Der Sauerstoffverbrauch de Insekten in abhangigkeit von der Korpergrosse. Z.Vergl.Physiol. 28,533.

KREBS, J.R., 1973. Behavioural aspects of predation. In perspective in ethology (P.P.G.Bateson, Klopfer P.H. eds.) New York,Plenum Press,73 p. Krebs, J.R.,Ryan,J.C. and Charnov,E.L.,1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. J. Anim. Behav. 22,953-964.

KREHAN, I.,1970. Die steuerung von Jahresrhytmik und Diapause bei Larval- und Imagouberwintern de Gattung Pterostichus (Col.,Carab.). Oecologia (Berl.),6;58-105.

LAING, J., 1938. Host finding by insect parasites.II. The change of Trichogramma evanescens finding its host. J.exp.Biol.,15,281-302.

MAC FADYEN, A., 1967. Methods of investigation of productivity of invertebrates in terrestrial ecosystems. (in: Secondary productivity of terrestrial ecosystems pp. 383-412, ed. K. Petrusewicz) Warszawa-Krakow: Polish. Acad. Sci.

LAROCHELLE, A., 1974a. Carabid beetles (Coleoptera,Carabidae) as prey of North American frogs. Gt. Lakes Entomol.7,147-148.

LAROCHELLE, A., 1974b. The American toad as champion carabid beetle collector. Pan-Pacif. Entomol. 50,203-204.

LAROCHELLE, A., 1975a. A list of mammals as predators of carabidae. Carabologia. 3,95-98.

LAROCHELLE, A., 1975b. A list of amphibians and reptiles as predators of North American Carabidae. Carabologia 3,99-103.

LUFF, M.L., 1974. Adult and larval feeding habits of Pterostichus madidus (F.)(Coleoptera,Carabidae). J. Natur.Hist.8,403-409.

MACNAB, R.M. and KOSHLAND, D.E., 1972. The gradient-sensing mechanism in bacterial chemotaxis. PNAS 69,2509-2512.

MANGA, N., 1972. Population metabolism of Nebria brevicollis (F.) (Coleoptera,Carabidae). Oecologia (berl.) 10,223-242.

MATHAVAN and MUTHUKRISHNAN, 1980. Use of larval weight and length as indices of gut content weight in some lepidopterous larvae. Oecologia (Berl.),44,317-318.

MITCHELL, B., 1963. Ecology of two carabid beetles Bembidion lampros (Herbst) and Trechus Quadristriatus (Schrank).I. Life cycles and feeding behaviour. J. Anim. Ecol.,32, 289-299.

MOLS, P.J.M., 1986. Predation in the carabid beetle *Pterostichus coerulescens* L. In:Feeding behaviour and accessibility of food for carabid beetles. P.J.den Boer, L.Grum and J.Szyszko (eds.), Rep. fifth meeting of European Carabidologists. Warsaw Agric. Univ.-SGGW-AR,49-58.

MOLS, P.J.M., VAN DIJK, TH.S. and Y. JONGEMA, 1981. Two laboratory techniques to separate eggs of carabids from a substrate. Pedobiologia,21, 500-501.

MURDIE, G., 1971. Simulation of the effects of predator/parasite models on prey/host spatial distribution. In: Statistical ecology.vol.1.(G.P.Patil, E.C. Pielou and W.E. Waters (eds)). Univ. Park.-Penn. State stat.series,215-233.

MURDIE, G., HASSEL, M.P., 1973. Food distribution, searching succes and predatory prey models. The matematical theory of biological populations. Academic Press, London,87-101.

MURDOCH, M.W. and OATEN A. 1975. Predation and population stability. In Advances in Ecological Research, ed. Mac Fadyen, 1-131. London, Academic Press.

NAKAMURA, K., 1968. The ingestion of wolf spiders.I. Capacity of gut of Lycosa pseudoannulata. Res.Popul. Ecol.10,45-53.

NAKAMURA, K., 1972. The ingestion in Wolf Spiders II. The expression of degree of hunger and amount of ingestion in relation to spiders hunger. Res. Popul. Ecol. 14,82-96.

NEUDECKER, C., THIELE, H.U., 1974. Die jahreszeiliche Synchronisation der Gonadenreifung bei Agonum assimile Payk. (Coleoptera,Carabidae) durch Temperatur und Photoperiode. Oecologia (berl.) 17,141-157.

OSBORNE, M.P. and FINLAYSON, L.H., 1962. The structure and topography of stretch receptors in representives of seven orders of insects. Quarterly Journal of Microscopical Science, 103, 227-42.
PAK, G.A., 1988. Selection of Trichogramma for inundative biological control. Ph.D thesis, Agricultural University Wageningen, pp. 224.
PENNEY, M.M., 1966. Studies on certain aspects of the ecology of Nebria brevicollis (F.) (Coleoptera,Carabidae). J.Anim.Ecol.35,505-512.
PENNEY, M.M., 1969. Diapause und reproduction in Nebria nebricollis (F.) (Coleoptera, Carabidae). J.Anim.Ecol. 38,219-233.
PETRUSEWICZ, K., 1967. Conceps in studies on the secondary productivity of terrestrial ecosystems. (in: Secondary productivity of terrestrial ecosystems pp.17-49, ed K. Petrusewicz). Warzawa-Krakow. Polish Acad. Sci.
PHILLIPSON, J., 1962. Respirometry ans the study of energy turn over in natural systems with particular reference to harvest spiders (Phalangiidae). Oikos, 13, 311-322.
PHILLIPSON, J. and WATSON, J., 1965. Respiratory metabolism of the terrestrial isopod Oniscus asellus L. Oikos, 16, 78-87.
RABBINGE, R., 1976. Biological control of the fruit-tree spider mite. Simulation Monographs. Pudoc Wageningen.
RIVARD, I., 1965. Dispersal of groundbeetles (Coleoptera: Carabidae) on soil surfaces. Can. J.Zool.43,465-473.
ROYAMA, T., 1970. Factors governing the hunting behaviour and food selection of the great tit (Parus major). J. Anim. Ecol.39,619-688.
ROYAMA, T., 1971. Evolutionary significance of predators response to local differences in prey density: a theoretical study. In P.J. den Boer and G.R. Gradwell (eds.). Proc.Adv.Study Inst. Dynamics Numbers Popul. Oosterbeek,344-357.
REICHLE, D.E., 1968. Relation of body size to food intake, oxygen consumption, and trace element metabolisme in forest floor arthropods. Ecology,49, 3, 538-542.
RUITER, L. DE, 1963. The physiology of vertebrate feeding behaviour towards a synthesis of the ethological and physiological approaches to problems of behaviour. Z. Tierpsychology 20,498-516.
SABELIS, M.W., 1981. Biological control of two-spotted spider mites using phytoseiid predators. Part I. Agricul. Research Rep. 910, Pudoc Wageningen, 242 p.
SANDNESS, J.N. and MC MURTRY, J.A.,1970. Functional response of three species of Phytoseiidae (acarina) to prey density. Can.Ent. 102,692-704.
SCHERNEY, F. 1955. Untersuchungen uber Vorkommen un Wirtschaftliche Bedeutung rauberisch lebender Kafer in Feldkulturen. Z.Pflanzenbau Pflanzenschutz 6,49-73.
SCHERNEY, F., 1960. Beitrage zur biologie und oconomische Bedeutung rauberisch lebender Kaferarten. (Untersuchungen uber das auftreten von Laufkafern (Carabidae) in Feldculturen. (Teil II). Z.Angew.Entomol. 47,231-255.
SCHERNEY, F.,1961. Beitrage zur Biologie un economische Bedeutung rauberisch lebender Kaferarten. (Beobachtungen und Versuche zur Uberwinteriung, Aktivitay und Ernarungsweise der Laufkafer (Carabidae) Teil III). Z.Angew. Entomol. 48,163-175.
SCHMIDT, G., 1956. Der Stoffwechsel de Carabiden (Ins. Coleopt.) und seine beziehungzum wasserhaushalt. Zool. Jb.Abt.Physiol., 66, 273-294.
SKUHRAVY, V., 1959. Die Nahrung der Feldcaraben. Acta Soc. Entomol.Csl,56,1-18.
SMIT, H., 1957, Onderzoek naar het voedsel van Calathus erratus Sahlb. en Calathus ambiguus Payk. aan de hand van hun magen. Entomol berichten. Amsterdam 17,199-209.
SMITH, J.N.M., 1974. The food searching behavior of two European thrushes. I. Description and analysis of the search path. Behavior 48,276-302.
SMITH, J.N.M. 1974. The food searching behavior of two European thrushes. II. the adaptiveness of the search patterns. Behavior 49, 1-61.
SMITH, J.N. and SWEATMAN, H.P.A. 1974. Food-searching behaviour of titmice in patchy environments. Ecology 55,1216-1232.
SOUTHWOOD, T.R.E., 1966. Ecological methods. Methuen, London, 391 pp.
SUNDERLAND, K.D. and G.P. VICKERMAN, 1980. Aphid feeding by some polyphogous predators in relation to aphid density in cereal fields. The journal of applied Ecology, 17(2), 389-391.

SUNDERLAND, K.D., CHAMBERS, R.J., STACEY D.L. and CROOK N.E., 1985. Invertebrate polyphagous predators and cereal aphids. IOBC-WPRS Bulletin VIII/3, 105-115.
TAYLOR, R.J., 1977. The value of clumping to prey. Experiments with a mammalian predator. Oecologia (berl.)30,285-294.
STOFFELANO, J.G.,1974. Control of feeding and drinking in diapausing insects. In Experimantal Analysis of insect behaviour. L Barton browne (ed.). Springer Verlag. 32-47.
THIELE, H.U., 1977. Carabid beetles in their environments. Springer Verlag, Heidelberg, 369 pp.
THOMSON A.J. and HOLLING, C.S., 1977. A model of carbohydrate nutrition in the blowfly Phormia regina (Diptera,Calliphoridae). Canad.Ent.109,1181-1189.
TINBERGEN, N., IMPEKOVEN, M. and D. FRANCK, 1967. An experiment on spacing out as a defence against predation. Behaviour,28,307-321.
TREHERNE, J.E., 1967. Gut absorption. Ann. Rev. Entomol. 12,43-58.
TROMBULAK, S.C. and KENAGY, G.K.,1980. Effect of seed distribution and competitors on seed harvesting efficiency in Heteromyid rodents. Oecologia (Berl.) 44, 342-346.
VARLEY, G.C., GRADWELL, G.R. and M.P.HASSEL, 1973. Insect population ecology: an analytical approach. Blackwell, Oxford.
WAAGE, J.K., 1979. Foraging for patchily-distributed hosts by the parasitoid Nemerites canescens. J.Anim.Ecol.,48, 353-371.
WALDBAUER, G.P., 1968. The consumption and utilisation of food by insects. Advances in Insect Physiology 5, 229-288.
WEIDEMANN, G., 1971a. Food and energy turn over of predatory arthropods of the soil surface. Ecol studies, 2, 110-118.
WEIDEMANN, G., 1971b. Zur biologie von Pterostichus metallicus F. (Coleoptera, Carabidae). Faun. Okol. Mitt.,4, 30-36.
WEIDEMANN, G., 1972. Die Stellung epigaischer Raubarthropoden im Okosystem Buchenwald. Verh.Dent Zool. ges. Helgold, 106-116.
WISHART, G., DOANE, J.F., and MAYBEE, G.E., 1956. Notes on beetles as predators of eggs of Hylemya brassicae (Bouche')(Diptera, Anthomyidae), Can.Ent., 88,634-639.
WIT, C.T., DE, GOUDRIAAN, J., 1978. Simulation of ecological processes. Ecological Monographs, Pudoc, Wageningen, 175 pp.
ZINKLER, D., 1966. Vergleichende Untersuchungen zur Atmungs-physiologie van Collembolen (Apterigota) und andere Boden klein Arthropoden. Z.vergl. Physiol.,52, 99-144.

APPENDIX I

The simulation model in this study is constructed according to the state variable approach (Forrester,1961; De Wit & Goudriaan,1978). The simulation language used is CSMP (Continuous System Modelling Program).

A characteristic of this approach is the implicit assumption that the state of an ecosystem at any particular time can be expressed quantitatively and that the changes in the system can be described by mathematical terms. The rates of change of the state variables between time t and time t+dt are calculated from the conditions at time t, or from other historical and environmental data. After calculation of the rates the changes of the states are executed by semi parallel integration over a small time interval. The length of this time interval (DELT) depends on the smallest time coeficient of the system.

This must be at least so short that the assumption that the rates are more or less constant is valid. The time interval is kept at a fixed value during the whole simulation. As integration method the Eulerian or rectilinear integration is used, which means that the new value of the state equals the sum of the old value plus the product of the rate of change and the time interval.

The model of the motivational state is constructed for an individual beetle. It is deterministic in its calculation of the internal flow of material. The values used to quantify the variables in the simulation model for the motivational state are the averages of the experiments described in the previous sections.

THE MODEL.

```
TITLE EGG PRODUCTION OF P. COERULESCENS 1985
***   THIS PROGRAM SIMULATES THE EGG PRODUCTION OF THE GROUNDBEETLE
***   PTEROSTICHUS COERULESCENS IN RELATION TO TEMPERATURE AND FOOD
FIXED INDEX,N,I,K
STORAGE MXTT(200),MNTT(200)
STORAGE EGG(11)
***
INITIAL
***TEMPERATURES

***   THE MAXIMUM AND MINIMUM TEMPERATURES AT EELDE (DRENTE) 1985
**
***   START AT 21 MARCH 1985 (DAY NUMBER 80), END OF TABLE 31 AUGUST
**
***
TABLE MXTT(1-164)=
  9.6,13.3,10.6,9.5,9.5,10.4,6.9,5.9,7.3,10.2, ...
  12.0,14.5,13.7,18.2,18.5,16.1,15.2,12.6,10.6,9.6,9.9, ...
  11.1,9.2,10.6,9.3,10.2,11.0,15.6,15.6,19.2,9.6, ...
  13,0,11.5,8.4,9.8,6.7,7.7,7.8,7.5,8.1,11.4, ...
  10,0,8.0,8.5,9.5,13.8,20.0,20.5,19.6,20.4,13.1, ...
  14.5,18.0,15.7,22.5,22.5,20.0,18.6,16.6,21.9,23.0, ...
  23.6,13.6,10.2,18.5,21.5,29.1,31.0,19.4,15.1,17.0,21.0, ...
  21.0,22.3,25.3,29.0,20.9,14.9,16.0,13.4,13.5,14.0, ...
  15.8,14.3,14.9,13.4,13.0,14.4,13.8,17.7,20.0,18.9, ...
  19.9,18.9,15.6,19.1,17.0,14.0,15.5,15.3,17.0,19.4, ...
  18.4,19.0,20.3,26.1,27.3,19.6,20.1,16.9,18.6,17.8, ...
  21.4,20.7,27.2,28.6,20.0,16.3,21.0,23.9,19.8,18.4, ...
  17.9,17.7,20.2,24.9,22.1,22.8,19.5,23.6,20.9,16.6,17.2, ...
  17.0,17.4,18.4,16.1,18.8,18.0,19.0,20.2,25.2,17.2, ...
  20.9,21.2,23.5,29.6,22.5,21.3,18.7,19.0,19.3,19.5, ...
  19.9,19.4,18.4,17.0,18.6,17.7,19.4,22.2,24.1,25.2,20.0

TABLE MNTT(1-164)=
  1.1,1.5,1.5,3.3,3.1,5.0,0.7,0.5,0.8,6.8, ...
  7.5,7.4,6.4,5.1,11.2,11.4,8.5,8.0,8.1,6.5,4.7, ...
  5.0,5.0,4.9,5.6,5.5,5.4,7.0,2.9,3.3,4.2, ...
  3.5,3.9,0.3,-1.9,1.6,-0.6,0.2,2.2,0.5,-0.1, ...
  4.7,2.5,4.9,3.4,5.3,8.6,9.4,10.0,8.6,8.2, ...
  8.6,9.0,9.6,9.0,8.0,8.6,7.9,8.0,9.9,12.0, ...
  10.2,9.7,5.9,7.2,12.0,11.9,15.7,9.1,7.6,6.4,3.3, ...
  9.0,7.6,5.9,11.5,12.6,10.4,9.0,5.1,6.4,9.2, ...
  6.4,9.4,8.2,5.9,5.8,4.1,5.6,6.0,9.0,10.0, ...
```

```
  6.9,10.1,10.1,8.5,8.5,7.2,6.2,9.1,10.7,11.4, ...
  10.6,8.6,7.2,11.9,14.7,8.5,7.0,8.0,12.7,10.3, ...
  9.3,14.4,14.0,16.3,10.2,10.8,10.6,13.0,11.8,9.1, ...
  8.8,10.9,10.5,9.4,12.5,13.7,12.4,11.7,13.5,12.8,13.5, ...

  9.7,10.8,10.1,9.6,11.9,8.8,8.8,12.5,12.7,10.7, ...
  9.8,11.7,10.8,13.5,10.5,10.6,10.0,9.4,11.1,14.0, ...
  11.6,11.3,13.0,13.3,11.0,8.5,7.5,11.2,14.6,12.5,11.8

***  INITIAL VALUES
***
START=80

TEMP= 0.
      DELX =1./DELT
PARAM MDAY =14.
PARAM PREY =50.
      EGGPRO=0.
PARAM F1=1.
PARAM EFF =.5
PARAM DEGGW=.23
PARAM FEGGW =.4
PARAM CRTEMP=8.
PARAM CRDAYL=12.
INCON EGGPRO=0.
INCON EGGOV =0.
INCON DEGGOV=0.

***  RATIO DRY TO FRESH WEIGHT OF EGGS
      DFREGG=DEGGW/FEGGW
      FDREGG=FEGGW/DEGGW

***  THE QUALITY OF THE PREY EXPRESSED IN DRY FRESH RATIO
PARAM DFRPR=.32
      FDRPR=1./DFRPR

***  SIZE AND SPACE IN ABDOMEN AND GUT
**PARAM LEWI =(18.,20.,22.,24.)
PARAM LEWI=22.7
      MAXFW  =EXP(.07*LEWI+2.831)
      MINFW  =EXP(.062*LEWI+2.297)
      ABDOM =MAXFW-MINFW
      MAXGUT=0.6*ABDOM
      MAXOV=.12*MAXFW
```

```
***   ALL THE EGG CLASSES ARE SET AT ZERO
NOSORT

      DO 222 I=1,11
      EGG(I) =0
 222  CONTINUE
SORT
*****************************************************************

DYNAMIC

***   COUNTING THE DAYS FOR THE MAXT AND MINT TABLES.
NOSORT
      K=TIME+1+START-80
      MAXT=MXTT(K)
      MINT=MNTT(K)
SORT

***   THE SPACE IN THE GUT IS LIMITED BY THE MAXIMUM EXTENSION
***   OF THE CROP OR BY THE SPACE LEFT BY THE OTHER ORGANS

      GUTCAP=AMIN1(MAXGUT,SPACE)
            SPACE =AMAX1(0.,ABDOM-(OVAR+EGGOV+FAT+HEMO))

***   THE GUT IS NOT COMPLETELY FILLED WHEN THE BEETLE CEASES INGESTION

NOSORT
      MEALW=.7*MAXGUT

***   THE MEAL SIZE DEPENDS ON THE REPRODUCTIVE STATE OF THE BEETLE
        IF(OVIP.EQ.0) MEALW=.85*MAXGUT

***   THE MEAL SIZE DEPENDS ON AN EXPERIMENTALLY FOUND RELATIONSHIP
        IF (GUTCAP.LT..85*MAXGUT) MEALW=2*GUTCAP-MAXGUT
        IF (GUTCAP.LT..5*MAXGUT) MEALW=0.
SORT
***   THE POTENTIAL SIZE OF THE MEAL DEPENDS ON THE GUT CONTENT ALSO
        PMEAL =AMAX1(0.,MEALW-GUTCON)

***   THE RELATIVE SATIATION LEVEL
      RSATL =LIMIT(0.,1.,GUTCON/(.00001*NOT(MEALW)+MEALW))
      HUNGER=1.-RSATL
***   THE GUT CONTENT RELATIVE TO THE GUT CAPACITY
      RELGUT =LIMIT(0.,1.,GUTCON/GUTCAP)
*****************************************************************
```

```
***
***   PREY CONSUMPTION
***
***   TIME OF FEEDING

***   DURING THE NIGHT THE BEETLE IS NOT ACTIVE
       A=INSW(HOUR-5.,0.,INSW(21.-HOUR,0.,1.))
***   THE BEETLE STARTS EATING WHEN RSATL IS SMALLER THAN THE THRESHOLD
***   FOR INGESTION (CONTD) AND WHEN THE TEMPERATURE EXCEEDS THE
***   CRITICAL TEMPERATURE

        CATCH =INSW(RSATL-CONTD,1.,0.)*A*INSW(TEMP-CRTEMP,0.,1.)


***   IT IS ALSO POSSIBLE TO FEED THE BEETLE AT SPECIFIC TIME INTERVALS
**     CATCH =IMPULS(.375,FOODIN)*A
***PARAM FOODIN=(.25,1.,2.,3.,4.,6.)
**PARAM FOODIN=.2
PARAM CONTD=0.7

***   DURING FEEDING A FRACTION OF THE PREY IS LOST
       PREYIN=PREY**.9
***    THE SIZE OF THE MEAL DEPENDS ON THE GUT DEFICIT AND ON THE PREY
***   SIZE
       MEAL   =AMIN1(PMEAL,PREYIN)*CATCH
***   TOTAL CONSUMPTION
       CONSUM=INTGRL(0.,MEAL*DELX)
***   DAILY CONSUMPTION
       PULS   =IMPULS(DELT,1.)
       EMCONS=PULS*DCONS*INSW(DCONS-.0001,0.,1.)
*************************************************************************
***
***   FOOD CONVERSION
***   THE STATE VARIABLES

      GUTCON=INTGRL(0,RGUT)
      FP     =INTGRL(0.,RFECES)
      HEMO   =INTGRL(2.,RHEMO)
      FAT    =INTGRL(10.,RFAT)
      OVAR   =INTGRL(0.1,ROVAR)
      EGGOV  =DEGGOV*FDREGG

***  FRESH AND DRY WEIGHTS
       NBODYW    =MINFW+HEMO+FAT+OVAR+EGGOV
       TOTW   =NBODYW+GUTCON
```

```
***   IN THE CALCULATION OF DRY WEIGHT TO FRESH WEIGHT A CORRECTION
***   HAS TO BE MADE FOR BEETLES OF OTHER SIZE
      DW     =(21/LEWI)*(.1*NBODYW)**1.7762
      MINDW  =(.1*MINFW)**1.7762
      FRES   =NBODYW-MINFW-EGGOV
      DRES   =DW-MINDW-DEGGOV

*** RATES OF FOOD CONVERSION
      RGUT   =MEAL*DELX-RGE
      RGE    =RRGE*GUTCON
      RFECES=(1-EFF)*RGE
      RASSIM=EFF*RGE
***CONVERSION TO BODY SUBSTANCE
      RASSHE=RASSIM*DFRPR*FRES/DRES
      RHEMO  =RASSHE-RFAT-TOOVAR+FROVAR-RESPIR


      RFAT   =TOFAT-FROFAT
      ROVAR  =TOOVAR-FROVAR-REGG
      TOFAT  =RRFAT*HEMO
      FROFAT=RRFDIS*FAT

***   EGG FORMATION DEPENDS ON TEMPERATURE, DAYLENGTH AND
***   OVIPOSITION PERIOD
      OVIP   =INTGRL(0.,ROVIP)
      ROVIP  =(1./OVIPP)*INSW(RDRTD-1.,0.,1.)
      OVIPP  =AFGEN(OVIPT,TEMP)

***REACTION TO CHANGE IN DAY LENGTH
      RRTD=(1./RTD)*INSW(DAYL-CRDAYL,0.,1.)
      RTD=AFGEN(RTDT,TEMP)
      RDRTD=INTGRL(0.,RRTD)
FUNCTION RTDT=-10.,10.,15.,10.,...
      19.,6.5,22.,3.7,27.,2.4,40.,2.

      TOOVAR=RRGE*HEMO*INSW(1.-OVIP,0.,1.)*INSW(RDRTD-1.,0.,1.)
      FROVAR=RRODIS*OVAR

***   RELATIVE DIGESTION DEPENDS ON REPRODUCTIVE STATE
***   AND DAILY RHYTHMICITY

      RRGE   =INSW(OVIP-1.,INSW(2.-OVAR,RDIGES,RRFAT),RRFAT)
      RDIGN  =AVDIGS+AMDIGS*COS(PI*TM/(24.-MDAY+RISS))
      RDIGD  =AVDIGS-AMDIGS*COS(PI*(HOUR-RISS)-(MDAY-RISS))
      RDIGES=INSW(AND(HOUR-RISS,MDAY-HOUR)-0.5,RDIGN,RDIGD)
```

```
      RISS   =MDAY-DAYL/2.
      TM     =INSW(HOUR-MDAY,HOUR+24.-MDAY,HOUR-MDAY)
      AVDIGS=AFGEN(AVDIGT,TEMP)
      AMDIGS=AFGEN(AMDIGT,TEMP)
      RRFAT =AFGEN(RRFATT,TEMP)
      RRFDIS=AFGEN(FATDTT,TEMP)
      RRODIS=AFGEN(OVADTT,TEMP)
      DAYL=AFGEN(DAYLT,DAY)
FUNCTION DAYLT=0.,8.5,1.,8.5,30.,9.1,60.,11.5,90.,13.6,120.,15.6, ...
150.,16.4,180.,17.3,210.,15.5,240.,14.3,270.,12.3,300.,10.2,330.,8.1

***   RESPIRATION DEPENDS ON THE BODY WEIGHT
      RESPIR=(.00074*FW*FW/DW)*EXP(0.102*TEMP)
      RESPT =INTGRL(0.,RESPIR)

FUNCTION OVIPT=-5.,500.,10.,250.,12.,67.,15.,32.4.,19.,35.7, ...
               22.,35.5,27.,41.,40.,42.
FUNCTION FATDTT=-5.,.001,0.,.001,10.,.01,12.,.025,15.,.07, ...


                19.,.13,22.,.18,27.,.25,40.,.3
FUNCTION RRFATT=-5.,0., 0.,0.,12.,.35,17.,.65,22.,.75,26.,1.6,40.,2.
FUNCTION OVADTT=-5.,0.,0.,0.,12.,.03,15.,.038,19.,.049,22.,.063, ...
               27.,.1,40.,.3
FUNCTION AVDIGT=-5.,0.,0.,0.,5.,.1,10.,.2,12.,.7,15.,1.2,19.,1.8, ...
               22.,2.2,27.,3.1,40.,3.6
FUNCTION AMDIGT=-5.,0.,0.,0.,5.,0.,10.,0.,12.,.5,15.,.9,19.,1.3, ...
               22.,1.4,27.,.5,40.,0.2

***   TEMPERATURE
***
      HOUR   =AMOD(TIME,1.)*24.

***    WHEN THE OVARY HAS REACHED ITS MAXIMUM SIZE ALL THE SURPLUS IS
***   DUMPED INTO THE OVIDUCT, AFTER RECALCULATION TO ITS SPECIFIC ***
***   WEIGHT.

      PUSH1 =INSW(OVAR-(MAXOV+(DEGGW*FRES/DRES)),0.,1.)
      REGG   =PUSH1*(OVAR-MAXOV)*DELX
      RDEGG=REGG*DRES/FRES

***   MATURATION TIME OF EGGS IN THE OVIDUCT

      PUSH2 =INSW(MATRT-.1,0.,1.)
      MATRT=INTGRL(0.,(1./MATT)-(PUSH2*DELX*MATRT))
```

```
      MATT=F1*AFGEN(MATRTT,TEMP)
FUNCTION MATRTT=-10.,200.,10.,100.,12.,12.,15.,4.,19.,2.,22.,1.5, ...
      27.,1.,40.,.5
***   THE RESIDENCE IN 10 EGG CLASSES
NOSORT
      EGG(1)=EGG(1)+RDEGG*DELT
      DEGGOV=0.
      DO 10 I=11,2,-1
      IF(PUSH2.NE.1.) GO TO 10
      EGG(I)=EGG(I-1)
 10   DEGGOV =DEGGOV+EGG(I-1)
      EGGPRO=EGGPRO+(EGG(11)/DEGGW)
      EGGNUM=DEGGOV/DEGGW
      EMEGGP=PULS*DEGGP
      DEGGP =DEGGP+(EGG(11)/DEGGW)-EMEGGP
      EGG(1)=EGG(1)*(1.-PUSH2)
      EGG(11)=0.
SORT
*************************************************************************
***
***   CALCULATION OF THE TEMPERATURE SUM ABOVE 10 DEGREES.
RTS=INSW(TEMP-10.,0.,TEMP-10.)

TS10=INTGRL(0.,RTS)
DTS10=INTGRL(0.,RTS-PULS*DTS10*INSW(DTS10-.0001,0.,1.)*DELX)
***
PRINT DTS10,OVAR,EGGNUM,DEGGP,EGGPRO,FAT,HEMO,TOTW
OUTPUT DAY,MAXT,MINT,DCONS,GUTCON,RSATL
*OUTPUT RELGUT,RSATL,GUTCON,OVAR,EGGNUM
*OUTPUT DEGGP,EGGPRO,FW,FAT,HEMO,RESPT,TOTW

FINISH OVIP=1.6
TIMER FINTIM=130.,DELT=0.02,PRDEL=1.,OUTDEL=1.
**TIMER FINTIM=10.,DELT=.02,PRDEL=.1,OUTDEL=.1
METHOD RECT


*     SINUS DOOR MAX EN MIN TEMPERATUUR
       INDEX=0.
CONST PI=3.1415927
*     DAY NUMBER
      DAY=START+TIME
*     LATITUDE LOCATION
PARAM LAT=52.
      RADL=PI/180.
```

```
PARAM LONG=-5.
      DLONG=AMOD((LONG+360.)/15.,1.)
*          COSINE LATITUDE
      CSLT=COS(RADL*LAT)
           SINE LATITUDE
      SNLT=SIN(RADL*LAT)
      DELX=1./DELT
      HOUR=AMOD(TIME,1.)*24.

*          ELEVATION OF THE SUN

*          DECLINATION OF THE SUN
      DEC=-23.45*COS(PI*(DAY+10.)/182.621)
*          COSINE DECLINATION
      COSDEC=COS(RADL*DEC)
*          SINE DECLINATION
      SINDEC=SIN(RADL*DEC)
*          HOUR ANGLE
      HA=PI*(HOUR+12.-DLONG)/12.
*          SINE ELEVATION
      SNHSS=SNLT*SINDEC+CSLT*COSDEC*COS(HA)
      SNHS=AMAX1(0.,SNHSS)
*
*          AIR TEMPERATURE IS CALCULATED FROM MINIMUM AND
*          MAXIMUM TEMPERATURE

PARAM RISEI=6.5
      RISE=RISEI+ZHOLD(AND(SNHSS,-LSNHS)-0.5,HOUR-SNHSS/...
      (NOT(SNHSS-LSNHS)+SNHSS-LSNHS)-RISEI)
*     TIME OF SUNRISE TODAY AND TOMORROW ARE TAKEN TO BE EQUAL
      LSNHS=INTGRL(-0.5,(SNHSS-LSNHS)*DELX)
*          SUN ELEVATION TODAY AT LAST TIME STEP

      VALAMP=0.5*(MAXT-MINT)
*          CALCULATION OF AMPLITUDE TEMPERATURE
      VALAV=0.5*(MAXT+MINT)
*          CALCULATION OF AVERAGE TEMPERATURE
      TIM=INSW(HOUR-14.,HOUR+10.,HOUR-14.)
      VALSR=VALAV-COS(PI*(HOUR-RISE)/14.-RISE))*VALAMP
      VALSS=VALAV+COS(PI*TIM/(10.+RISE))*VALAMP
*          CALCULATION OF VALUE AT SUNRISE AND SUNSET
      TEMP=INSW(AND(HOUR-RISE,14.-HOUR)-0.5,VALSS,VALSR)
END
STOP
ENDJOB
```

APPENDIX II

List of symbols.

Symbol	Unit	Definition
A		Activity parameter. At day time 1, during night 0.
ASS	mg	Weight of food in the gut to be assimilated.
ABDOM	mg	Weight of the abdomen. Difference between maximum and minimum fresh weight.
AMDIGS		Amplitudo of the relative gut emptying rate.
AMDIGT		Table of the relative gut emptying rate in relation to temperature.
AVDIGS	1/day	Average relative gut emptying rate.
AVDIGT		Table of the relative gut emptying rate in relation to temperature.
CATCH		Variable whicht is one when a prey is caught other, wise zero.
CONSUM	mg	Summation of the ingested food.
CRDAYL	hour	Critical daylength for ovarioles development.
CRTEMP	oC	Threshold temperature for development of the ovaries.
CONTD		Threshold of RSATL for ingestion.
DAY		Number of the day, days are consecutively numbered with january 1-st as day one.
DAYL	hour	Length of the light period of the day.
DAYLT		Table of daylength and day number.
DCONS	mg	Total quantity of food ingested during one day.
DEGGP	number	Number of eggs produced during one day.
DEGGW	mg	Dry weight of one egg.
DELT	day	Time step if integration.
DEGGOV	mg	Dry weight of eggs in the oviduct.
DFREGG		Dry:fresh ratio of eggs.
DRES	mg	Dry weight of HEMO + OVAR + FAT
DRFRPR		Dry:fresh ratio of the prey.
DTS10	°C.day	Daily temperature sum above 10 °C.
DW	mg	Dry weight of the beetle without gut content.
EFF		Efficiency of food assimilation.
EGG 1-11		Egg maturation classes in oviduct.
EGGNUM	number	Total number of eggs in the oviduct.

EGGOV	mg	Total weight of the eggs in the oviduct.
EGGPRO	number	Total egg production.
EGGW	mg	Weight of one egg.
EMCONS	mg	Summation of the weight of ingested food during one day.
EMEGGP		Dummy for emptying DEGGP at the beginning of the day.
FAT	mg	Weight of stored products.
FATDDT		Table of RRFDIS and temperature.
FEGGW	mg	Fresh weight of one egg.
FDREGG		Fresh:dry ratio of eggs.
FOODIN	day	Time when food is offered.
FP	mg	Total faeces production.
FRDRPR		Fresh:dry ratio of prey.
FRES	mg	Fresh weight of HEMO+OVAR+FAT
FROFAT	mg/day	Rate of transport of stored products to HEMO.
FROVAR	mg/day	Rate of egg resorption.
GUTCAP	mg	Gut capacity. The maximum meal weight, either depending on crop volume or on the room left in the abdomen.
GUTCON	mg	Gut content.
GUTDEF	mg	The empty room in the gut that can be filled by food.
HEMO	mg	The weight of the haemolymph.
HOUR	hour	Hour of the day.
HUNGER		1- Relative satiation level.
LEWI	mm^2	Length times width of an elytrum. It is a measure for the size of a beetle.
MATRT	day	Residence time of eggs in one egg class in the oviduct.
MATRTT		Table of the residence time of eggs in the oviduct.
MATT	day	Residence time of the eggs in the oviduct.
MAXDW	mg	Maximum dry weight of a beetle with a certain size.
MAXFW	mg	Maximum fresh weight of a beetle with a certain size.
MAXGUT	mg	Maximum gut content. The highest meal weight that can be ingested by an individual beetle.
MAXOV	mg	Maximum weight of the ovarioles.
MAXT	°C	Maximum temperature of the day.
MDAY	hour	Middle of the day.
MEAL	mg	Weight of the actual ingested meal.
MEALW	mg	Weight of a meal to satiate a beetle that starts eating with an empty gut.

MINDW	mg	Minimum dry weight.
MINFW	mg	Minimum fresh weight. The weight of cuticula and vegetative tissues when the beetle just stays alive.
MINT	°C	Minimum temperature of the day.
MNTT		Table of the minimum temperature.
MXTT		Table of the maximum temperature.
NBODYW	mg	The fresh weight of the beetle without gut content.
OVAR	mg	Weight of the ovarioles.
OVIP	day	Summation of days that the beetle forms eggs.
OVIPP	day	Estimated duration of the egg formation period.
OVIPT		Table of egg formation and temperature.
PMEAL	mg	Difference between MEALW and GUTCON.
PREY	mg	Weight of prey item.
PREYIN	mg	Potential prey weight to be ingested.
PULS		Switch which is one at the beginning of the day, otherwise zero.
PUSH1		Switch which is one when the ovaries exceed their maximum weight, otherwise zero.
PUSH2		Switch which is one when the residence time of the eggs in one egg class is over, otherwise zero.
RASSIM	mg/day	Rate of food assimilation from gut into haemolymph.
RASSHE	mg/day	Assimilated food converted to body weight.
RDIGD	1/day	Relative gut emptying rate during day time.
RDIGES	1/day	Relative gut emptying rate.
RDIGN	1/day	Relative gut emptying rate during the night.
RDRTD	day	Time already passed through the reaction period to change in daylength.
REGG	mg	Rate of transport of eggs from ovarioles to oviduct.
RELGUT		Relative gut content (GUTCON/GUTCAP).
RESPIR	mg/day	Weight loss by respiration.
RFAT	mg/day	Rate of change of stored products.
RFECES	mg/day	Rate of faeces production.
RGE	mg/day	Rate of gut emptying.
RGUT	mg/day	Rate of change of the gut content.
RHEMO	mg/day	Rate of change of haemolymph weight.
RISS	hour	Time of sun rise.
ROVAR	mg/day	Rate of change of ovariole weight.
ROVIP	1/day	Relative rate at which the egg formation time is passed through.
RRFAT	1/day	Relative rate of formation of stored products.
RRFATT		Table of RRFAT and temperature.

RRFDISS	1/day	Relative rate of transport of products from FAT to HEMO.
RRODISS	1/day	Relative rate of egg resorption.
RRTD	1/day	Rate of passage through the reaction period to change in daylength.
RSATL		Relative satiation level.
RTD	day	Duration of reaction time to change in daylength.
RTDT		Table of reaction period versus temperature.
RTS	°C	Rate of increase of the temperature sum.
SATW	mg	Weight of a satiated beetle.
SPACE	mg	Room left in the abdomen.
START		Day number of the year at which the simulation is started.
TEMP	°C	Temperature throughout the day.
TOFAT	mg/day	Rate of transport of products to FAT.
TOOVAR	mg/day	Rate of transport of products to the ovarioles.
TS10	°C.day	Temperature sum above 10°C.
WEIGHTLOSS	mg	Loss in weight of a beetle by egestion.
WEIGHTGAIN	mg	Increase of weight by ingestion.